



Insights into the *Tricholomataceae* (*Agaricales*, *Agaricomycetes*): a new arrangement of *Biannulariaceae* and *Callistosporium*, *Callistosporiaceae* fam. nov., *Xerophorus* stat. nov., and *Pleurocollybia* incorporated into *Callistosporium*

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Abstract

A new classification of the taxa formerly ascribed to *Biannulariaceae* (≡ *Catathelasmataceae*), viz. *Catathelasma* (type), *Callistosporium*, *Pleurocollybia*, *Macrocybe*, *Pseudolaccaria*, *Guyanagarika* and *Anupama* is here proposed. Phylogenetic inference of the *Tricholomataceae* based on the analysis of a combined dataset of nuclear genes including ITS, 18S and 28S rDNA, *tef1* and *rpb2* data supports significantly a monophyletic origin of the aforementioned genera with the exception of *Catathelasma*, which is significantly related with *Bonomycetes* and *Cleistocybe*. *Biannulariaceae* is therefore emended to include the clade formed by *Catathelasma*, *Bonomycetes* and *Cleistocybe*. Consequently, the new family *Callistosporiaceae* is proposed to name the clade containing *Callistosporium* (= *Pleurocollybia*) and related genera. Species of *Callistosporium* with distant lamellae, long hygrophoroid basidia and large amygdaliform spores are accommodated in the new genus *Xerophorus*. Finally, the new species *Callistosporium pseudofelleum* and *Macrocybe sardoa* are described, *Clitocybe hesleri* and *C. fellea* are combined into *Callistosporium* and *Pseudolaccaria*, respectively, and *Callistosporium olivascens* var. *donadinii* is upgraded to species rank and combined into *Xerophorus*.

Keywords Basidiomycota · Tricholomatoid clade · Catathelasma clade · Multigene phylogenetic analysis · Taxonomy

Introduction

The suborder *Tricholomataceae* Aime, Dentinger & Gaya is one out of the seven suborders currently recognized within the *Agaricales* Underw. (Dentinger et al. 2016). This suborder corresponds quite well to the Tricholomatoid clade s. Matheny et al. (2006), except for the exclusion of *Mycenaceae* Overeem and the inclusion of *Infundibulicybe gibba* (Pers.) Harmaja, and to the Tricholomatoid clade of Binder et al. (2010). It includes six families, viz. *Tricholomataceae* R. Heim ex Pouzar, *Biannulariaceae* Jülich, *Entolomataceae* Kotl. & Pouzar, *Macrocytidiaceae* Kühner, *Lyophyllaceae* Jülich and *Pseudoclitocybaceae* Vizzini, Consiglio, P.-A. Moreau, P. Alvarado, as well as the *Clitocybeae* Fayod lineage and many *incertae sedis* genera such as *Aspropaxillus* Kühner & Maire, *Bonomycetes* Vizzini, *Cleistocybe* Ammirati, A.D. Parker & Matheny, *Giacomia* Vizzini & Contu, *Infundibulicybe* Harmaja, *Notholepista* Vizzini & Contu, *Pseudoclitopilus* Vizzini & Contu and *Pseudooomphalina* (Singer) Singer (Matheny et al. 2006; Binder et al. 2010;

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Sánchez-García et al. 2014, 2016; Lavorato et al. 2015; Dentinger et al. 2016; Alvarado et al. 2018a, b). At least 32 genera can be assigned to this suborder following Sánchez-García et al. (2014) and Alvarado et al. (2018a). Members of *Tricholomataceae* show high variation in nutritional mode and ectomycorrhizal symbionts, saprotrophs, bryophyte parasites, mycoparasites and termite-associates are included (Matheny et al. 2006; Hofstetter et al. 2014).

In particular, the family *Biannulariaceae* (a priority synonym over *Catahelasmataceae* Wasser; Sánchez-García 2016; Raj et al. 2019) was recently resurrected and amended to name a clade including *Callistosporium* Singer, *Catahelasma* Lovejoy, *Macrocybe* Pegler & Lodge, *Pleurocollybia* Singer, *Pseudolaccaria* (Fr.) Vizzini, Contu & Z.W. Ge and *Clitocybe fellea* Peck (Sánchez-García et al. 2016). Recently Raj et al. (2019) added to this family the new monotypic Indian genus *Anupama* K.N.A. Raj, K.P.D. Latha & Manim. As circumscribed by Sánchez-García et al. (2016) and Raj et al. (2019) based on genetic inference, *Biannulariaceae* is a cluster of genera with most diverse morphological and ecological features and with no evident shared synapomorphies.

The aim of the present work was to review the taxonomy of *Biannulariaceae* after the analysis of new morphological and genetic data obtained from multiple collections of *Callistosporium*, *Catahelasma* and *Macrocybe*, which were underrepresented in the former studies.

Materials and methods

Collections studied

Samples studied are identified with the code of the public herbaria (Thiers, continuously updated) where they are stored: AMB, ARAN-Fungi, BRNM, CORT, CFMR, DAOM, DBG-F, EMB, FLAS-F, H, JBSD, K-M, LIP, LUG, MCVE, SFSU-F, TUR, UTK, WRSL, WTU-F, ZT-Myc, or else the private collection of their owner: ALV, P. Alvarado; CA, C. Agnello; ChP, P. Chachuła; PBM, P.B. Matheny; RRy, R. Rutkowski.

Morphological studies

Macroscopic morphological features were studied in fresh specimens. The following abbreviations are employed: L = number of lamellae reaching the stipe, l = number of lamellulae between each pair of lamellae. Microscopic structures were examined in dried material using different mounting media: water, L4 (Clémençon 1972), Melzer's reagent, ammoniacal Congo red, phloxine, Cresyl blue and Cotton blue. Dried pieces of the samples were rehydrated in water and mounted in L4. All microscopic measurements were carried out with a Nikon Eclipse 80i microscope, using

immersion oil at $\times 1000$. Spore measurements were made by capturing images of a single visual field with multiple spores (taken from lamellar squashes of exsiccate material of mature specimens) which were then measured using the DS-L1 Nikon camera control unit. Spore dimensions do not include the hilar appendix, and are reported as follows: average minus standard deviation of length – average plus standard deviation of length \times average minus standard deviation of width – average plus standard deviation of width; Q = average minus standard deviation – average plus standard deviation of ratio length/width; Q_m = average of the ratio length/width; V = average minus standard deviation – average plus standard deviation of the volume [μm^3]; V_m = average of the volume [μm^3]. The approximate spore volume was calculated as that of an ellipsoid (Gross 1972; Meerts 1999). The notation [n/m/p] indicates that measurements were made on "n" randomly selected spores from "m" basidiomes of "p" collections. The width of the basidia was measured at the widest part, and the length was measured from the apex (sterigmata excluded) to the basal septum. Microscopy images were taken using a Nikon DS 5M digital connected to the microscope with both brightfield and interferential contrast optics. Macro- and microchemical testing of pigments were performed using basic solutions (5% KOH and 10% ammonia, separately). Scanning electron micrographs were made with a Zeiss DSM 950 device following the methods described by Moreno et al. (1995).

DNA extraction, amplification and sequencing

Total DNA was extracted from dry specimens (Supplementary Material Table 1) employing a modified protocol based on Murray and Thompson (1980). PCR amplification (Mullis and Falloona 1987) included 35 cycles with an annealing temperature of 54 °C. Primers ITS1F and ITS4 (White et al. 1990; Gardes and Bruns 1993) were employed for the ITS rDNA region, while LR0R and LR5 (Vilgalys and Hester 1990; Cubeta et al. 1991) were used to amplify the LSU/28S rDNA region, NS19b and NS41 for SSU/18S rDNA ribosomal region (Hibbett 1996), EF1-728F, EF1-983F and EF1-1567R (Carbone and Kohn 1999; Rehner and Buckley 2005) for the translation elongation factor 1a (*tef1*) gene, and bRPB2-6F2 (reverse of bRPB2-6R2), bRPB2-7.1R2 and bRPB2-7R2 for the RNA polymerase II second largest subunit (*rpb2*) gene (Liu et al. 1999; Matheny et al. 2007). PCR products were checked in 1% agarose gels, and positive reactions were sequenced with one or both PCR primers. Chromatograms were checked searching for putative reading errors, and these were corrected.

Phylogenetic analyses

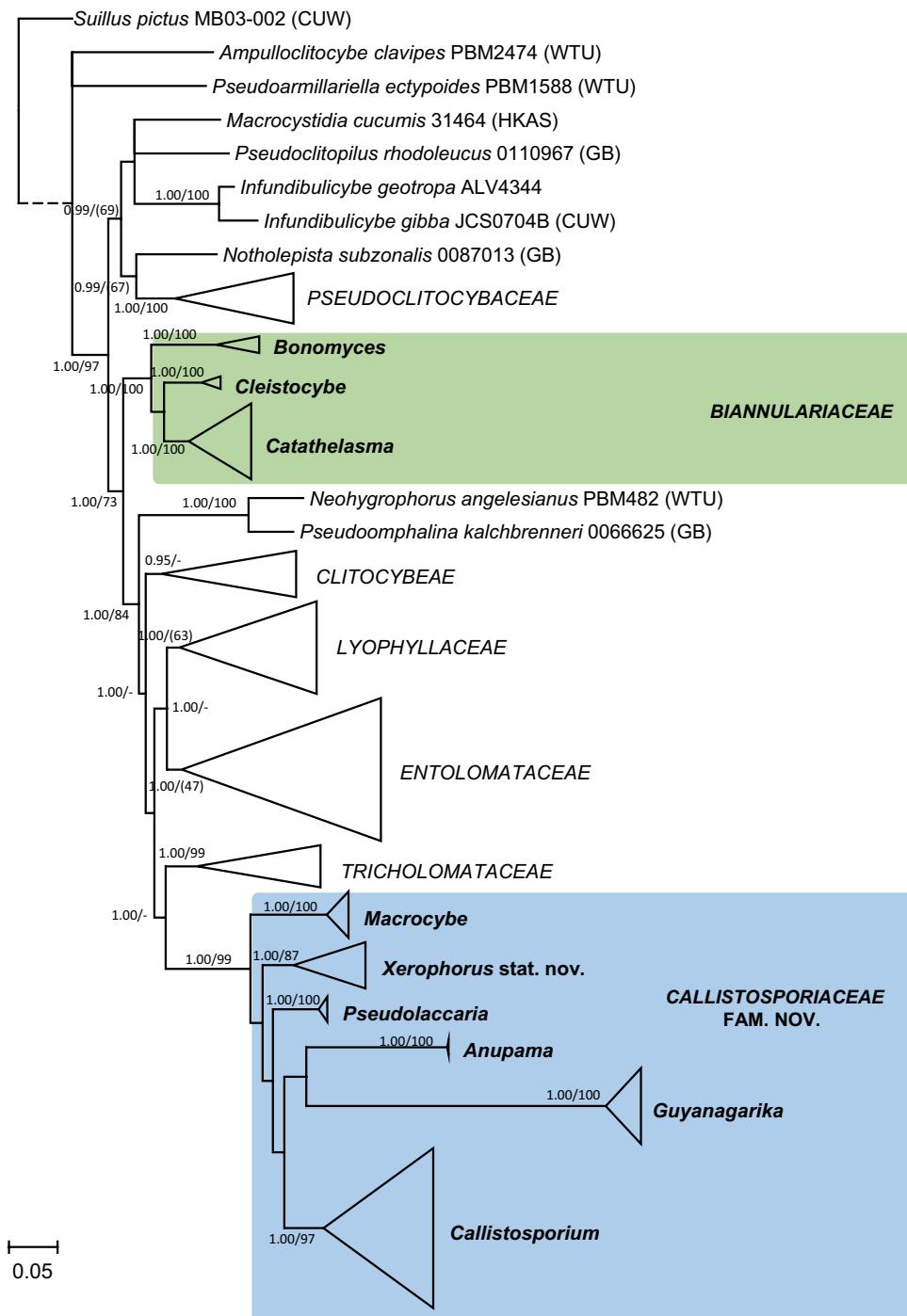
BLAST (Altschul et al. 1990) was used to select the most closely related sequences from public databases (INSDC/GenBank <https://www.ncbi.nlm.nih.gov/genbank/>, UNITE <https://unite.ut.ee/>, BOLD <http://www.boldsystems.org/>). Three distinct alignments were built. (1) First, a combined alignment including 18S rDNA, 28S rDNA, *tef1* (introns excluded) and *rpb2* sequences from representative species of the major lineages in the *Tricholomataceae* found in previous phylogenetic studies (Matheny et al. 2006; Sánchez-García et al. 2014, 2016; Bellanger et al. 2015; Alvarado et al. 2015, 2018a, b). *Suillus pictus* (Peck) Kuntze, *Pseudoarmillariella ectypoides* (Peck) Singer and *Ampulloclitocybe clavipes* (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys, were used as outgroups to root the tree, because of their phylogenetic position external to the *Tricholomataceae* (Matheny et al. 2006). (2) Second, a combined alignment of ITS, 18S and 28S rDNA, *tef1* (introns excluded) and *rpb2* data of genus *Catathelasma* and related lineages including sequences obtained by Alvarado et al. (2018b). (3) Third, a combined alignment of ITS, 18S and 28S rDNA, *tef1* (introns excluded) and *rpb2* data of the genus *Callistosporium* and related genera, including sequences obtained by Sánchez-García et al. (2016), Alvarado et al. (2018b) and Raj et al. (2019). Sequences (Supplementary Material Table 1) were first aligned in MEGA 6.0 (Tamura et al. 2013) software with its MUSCLE application (Edgar 2004) and then corrected manually. No significant incongruence between the phylogenetic signal from *rpb2*, ITS rDNA and 28S rDNA was observed after independent Bayesian and Maximum likelihood analyses of each of these genes from the Catathelasma and Callistosporium clades (Supplementary Material Figs. 1–3). A putative error in the *Catathelasma ventricosum* *rpb2* sequences DQ470830 (obtained from AFTOL-ID 1488, PBM 2403, 45682 WTU-F) and KP255469 (obtained from 221514 DAOM) was detected, since both sequences match instead *Callistosporium graminicolor* (KJ424369 from PBM 2341 WTU-F, not included in the final analyses as it covers a different region of the *rpb2* gene). To check if these sequences represented parologue genes, alternative primer pairs were tested in several samples of *Catathelasma* (including PBM 2403): fRPB2-5F/bRPB2-7R2 produced a ~ 1100 bp amplicon identical to the sequences obtained in the present work, while fRPB2-5F/bRPB2-7R produced a smaller product ~ 300 bp with no close matches in databases, but only 80% similarity with some RNA polymerase III sequences. Another putative error was found in the ITS rDNA sequence KP255469 (obtained from *C. ventricosum* 221514 DAOM), which matches instead sequences of *C. imperiale* (Supplementary Material Fig. 2).

The Bayesian analysis was performed through the CIPRES Science Gateway platform (Miller et al. 2010) by

using the MrBayes v. 3.2.6 algorithm with ITS, 28S and 18S rDNA, *tef1*, *rpb2* data partitioned (one partition for each codon position in *tef1* and *rpb2* exons), two simultaneous runs, four chains, temperature fixed at 0.2 and sampling every 1000 generations until reaching the convergence parameters (standard deviation less than 0.01). The first 25% trees were discarded as burn-in. The final multigenic alignment of the *Tricholomataceae* is composed of 212 OTU and contained 2939 total nucleotide positions: 956 positions from LSU/28S rDNA (208 sequences), 757 positions from SSU/18S rDNA (93 sequences), 519 positions from *tef1* (76 sequences) and 707 positions from *rpb2* (139 sequences). The alignment of the *Biannulariaceae* (the Catathelasma clade) is composed of 48 OTU and contained 3347 nucleotide positions: 875 positions from LSU/28S rDNA (26 sequences), 749 positions from SSU/18S rDNA (16 sequences), 412 positions from *tef1* (9 sequences), 594 positions from *rpb2* (10 sequences), and 717 from ITS rDNA (43 sequences). Finally, the alignment of *Callistosporiaceae* (the Callistosporium clade) is composed of 149 OTUs and contained 3372 nucleotide positions: 916 positions from LSU/28S rDNA (85 sequences), 753 positions from SSU/18S rDNA (33 sequences), 483 positions from *tef1* (14 sequences), 717 positions from *rpb2* (41 sequences), and 503 positions from ITS rDNA (132 sequences).

Bayesian analyses reached convergence after 8.76 M (*Tricholomataceae*), 0.39 M (Catathelasma clade) and 3.6 M (Callistosporium clade). As both Bayesian and Maximum likelihood analyses produced similar topologies, only the Bayesian trees with both PP and BP values are shown (Figs. 1–3). No evidence of non-convergence between chains was found in the analysis of the Catathelasma and Callistosporium clades after checking the analysis files in RWTY (Warren et al. 2017). However, a new analysis of the Callistosporium clade was run for 5 M generations to assure convergence. Significant changes in tree topologies and posterior probabilities of selected nodes were observed in one of the chains of the *Tricholomataceae* analysis after about 4 M generations. Therefore, a new analysis was run for 20 M generations where only a smaller change in posterior probabilities occurred in one of the runs shortly before 2.5 M generations, but the trees sampled before this event were removed by the 25% burn-in. Finally, a full search for the best-scoring Maximum likelihood tree was performed in RAxML v.8.2.10 (Stamatakis 2014) using the standard search algorithm (data partitioned as in Bayesian analysis, GTRCAT model, 2000 bootstrap replications). Significance threshold was set ≥ 0.95 for posterior probability (PP) and $\geq 70\%$ for bootstrap proportions (BP).

Fig. 1 50% majority rule 18S rDNA-28S rDNA-*tef1-rpb2* consensus phylogram of the Tricholomatinae (with *Suillus pictus*, *Pseudoarmillariella ectypoides*, and *Ampulloclitocybe clavipes* as outgroups) obtained in MrBayes from 65700 sampled trees. Nodes were annotated if supported by ≥ 0.95 Bayesian PP (left) or $\geq 70\%$ ML BP (right). Non-significant support values are exceptionally represented inside parentheses



Results

Phylogenetic analyses

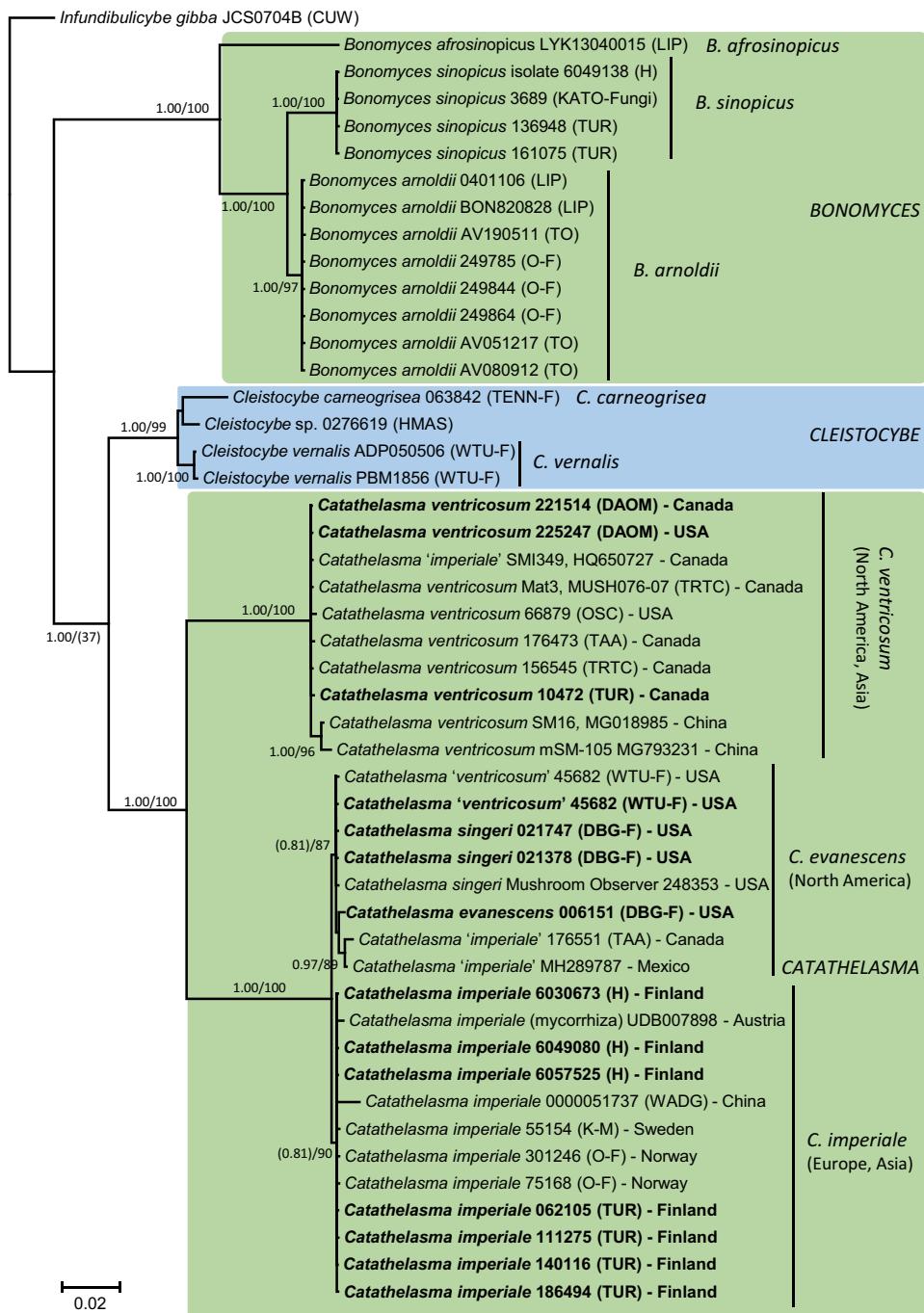
The overall topology of the Tricholomatinae obtained from the partitioned analysis of 18S rDNA, 28S rDNA, *tef1* and *rpb2* (Fig. 1) was consistent with those published in previous studies (Sánchez-García et al. 2014, 2016;

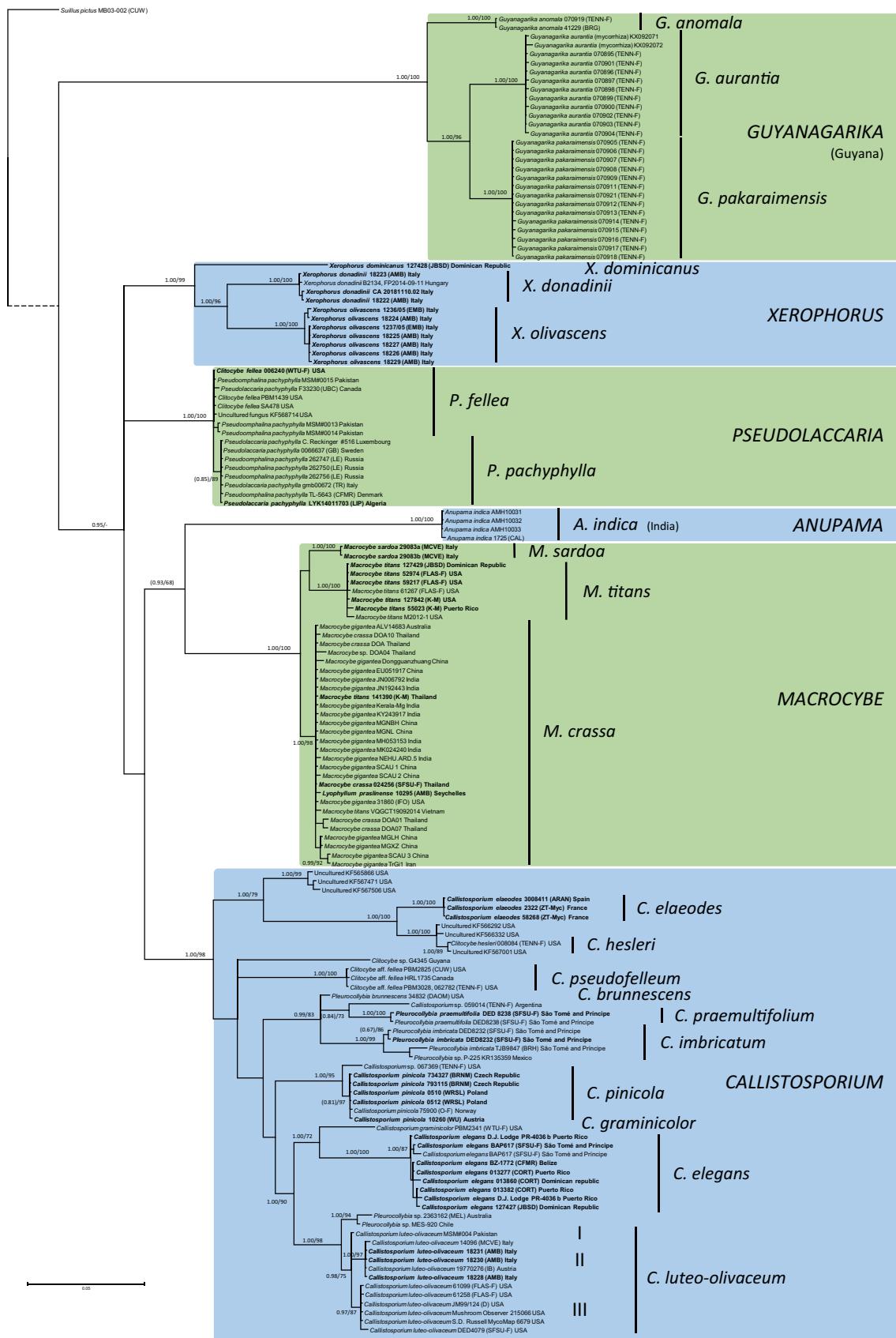
Alvarado et al. 2015, 2018a, b; Raj et al. 2019) excepting for the position of genus *Catathelasma*. Sequences analysed grouped in two main clades: (i) one composed of the family *Pseudoclitocybaceae* and the lineages of *Infundibulicybe*, *Notholepista*, *Macrocytida* Joss and *Pseudoclitopilus* (PP = 0.99, BP = 69%), and (ii) another clade containing the remaining taxa (PP = 1.00, BP = 73%). This second clade was composed of two different

lineages with significant support, one formed by *Catathelasma*, *Bonomycetes* and *Cleistocybe* (PP = 1.00, BP = 100%), and another one containing the families *Entolomataceae*, *Lyophyllaceae*, *Tricholomataceae* as well as the *Clitocybeae*, the lineage of *Pseudooomphalina* and *Neohygrophorus*, and a monophyletic clade containing the genera formerly associated with the *Biannulariaceae*: *Anupama*, *Callistosporium* (= *Pleurocollybia*), *Guyanagarika*, *Macrocybe* and *Pseudolaccaria* (PP = 1.00, BP = 99%). In light of these results, the family *Biannulariaceae*

is amended below, while a new family name is proposed to accommodate *Callistosporium* and related clades. Bayesian analysis provided significant support (PP = 1.00) for a monophyletic origin of this clade and the family *Tricholomataceae*, but Maximum likelihood did not. The analysis of *Catathelasma* and related clades (Fig. 2), significantly supported the existence of three distinct genetic lineages within *Catathelasma*, which match the taxonomic concepts of *C. imperiale*, *C. ventricosum* and *C. evanescens*.

Fig. 2 50% majority rule ITS rDNA-18S rDNA-28S rDNA-*tef1-rpb2* consensus phylogram of the family *Biannulariaceae* (Catathelasma clade) (with *Infundibulicybe gibba* as outgroup) obtained in MrBayes from 2925 sampled trees. Nodes were annotated if supported by ≥ 0.95 Bayesian PP (left) or $\geq 70\%$ ML BP (right). Non-significant support values are exceptionally represented inside parentheses





◀Fig. 3 50% majority rule ITS rDNA-18S rDNA-28S rDNA-*tef1-rpb2* consensus phylogram of the family *Callistosporiaceae* (Callistosporium clade) (with *Suillus pictus* as outgroup) obtained in MrBayes from 27000 sampled trees. Nodes were annotated if supported by ≥ 0.95 Bayesian PP (left) or $\geq 70\%$ ML BP (right). Non-significant support values are exceptionally represented inside parentheses

A partially significant relationship (PP = 1.00, BP = 37) was found between *Catathelasma* and *Cleistocybe*.

The analysis of the *Tricholomataceae* (Fig. 1) and that of genus *Callistosporium* and related genera (Fig. 3) suggest that the traditional concept of *Callistosporium* (Bon 1976, 1984, 1991; Singer 1986) is polyphyletic, since its species form two different, non-related clades: (i) a first one, hereafter named as *Callistosporium*, including *Callistosporium elaeodes* (Romagn.) Bon, *C. elegans* Desjardin & B.A. Perry, *C. graminicolor* Lennox, *C. luteo-olivaceum* (Berk. & M.A. Curtis) Singer, *C. pinicola* Arnolds, *Clitocybe hesleri* H.E. Bigelow, *C. aff. fellea* Peck, *Pleurocollybia brunneascens* (Earle) Singer, *P. imbricata* T.J. Baroni, Lodge & D.L. Lindner, and *P. praemultifolia* (Murrill) Singer as well as several lineages lacking a confirmed name; (ii) a second clade including *Callistosporium olivascens* (Boud.) Bon, *C. donadini* (Bon) Contu and a third lineage putatively representing a new species. The first group is here considered to represent the original concept of *Callistosporium* because the species included show morphological characters that match better those of the type species (see below), while a new genus name is proposed below for the second one. Based on these phylogenetic results, an updated taxonomic arrangement of these lineages is proposed.

Taxonomy

Biannulariaceae Jülich, Higher taxa of Basidiomycetes, *Bibliotheca Mycologica* 85: 356 (1981)

≡ ***Biannulariae*** Singer ex Bas, *Persoonia* 14: 235 (1990)

= ***Catathelasmataceae*** Wasser in Agarikovye griby SSSR (Kiev): 29 (1985)

Type genus: *Catathelasma* Lovejoy, *Bot. Gaz.* 50: 383 (1910)

Emended here to encompass also the genera *Bonomyces* and *Cleistocybe*.

Description: Habit tricholomatoid, clitocyboid or pleurotoid. Lamellae adnate, adnexed, sinuate, emarginated to decurrent. Partial veil present (simple or double) or inconsistent and reduced to a granular, pseudoanular zone at stipe apex. Tendency to form scales and/or granules on pileus and stipe. Smell usually farinaceous. Spore print white. Spores ellipsoid to fusoid, cylindrical, hyaline, smooth, inamyloid or

amyloid, acyanophilous or cyanophilous. Cheilocystidia present or absent, pleurocystidia absent, if present then only as pseudocystidia. Hymenophoral trama regular to bilateral becoming regular. Pileipellis a cutis, an ixocutis or a cutis becoming a trichoderm. Context (pileitrama and stipititrama) formed by densely arranged slender hyphae which give rise to a dry and fibrous consistency. Clamp connections present. On soil or rotten wood. Saprotrophic or ectomycorrhizal in conifer forests. Europe, Asia, North and Central America.

Genera included: *Catathelasma*, *Cleistocybe* and *Bonomyces*.

Catathelasma Lovejoy, *Bot. Gaz.* 50(3): 383 (1910)

= ***Biannularia*** Beck, *Pilz- und Kräuterfreund* 5(5–8): 231 (1922)

Type species: *Catathelasma evanescens* Lovejoy, *Bot. Gaz.* 50(3): 384 (1910)

Description: Habit tricholomatoid, basidiomata fleshy and sturdy, development bivelangiocarpic; lamellae adnate to decurrent, double veil present (stipe with two annuli), stipe tapered and rooting (often buried), smell farinaceous, hymenophoral trama divergent in young basidiomata, bilateral, later more regular, at least in the central part of lamellae, clamp connections present, spores oblong to cylindrical, amyloid.

Ecology: terrestrial and ectomycorrhizal under conifers.

Comments: The genus *Catathelasma* includes boreal to hemiboreal species usually associated with *Pinaceae* (*Abies*, *Picea*, *Pseudotsuga*, *Tsuga*, *Pinus*) in Europe (Breitenbach and Kränzlin 1991; Vellinga 1995; Vesterholt 2012a), North America (Mitchel and Smith 1978; Miller 1985; Hutchison 1992; Miller and Miller 2006; Phillips 2010; Desjardin et al. 2015), Central America (Flores Arzú et al. 2012) and Asia (Imazeki and Hongo 1957; Singer 1978b; Imazeki et al. 1988). Five species were recognized by Singer (1978b, 1986) within *Catathelasma*. The only known collection of *Armillaria macrospora* Peck found at Colorado (USA), which was invalidly combined into *Catathelasma* by Singer (1940), has a whitish viscid pileus usually brown-spotted in the centre and spores measuring 6–8 µm wide (Peck 1900), slightly wider than those of the other species of *Catathelasma* (Bon 1978; Mitchel and Smith 1978; Vellinga 1995; Miller and Miller 2006; Vesterholt 2012a). *Catathelasma singeri* Mitchel & A.H. Sm. was also found for the first time in Colorado, but has a *Hygrophorus*-like habit with a dull yellow ochraceous slimy pileus up to 60 mm broad, a relatively soft context and a peculiar, non-farinaceous smell (Mitchel and Smith 1978). Recent collections from Colorado determined as *C. singeri* (021378 DBG-F and 021747 DBG-F) were not significantly different from those of *C. evanescens* (Fig. 2). Therefore, *Catathelasma* includes by



Fig. 4 *Catathelasma imperiale*. **a** Fresh basidiomes (18232 AMB). **b** Pileipellis (062105 TUR, neotype). **c** Cheilocystidia (062105 TUR, neotype). **d** Cheilocystidia (021747 DBG-F as *C. singeri*). **e** Spores (062105 TUR, neotype). **f** Spores (062105 TUR, neotype). *Catathelasma evanescens*. **g** Fresh basidiomes (45682 WTU-F, epitype). **h** Spores (45682 WTU-F, epitype). **i** Spores (021747 DBG-F). *Cat-*

athelasma ventricosum. **j** Cheilocystidia (225247 DAOM). **k** Spores (225247 DAOM). **l** Spores (221514 DAOM). **b-d, h, i, j-l** in ammoniacal Congo red; **e** in ammoniacal Congo red-interferential contrast; **f** in Melzer's reagent. Bars: **a** = 100 mm; **g** = 20 mm; **b-f** and **h-l** = 10 µm. Photographs: **a** by G. Consiglio; **g** by P.B. Matheny; **b-f** and **h-l** by M. Marchetti

now three significantly distinct genetic lineages, formed by samples which match the species concept of *C. imperiale*, *C. ventricosum* and *C. evanescens* (Fig. 2).

***Catathelasma imperiale* (P. Karst.) Singer, Revue Mycol., Paris 5: 9 (1940) Fig. 4a-f**

Basionym: *Armillaria imperialis* P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 20 (1879)

≡ *Agaricus imperialis* Fr. in N. Lund, Consp. Hymen. Holm (Christianiae): 5 (1845) nom. illegit., (Art. 53.1) (preoccupied by *Agaricus imperialis* Batsch 1783)

≡ *Omphalia imperialis* (P. Karst.) Quél., Enchir. fung. (Paris): 19 (1886)

- ≡ *Mastoleucomyces imperialis* (P. Karst.) Kuntze, Revis. gen. pl. (Leipzig) 2: 861 (1891)
 ≡ *Clitocybe imperialis* (P. Karst.) Ricken, Die Blätterpilze: 361 (1914)
 ≡ *Biannularia imperialis* (P. Karst.) Beck, Pilz- und Kräuterfreund 5(5–8): 231 (1922)
 ≡ *Armillariella imperialis* (P. Karst.) Konrad & Maubl., Icon. Select. Fung. 3: 280 (1926)
 = *Armillaria nobilis* Murrill, N. Amer. Fl. (New York) 10(1): 38 (1914)

Type specimen: **FINLAND**: Varsinais-Suomi, Salo, Merikulma, near Berliinintie, grassy slope, under *Picea abies*, leg. S. Tuominen, 21-VIII-1977, 062105 (TUR) (**neotype** here designated) (Mycobank MBT 387434).

Description: Habit tricholomatoid, basidiomes fleshy, with two annuli. *Pileus* 80–200(–400) mm in diam., hemispherical to convex, becoming plano-convex or nearly applanate with decurved margin, finally sometimes depressed, surface sticky, subviscid when young but soon dry, not hygrophanous, often cracking up in maturity, greyish-brown, reddish-brown, with dark brown pressed-down patches. *Lamellae* decurrent, narrow, crowded, sometimes forked, pale cream with an even concolorous edge. *Stipe* 50–130(–180) × 30–60(–80) mm, compact and solid, cylindrical, tapering to the base and usually rooting, sometimes almost completely buried, whitish above the annuli, pale buff with yellowish patches below; *partial veil* membranous, forming two annuli (double ring): the upper annulus is persistent, grey-brownish outside and cream, lined to sulcate inside; the lower annulus is evanescent, concolorous with the stipe outside and brownish inside. *Context* very thick, firm, compact, white, not changing on exposure. *Smell* and *taste* strongly farinaceous (cucumber-like, cucumber or watermelon rind). *Spore print* white.

Spores [260/7/7] 12.7–16.0 × 5.3–6.4 µm (on average 14.3 × 5.8 µm), Q = 2.2–2.7 (Q_m = 2.5), V = 184–337 µm³ (V_m = 261 µm³), narrowly ellipsoid, elongated-ellipsoid, subcylindrical to fusiform (boletoid, *Boletus*-like) (in side view), sometimes with a median constriction, partly with a suprahilar depression, apex rounded or rarely blunt, hilar appendix well-developed and up to 0.5–0.8 µm long, smooth, thin-walled, usually multiguttulate, amyloid, conophilous, cyanophilous. *Basidia* 50–70(–80) × 8–10 µm, narrowly clavate, four-spored, sterigmata up to 10 µm long, with basal clamp-connections, hyaline or with a multiguttulate green content. *Subhymenium* well-developed, consisting mainly of short elements, 3–6 µm wide. *Hymenophoral trama* divergent in young basidiomata then regular to subregular with cylindrical to claviform, thin-walled, 3–10(–14) µm wide elements, sometimes intermixed with thromboplerous hyphae (with greyish contents) and polymorphic

crystals. *Cheilocystidia* 40–60 × 3–5 µm, abundant, hyaline, thin-walled, undulate, sometimes lobate/forked, with rounded apex, sometimes subcapitate. *Pleurocystidia* absent. *Pileipellis* an ixocutis (with some ascending/repent hyphae) of loosely interwoven, sometimes undulate, cylindrical hyphae, 3–7 µm wide, embedded in a thick gelatinous matrix, with yellow-brown, yellow-reddish cytoplasmatic contents; presence of polymorphic crystals. *Subcutis* of interwoven, sometimes undulate hyphae, with thromboplerous hyphae (with greyish contents). *Clamp connections* common everywhere.

Ecology: associated with boreal or alpine conifers, often found in calcareous soils of Europe and maybe also Asia.

Specimens examined: **FINLAND**: Varsinais-Suomi, Salo, Merikulma, near Berliinintie, grassy slope, under *Picea abies*, leg. S. Tuominen, 21-VIII-1977, 062105 (TUR) (**neotype**); Satakunta, Mellilä commune, Rahkio, NE side of Kakarlampi, margin of dry heath forest on sandy soil (Haarukangas), planted forest with *Picea abies* on former field, with scattered *Pinus*, *Betula* and *Alnus*, leg. R. Knutila & J. Vauras, 21-IX-2000, 140116 (TUR); Varsinais-Suomi, Lieto, Liedon asema, Arosuo, Arosuontie 141, leg. K. Kulmala, 14-IX-2009, 186494 (TUR); Nylandia (N/U), Espoo, Luukkaan ulkoilualue (Luukki), leg. T. v. Bonsdorff, 25-VIII-2011, 6049080 (H); Pohjois-Karjala (PK/Kb), Lieksa, Koli national park, along Tarhapuro brook, moist mixed forest, leg. E. Ohenoja, 14-IX-2011, 6030673 (H); Perä-Pohjanmaa (PeP/Obu), Rovaniemi, Vaattunkikongas, Könkaansääri, 31-VIII-2015, 6057525 (H); V. Merimasku, school, Iskola, leg. M. Mikkonen, 28-VIII-1993, 111275 (TUR). **ITALY**: Trentino-Alto Adige, Trento, Predazzo, Bellamonte, under *Picea abies*, leg. G. Consiglio, 12-IX-2015, 18232 (AMB).

Comments: This species, originally described from Scandinavia (Karsten 1879) can be discriminated because of its very large basidiomes with a brown to reddish brown pileus up to 400 mm broad, often with olive tinges at the margin, sticky when young (thin ixocutis), a thick stipe up to 60 mm broad, a strongly farinaceous (mealy) smell and taste, hygrophoroid slender basidia up to 80 µm long and spores exceeding 14 µm long on average (Bon 1978; Singer 1978b; Miller 1985; McKnight and McKnight 1987; Imazeki et al. 1988; Breitenbach and Kränzlin 1991; Vellinga 1995; Miller and Miller 2006; Vesterholt 2012a). *Catathelasma imperiale* seems to be the only species of *Catathelasma* present in Europe (Bon 1978; Vellinga 1995; Jeppson and Jeppson 2010; Vesterholt 2012a). It has been reported also from Japan (Hutchison 1992), and a sequence from Tibet (China) is available in GenBank (KX008987 from WADG 0000051737, Kang et al. 2016), but it presents some differences with the European samples, suggesting that further

sampling and sequencing could reveal the existence of one or more isolated Asian lineages. To date there is no genetic evidence of the presence of *C. imperiale* in North America (Fig. 2), since all specimens analyzed belong to the sympatric *C. evanescens* or *C. ventricosum* (see below). In absence of original material, selecting a neotype is in order to give *C. imperiale* a stable genetic identity. An abundant, well-documented, and genetically characterized collection (062105 TUR) was selected among samples from Scandinavia because its morphological and ecological features match perfectly those reported in the protologue and the most relevant European literature (Bon 1978; Breitenbach and Kränzlin 1991; Vellinga 1995; Vesterholt 2012a).

***Cataethelasma ventricosum* (Peck) Singer (1940)**, Revue Mycol., Paris 5: 9 (1940) Fig. 4g–i

Basionym: *Lentinus ventricosus* Peck, Bull. Torrey bot. Club 23(10): 414 (1896)
 \equiv *Armillaria ventricosa* (Peck) Peck, Bull. Torrey bot. Club 34: 104 (1907)
 \equiv *Biannularia ventricosa* (Peck) Pomerl., Naturaliste Can. 107: 303 (1980)

Type specimen: **USA:** Alabama, Lee, Auburn, Alabama, 00-XI-1895, leg. L. M. Underwood, NYS-F-003346 (**holotype**).

Description: Habit fleshy, tricholomatoid, with two annuli. *Pileus* 70–150(–200) mm in diam., convex to broadly convex with enrolled to incurved margin, becoming irregularly convex or nearly flat, surface dry, smooth, with scattered pressed-down fibers or subareolate in age, not hygrophanous, whitish to pale grey, often in age with gray-brown areas. *Lamellae* decurrent, narrow, crowded, white to pale tan, with an even concolorous edge. *Stipe* 50–150 × 25–60 mm, solid, hard, cylindrical (sometimes swollen in the middle) above a tapered base, usually rooting, sometimes almost completely buried, smooth to appressed-fibrillose, dull, dry, white to yellow-brown (discoloring brownish or greyish) with a flaring, double ring; partial veil superior, persistent, two layered, membranous, somewhat elastic, white, leaving a narrow annulus and often an appendiculate margin. *Context* compact, thick, firm, hard, white, not changing on exposure. *Smell* and *taste* not distinctive or slightly unpleasant-farinaceous. *Spore print* white.

Spores [50/2/2] 9.8–12.2 × 4.0–4.7 μm (on average 11.0 × 4.4 μm), $Q = 2.3–2.8$ ($Q_m = 2.5$), $V = 88–136 \mu\text{m}^3$ ($V_m = 112 \mu\text{m}^3$), elongated-ellipsoid, subphaseoliform to fusoid (boletoid) in side view, sometimes with a median constriction, mainly ellipsoid in front view, partly with a suprahilar depression, apex rounded or rarely blunt, hilar appendix well-developed and up to 0.5–0.8

μm long, smooth, thin-walled, usually multiguttulate, amyloid, congophilous, cyanophilous. *Basidia* 40–55(–60) × 8–9.5(–10) μm , usually less than 45 μm long, four-spored, strictly clavate, sterigmata 4–6 μm long, with basal clamp-connections, hyaline or with a multiguttulate green content. *Subhymenium* poorly differentiated of short, up to 3–6 μm wide elements. *Hymenophoral trama* divergent in young basidiomata then regular to subregular with cylindrical to claviform, thin-walled, 3–10(–14) μm wide elements, sometimes intermixed with thromboplerous hyphae (with greyish contents) and polymorphic or rosetta-like crystals. *Cheilocystidia* 40–60 × 3–5(–7) μm abundant, thin-walled, hyaline, undulate, with rounded apex, sometimes lobate or beaked. *Pleurocystidia* absent. *Pileipellis* an ixocutis (with some ascending/repent hyphae) of loosely interwoven, sometimes undulate or moniliform, cylindrical hyphae, 3–8 μm wide, embedded in a thick gelatinous matrix, often with grey-brown cytoplasmatic contents. *Subcutis* of loosely interwoven, sometimes undulate hyphae, with abundant thromboplerous hyphae (with greyish contents) and polymorphic crystals. *Clamp connections* common everywhere.

Ecology: solitary, scattered, rooting, occurring in deep humus under conifers (primarily *Abies* and *Picea*). North America (Alabama (type), Quebec, Ontario, Washington) and Asia (China).

Specimens examined: **CANADA:** Ontario, Petawawa Forestry Station, under closed canopy of Norway spruce, emerging from needle bed, leg. S.A. Redhead, E. Fox, L. Duchesne, L. Clark, det. S.A. Redhead, 14-IX-1994, 221514 (DAOM); Québec, St. Aubert, L'Islet Co., leg. J.W. Groves, 23-VIII-1966, 10472 (TUR) (as *Armillaria ventricosa*). **USA:** Washington, Clallan Co., Olympic National Park, Soleduc Valley, leg. G. Barron, S.A. Redhead, L. Norvell, det. D.E. Desjardin, 14-X-1992, 225247 (DAOM) (as *Cataethelasma imperiale*).

Comments: This species was originally described from Alabama (USA) by Peck (1896). It usually produces medium-sized basidiomes with a whitish to pale grey, ash-grey dry pileus up to 150(–200) mm broad, a usually non-farinaceous smell and taste, short basidia not exceeding 45 μm long and spores hardly reaching 12 μm in length (Peck 1896; Singer 1940; Miller 1985; Castellano et al. 2003; Phillips 2010; Desjardin et al. 2015). *Cataethelasma ventricosum* is mainly found in eastern North America but has been recorded also in the Pacific Northwest (Peck 1896; Singer 1978b; Desjardin et al. 2015), Guatemala (Flores Arzú et al. 2012), and in the northeast coast of Asia (Singer 1978b).

It could be confused with *C. imperiale* which shows larger basidiomes with a brownish-red pileus, a mealy smell, longer spores and longer basidia. There seems to be

some confusion between these two species in North America as evidenced above. *Catathelasma ventricosum* may be confused in the field with *C. evanescens* (see below) or with *Tricholoma magnivelare* (Peck) Redhead, which is easily distinguished by its strong spicy-sweet smell, softer context, more fragile basidiomes, and inamyloid spores (Bessette et al. 2013). Genetically, two sequences coming from Chinese samples of mycelium (MG018985 and MG793231) seem to be slightly different from those coming from Canada and USA (Fig. 2). Further sampling and sequencing are needed to decide if they represent a distinct (maybe cryptic) species, or a partially isolated lineage encompassed within the intraspecific variability of *C. ventricosum*.

Catathelasma evanescens Lovejoy, Bot. Gaz. 50(3): 384 (1910) Fig. 4j–l

Type specimen: **USA**: Wyoming, Carbon, Brooklyn Lake, Snowy Range, in open balsam and spruce woods, occurring singly in sod on thick humus, 3500 m a.s.l., leg. R.H. Lovejoy, 08-IX-1909, MICH 10102 (**isotype**); Washington, Kittitas Co., Table Mtn., Naneum Meadows, scattered singly on base soil under *Picea*, 1676 m a.s.l., leg. P.B. Matheny & S.D. Matheny, 21-IX-2002, PBM 2403, 45682 (WTU-F) (**epitype** here designated) (Mycobank MBT 38889).

Description: Habit tricholomatoid. *Pileus* 40–130 mm, convex with slight central depression to vas-shaped with an uplifted margin, edge of margin inrolled, dry, whitish when young, whitish with cinnamon brown tones towards margin in age, surface smooth but cracked due to desiccation on youngest specimens, with sandy soil adhering to surface of largest specimen. *Lamellae* crowded, decurrent, with few tiers of lamellulae, occasionally forked, narrow to broad, pallid or whitish, edges entire and even. *Stipe* 40–90 × 15–35 mm at apex, tapered to a point below, slightly ventricose near the centre (this 30–38 mm wide); *annulus* double, membranous, upper ring flaring, striate on upper side, lower ring less conspicuous but membranous; white or pallid, in age with slight brownish tone. *Context* confluent, white, unchanging, smell farinaceous when young but mixed farinaceous-antiseptic or unpleasant with age. Spore-print white (on upper side of upper annulus).

Spores [119/3/3] 13.5–16.7 × 5.1–6.1 µm (on average 15.1 × 5.6 µm), $Q = 2.39\text{--}3.10$ ($Q_m = 2.74$), $V = 185\text{--}319 \mu\text{m}^3$ ($V_m = 252 \mu\text{m}^3$), oblong to boletoid in side view, at times constricted in the middle, with often rounded apex, smooth, thin-walled, with apicule evident, amyloid, con-gophilous, cyanophilous, with many greenish small drops. *Basidia* 50–70(–80) × 8–11 µm, tetrasporic, long clavate, with up to 10 µm sterigmata, with basal clamp connections, with many greenish small drops. *Hymenophoral*

trama regular to subregular, composed of cylindrical to claviform, 3–12(–15) µm wide, hyphae. *Cheilocystidia* 40–60 × 3–6 µm, hyaline, flexuous, with rounded apex, often lobed or rostrate, at times subcapitate. *Pleurocystidia* not observed. *Pileipellis* an ixocutis of repent, loose, intertwined, cylindraceous, 2–7 µm wide hyphae, embedded in a gelatinose matter. *Subcutis* of loosely interwoven, sometimes undulate, 6–12 µm hyphae, with abundant thrombo-plerous hyphae (with greyish contents) and polymorphic crystals. *Clamp connections* present.

Ecology: isolated basidiomes fruit scattered on bare ground in coniferous forests. So far known only North America (Canada, USA and Mexico).

Specimens examined: **USA**: Washington, Kittitas Co., Table Mtn., Naneum Meadows, scattered singly on base soil under *Picea*, 1676 m a.s.l., leg. P.B. Matheny & S.D. Matheny, 21-IX-2002, PBM 2403, 45682 (WTU-F) (**epitype**) (as *C. ventricosa*); Colorado, Front Range, leg. Mycological Society, 16-VIII-2003, 021378 (DBG-F) (as *C. singeri*); Colorado, Gilpin County, Roosevelt National Forest, Rollinsville area, Rd. 132, leg. C. Harwick & Mycological Society, 21-VIII-2004, 021747 (DBG-F) (as *C. singeri*); Colorado, Pitkin County, Aspen Conference, leg. Mannie Salzmann's Boys, 13-VIII-1975, 006151 (DBG-F) (as *C. evanescens*); Colorado, Pitkin County, White River National Forest, Montezuma Rd., 3 miles from Ashcroft, leg. A.H. Smith, 14-VIII-1975, 006150 (DBG-F) (as *C. evanescens*).

Comments: A sequenced North American collection of *C. evanescens*, 45682 (WTU-F), with morphological and ecological features perfectly fitting those reported in the protologue is here selected as epitype to stabilize the identity of this taxon. Lovejoy (1910) proposed the new genus *Catathelasma* and the new species *C. evanescens* to accommodate a single basidiome found in a *Abies/Picea* stand at 3500 m a.s.l. in Wyoming (USA) characterized by a 130 mm broad white pileus with a dark cream centre (becoming intensely ochre with reddish tinges after drying), a very short stipe (10 × 40 mm), an “*annulus delicate, evanescent, situated on stipe just below gills: volva large, white, smooth, opening around top leaving a thick even white margin, persistent and closely embracing base of stipe*”, and ellipsoid to fusiform spores (14–17.5 × 3–5 µm).

The original description is based on a probably young specimen presenting a still compressed and not completely expanded stipe, and the outermost ring remains still basal simulating the presence of a volva-like structure. Considered until today an elusive phantom species, *Catathelasma evanescens* was never reported again after the original description, probably because it was confused with other taxa. In fact, *C. evanescens* resembles *C. ventricosum* because of its small to medium-sized whitish pileus that

turns ochre in spots with age and a similar non-farinaceous context, but its microscopic characteristics (spores > 14 µm long on average, basidia > 50 µm long) are more similar to those of *C. imperiale*. The clade of *C. evanescens* (Fig. 2) includes three collections from Colorado (USA) originally determined as *C. singeri*, as well as one from Washington (USA) identified as *C. ventricosum*, and two more (from Canada and Mexico), as *C. imperiale*, proving how deceptive this species can be. Morphologically, *C. imperiale* differs mainly by a larger pileus reaching 200(–400) mm, which has reddish-brown tinges, and a strong farinaceous or cucumber-like smell (Bon 1978; Breitenbach and Kränzlin 1991; Vellinga 1995; Vesterholt 2012a; present work). *Catathelasma ventricosum* shows smaller spores and basidia (Singer 1940; Miller 1985; Castellano et al. 2003; Desjardin et al. 2015; present work). The collection of *C. ventricosum* with up to 16 µm long spores described in Miller and Miller (2006) is probably *C. evanescens*. Finally, *C. singeri*, a species proposed for a single basidiome found in Aspen (Colorado, USA), has a 60 mm broad pileus, dull pale ochraceous in the margin and dingy olive at centre, as well as spores measuring 9.5–13 × 6–7.5 µm (Mitchel and Smith 1978). However, a re-examination of the holotype of *C. singeri* by O. Miller and H. Miller and Vera S. Evenson and Rosa-Lee Brace (<http://mycoportal.org/portal/collections/individual/index.php?occid=11673>) revealed much smaller spores measuring 9.9–13.5 × 4.5–5.4 (on average 11.4 × 4.9 µm), suggesting that *C. singeri* could be closer to *C. ventricosum*.

Cleistocybe Ammirati, A.D. Parker & Matheny, Mycoscience 48(5): 283 (2007)

Type species: *Cleistocybe vernalis* Ammirati, A.D. Parker & Matheny, Mycoscience 48(5): 284 (2007)

Description: Habit clitocyboid to pleurotoid, veil present or ephemeral. *Pileus* 20–50 mm, convex to plane becoming depressed, margin enrolled to incurved or decurved, surface non-viscid or viscid, appressed fibrillose to squamulose or with agglutinated fibrils, non-hygrophanous. *Lamellae* decurrent to long decurrent, close, crowded or subdistant to distant, relatively narrow, light pinkish brown, pale pinkish grey to light grey. *Stipe* central, equal to clavate or tapered slightly downward, solid, surface dry, appressed fibrillose to squamulose below; *smell* and *taste* strongly farinaceous. *Spore print* white. *Spores* in front view usually ellipsoid to ellipsoid oblong, in side view ellipsoid to ovoid or subfusoid to subcylindrical, often strongly inequilateral, smooth, distinctly apiculate, relatively thin-walled, inamyloid, acyanophilous. *Basidia* narrowly clavate to clavate, usually 4-spored but sometimes 1–3-spored, typically colourless

or with granular contents; *hymenophoral cystidia* absent. *Hymenophoral trama* interwoven to subparallel but more or less divergent when young, hyphae cylindrical, with a tendency to undulate, colorless; thromboplerous hyphae present. *Pileipellis* interwoven, non-gelatinous or gelatinous, hyphae cylindrical, narrow, often flexuous, sometimes encrusted, colourless, yellowish, orange or orange-brown. *Clamp connections* present.

Ecology: terrestrial, solitary to caespitose, or in clusters on soil under mixed conifers (*Abies*, *Larix*, *Platycladus orientalis*, *Pseudotsuga*, *Thuja*) or conifers mixed with Betulaceae (*Alnus*, *Betula*). It has not been ascertained if it is ectomycorrhizal or saprotrophic but C and N stable isotopes data produced by Sánchez-García and Matheny (2017) suggest a saprotrophic lifestyle.

Comments: This genus was proposed by Ammirati et al. (2007) to accommodate the new species *Cleistocybe vernalis* Ammirati, A.D. Parker & Matheny, found in mixed forests in Washington state (USA), and combine *Clitocybe gomphidioides* A.H. Sm. *Cleistocybe* is characterized by the presence of an ephemeral veil, pinkish gray to vinaceous buff decurrent lamellae, a stipe usually rooting, spores inamyloid, amygdaliform to fusiform with an acute base, subfuscoid or subcylindric, long narrow hygrophoroid basidia, and divergent to interwoven hyphae in the lamellar trama and pileipellis. Three additional species were later added to *Cleistocybe*: *C. carneogrisea* (Malençon) Vizzini, *C. pleurotoides* J. Favre ex Vizzini (Vizzini 2009) from North Africa and Europe, and *C. vernaloides* H.M. Wu, J.Q. Luo, Ke Wang & Y.J. Yao from China (Wu et al. 2018). Moreau (2009) proposed the provisional name *Cleistocybe malenconii* P.-A. Moreau (nom. inval.) for a caespitose collection from Morocco, so far only documented by G. Malençon's notes and aquarelle.

A close phylogenetic relationship between *Cleistocybe* and the *Catathelasma* clade was already suggested by some authors (Ammirati et al. 2007; Vizzini and Ercole 2012; Sánchez-García and Matheny 2017), while in other studies, *Cleistocybe* was considered an *incertae-sedis* genus because it was not significantly related with any known family (Sánchez-García et al. 2014, 2016; Alvarado et al. 2018a), although a relationship with *Bonomycetes* was recently suggested (Alvarado et al. 2018b). In the present analysis of the *Tricholomataceae* (Fig. 1), *Bonomycetes* and *Cleistocybe* are significantly related with *Catathelasma* (PP = 1.00, BP = 100%), and both are therefore considered members of the family *Biannulariaceae*. In the analysis focused on *Biannulariaceae* (Fig. 2), *Cleistocybe* is sister to *Catathelasma* (PP = 1.00, BP = 37%). Morphologically, *Catathelasma* differs from *Cleistocybe* because of its double annulus and amyloid spores, while *Bonomycetes* has salmon to reddish tones, pale lamellae, non-rooting stipe, ellipsoid spores with obtuse base, and lack a developed veil. *Cleistocybe gomphidioides* was not included in the present analysis because it probably

does not belong to either *Biannulariaceae* or *Callistosporiaceae*, and is therefore outside the focus of the present work.

Bonomyces Vizzini, Index Fungorum 159: 1 (2014)

Type species: *Bonomyces sinopicus* (Fr.) Vizzini, Index Fungorum 159: 1 (2014)

Description: Basidiomata clitocyboid, veil absent or primordial. Pileus 50–100 mm, convex to plane or umbilicate with slightly enrolled margin when young, later irregularly funnel-shaped with undulating and uplifted margin; surface smooth, dull, reddish brown, pale brick, salmon color to light brown and darker at the center, non-hygrophanous. Lamellae crowded or distant, more or less decurrent, broad, with entire edge, white to beige and wood colour when mature. Stipe 40–50 × 5–12 mm, cylindrical, sometimes tapering or larger toward the base, longitudinally fibrillose, with a large rhizomorph cluster at the base. Context white when young, later light champagne, smell farinaceous, taste mild to slightly bitter. Spore print whitish to cream. Spores ellipsoid to cylindric, not lacrymoid with obtuse, not confluent base, multiguttulate, smooth, thin-walled, with a thick lateral apiculus, acyanophilous. Basidia cylindrical to clavate, mostly colourless, with short broad sterigmata. Lamellae edge fertile, with frequent hair-like cystidioles with long neck and inflate base, absent in the faces. Hymenophoral trama with a slightly divergent hymenopodium and a mediostratum made of parallel hyphae. Pileipellis an ixocutis with mainly cytoplasmatic pigment. Clamp connections present at all septa.

Ecology: terricolous, under conifers, probably saprotrophic, the genus has been found in Europe, North Africa and Turkey. *Clitocybe sinopica* has also often been reported from burned sites (Moser 1949; Mornand 1978; Bigelow 1982, 1985; Breitenbach and Kränzlin 1991; Crozes 1999; Horak 2005; Vesterholt 2012b).

Comments: *Bonomyces* was proposed by Vizzini (2014) as a new genus for *Clitocybe sinopica* (Fr.) P. Kumm. because of its deviant morphological and genetical features compared with other *Clitocybe* species. Alvarado et al. (2018b) confirmed this decision after the analysis of several samples which led to the addition of two species more, *B. arnoldii* (Boud.) P.-A. Moreau, Vizzini & P. Alvarado and *B. afrosinopicus* (P.-A. Moreau) P. Alvarado, P.-A. Moreau, Youcef Khodja & Contu, as well as the synonymization of *Clitocybe subsinopica* Harmaja and *B. sinopicus*. *Bonomyces* species have (i) a pileus with reddish brown to pale brick tinges, (ii) a very hard, filamentous stipe made of narrow and crowded hyphae, similar to that observed in *Infundibulicybe*, (iii) ellipsoid and multiguttulate spores with a thick lateral apiculus, and (iv) the mediostratum of lamellae is made of not completely parallel inflate hyphae as well as some often

bifurcate vesicular elements that introduce irregularities in the otherwise rather parallel structure of the trama (Alvarado et al. 2018b). *Bonomyces* is quite similar morphologically to *Cleistocybe* (Alvarado et al. 2018b). However, *Bonomyces* species show salmon to reddish overall tones, with white, pale, or at most yellow lamellae, non-rooting stipe, ellipsoid spores with obtuse base, and lack a well-developed veil (in *B. arnoldii* a pseudo-annular zone delimited by granules may be present). In the present analyses (Figs. 1, 2) *Bonomyces* is sister to a monophyletic clade consisting of *Catathelasma* and *Cleistocybe*.

Callistosporiaceae Vizzini, Consiglio, M. Marchetti & P. Alvarado, fam. nov.

Mycobank MB 831396

Type genus: *Callistosporium* Singer, Mycologia 36(4): 363 (1944)

Diagnosis: Habit tricholomatoid, collybioid or pleurotoid, veils absent. Lamellae adnate, adnexed, sinuate, emarginated to decurrent. Spore print white. Spores ellipsoid, hyaline, smooth, inamyloid or amyloid (*Pseudolaccaria*), cyanophilous or acyanophilous. Basidia lacking siderophilous inner bodies. Cheilocystidia present or absent, pleurocystidia absent, if present then only as pseudocystidia. Hymenophoral trama regular to slightly bilateral becoming regular. Pileipellis arranged as a cutis, ixocutis or cutis becoming a trichoderm. Clamp connections usually absent, very rarely present (in *Xerophorus*, partim; in *Callistosporium imbricatum* at the base of basidia). On soil or rotten wood. Saprotrophic or ectomycorrhizal.

Genera included: *Callistosporium* (including *Pleurocollybia*), *Anupama*, *Guyanagarika*, *Macrocybe*, *Pseudolaccaria*, *Xerophorus* stat. nov.

Callistosporium Singer, Mycologia 36(4): 363 (1944)

= *Pleurocollybia* Singer, Mycologia 39(1): 80 (1947)

Emended here to include also the genus *Pleurocollybia* and *Clitocybe hesleri*, and to exclude species of *Xerophorus*.

Type species: *Gymnopus palmarum* Murrill, Bull. Torrey bot. Club 66: 32 (1939)

Description: Habit collybioid, collybioid-pleurotoid or pleurotoid; veils absent; pileus small-sized, convex to planar, stipe central, eccentric or lateral, sometimes absent; lamellae usually crowded and very narrow, adnate, adnexed, or emarginate-adnexed; small spores (usually < 8 µm long), white-colored in mass deposits, smooth, inamyloid, cyanophilous; basidia up to 35 µm long, lacking siderophilous bodies; hymenial cystidia, present only as cheilocystidia (if at all); spores, basidia and hyphae of the trama with or without necropigments (at least in part as dimeric anthraquinone pigments such as skyrin and hypericin); clamp connections usually absent (present in *C. imbricatum* at the base of

basidia); habitat usually lignicolous on rotting wood or wood debris, found in Europe, North Africa, America and Asia.

Comments: The genus *Callistosporium* was described by Singer (1944) for *C. palmarum* (Murrill) Singer (basionym *Gymnopus palmarum* Murrill), a species known only from the type collection. Since then, several new *Callistosporium* taxa have been recognized, and new combinations made. There are about 25 *Callistosporium* species names published (Kirk 2019). Most of the species has a collybioid habit, central stipe, abundant bright yellow necropigments in the spores, basidia and tramal hyphae usually turning lilac-purple in basic solutions, lacking clamp connections, and occurring in the Neotropics (Singer 1944; Bon 1976, 1984, 1991; Verde and Calonge 1979; Redhead 1982; Gulden 1992; Noordeloos 1995; Vesterholt and Holec 2012; Jančovičová et al. 2016). It is thought that the yellow and brown colours of *Callistosporium* basidiomes are due to unstable, dimeric anthraquinone pigments that oxidate producing colour shifts (darkening) in living and dried basidiomes (Høiland 1984; Moser 1986).

Bon (1990, 1991) recognized two subgenera within *Callistosporium*: (i) subgen. *Callistosporium* with crowded thin lamellae, regular hymenophoral trama, non hygrophoroid basidia up to 30 µm long, pileipellis hyphae with cytoplasmatic or parietal pigment but without extracellular incrustations reacting in basic solutions, spores < 8.5 µm long, fruiting on wood or wood debris; and (ii) subgen. *Xerophorus* Bon for the European species with spaced thicker lamellae, subdivergent hymenophoral trama, hygrophoroid basidia up to 45(–50) × 8–10 µm, abundant extracellular pigment turning blue-green in basic solutions (as in *Hygrophorus persoonii*), spores up to 10(–11) µm long, fruiting mainly on soil. Contu (1992) downgraded subgen. *Xerophorus* at the section level.

Pleurocollybia was originally proposed by Singer (1947) to accommodate *Gymnopus praemultifolius* Murrill (Murrill 1945), a species first found in Florida (USA), based on several divergent features: eccentric stipe, clampless hyphae, minute basidiospores (very small for an agaric, e.g. “2.7–3.5 × 2.5–3.2 µm”), and lack of necropigments. Singer (1947) compared *Pleurocollybia* with two morphologically similar genera, *Callistosporium* and *Podabrella* Singer (the latter is now considered a synonym of *Termitomyces* R. Heim, Frøslev et al. 2003), but considered *Pleurocollybia* a distinct genus because of its eccentric stipe and smaller spores. Since 1947, five new species of *Pleurocollybia* have been described from the Neotropics (Singer 1955, 1963, 1969, 1978a; Baroni et al. 2008), and five more have been combined from existing genera, two of them occurring in the Neotropics (Singer 1970, 1986); one from Sri Lanka and Africa (Pegler 1977), one from New Zealand (Horak 1971)

and another one from Florida, USA (Baroni et al. 2008). In total, eleven species of *Pleurocollybia* have been so far described, nine of them occurring in the tropics (Baroni et al. 2008). *Pleurocollybia imbricata* T.J. Baroni, Lodge & Linder and *P. praemultifolia* (Murrill) Singer have been reported also from the Republic of São Tomé and Príncipe in western Africa (Desjardin and Perry 2017). Recently, *Pleurocollybia cibaria* Singer from Peru was combined into *Gerhardtia* Bon in the *Lyophyllaceae* based on morphological and rDNA data (Matheny et al. 2017).

According to the original description by Singer (1947) and the features of the species described after it (Singer 1986; Baroni et al. 2008), *Pleurocollybia* is characterized by a pleurotoid or collybioid-pleurotoid habit; stipe eccentric, lateral or absent (a truly central stipe is known only for two species); lamellae crowded and very narrow, adnate or adnexed or emarginate-adnexed; spores small and white in mass deposits, smooth, inamyloid; basidia lacking siderophilous bodies; spores, basidia and hyphae of the trama without necropigments; clamp connections may be present or absent; habitat typically lignicolous on rotting wood.

A close phylogenetic relationship between *Pleurocollybia* and *Callistosporium* (as originally suspected by Singer 1947) was later suggested by the genetic works by Moncalvo et al. (2002) and Lavorato et al. (2015), where both genera were significantly related with the so-called /callistosporioid clade, as well as by Ammirati et al. (2007), Sánchez-García et al. (2016), Sánchez-García & Matheny (2017), and Alvarado et al. (2018a, b), where both genera are supposed to belong to the lineage called Catahelasma clade, *Catahelasmataceae* or *Biannulariaceae*. The present analyses (Figs. 1, 3) suggest a wider generic concept of *Callistosporium*, which is here applied to a significantly monophyletic clade including *Callistosporium* s. str., *Pleurocollybia*, *Clitocybe* aff. *fellea*, and *Clitocybe hesleri* (type collection), as well as several other lineages lacking a confirmed name. Consequently, the absence/presence of necropigments and the position of the stipe do not seem to have a phylogenetic meaning at the genus level in this group (Singer 1986; Baroni et al. 2008), although they could still play a role at the supraspecific level, since most species of *Pleurocollybia* (*P. brunnescens*, *P. praemultifolia*, *P. imbricata*) form a significantly monophyletic clade (PP = 0.99, BP = 83%) within *Callistosporium*. Finally, the species of *Callistosporium* subgenus *Xerophorus* form an independent lineage within *Callistosporiaceae* which is here upgraded to genus level.

Callistosporium palmarum (Murrill) Singer, Mycologia 36(4): 363 (1944) Fig. 5

Basionym: *Gymnopus palmarum* Murrill, Bull. Torrey bot. Club 66: 32 (1939)

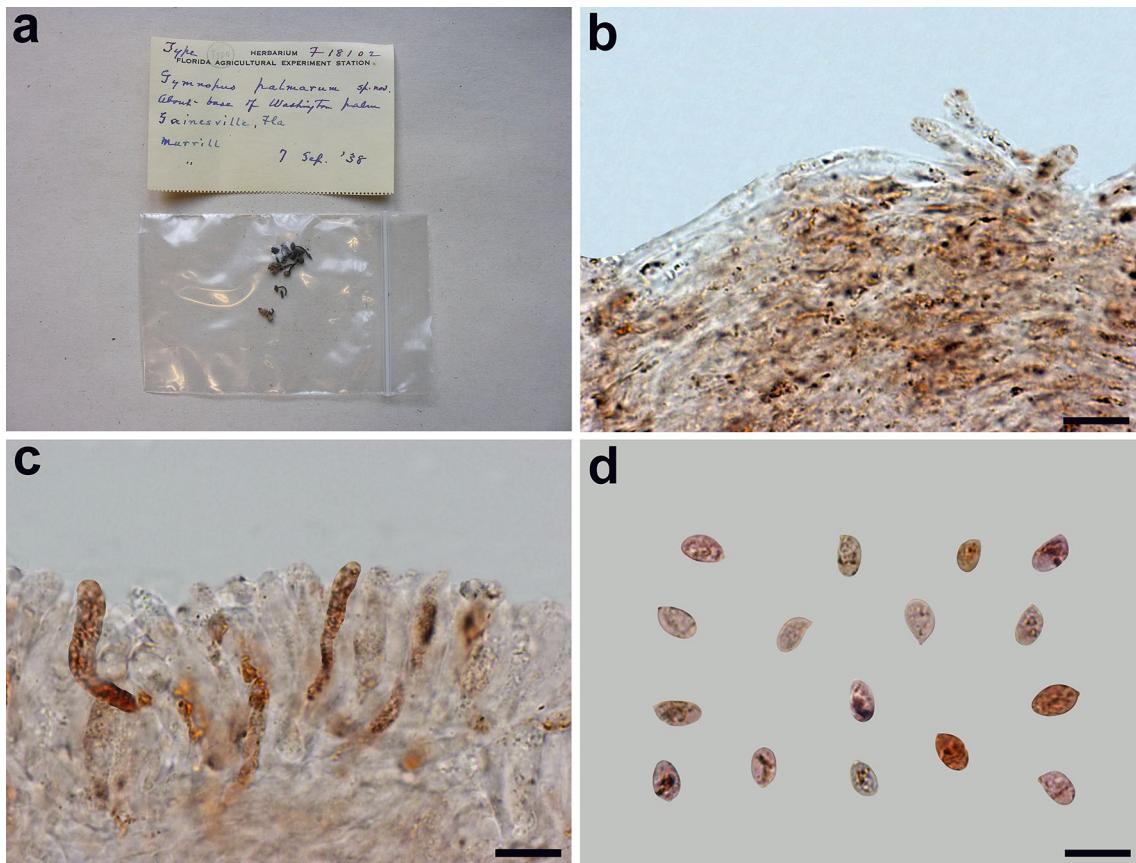


Fig. 5 *Callistosporium palmarum* (18102 FLAS-F, holotype). **a** Herbarium collection. **b** Pileipellis. **c** Hymenial elements. **d** Spores. **b-d** in 10% ammonia. Bars = 10 µm. Photographs by M. Marchetti

≡ *Collybia palmarum* (Murrill) Murrill, Bull. Torrey bot. Club 66: 37 (1939)

Description: Spores [40,1,1] 6.2–7.0 × 3.9–4.6 µm (on average 6.6 × 4.3 µm), Q = 1.1–2.3 ($Q_m = 1.7$), V = 51–75 µm³ ($V_m = 63 \mu\text{m}^3$), ellipsoid to subamygdaliform in side view, ellipsoid in front view, often with a rounded and sometimes attenuated apex, smooth, thin-walled, frequently with an evident apicule, inamyloid, cyanophilous; cytoplasmatic content hyaline with a central guttule or with several polymorphic guttules, green-colored under light microscope; some of them produce a more or less light vinous red colour with basic solutions. Basidia 20–30 × 5.6–7.4 µm, tetrasporic, rarely also bisporic, often enlarged at the apex, with 3–5 µm long sterigmata, lacking basal clamp connections, with a granulose greenish pigment, some of them with a vinous red cytoplasmatic content, turning more or less intensely purplish-red in basic solutions (in spots or completely). Hymenophoral trama regular to subregular, composed of thick-walled hyphae up to 110 µm long × 3–10 µm wide, with granulose epiparietal pigment, vinous red with basic solutions. Cheilocystidia rare, 15–28 × 3–5 µm, hyaline,

flexuous, with rounded apex. *Pleurocystidia* not observed. *Pileipellis* formed by repent cylindrical hyphae 4–10 µm wide, with some claviform terminal elements emerging, and with intracellular and granulous epiparietal pigments becoming vinous red in basic solutions. *Stipitipellis* composed of cylindrical to fusiform hyphae 2–10 µm wide, at times constricted at septa; in the external ones the cytoplasmatic content as well as the dense granulous epiparietal pigment (up to 1.2 µm thick) stain vinous red with basic solutions. *Clamp connections* absent everywhere.

Specimens examined: USA: Florida, Alachua, Gainesville, around the base of Washington palm, leg. W.A. Murrill, 07-IX-1938, 18102 (FLAS-F) (**holotype**).

Comments: All attempts made to produce genetic data from the type collection failed, either with the traditional Sanger sequencing technique or with the next generation sequencing tools (already tested successfully on old ascomycetous herbarium specimens by Forin et al. 2018). The original description by Murrill (1939) reports small basidiomes with a 4–6 mm broad pileus fruiting on the soil about the base

Fig. 6 Fresh basidiomes of *Callistosporium* spp. **a** *C. elaeodes* (958 ZT-Myc). **b** *C. luteo-olivaceum* (18220 AMB). **c** *C. luteo-olivaceum* (18221 AMB). **d** *C. luteo-olivaceum* (18113 AMB). **e** *C. pinicola* (691390 BRNM). **f** *C. pinicola* (709 ZT-Myc). **g–h** *C. graminicolor* (PBM 2341-WTU-F). Photographs: **a–f** by M. Wilhelm; **b–d** by G. Consiglio; **e** by V. Antonín; **g–h** by P.B. Matheny



of a Washington palm (*Washingtonia* sp.) (maybe on rotten debris?). Microscopic features described by Horak (1968) and the present study confirm the presence of necropigments turning purple-red in basic solutions in tissues, basidia and spores, absence of extracellular incrustations becoming green in basic solutions, small spores < 8 µm long, and small basidia < 30 µm long. These characters suggest a closer relationship with *Callistosporium* s.s., than to *Xerophorus*.

***Callistosporium luteo-olivaceum* (Berk. & M.A. Curtis)**
Singer, Lloydia 89: 117 (1946) Figs. 6b–d, 8a–c

Basionym: *Agaricus luteo-olivaceus* Berk. & M.A. Curtis, Ann. Mag. nat. Hist., Ser. 3 4: 286 (1859)
≡ *Collybia luteo-olivacea* (Berk. & M.A. Curtis) Sacc., Syll. fung. (Abellini) 5: 215 (1887)
= *Agaricus coloreus* Peck, Bull. Buffalo Soc. nat. Sci. 1(2): 46 (1873) [1873–1874]

- ≡ *Collybia colorea* (Peck) Sacc., Syll. fung. (Abellini) 5: 230 (1887)
 = *Agaricus rubescens* Peck, Rep. (Annual) Trustees State Mus. Nat. Hist., New York 39: 38 (1887) [1886]
 ≡ *Collybia rubescens* (Peck) Peck, Rep. (Annual) Trustees State Mus. Nat. Hist., New York 41: 83 (1888)
 ≡ *Tricholoma rubescens* (Peck) Sacc., Syll. fung. (Abellini) 9: 15 (1891)
 ≡ *Collybia colorea* var. *rubescens* (Peck) Peck, Ann. Rep. Reg. N.Y. St. Mus. 49: 65 (1897) [1896]
 = *Calocybe olivascens* (Maire) Singer, Annls mycol. 41(1/3): 107 (1943)
 = *Psilocybe floridana* Murrill, Proc. Fla Acad. Sci. 7(2/3): 126 (1945) [1944]
 = *Callistosporium psilocybe* Murrill & Singer, Mycologia 36(4): 363 (1944)
 = *Callistosporium luteofuscum* Singer, Lilloa 26: 115 (1954) [1953]
 ≡ *Callistosporium luteofuscum* var. *major* Singer [as 'maior'], Beih. Nova Hedwigia 29: 53 (1969)
 = (?) *Collybia xanthophylla* Malençon & Bertault, Trav. Inst. Sci. Chérifien, Sér. Bot. Biol. Vég. 33: 406 (1975)
 ≡ (?) *Callistosporium xanthophyllum* (Malençon & Bertault) Bon, Docums Mycol. 6(no. 24): 52 (1976)
 = *Callistosporium majus* Singer, Sydowia 30(1–6): 262 (1978) [1977], nom. inval., Art. 39.1 (Shenzhen)

Description: Habit collybioid, basidiomes usually clustered. *Pileus* 10–45 mm broad, hemispherical, convex to flat-convex, with or without an umbo, slightly depressed to umbilicate at the centre when old, margin inflexed to straight, flat to undulate, entire, slightly translucently striate, surface smooth, dry, hygrophanous, glabrous to rugulose, sometimes apparently velutinous, yellowish-brown to olive brown. *Lamellae* crowded, $L = 35–50$, $l = (1–)3–4(–5)$, up to 3 mm wide, ventricose, emarginate, bright yellow when young, then rusty yellow or olive yellow, edge entire, concolorous or somewhat paler. *Stipe* 20–80 × 2–8 mm, central to slightly eccentric, fused into a cluster, thicker at the centre and tapering upwards and downwards, curved, sometimes longitudinally compressed, fistulose, yellowish brown to olive brown, fibrillose, minutely pruinose-floccose at the top, with a white tomentum at the base. *Context* of the pileus up to 2 mm thick, yellowish, olive brown. *Smell* indistinct, *taste* mild or slightly bitter. *Spore print* white. *Macrochemical reactions*: surface of the basidiome turning red-purple with a drop of basic solutions.

Spores [122, 3, 3] 4.7–6.0 × 3.3–4.1 μm , (on average 5.5–3.7 μm), $Q = 1.3–1.8$ ($Q_m = 1.5$), $V = 29–49 \mu\text{m}^3$ ($V_m = 39 \mu\text{m}^3$), ellipsoid, adaxially flattened in side view, ellipsoid in front view, hyaline, thin-walled, with apicule evident, with a large greenish-yellow droplet when observed in water, which stains reddish in basic solutions, inamyloid,

cyanophilous, mostly congophobic. *Basidia* 20–32 × 5.0–6.7 μm , cylindric to cylindric-clavate, tetrasporic, with sterigmata up to 5 μm long, sometimes bisporic or monosporic with sterigmata up to 7 μm long, lacking basal clamp connections, with a granulose greenish cytoplasmatic content, which stains more or less strongly purplish red in basic solutions. *Cheilocystidia* 22–35 × 3.5–5 μm , poorly differentiated, cylindraceous or sometimes flexuose, often constricted in the middle and subcapitulated, purplish red in basic solutions. *Pleurocystidia* not observed. *Subhymenium* well differentiated, thick, mostly composed of short elements, 3–6 μm wide. *Hymenophoral trama* regular, with hyphae 4–12(–14) μm wide, cylindrical to rounded at septa, with a hyaline wall up to 0.5(–1.0) μm thick. *Pileipellis* a cutis with intertwined hyphae 3–10 μm wide, sometimes with a vinous red cytoplasmatic content and patches of reddish brown epiparietal pigment in basic solutions, with scattered emergent terminal elements, often forming tufts, flexuose to cylindric or clavate, measuring 25–35 × 4–8 (–15) μm , hyaline to lilac-pink. *Hypoderm* regular with hyphae 4–12(–15) μm wide, presenting walls up to 1(–1.2) μm thick, sometimes with small reddish brown plates of epiparietal pigment. *Stipitipellis* composed of hyphae 2–10(–12) μm wide, of variable length, cylindraceous, sometimes rounded at septa, with walls up to 1 μm thick, with small brownish plates of epiparietal pigment and red to vinous red intracellular pigment. *Caulocystidia* 30–50 (70) × 5–10 (–14) μm , cylindrical to clavate, sometimes flexuose, lageniform, bilobed, emergent to repent, with rounded to subcapitulated apex. *Clamp connections* absent.

Ecology: usually on decaying wood of *Pinus* spp., North and South America, the Caribbean, Europe, North Africa and Asia.

Specimens examined: **ITALY:** Friuli Venezia Giulia, Trieste, Miramare Park, on a large decaying domestic pine tree stump, leg. P. Picciola, 11-XII-2016, 18228 (AMB); Lazio, Latina, Retroduna di Sabaudia, on dead pine wood, leg. G. Consiglio, G. Perdisa & L. Setti, 03-XI-2007, 18230 (AMB); Tuscany, Livorno, Piombino, Rimigliano, on dead holm wood, leg. G. Consiglio, E. Franceschini & G. Perdisa, 02-XII-2006, 18231 (AMB).

Comments: This species was originally proposed by Berkeley and Curtis (1859) from New England (USA). According to Singer (1944, 1946, 1970, 1978a), Murrill (1945), Josserand (1959, as *Collybia exculta* (Fr.) Gillet), Dennis (1961, 1970), Malençon and Bertault (1975 as *Collybia xanthophylla*), Bon (1976, 1984, 1991), Lennox (1979), Alessio (1982 as *Collybia xanthophylla*), Redhead (1982), Hongo (1981), Pegler (1983), Moser (1986), Horak (1987), Stålberg (1987 as *Callistosporium olivascens*), Manimohan and Leelavathy (1989), Antonín and Vágner (1994),

Cacialli et al. (1995) as *Callistosporium xanthophyllum*), Panchetti (2004), Cheype (2005) as *Callistosporium xanthophyllum*), Antonín (2006), Gándara and Guzmán (2006), Daniels and Moreno-Arroyo (2008), Eyssartier and Roux (2011), Martin (2012), Vesterholt and Holec (2012), Saba and Khalid (2014), Bañares-Baudet and Beltrán-Tejera 2015, Jančovičová et al. (2016), Picciola and Zugna (2017). *C. luteo-olivaceum* can be found in temperate or tropical forests in North and South America, the Caribbean, Europe, North Africa and Asia, while it is very rare in the boreal and subalpine areas. It grows saprotrophically usually on decaying conifer wood (logs, trunks, stumps, debris), mostly *Pinus* spp. Redhead (1982) reviewed the species of *Callistosporium* resembling *C. luteo-olivaceum* (pileus with yellow olive tinges, crowded yellowish lamellae and fruiting in clusters on wood), namely *C. elaeodes* Bon, *C. favrei* Singer, *C. graminicolor*, *C. luteofuscum*, *C. luteofuscum* var. *major*, *C. majus*, and *C. xanthophyllum*, and considered them all synonyms of *C. luteo-olivaceum* because the features used to discriminate them (mainly their spore size) intergrade. This hypothesis was later followed by, for example, Noordeloos (1995), Antonín and Noordeloos (1997), Horak (2005), and Antonín (2009). However, the phylogenetic analyses conducted in the present work (Figs. 1, 3) suggest that *C. elaeodes* and *C. graminicolor* are distinct species (see below), and spore size is a diagnostic feature in this species complex. Genetic data agree also with the conclusions obtained by Moser (1986) after the study of anthraquinone pigments, where the existence of several taxa within the *C. luteo-olivaceum* complex was already suggested. *Callistosporium luteo-olivaceum* is characterized by a pileus with yellow-olive tinges, bright yellow (when young) crowded lamellae (always distinctly contrasting in colour with the pileus), basidiome surface turning lilac-purple in basic solutions, presence of skyrin and hypericin (dimeric anthraquinone pigments), and spores hardly reaching 7 µm in length (Moser 1986; Vesterholt and Holec 2012, Saba and Khalid 2014; Martin 2012; Jančovičová et al. 2016; Picciola and Zugna 2017 and this work), in fact these measure 4–6.5 × 3–4 µm in the type collection according to Roberts (2008). *Callistosporium graminicolor*, a species proposed by Lennox (1979) for specimens found in the state of Washington (USA), differs from *C. luteo-olivaceum* mainly because of its larger spores (6–8 × 4–5.5 µm), and seems to represent an autonomous species (Fig. 3) based on the genetic data obtained from collection PBM 2341 (WTU-F), found in the trail to Barclay Lake, Snohomish County, Washington state (USA), on rotten conifer stump, 670 m a.s.l., on 14-Jul-2002, leg. P.B. Matheny; smell and taste not remarkable; 3% KOH dark reddish to dark reddish brown on lamellae and stipe; spores mostly 6–7.5 × 4–5 µm; (Fig. 6g–h, P.B. Matheny, pers. comm.). In the phylogenetic tree of *Callistosporiaceae* (Fig. 3), *C. luteo-olivaceum* is composed

of three significantly distinct clades (I–III) with different geographical distribution: clade I is formed by a single collection coming from Asia, clade II by European collections, and clade III by American collections. Since no evident morphological differences were found between them, they are by now considered partially isolated lineages of a single species, although future analyses based on more collections and sequences could confirm that they are fully isolated from each other, deserving to be treated as independent, but maybe cryptic, species. In this case, the name *Callistosporium luteo-olivaceum* should be assigned to the American lineage, and *C. xanthophyllum* to the European clade, while the Asian species would need a new name. In addition, *C. luteo-olivaceum* is significantly related with two samples of *Pleurocollybia* sp. (MEL 2363162, MES-920).

Callistosporium elaeodes (Romagn.) Bon, Docums Mycol. 6(22–23): 282 (1976) Figs. 6a, 8i–l

Basionym: *Tricholoma elaeodes* Romagn., in Kühner & Romagnesi 1954, Bull. Soc. nat. Oyonnax 8: 96.

Description: Habit collybioid. Pileus 5–20 mm broad, hemispherical to convex, with inflexed margin, sometimes with a small obtuse umbo, later slightly convex or concave, with flat or somewhat depressed centre, and deflexed to straight margin, slightly hygrophanous, not striate, dry, minutely pruinose to felted, bright olive yellow to olive brown when moist, with a paler yellowish green margin, pallescent to pale dull olive buff upon drying. Lamellae quite spaced, L = 20–25, l = (1–)2–4–(5), deeply emarginated to almost free, narrowly segmentiform to subventricose, moderately thick, sometimes forked or anastomosed, pale olive-yellow, to greyish-olive, with a slightly fimbriate concolorous edge. Stipe 15–30 × 0.7–3.0 mm, slightly tapering towards the top or the base, sordid olive yellow to olive brown, minutely floccose at the top, appressed silky fibrillose with a very fine yellow-grey to olive-brown fibrillose covering in the lower half, as well as minute white rhizomorphs at the base. Context thin at the pileus centre, pale greyish yellow to yellowish. Smell indistinct and taste mild. Spore print white. Macrochemical reactions: surface of the basidiome turning faintly vinous red with a drop of basic solutions.

Spores [97, 4, 4] 5.9–7.6 × 3.3–4.3 µm (on average 6.7 × 3.8 µm), Q = 1.5–2.1 ($Q_m = 1.82$), V = 35–69 µm³ ($V_m = 52 \mu\text{m}^3$), broadly ellipsoid to ellipsoid, often adaxially flattened in side view, sometimes apically attenuated, smooth, hyaline or pale cream, thin-walled, inamyloid, cyanophilous, sometimes with one or more greenish droplets, with an evident apicule up to 1.3 µm long. Basidia 25–35 × 6–9 µm, subcylindric to claviform, hyaline, tetrasporic or sometimes bisporic, with sterigmata up to 10 µm long, smooth or with granulose greenish content that turns vinose red in basic

solutions. Hymenial cystidia absent. Hymenophoral trama regular composed of smooth, parallel hyaline hyphae 4–12 µm wide, with walls up to 0.5 µm thick. *Pileipellis* poorly differentiated, consisting of a cutis of regular to intertwined cylindrical hyphae, often rounded or inflated at the septa, measuring up to 10 (–15) µm wide, thin-walled. *Stipitipellis* regular, composed of smooth, parallel, more or less cylindrical thin-walled hyphae 3–10 µm wide. *Clamp connections* absent.

Ecology: mainly on broadleaved dead wood debris, in temperate areas of south-western Europe.

Specimens examined: **FRANCE:** Alsace, Ried d'Elsenheim, on mossy wood, Riedwald, leg. M. Wilhelm, 29-IX-1995, 2322 (ZT-Myc); Alsace, St. Louis, Petite Camargue Alsacienne, on buried wood (*Prunus?*), leg. M. Wilhelm, 08-IX-2000, 2549 (ZT-Myc); Alsace, Hirzfelden, Bois de Rotlaible, at the base of a *Quercus* among mosses, leg. M. Wilhelm, 20-X-2006, 58268 (ZT-Myc); ibidem, leg. M. Wilhelm, 20-X-2006, 958 (ZT-Myc). **SPAIN:** Basque Country, Guipúzcoa, Donostia/San Sebastián, on dead trunk of pine, in a flower bed under a palm tree, leg. Pedro Arrillaga, 17-IX-2012, 3008411 (ARAN Fungi) (as *Callistosporium luteo-olivaceum*).

Comments: This species, synonymized with *Callistosporium luteo-olivaceum* by Redhead (1982), was originally proposed for specimens collected on broadleaved trees wood in France (Kühner and Romagnesi 1953, 1954), and further reported from France (Bon 1984, 1991; Laurent 1999; Sarraillon 2006; Wilhelm 2007; Martin 2015; Tanchaud 2018), Germany (Kriegelsteiner and Enderle 1986; Ludwig 2001), Austria (Hausknecht et al. 2006), and Spain (Rubio and Miranda 2008). *Callistosporium elaeodes* can be discriminated from *C. luteo-olivaceum* because of its bright olive-green pileus, thicker and more spaced olivaceous lamellae, larger spores, and preference for broadleaved trees (Kühner and Romagnesi 1953, 1954; Bon 1976, 1984, 1991; Ludwig 2001 and our observations). Spore dimensions observed in the present work agree with those reported from the holotype by Bon (1976), 6.5–7.5(–8.5) × 3.5–4.4(–5) µm. Furthermore, Moser (1986) noticed the absence of skyrin and hypericin in *C. elaeodes*, pigments present in *C. luteo-olivaceum*, and Wilhelm (2007) highlighted that the lamellae of *C. elaeodes* produce a faint to negative reaction to basic solutions (observed also in the collections studied in the present work), which is intensely purplish red in *C. luteo-olivaceum*. Some collections found in the Netherlands (Noordeloos 1995), and the UK (Roberts 2008) identified as *C. luteo-olivaceum* following the work of Redhead (1982), could belong instead to *C. elaeodes* due to their spaced lamellae, large spores, and preference for broadleaved trees. The colour picture published in Roberts (2008) shows basidiomes

strongly resembling *C. elaeodes*. A partially significant genetic relationship (PP = 1.00, BP = 100%) was found between *C. elaeodes* and *C. hesleri* (Fig. 3).

Callistosporium pinicola Arnolds, Acta Mycologica, Warszawa 41(1): 32 (2006) Figs. 6e, f, 8d–h

= *Callistosporium xanthophyllum* f. *minor* Bon ad int., in “Flore mycologique d'Europe”, Doc. Mycol. Mém. hors Sér. 2: 95. 1992 (invalid name, ICBN Art. 32.1)

= *Callistosporium luteo-olivaceum* f. *minor* Verbeken & Walleyn, Doc. Mycol. 32(127–128): 3. 2003

Callistosporium xanthophyllum var. *minor* (Verbeken & Walleyn) P. Roux, Docums Mycol. 34(135–136): 41 (2008)

= *Callistosporium minor* (Verbeken & Walleyn) Wilhelm, Schw. Z. Pilzk. 85(4): 137. 2007 (invalid name, ICBN Art. 52.1);

Misapplied names: *Calocybe cerina* (Pers.: Fr.) Donk sensu Arnolds and Becker in Coolia 36: 70 (1993), sensu Moser in Kleine Kryptogamenflora IIb/2: 135 (1983), sensu Kalamees (2004) according to Arnolds (2006).

Description: Habit collybioid, basidiomes isolated, gregarious or clustered in small groups. *Pileus* 5–32 mm broad, first hemispherical then flat-convex to applanate, slightly depressed at the centre when old, sometimes with an indistinct broad umbo inside the depression, margin involute turning inflexed or straight, not striate, with the cuticle slightly exceeding the lamellae when young, surface dry, smooth, weakly or not hygrophanous, apparently glabrous and slightly greasy-shiny when moist, finely tomentose-pruinose (especially in the centre) to slightly radially fibrillose after drying, yellowish-brown to orange-brown, rust-brown, reddish-brown or dark brown, occasionally with an olivaceous hue near the centre. *Lamellae* moderately distant, thin, L = 26–36, l = (1–)2–6, adnate to strongly emarginate, up to 4 mm broad, then ventricose, lemon-yellow to yellow at first, then rust-yellow to olive-yellow or brownish-olive when old, with an entire to irregular concolorous edge. *Stipe* 10–40 × 1.5–4 mm, central or slightly eccentric, curved, cylindric or sometimes slightly compressed, occasionally inflated in the upper half, first solid and then narrowly fistulose, longitudinally finely fibrillose or fibrillose-pruinose, slightly pruinose-squamulose at the top, and often with a yellowish-white tomentum at the base, more or less concolorous with the pileus. *Context* thin, up to 2 mm thick at the pileus centre, fragile, concolorous with the surface. *Smell* indistinct or farinaceous, *taste* mild to slightly bitter. *Spore print* white to pale cream. *Macrochemical reactions:* all parts of fresh and dried basidiomes stain immediately dark red-brown to violet-brown with basic solutions.

Spores [131, 3, 3] 3.4–4.1 × 2.5–3.0 µm (on average 3.7 × 2.7 µm), Q = 1.2–1.6 (Q_m = 1.4), V = 12–18 µm³ (V_m = 15 µm³), broadly ellipsoid to ellipsoid or sometimes

subglobose, with rounded apices, smooth, hyaline or pale cream, thin-walled, sometimes with one or more greenish droplets and evident apicules, the cytoplasmatic content stains more or less intensely vinous red in basic solutions, inamyloid, cyanophilous. *Basidia* 17–24 × 3.5–6 µm, subcylindrical to clavate, hyaline, tetrasporic or sometimes bisporic, with a brownish granulose content, staining vinous red in basic solutions. *Hymenial cystidia* not detected. *Hymenophoral trama* regular consisting of parallel hyaline hyphae, smooth but often with brownish granules, 4–14 µm wide, with a wall up to 0.5 µm thick, staining vinous red in basic solutions. *Pileipellis* poorly differentiated, composed of a cutis of intertwined, cylindrical hyphae 4–10 µm wide, often enlarged at septa, with a wall up to 0.4 µm thick. *Subpellis* regular, composed of parallel, more or less cylindrical, smooth thin-walled hyphae about 3–10 µm wide. *Stipitipellis* regular, composed of parallel, more or less cylindrical smooth, hyphae, with a wall up to 0.3 (–0.5) µm thick; on the external surface there are some intertwined cylindrical to clavate, subcapitate or lageniform elements (*caulocystidia*). *Clamp connections* absent.

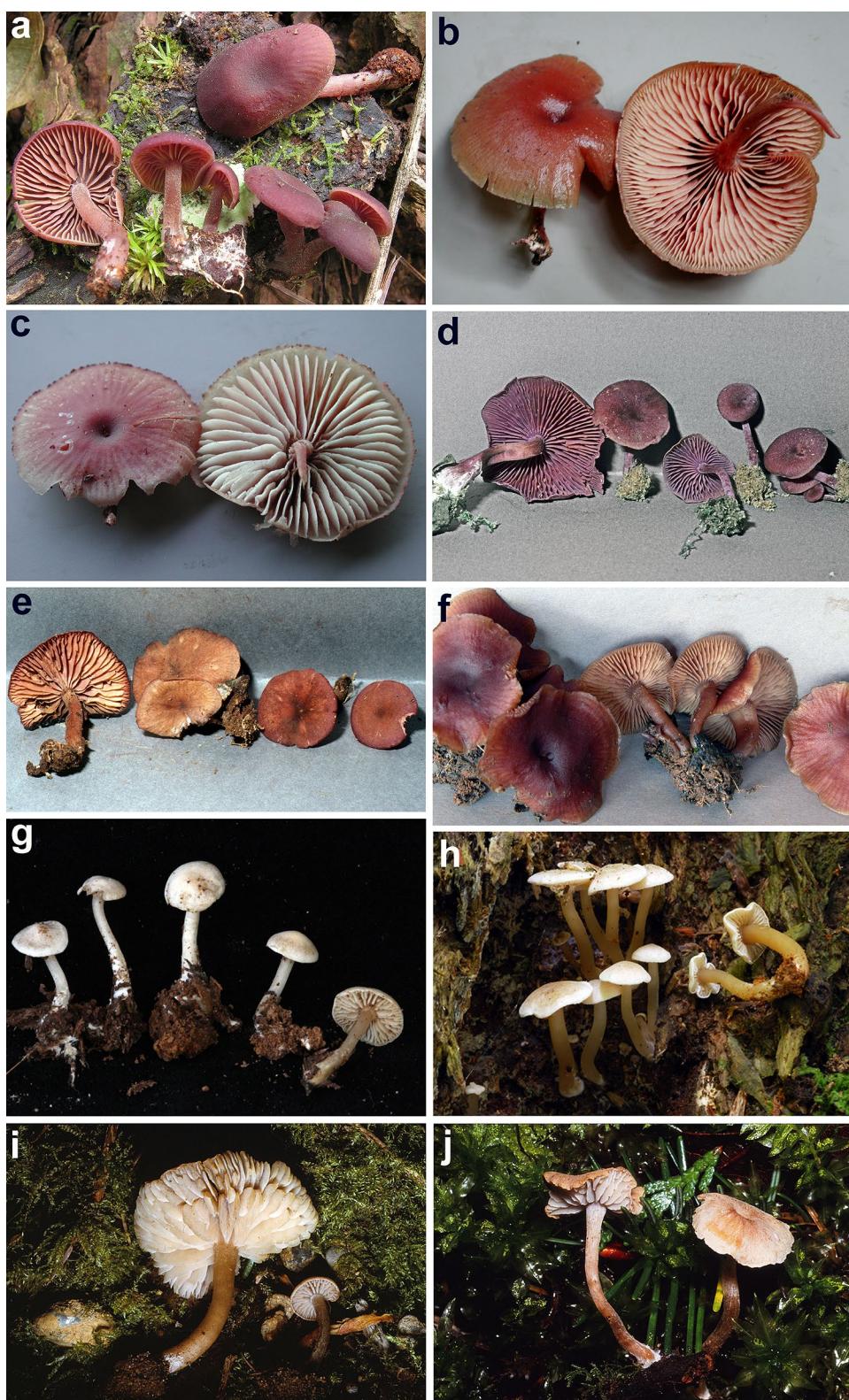
Ecology: on fallen logs in advanced decay, in pure conifer or mixed stands, mainly on acidic, sandy and loamy soils. Apparently widespread but rare in temperate Europe.

Specimens examined: **AUSTRIA:** Steiermark, Gleichenberg, Trautmannsdorf, on a dead trunk of *Pinus sylvestris*, leg. W. Wofar & A. Hausknecht, 21-VIII-2003, 10260 (WU). **CZECH REPUBLIC:** Moravskoslezské Beskydy Mts., Bílá, Salajka National Nature Reserve, on strongly decayed wood of *Abies alba*, leg. V. Antonín, 05-VIII-2004, 691390 (BRNM); ibidem, on strongly decayed wood of *Abies alba*, leg. V. Antonín, 31-VII-2008, 712716 (BRNM); Dobřejovice near Hosín, Libochovka Nature Reserve, on decaying stem of *Abies alba*, leg. P. Špinar & V. Antonín, 29-X-2010, 734327 (BRMN); Luže - Předhradí, Údolí Krounky a Novohradny Natural Park (Krounka and Novohradka valey), on thicker stump of *Picea*, leg. H. Ševčíková, 26-VII-2017, 793115 (BRNM). **FRANCE:** Alsace, Alsatian Hardt, Schlierbach, Oak-hornbeam forest with *Pinus*, leg. M. Wilhelm, 16-IX-1998, 2447 (ZT-Myc); Alsace, Sondersdorf (North), 550 m a.s.l., oak-beech forest with *Pinus*, on *Pinus*, leg. M. Wilhelm, 31-VII-2000, 2653 (ZT-Myc); ibidem, on a fallen tree of *Abies* or *Pinus*, leg. M. Wilhelm, 31-VII-2000, 709 (ZT-Myc). **POLAND:** Podlaskie, Wigierski National Park, on powdered rests of wood (strongly decayed), fallen/broken wood of coniferous trunk, leg. M. Halama, 03-X-2012, 0510 (WRSL); ibidem, 25-VII-2013, 0512 (WRSL); Śląskie, Śrubita nature reserve Beskidzie Żywiecki mountains, on powdered rests of wood (strongly decayed), fallen/broken wood of coniferous trunk, leg. R. Rutkowski, 27-VI-2013, RRy-2013-0003; Małopolskie, Pieniński Park Narodowy within Poreba forest, on wood of trunk/branch of fallen/

broken coniferous tree, leg. P. Chachula, 07-IX-2014, ChP-2014-0001.

Comments: *Callistosporium pinicola* is known so far from Austria (Kalamees 2004, as *Calocybe cerina* (Pers.) Donk fide Arnolds 2006), the Czech Republic (Antonín et al. 2009), France (Bon 1991; Wilhelm 2003, 2007; Arnolds 2006; Roux 2006 as *Callistosporium xanthophyllum*), Germany (Ludwig 2001; Wilhelm 2003, 2007), Italy (Arnolds 2006), the Netherlands (Arnolds and Becker 1993 as *C. cerina* fide Arnolds 2006), Belgium (Verbeken and Walleyn 2003), Switzerland (Kalamees 2004 fide Arnolds 2006), Slovakia (Jančovičová et al. 2016), Ukraine (Antonín et al. 2009), Sweden (Vesterholt and Holec 2012), Poland (Halama and Rutkowski 2014), Norway (Gulden and Fonneland 2015), United Kingdom (Aron 2014). It grows saprotrophically associated with *Abies alba*, *Picea abies* and *Pinus sylvestris* (Wilhelm 2003; Kalamees 2004; Arnolds 2006; Antonín et al. 2009). There are also records from *Pinus pinea* (Arnolds 2006), and *Fagus sylvatica* (Verbeken and Walleyn 2003; Antonín et al. 2009). *Callistosporium pinicola* was initially described as a variety or form of *C. luteo-olivaceum*, but later considered an independent species (Arnolds 2006), because of its small-sized basidiomes, pileus usually lacking green tinges, medium-crowded lamellae, farinaceous smell and moderately bitter taste, small spores < 5 µm long, all tissues turning immediately violet in basic solutions (staining even surrounding liquid), and associated with conifers (Arnolds 2006; Antonín et al. 2009; Vesterholt and Holec 2012; Halama and Rutkowski 2014; Gulden and Fonneland 2015). The genetic data produced in the present work suggest that *C. pinicola* is an autonomous species (Fig. 3). The presence of caulocystidia (simple ascending terminal elements of the stipitipellis), reported for the first time by Antonín et al. (2009), was observed also in the specimens studied here. *Callistosporium luteo-olivaceum* is the species most closely resembling *C. pinicola*, but differs because of its somewhat larger and more frequently fasciculate basidiomes presenting evident green tinges in the pileus, more crowded lamellae, and larger spores (see above). Basidiomes of *C. pinicola* may also recall *C. elaeodes*, but the latter has a yellow-green or olive-green pileus, quite distant green-yellow to olive-brown lamellae, clearly larger spores (6.5–8.5 × 3.5–5.0 µm), a faint to negative reaction to ammonia solution in lamellae and basidiome surface, and preference for broadleaved trees (Wilhelm 2003 and the present work). *Callistosporium pinicola* is significantly related with a collection, 067369 (TENN-F), identified as *Callistosporium* sp. Further sampling is needed to ascertain whether this collection represents a different sister species, or else it is encompassed within the intraspecific variability of *C. pinicola*.

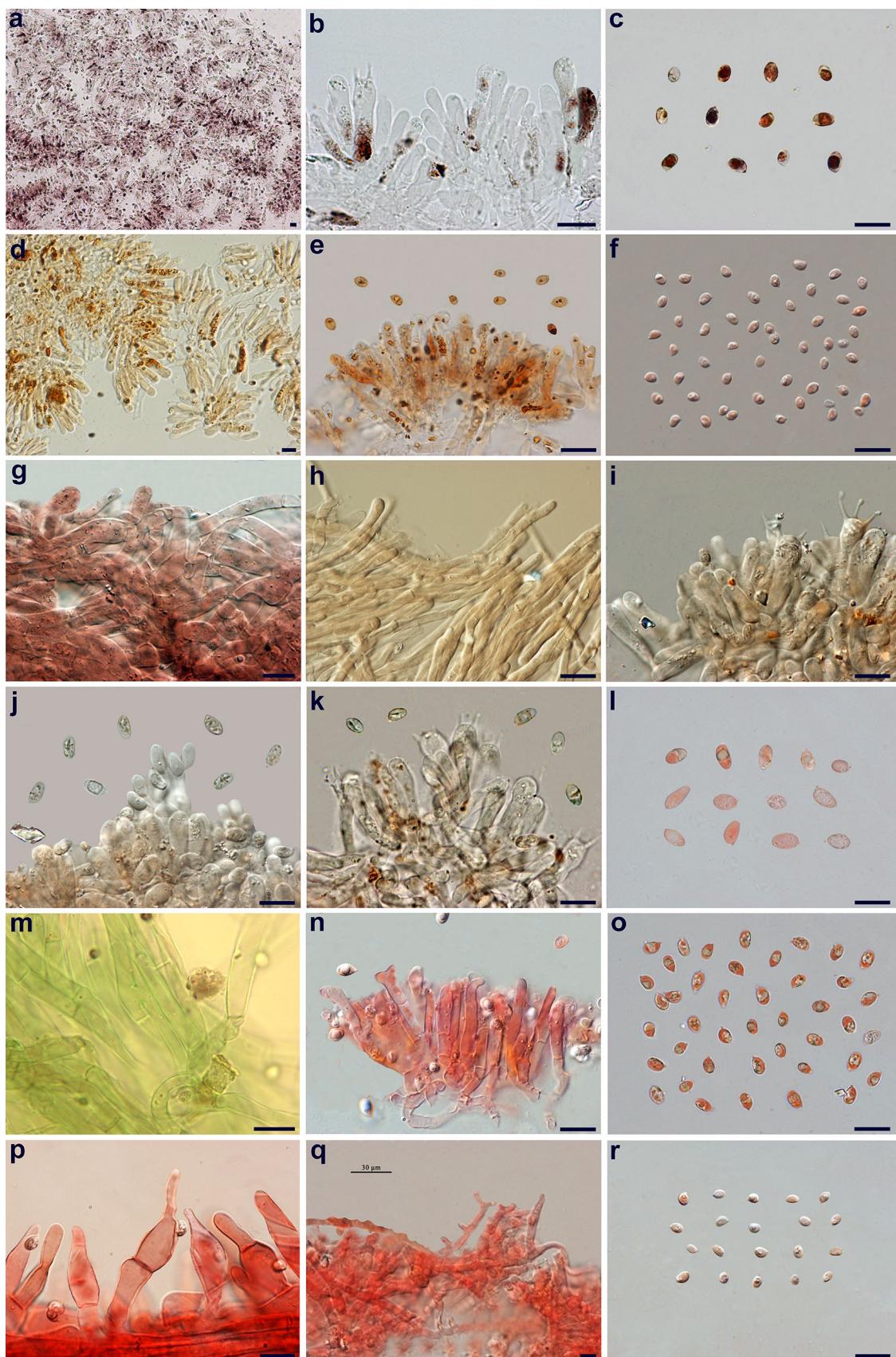
Fig. 7 Fresh basidiomes of *Callistosporium* spp. *C. elegans*. **a** (JBSD127427), **b** (BZ-1772, CFMR), **c** (BZ-1875 CFMR), **d** (013277 CORT), **e** (013382 CORT), **f** (013860 CORT). *C. pseudofelleum*. **g** (063882 TENN-F), **h** (071105 TENN-F). *Pseudolaccaria fellea*. **i** (006239 WTU-F), **j** (006230 WTU-F). Photographs: **a** by C. Angelini; **b**, **c** D.J. Lodge; **d–f** by T.J. Baroni; **g**, **i**, **j** by P. B. Matheny; **h** by R. Lebeuf



Callistosporium elegans Desjardin & B.A. Perry, Mycosphere 8(9): 1333 (2017) Figs. 7a–f, 8m–p

= ***Callistosporium caribaeus*** S.A. Cantrell & Lodge, Biodiversidad de Puerto Rico: Agustín Stahl, Flora, Hongos. Serie

de Historia natural; Capítulo 4: 289 (2008), nom. inval., Art. 32.1(c) (Melbourne)



◀Fig. 8 Microscopical features of *Callistosporium* spp. *C. luteo-olivaceum* (18221 AMB). **a** Hymenial elements. **b** Basidia and hymenial elements. **c** Spores. *C. pinicola*. **d** Hymenial elements (10260 WU). **e** Hymenial elements and spores (2447 ZT-Myc). **f** Spores (0512 WRSL). **g** Pileipellis (2447 ZT-Myc). **h** Caulocystidia (10260 WU). *C. elaeodes*. **i** Hymenial elements (2322 ZT-Myc). **j** Basidia and spores (2322 ZT-Myc). **k** Basidia and spores (2549 ZT-Myc). **l** Spores (3008411 ARAN Fungi). *C. elegans*. **m** Elements of the pileipellis (BZ-1772 CFMR). **n** Cheilocystidia and spores (PR-4036, UTK). **o** Spores (PR-4036, UTK). **p** Caulocystidia (PR-4036, UTK). *C. praemultifolium* (17468 FLAS-F). **q** Pileipellis. **r** Spores. **a–e, g, i–k** in 10% ammonia; **f–h** in 10% ammonia-interferential contrast; **l, n–p** in ammoniacal Congo red; **m** in Cotton blue in Lactic acid; **q, r** in ammoniacal Congo red-interferential contrast. Bars = 10 µm. Photographs: **a–l, n–r** by M. Marchetti; **m** by D.J. Lodge

Description: Habit collybioid, solitary. *Pileus* 10–31 mm diam., hemispheric to broadly convex, slightly to moderately depressed or umbilicate in the center, margin inrolled when young, rarely flared, sometimes exceeding the lamellae; surface dry, hygrophanous, glabrous but granulose at the centre, often dull and minutely grainy over the whole surface, predominantly wine colored to near Maroon or Brick red, changing to burnt Sienna, warm sepia or Army brown with a cinnamon drab centre; margin pale pinkish buff with darker striae when young, a few of them faintly sulcate-striate, becoming concolorous with the whole pileus and non-striate with age. *Lamellae* adnate, sinuate or sub-arcuate-decurrent, regular or rarely forked (strongly forked in the African collection studied), 1–5 mm broad, distant, 1–2/mm at the margin, 1/mm half-way to margin, with lamellulae of two or three lengths, buff yellow suffused with deep vinaceous or mauve near pileus; russet-vinaceous at the centre of the lamella with the edge concolorous or slightly paler; edge even. *Stipe* central or slightly eccentric, 10–25 × 2–5 mm, equal or subclavate, hollow; concolorous with the pileus or else drab-coloured with deep vinaceous tones at the top, minutely pubescent especially at the top; with a delicate pale mycelial attachment. *Pileus context* rubbery, buff yellow to drab gray, smell none or fungoid, taste fungoid. *Spore print* white.

Spores [198, 5, 5] 4.4–5.3 × 3.0–3.7 µm (on average 4.9 × 3.3 µm), Q = 1.2–1.75 ($Q_m = 1.47$), V = 21–37 µm³ ($V_m = 29 \mu\text{m}^3$), ellipsoid to ovoid, sometimes adaxially flattened in side view, with an evident apicule up to 1 µm long, smooth, thin-walled, mostly with a pale greenish drop, the cytoplasmatic content staining light lilac to reddish in basic solutions, inamyloid, cyanophilous, congophilous. *Basidia* 20–26 × 5.5–7 µm, cylindraceous to cylindrical-clavate, usually tetrasporic, sometimes 1–2 sporic, with up to 5 µm long sterigmata, lacking basal clamp connections, with a smooth to granulose cytoplasmatic content, sometimes with a vinaceous brown necropigment. *Cheilocystidia* 20–25 × 2.5–5 µm, cylindraceous, subcapitate to bilobed, smooth, hyaline, sometimes with a purplish content. *Pleurocystidia* absent.

Subhymenium subcellular of 3–6 µm wide hyphae. *Hymenophoral trama* regular, composed of cylindraceous hyphae 4–12 (–14) µm wide, rounded at septa, thin-walled, smooth, hyaline or with violaceous brown cytoplasmatic content. *Pileipellis* a cutis made of intertwined violaceous brown hyphae 4–12 µm wide, with scattered to dense clusters of upturned cylindraceous to subclavate hyphal ends 20–30 × 2–5 µm (*pileocystidia*). *Hypoderm* regular composed of 4–12 µm wide hyphae with walls up to 1(–1.2) µm thick, as well as some terminal and hypodermal elements encrusted with purple pigment that turns green in basic solutions. *Stipitipellis* composed of 4–12 µm wide hyphae with variable length, rounded at septa to clavate, with walls up to 1.2 µm thick, and a hyaline to purplish cytoplasmatic pigment. *Caulocystidia* abundant, measuring 15–30 (–35) × 4–12 µm, in tufts, cylindraceous to clavate, sometimes with a long apical appendix, presenting an often rounded but sometimes attenuated apex. *Clamp connections* absent.

Ecology: on wood in advanced decay, in wet and moist forests of tropical regions of Africa and America

Specimens examined: **BELIZE:** Cayo district, Maya Mountains, Northern Foothills, Caves Branch, Ian Anderson's Adventure Camp, Nature Trail, soil, 72 m a.s.l., leg. M. McReynolds & B. Ortiz-Santana, 28-X-2002, BOS423, BZ-1772 (CFMR); La Milpa Field Station, behind La Milpa, on a log, leg. L. Ryvarden, 24-X-2002, BZ-1875 (CFMR). **DOMINICAN REPUBLIC:** La Vega Province, Jarabacoa Golf Course, lignicolous, mostly caespitose, on well rotted wood of *Pinus occidentalis*, leg. T.J. Baroni, 13-XI-2003, 9783 TJB, 013860 (CORT); La Vega Province, Jarabacoa, 8 specimens collected on trunk on the ground of *Pinus* (*Pinus occidentalis*), leg. C. Angelini, 08-XII-2016, 127427 (JBSD). **PUERTO RICO:** Mun. Río Grande, Caribbean National Forest, Luquillo Mts., El Verde Research Area, 350 m a.s.l., on rotting log, leg. D.J. Lodge, 19-II-1996, D.J. Lodge PR-4036 (UTK); Orocovis Municipio, El Toro Negro State Forest Reserve, near Bosque Estatal de Toro Negro Oficina and campground, on soil under or near *Eucalyptus* (alien planted), in mixed tropical forest, leg. T.J. Baroni, 09-XI-1996, 8255 TJB, 013277 (CORT); Rio Grande Municipio, Caribbean National Forest, El Yunque, El Verde LTER site (El Verde Research Station), gregarious to sub-caespitose on well rotted wood (wood type undetermined) in mixed tropical rainforest, 04-VI-1998, leg. T.J. Baroni, 8759 TJB, 013382 (CORT). **SÃO TOMÉ AND PRÍNCIPE:** São Tomé, Parque Nacional Obo, trail to Lagoa Amelia, leg. D.E. Desjardin & B.A. Perry, 14-IV-2008, MF100991, BAP 617 (SFSU-F) (**holotype**).

Comments: This species was originally described from São Tomé and Príncipe (West Africa) on rotten wood (Desjardin and Perry 2017), but the present results (Fig. 3) suggest

it is also present in the Caribbean (so far found in Belize, Dominican Republic and Puerto Rico). *Callistosporium elegans* is characterized by its small, usually violet (collection from São Tomé) to purple-wine basidiomes (collections from the Caribbean), minute ellipsoid spores hardly reaching 5 µm in length, a sterile lamellar edge composed of cylindrical-subcapitate cheilocystidia, a cutis-type pileipellis with scattered erect terminal elements (pileocystidia), clustered and irregularly cylindrical caulocystidia, spores and hymenial elements with purple necropigments, hypodermal elements encrusted with purple pigments that turn green in basic solutions, and growth on decaying wood. A certain chromatic variability has been observed in this species: the purple tinges on pileus, stipe and lamellae can be replaced by reddish-brown colours in some collections (Fig. 7e–f). The most similar vinaceous to purple-violet pigmented species of *Callistosporium* are *C. vinosobrunneum* Desjardin & Hemmes, first found in the Hawaiian Islands (USA), and *C. amazonicum* Singer from Brazil. *Callistosporium vinosobrunneum* differs from *C. elegans* mainly by its larger spores measuring 6.5–8 × 5–6.5 µm, and 7.1 × 5.6 µm on average (Desjardin and Hemmes 2011), while *C. amazonicum* has a pellucid-striate pileus, a smaller and more gracile stipe about 14–17 × 1.5–2.5 mm, pinkish grey lamellae, a farinaceous smell, and narrower spores measuring 1.7–3.5 µm wide vs. 2.8–3.8 µm in *C. elegans* (Singer 1978a). *Callistosporium purpureomarginatum* Fatto & Bessette, proposed for collections found in the southern Appalachians (USA), has purple lamellar edges (which are concolorous or paler than the rest of the lamella in *C. elegans*), and narrower caulocystidia measuring 3.2–7.8 µm (5–13.5 µm in *C. elegans*) that are never turbinate or pyriform (Fatto and Bessette 1996). Genetically, *C. elegans* presents some intraspecific variability, and is significantly related with *C. graminicolor*, and also *C. luteo-olivaceum* (Fig. 3).

Callistosporium praemultifolium (Murrill) Vizzini, Consiglio & M. Marchetti, comb. nov. Fig. 8q–r

MycoBank MB 831397

Basionym: *Gymnopus praemultifolius* Murrill, Proc. Fla Acad. Sci. 7(2/3): 109 (1945) [1944]
 ≡ *Collybia praemultifolia* (Murrill) Murrill, Proc. Fla Acad. Sci. 7(2/3): 127 (1945) [1944]
 ≡ *Pleurocollybia praemultifolia* (Murrill) Singer, Mycologia 39(1): 80 (1947)
 = *Clitocybe microspora* R.E.D. Baker & W.T. Dale, Mycol. Pap. 33: 85 (1951) fide Pegler 1983, nom. illegit., Art. 53.1, preoccupied by *Clitocybe microspora* Peck 1909, Bull. Torrey bot. Club 36(6): 331 (1909)

Description: Habit pleurotoid, basidiomes densely imbricate. Pileus 10–45(–100) mm broad, asymmetrically

plano-convex with a broad low umbo at first, later slightly depressed at the centre, margin undulate, lobed, decurved, split with age, not striate, surface dull, moist, hygrophanous, canescent, chestnut brown to light brown, fading to pale greyish orange or light ivory yellow. Lamellae adnexed to adnate, arcuate, extremely crowded with 5 series of truncate lamellulae, narrow (1–2 mm broad), dingy beige to cream or hazelnut-color. Stipe 5–55 × 1.5–6 mm, usually very eccentric or almost lateral, curved, cylindrical, sometimes compressed, solid to fistulose and then hollow, tough; surface dull, dry, longitudinally fibrillose-pruinose, glabrescent, whitish to light brown, or pale ivory yellow. Context thin, 1–3 mm thick at the centre, soft, aqueous, pale greyish orange to pale brown. Smell not distinctive to anise, taste bitter. Spore print white.

Spores [26, 1, 1] 3.3–4.0 × 2.4–2.8 µm (on average 3.7 × 2.6 µm), Q = 1.3–1.5 ($Q_m = 1.4$), V = 10–17 µm³ ($V_m = 13 \mu\text{m}^3$), ellipsoid to ovoid, at times subglobose or adaxially flattened in side view, smooth, hyaline, thin-walled, with one or more pale greenish drops in basic solutions, with an evident apicule, inamyloid, cyanophilous. Basidia 12–16 × 4–5 µm, subcylindrical to clavate, hyaline, tetrasporic, smooth or with a granulose greenish yellow content, lacking basal clamp connections. Hymenophoral trama regular, composed of parallel smooth hyphae, cylindraceous to inflated at the apex, 4–12(–16) µm wide, thin- to thick-walled, with reddish yellow-brown granules. Hymenial cystidia absent. Pileipellis a cutis of mostly intertwined cylindrical hyphae 2–7 µm wide, often thickened at the septa, thin-walled, non-gelatinose, often digitate to diverticulate or even nodulose. Stipitipellis a cutis of cylindrical or irregular hyaline hyphae 2–4 µm wide, smooth or with a few scattered knobs, inamyloid, non-incrusted, non-gelatinous, thin-walled; stipititrama consisting of cylindrical, hyaline hyphae 5–16 µm wide, with walls 0.5–1.5 µm thick, inamyloid, non-gelatinose. Caulocystidia absent. Clamp connections absent everywhere.

Ecology: on dead trees in tropical broadleaved forests.

Specimens examined: SÃO TOMÉ AND PRÍNCIPE: Príncipe, Parque Nacional Obo, trail to Lagoa Amelia, between N00°17.112', E06°35.967' and N00°16.922', E06°36.062', leg. D.E. Desjardin, 14-IV-2008, MF100956, DED 8238 (SFSU-F). USA: Florida, Alachua County, Gainesville area, on decaying broadleaved log, shade, leg. and det. W.A. Murrill, 07-VII-1938, FLAS-F-17468 (holotype).

Comments: *Pleurocollybia praemultifolia* (type species of the genus *Pleurocollybia*) has been recorded in North America (Florida) (Murrill 1944), the Caribbean (Dominica, Guadeloupe, Martinique, Trinidad) (Pegler 1983), South America (Bolivia) (Singer 1970) and Africa (São Tomé and Príncipe) (Desjardin and Perry 2017). This species is

characterized by a light brown, hygrophanous, flat-convex pileus, extremely crowded, narrow, orangish-white lamellae, a very eccentric, greyish-orange stipe, very small spores ($3.7 \times 2.6 \mu\text{m}$ on average), absence of hymenial cystidia and caulocystidia, a cutis-type pileipellis, and a stipitipellis with smooth or slightly diverticulate (*Marasmiellus*-like) hyphae (Singer 1970; Pegler 1983; Desjardin and Perry 2017, and the present work). Baroni et al. (2008) found cylindrical-contorted to narrowly clavate or sometimes branched cheilocystidia in the type collection. Genetically, *C. praemultifolium* is significantly related with *C. brunnescens* and *C. imbricatum*, all of them former species of *Pleurocollybia*, although other samples of this genus (MEL 2363162, MES-920), are not phylogenetically related with the clade of *C. praemultifolium* (Fig. 3).

Callistosporium brunnescens (Earle) Vizzini, Consiglio & M. Marchetti, comb. nov.

Mycobank MB 831398

Basionym: *Geopetalum brunescens* Earle, Inf. an. Estac. Cent. agr. Cuba 1: 235 (1906)
 ≡ *Pleurotus brunescens* (Earle) Sacc. & Traverso [as ‘brunneus’], Syll. fung. (Abellini) 20: 448 (1911)
 ≡ *Micromphale brunescens* (Earle) Murrill, N. Amer. Fl. (New York) 9(5): 308 (1916)
 ≡ *Pleurocollybia brunescens* (Earle) Singer, Beih. Sydowia 7: 17 (1973)

Comments: This species, originally described by Earle (1906) from Cuba, was later found also in other areas of the Caribbean such as Martinique, Guadeloupe, Dominica and Trinidad and Tobago (Dennis 1953; Singer 1973; Pegler 1983). It is characterized by a spatulate pale grayish-brown pileus, a white and silky lateral stipe, dark brown lamellae on drying, and subglobose spores $3–4 \mu\text{m}$ in diam. (Earle 1906; Dennis 1953; Pegler 1983). As mentioned above, *C. brunescens* is significantly related with *C. imbricatum* and *C. praemultifolium*, all of them former species of *Pleurocollybia*.

Callistosporium imbricatum (T.J. Baroni, Lodge & D.L. Lindner) Vizzini, Consiglio & M. Marchetti, comb. nov.
 MycoBank MB 831399

Basionym: *Pleurocollybia imbricata* T.J. Baroni, Lodge & D.L. Lindner, Mycotaxon 103: 355 (2008)

Description: see Desjardin and Perry (2017, p. 1329–1331).

Specimens examined: SÃO TOMÉ AND PRÍNCIPE: Parque Nacional Obo, on trail to Lagoa Amelia, leg. D.E. Desjardin, 14-IV-2008, MF100955, DED 8232 (SFSU-F).

Comments: Proposed for collections found in Belize (Baroni et al. 2008), this species has been recently reported again from São Tomé and Príncipe (Desjardin and Perry 2017). *Callistosporium imbricatum* is easily distinguishable from the other pleurotoid species of *Callistosporium* because of its densely imbricate, spatulate to conchate pale brownish grey hoary pilei with deeply incised and frequently lobed margin, lacking a stipe (or present but very reduced), and having instead a tomentose whitish lateral attachment point arising from a thick whitish subiculum on decaying wood, as well as white rhizomorphs, distinct, irregularly cylindrical, subcapitate cheilocystidia, and subglobose to broadly ellipsoid spores measuring $3–4 \times 2–3.2 \mu\text{m}$ (Baroni et al. 2008; Desjardin and Perry 2017). Baroni et al. (2008) reported that clamp connections were absent from all tissues excepting at the base of basidia in the collection from São Tomé and Príncipe (Desjardin and Perry 2017). As mentioned above, *C. imbricatum* is significantly related with *C. brunescens* and *C. praemultifolium*, all of them former species of *Pleurocollybia*.

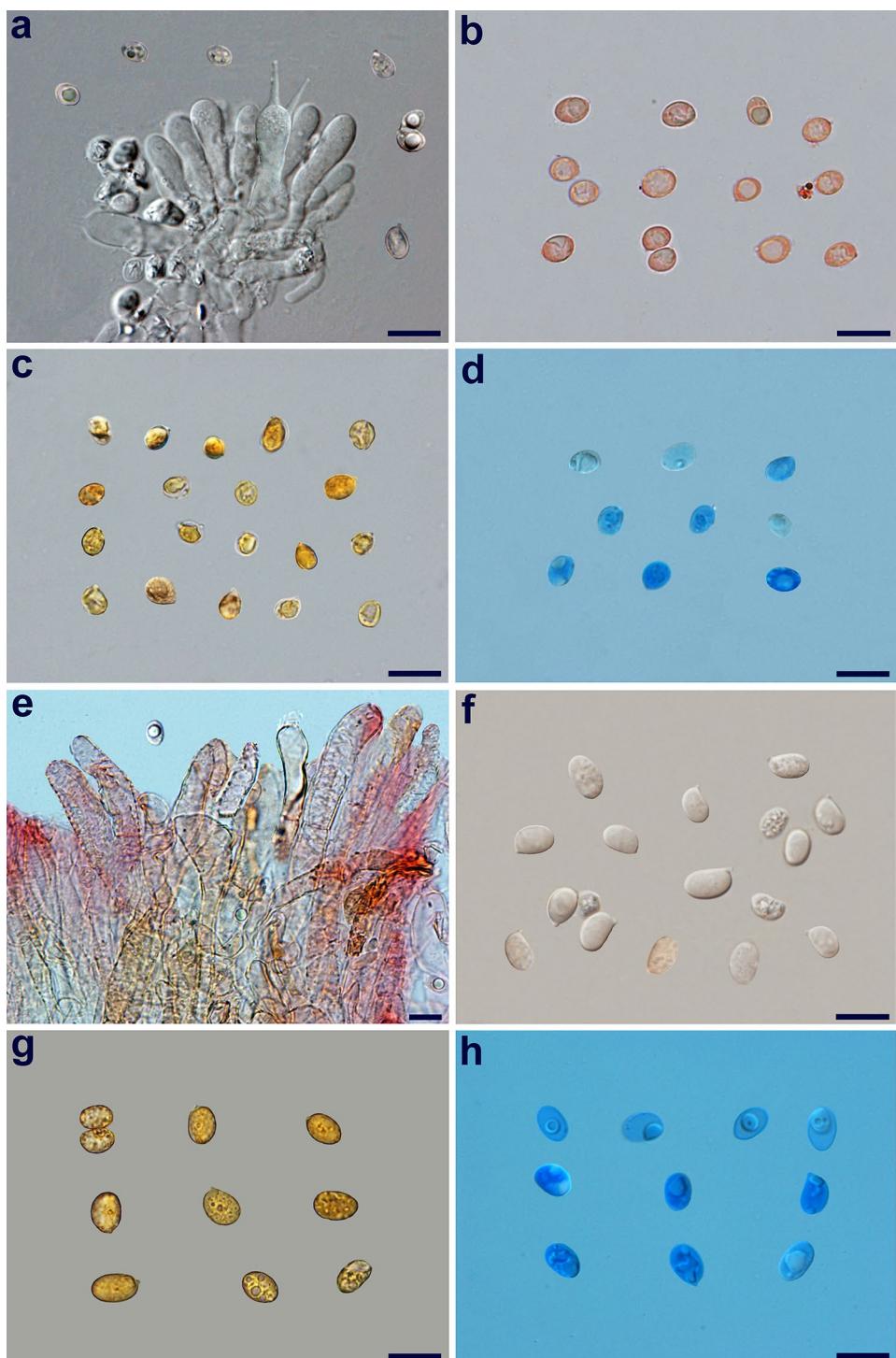
Callistosporium hesleri (H.E Bigelow) Vizzini, Matheny, Consiglio & M. Marchetti, comb. nov.

Mycobank MB 831400

Basionym: *Clitocybe hesleri* H.E. Bigelow, Cryptog. Mycol. 4(1): 97 (1983)

Comments: The phylogenetic analysis of the family *Callistosporiaceae* based on five genetic markers (Fig. 3) suggests that this species belongs to genus *Callistosporium*. Bigelow (1983) proposed it for collection 8084 (TENN-F), found by L.R. Hesler at Roan Mountain, Mitchell Co., North Carolina (USA). It was described as a small-sized clampless collybioid to omphalinoid *Clitocybe* with a hygrophanous, brownish-grey striate pileus, adnate to decurrent or almost subdistant grey lamellae, a smooth stipe with white mycelium at its base, ellipsoid to cylindrical or fusiform spores measuring $7–9 \times 3–4 \mu\text{m}$, small 1–4 spored basidia $27–31 \times 5.5–8 \mu\text{m}$, pileipellis a cutis with finely encrusting brown pigment, not changing in basic solutions, and occurring on soil and decayed wood of montane or subalpine mixed forests. These features are, even without considering genetic evidence, perfectly compatible with the concept of *Callistosporium* proposed in the present work. *Clitocybe hesleri* was not reported again after the original description, but three 28S rDNA/LSU environmental sequences (KF566292, KF566332 and KF567001) obtained by Mueller et al. (2014) from soil samples of a loblolly pine (*Pinus taeda*) plantation at the Duke Forest, North Carolina (USA), are not significantly different from those obtained from the holotype of *C. hesleri* (PP = 1.00, BP = 100%), suggesting that they could represent new findings of this taxon. Finally, the lineage of *C. hesleri* is significantly related with that of *C. elaeodes* (Fig. 3).

Fig. 9 *Callistosporium pseudofelleum*. **a** Hymenial elements and spores (062616 TENN-F, holotype). **b** Spores (071105 TENN-F). **c** Spores (062616 TENN-F, holotype). **d** Spores (062616 TENN-F, holotype). *Pseudolaccaria fellea* (006240 WTU-F). **e** Pileipellis elements. **f** Spores. **g** Spores. **h** Spores. **a** in 10% ammonia-interferential contrast; **b, e** in ammoniacal Congo red; **c, g** in Melzer's reagent; **d, h** in Cotton blue in Lactic acid; **f** in ammoniacal Congo red-interferential contrast. Bars = 10 µm. Photographs by M. Marchetti



Callistosporium pseudofelleum Vizzini, Matheny, Consiglio & M. Marchetti, sp. nov. Figs. 7g–h, 9a–d
Mycobank MB 831401

Etymology: the epithet highlights the similarity of this species to *Pseudolaccaria fellea*.

Type specimen: USA: Massachusetts, Middlesex, Flint's Pond, scattered singly on rotten wood in mixed forest of *Quercus*, *Carya*, *Pinus*, *Betula*, and *Tsuga*, leg. P.B. Matheny, 09-IX-2006, 062616 TENN-F (**holotype**).

Diagnosis: Habit collybioid. Pileus 5–15 mm broad, first convex to conico-convex, then flat-convex with a small

mammillate umbo with age, margin at first decurved, becoming uplifted and depressed at the center (but with a small umbo) with age, dry, hygrophanous, faintly translucently striate when moist, surface glabrous when moist but finely-fibrillose and often canescent when dry; near Isabella colour to honey yellow or cream buff to Chamois when fresh, then faded near Cartridge buff or ivory yellow. *Lamellae* adnate to sinuate or uncinate, moderately close to subdistant, L = 16–20, with several tiers of lamellulae, medium-sized to broad ventricose, somewhat thickened, Cartridge buff or light buff (not white), edges somewhat eroded with age and more or less concolorous with the rest of the lamella. *Stipe* 12–20 × 1–2 mm at the top, terete, central, stuffed at first but becoming hollow, slightly thickened at the base, often flexuous, somewhat brittle, veil absent; pale or buff (Cartridge Buff or near Honey Yellow), surface finely-fibrillose or silky-fibrillose above the base, white-myceloid at the attachment point. *Context* thin-fleshed, white, *smell* and *taste* not remarkable and not farinaceous. *Spore print* white.

Spores [37, 2, 2] 5.5–6.9 × 4.0–5.1 µm (on average 6.2 × 4.6 µm), Q = 1.27–1.46 ($Q_m = 1.36$), V = 46–93 µm³ ($V_m = 70 \mu\text{m}^3$), ellipsoid, smooth, thin-walled, with an evident apicule up to 0.4 (–0.5) µm long, often with one or sometimes two greenish drops, cyanophilous. *Basidia* 20–30 × 6–8 µm, tetrasporic but sometimes also monosporic or bisporic, subcylindrical to clavate or even subcapitate, with up to 6 µm long sterigmata (up to 12 µm long sterigmata in mono- or bisporic basidia), lacking basal clamp-connections. *Hymenophoral trama* regular, composed of cylindrical thin-walled hyaline hyphae 4–8 (–10) µm wide, some of them claviform, inflated up to 14 µm at the apex, cyanophilous. *Subhymenium* poorly differentiated. *Hymenial cystidia* not observed. *Pileipellis* a regular cutis, composed of cylindrical hyphae 4–10(–12) µm wide and variable in length, thin-walled, with some clavate terminal elements. *Stipitipellis* composed of parallel, cylindrical or sometimes fusiform hyaline hyphae 2–8(–10) µm wide, often with short elements, thin-walled. *Clamp connections* absent.

Ecology: isolated or in small groups on rotten wood in broadleaved and mixed forests of eastern North America.

Specimens examined: CANADA: Québec, Vaudreuil-Soulanges, Île Perrot, leg. R. Lebeuf, 04-VIII-2014, HRL1735, 071105 (TENN-F) (as *Clitocybe fellea*). USA: Massachusetts, Middlesex, Flint's Pond, scattered singly on rotten wood in mixed forest of *Quercus*, *Carya*, *Pinus*, *Betula*, and *Tsuga*, leg. P.B. Matheny, 09-IX-2006, PBM 2825, 062616 (TENN-F) (**holotype**) (as *Clitocybe* aff. *fellea*); West Virginia, Coopers Rock State Forest, scattered singly on rotten white-rotted hardwood log in mixed hardwood forest of mostly *Acer* and *Quercus*, leg. P.B. Matheny, 09-VIII-2008, PBM 3009, 063882 (TENN-F).

Comments: This species resembles *Pseudolaccaria fellea* (see below, *inde nomen*), because of its collybioid habit, a cream-ochre pileus surface, and subdistant lamellae, but differs from it because of its lignicolous habitat, a non-farinaceous smell, a mild taste, the pileipellis hyphae lacking encrusting pigment, inamyloid spores, and absence of clamp connections. Genetically, it represents an independent lineage within *Callistosporium*, with no known significant similarities with other species of this genus.

Pseudolaccaria Vizzini, Contu & Z.W. Ge, in Lavorato, Vizzini, Ge & Contu, Phytotaxa 219(1): 53 (2015)

Description: Habit Laccaria-like. Pileus convex, slightly depressed when old, dry, squamulose, lamellae thick, distant, emarginate. Spore print white. Spores thin-walled, smooth, amyloid, cyanophilous, pileipellis a cutis with repent hyphae, pigment parietal and encrusting. Clamp connections present. Terricolous.

Type species: ***Pseudolaccaria pachyphylla*** (Fr.) Vizzini & Contu, in Lavorato, Vizzini, Ge & Contu, Phytotaxa 219(1): 53 (2015)

Basionym: *Agaricus pachyphillus* Fr., Observations mycologicae 1: 76 (1815).

- ≡ *Clitocybe pachyphylla* (Fr.) Gillet, Hyménomycètes (Alençon): 169 (1874) [1878]
- ≡ *Camarophyllum pachyphylum* (Fr.) P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 230 (1879)
- ≡ *Omphalia pachyphylla* (Fr.) Quél., Enchir. fung. (Paris): 26 (1886)
- ≡ *Pseudooomphalina pachyphylla* (Fr.) Knudsen, Nordic Jl Bot. 12(1): 76 (1992)
- = *Agaricus absinthiatus* Lasch, Linnaea 3: 382 (1828)
- ≡ *Agaricus pachyphillus* var. *absinthiatus* (Lasch) Fr., Epicrisis Systematis Mycologici: 80 (1838)
- ≡ *Omphalia pachyphylla* var. *absintiaca* (Lasch) Quélet, Enchiridion Fungorum in Europa media et praesertim in Gallia Vigentium: 26 (1886)
- ≡ *Clitocybe absinthiata* (Lasch) Sacc., Sylloge Fungorum 5: 192 (1887)
- ≡ *Pseudooomphalina absinthiata* (Lasch) Knudsen, Nordic Journal of Botany 11 (4): 480 (1991)
- = *Collybia incomis* P. Karst., Bidrag till Kändedom av Finlands Natur och Folk 32: 164 (1879)
- ≡ *Clitocybe incomis* (P. Karst.) Sacc., Sylloge Fungorum 5: 192 (1887)
- = *Omphalopsis pallida* Murrill, Mycologia 9 (1): 41 (1917)

- ≡ *Mycena pallida* (Murrill) A.H. Sm., North American species of *Mycena*: 361 (1947)
 = *Omphalia clusiformis* Kühner & Romagn., Flore Analytique des Champignons Supérieurs: 125 (1953) (nom. nud.)
 ≡ *Pseudoomphalina clusiformis* (Kühner & Romagn.) Bon, Documents Mycologiques 9 (33): 13 (1978)
 = *Clitocybe vulgaris* Singer, Sydowia 15 (1–6): 48 (1962)
 = *Omphalina psammophila* Shtshukin, Folia Cryptogamica Estonica 18: 5 (1985)

Comments: Recently segregated from *Pseudoomphalina* (Lavorato et al. 2015), *Pseudolaccaria* is so far a monotypic genus accomodating only *Agaricus pachyphyllus* Fr. It is characterized by its *Laccaria*-like habit, rimose-squamulose pileus, ventricose-emarginate and distant thick lamellae, bitter taste, pileipellis hyphae very incrusted (not changing colour in basic solutions), weakly amyloid and ellipsoid thin-walled spores, and terricolous habitat (Kotlaba and Pouzar 1995; Kuyper 1995; Migliozzi and Coccia 1998; Watling and Turnbull 1998; Consiglio et al. 2006; Malysheva et al. 2011; Knudsen 2012; Lavorato et al. 2015). It is so far known only from Europe.

Pseudolaccaria fellea (Peck) Vizzini, Matheny, Consiglio & M. Marchetti, comb. nov. Figs. 7i–j, 9e–h
 MycoBank MB 831402

Basionym: *Clitocybe fellea* Peck, Ann. Rep. Reg. N.Y. St. Mus. 51(1): 284 (1898)

Description: Habit collybioid. *Pileus* (6–) 10–25 (–30) mm broad, hemispheric, convex at first, then broadly convex to flat, shallowly or rarely deeply depressed when old; margin inrolled, becoming either flat or facing upwards, thin, undulate, splitted or crisped in age, non-striate or faintly striatulate when soaked; surface dry, minutely fibrillose-pruinose to scaly (especially in the central depression), not hygrophanous; colour dingy yellowish to ochraceous, Sayal brown to cinnamon or pinkish buff, darker when young and paler with age, becoming sordid tan to yellowish. *Lamellae* broadly adnate, ventricose, later shortly decurrent, subdistant, 3–6 mm broad, $L = 18–25$, $l = 2–3$, moderately thick, sometimes triangular, white to pallid (tilleul buff), hazelnut-colour, with a concolorous eroded edge. *Stipe* (15–)20–40(–70) × 2–3 (–6) mm, cylindrical (or slightly enlarged at the top), sometimes compressed, often curved, sinuous, first solid but becoming fistulose, surface pallid or more or less concolorous with the pileus, appressed white silky-fibrillose but soon glabrescent, usually with scattered white rhizomorphs. *Context* thin (1–1.5 mm thick at the centre of the pileus), firm but rather brittle, white to washed white. *Smell* variable, intensely fungoid to subnauseous and farinaceous, but fading, *Pleurotus*

ostreatus-like according to P.B. Matheny (pers. comm.), *taste* bitter to very bitter and farinaceous, unpleasant. *Spore print* white.

Spores [59, 2, 2] 7.0–8.4 × 4.8–5.8 µm (on average 7.7 × 5.3 µm), $Q = 1.3–1.6$ ($Q_m = 1.46$), $V = 83–150 \mu\text{m}^3$ ($V_m = 114 \mu\text{m}^3$), ellipsoid, adaxially flattened or sometimes subcylindrical in side view, ellipsoid in front view, with an obtuse apex, with or without a low suprahilar depression, smooth, thin-walled, hyaline, cyanophilous, amyloid, often with a greenish drop and an evident tubular apicule, up to 1 µm long. *Basidia* 25–34 × 8.5–11 µm, tetrasporic or sometimes bisporic, subcylindrical to clavate or subcapitate, with up to 6 µm long sterigmata. *Hymenophoral trama* regular, composed of cylindrical to fusiform parallel hyaline hyphae 3–12 µm wide, thin-walled, sometimes enlarged at septa, cyanophilous. *Subhymenium* poorly differentiated. *Hypoderm* composed of parallel hyaline hyphae 3–10 µm wide, with a smooth or slightly pigmented wall. *Hymenial cystidia* not observed. *Pileipellis* a regular cutis, composed of cylindrical hyphae 4–10(–12) µm wide and variable in length, thin- to thick-walled, with some clavate terminal elements, with a hyaline to brownish cytoplasmatic content and parietal encrusting pigment. The surface of the pileus has scattered tufts of erect or repent hyphae about 5–12(–15) µm wide, with brownish encrusting epiparietal pigment, and versiform to cylindrical, subcapitate or clavate terminal elements, sometimes attenuated at the apex. *Stipitipellis* composed of mostly cylindrical or sometimes fusiform hyaline hyphae 2–8(–10) µm wide, thin-walled, often with short elements. *Clamp connections* present but sporadic.

Ecology: basidiomes isolated or gregarious, growing among grass or moss on soil in open conifer woods (hemlock, pines). So far known only from North America and Asia (Pakistan? see below).

Specimens examined: USA: Washington, King, Hazel Wolf Wetlands, under conifers and alder, leg. P.B. Matheny, PBM 1439, 006240 (WTU-F); Washington, King, Saddle Swamp, 1283 m a.s.l., leg. P.B. Matheny, 02-V-1997, PBM 426, 006239 (WTU-F); Washington, King, Saddle Swamp, one on a stick, other appearing in soil on moss, 1283 m a.s.l., leg. P.B. Matheny, 10-V-1998, PBM 964, 006230 (WTU-F).

Comments: Bigelow (1985) already noticed that the generic position of *Clitocybe fellea* was puzzling, placing it in the *incertae sedis* *Clitocybe*. *Pseudolaccaria fellea* seems to be a rare species endemic to North America, even though two collections from Pakistan (MSM#0013 and MSM#0014 are genetically close to the American collections (Fig. 3). It can be easily identified because of its minutely scaly and pale yellowish brown pileus, its pallid and distant thick lamellae, and very unpleasant bitter taste (Peck 1898; Smith

1944; Bigelow 1982, 1985). Previous phylogenetic analyses (Lavorato et al. 2015; Sánchez-García et al. 2016) revealed that *C. fellea* belongs in the genus *Pseudolaccaria*, close to the European *P. pachyphylla*, although genetic data were not enough to resolve if they actually represent one or more species. The present phylogenetic results (Fig. 3) suggest that some reproductive isolation exists between *P. pachyphylla* and *C. fellea*, with partially significant support values for *P. pachyphylla* (PP = 0.85, BP = 89%). In addition to an apparently different geographic distribution, both lineages have diagnostic morphological features, namely the presence of cheilocystidia and caulocystidia in *P. pachyphylla*, and its slightly larger spores which are only weakly amyloid ($6.5\text{--}9 \times 4.5\text{--}6 \mu\text{m}$) (Kotlaba and Pouzar 1995; Kuyper 1995; Migliozzi and Coccia 1998; Watling and Turnbull 1998; Consiglio et al. 2006; Knudsen 2012; Lavorato et al. 2015). Therefore, both names are considered here independent species, although further sampling and sequencing is needed to confirm their status. Smith (1944) and Bigelow (1985) reported the spores of *Clitocybe fellea* as non-amyloid. Given that in *Pseudolaccaria* spore positive amyloid reaction is rather weak and can go unnoticed, it would be advisable the use of standardized methods, such as the one presented in Alvarado et al. (2018a).

Xerophorus (Bon) Vizzini, Consiglio & M. Marchetti, stat. nov.

MycoBank MB 831417

≡ *Callistosporium* subg. *Xerophorus* Bon, Documents Mycologiques 20 (79): 57 (1990)

≡ *Callistosporium* sect. *Xerophorus* (Bon) Contu, Boletim da Sociedade Broteriana 65: 80 (1992)

= Sect. *Olivascentia* Bon & Perco, in Perco, Bollettino AMER 15: 9 (1988)

Type species: *Xerophorus olivascens* (see below)

Description: Habit collybioid, gymnocarpic development (without veils). *Pileus* dry, smooth to furfuraceous. *Lamellae* adnate, emarginated to subdecurrent, distant and thick. Spore-print white. Spores smooth, amygdaliform, papillate, usually longer than $8 \mu\text{m}$, thin-walled, without iodine reactions, non-amyloid, cyanophilous, with a large central oil drop that turns green in basic solutions. *Hymenophoral trama* at first slightly bilateral (divergent), soon regular. *Basidia* hygrophoroid, up to $50\text{--}60 \times 6\text{--}8\text{--}11 \mu\text{m}$, filled with granules that turn green in basic solutions. *Cheilocystidia* poorly differentiated or absent. *Pleurocystidia* absent. *Pileipellis* a cutis to subtrichoderm of cylindrical hyphae; pileipellis, subpellis and hypoderm elements usually with parietal-incrusting and extracellular pigments that turn green-light blue in basic solutions. *Clamp connections* present or absent.

Ecology: on soil. Presumably saprotrophic. Europe and Greater Antilles (Dominican Republic).

Xerophorus olivascens (Boud.) Vizzini, Consiglio & M. Marchetti, comb. nov. Figs 10 a–d, 11 a–g
MycoBank MB 831418

Basionym: *Tricholoma olivascens* Boud., Bull. Soc. mycol. Fr. 33(1): 7 (1917)

≡ *Callistosporium olivascens* (Boud.) Bon, Documents Mycol. 6 (22–23): 283 (1976)

= (?) *Collybia aerina* Quél., Assoc. Franç. Avancem. Sci., Congr. Rouen 1883 12: 498 (1884) [1883]

= (?) *Callistosporium olivascens* var. *aerinum* (Quél.) Bon, Documents Mycol. 6 (22–23): 286 (1976)

Description: Habit collybioid. *Pileus* 15–50 mm broad, first hemispherical to convex, with a narrow involute margin, sometimes with a flattened broad umbo; with age flat-convex to flattened, with a straight sinuose-undulate and slightly excedent margin, often a bit depressed at the centre; surface slightly hygrophanous, not translucently striate, dry, minutely tomentose-felted to pruinose, sometimes zonated towards the margin, brown-olive, ochraceous olive, grey-olive, sometimes with ochraceous Brick-red tinges, dark grey-brown in the chromatic variant/phenotype by some authors referred to as “*C. olivascens* var. *aerinum* (Quél.) Bon” (Bon 1976, 1984, 1991; Perco 1988; Ludwig 2001). *Lamellae* distant, spaced, $L = 15\text{--}25$, $l = 2\text{--}5$, up to 6 mm broad, ventricose, emarginated to slightly decurrent, *Hygrocybe*-like (thick and slightly ceraceous), often anastomosing, yellowish to olive yellow, ochraceous-olive or grey-olive; edge entire, colorous or somewhat paler. *Stipe* 18–55 \times 2–9 mm, elastic, cylindrical to laterally compressed, often slightly excentric, straight to somewhat curved, flexuose, sinuose, often tapering towards the base, at first fistulose and later hollow; surface dry, fibrillose, at first with a white felt-like covering over an ochraceous background that disappears soon; base with abundant white rhizomorphs incorporating substrate particles. *Context* thin (< 1.5 mm thick in the centre of the pileus), soft in the pileus but elastic-fibrous in the stipe, cream to yellowish. *Smell* indistinct or sometimes of rancid flour, *taste* indistinct or slightly bitter. *Spore print* whitish.

Macrochemical reactions: the surface of the whole basidioma (both fresh and dried) turns bluish green in basic solutions.

Spores [80, 3, 3] $8.1\text{--}10.4 \times 4.7\text{--}5.7 \mu\text{m}$, (on average $9.2 \times 5.2 \mu\text{m}$), $Q = 1.6\text{--}1.9$ ($Q_m = 1.70$), $V = 103\text{--}133 \mu\text{m}^3$ ($V_m = 118 \mu\text{m}^3$), amygdaliform with ogival apex in side view and ellipsoid in front view, hyaline, thin-walled, with an evident apicule, mostly with a big greenish-grey drop, turning green in basic solutions, inamyloid, congophilous, cyanophilous. *Basidia* $35\text{--}60 \times 7.0\text{--}11 \mu\text{m}$, clavate to cylindrical-clavate,

Fig. 10 Fresh basidiomes of *Xerophorus* spp. *Xerophorus olivascens*. **a** (1236/05 EMB). **b** (1236/06 EMB). **c** (18226 AMB). **d** (18227 AMB). *X. donadinii*. **e** (18223 AMB). **f** (18222 AMB). **g** (CA 20181110.02). *X. dominicanus*. **h** (127428 JBSD, holotype). Photographs: **a, b** by C. Papetti; **c, d** by G. Consiglio; **e, f** by M. Maletti; **g** by C. Agnello; **h** by C. Angelini



tetrasporic, with up to 8 µm long sterigmata, sometimes also bi- or monosporic, and then with sterigmata up to 12 µm long; without basal clamp connections, with a granulose greenish cytoplasmatic content, staining deep green in basic solutions. *Subhymenium* well differentiated, thick, mostly composed of short elements 3–6 µm wide. *Hymenophoral trama* composed of regular hyaline hyphae 8–20 µm wide, generally cylindrical but rounded at the septa, with walls up to 0.5(–1.0) µm thick. *Cheilocystidia* 30–50 × 6–8.5 µm, poorly differentiated, cylindraceous or sometimes flexuose, weakly mucronated, or also subcapitate, smooth, thin-walled, basidiole-like, scattered. *Pleurocystidia* not

observed. *Pileipellis* a cutis tending to a subtrichoderm of intertwined hyphae 10–20 µm wide, with a smooth greenish cytoplasmatic pigment and an epiparietal greenish yellow pigment (sometimes encrusting in small plates) which turns green-blue with basic solutions, as well as some terminal elements emerging in tufts, cylindrical to flexuose, cylindrical-clavate or subglobose, 14–25(–30) × 4–8(–15) µm, generally smooth. *Stipitipellis* composed of cylindraceous to rounded at septa or sometimes claviform hyphae 4–12 µm wide and variable in length, with walls up to 1.0 µm thick and epiparietal pigment in small plates. *Caulocystidia* cylindraceous to clavate, sometimes flexuose, lageniform or

bilobed, emerging or repent, with rounded apex or sometimes subcapitate, measuring $30\text{--}50(70) \times 4\text{--}8(14)$ μm . *Clamp connections* absent.

Ecology: solitary or gregarious, rarely subcaespitose in small clusters, usually under cedars in parks and gardens of southern Europe.

Specimens examined: **ITALY:** Emilia-Romagna, Ravenna, Bassa del Bardello, meadows, leg. G. Consiglio, M. Caldironi & A. Zuccherelli, 18-XI-2010, 18227 (AMB); ibidem, 30-X-2013, 18226 (AMB); Friuli Venezia Giulia, Trieste, Campi Elisi, in a flower bed with cedars, leg. P. Picciola, 25-X-2016, 18229 (AMB); Lombardia, Brescia, in the park in front of S. Anna hospital, numerous specimens, someones fasciculate, in the herb near a cedar, leg. M. Chiari & C. Papetti, 12-XII-1999, 1236/05 EMB; Brescia, in the park of Domus Salutis hospital, leg. C. Papetti, 23-X-2003, 1237/05 EMB; Sardinia, Olbia-Tempio, Aglientu, Rena Majore, on pine wood, leg. G. Consiglio, D. Antonini, M. Antonini & G. Perdisa, 02-XI-2000, 18224 (AMB); Sassari, Alghero, Baratz lake, on pine wood, leg. G. Consiglio, L. Perrone & L. Setti, 03-XI-2008, 18225 (AMB).

Comments: *Callistosporium olivascens* occurs in southern Europe especially under cultivated cedars in anthropic environments, such as gardens and city parks, although its trophic status remains unknown (Boudier 1917; Josserand 1943; Kühner and Romagnesi 1954; Bon 1976, 1984, 1991; Lanzoni 1986; Moser 1986; Bidaud 1988; Perco 1988; Bizio 1991; Courtecuisse 1993; Consiglio and Papetti 2001; Ludwig 2001; Horak 2005; Boccardo et al. 2008; Picciola and Zugna 2017; Tanchaud 2018). Interestingly, it was not reported from the extensive natural forests of *Cedrus atlantica* at the Moroccan Atlas (Malençon and Bertault 1975). Occasionally, it has been reported to grow among *Cupressaceae* (Bon 1984; Consiglio and Papetti 2001; Bizio 2012), *Pinus* spp. (Moser 1986; Picón 2008) and under *Cistus* (Lavorato 1991), as well as in sand dunes (Picón 1995, 2008; Bizio 2012; Conca et al. 2017). It can be discriminated mainly because of its dark colours, large amygdaliform spores about $8\text{--}13 \times 5.0\text{--}7.0$ μm , and more or less cylindrical marginal cystidia (Josserand 1943; Bon 1976, 1984, 1991; Moser 1986; Bidaud 1988; Ludwig 2001; Horak 2005; Picciola and Zugna 2017). The specimens sequenced in the present work, both those with typical brown-olive to ochraceous olive pileic colours (e.g. 1236/05 EMB) and those with dark grey-brown tinges (e.g. 18226 AMB, 18227 AMB) proved to be conspecific (Fig. 3), suggesting that “*C. olivascens* var. *aerinum* (Quél.) Bon” is only a chromatic form of the type without any taxonomic significance. As a matter of fact, the name *Collybia aerina* is older (1884) than *Tricholoma olivascens* (1917) and if their conspecificity were demonstrated in the future, the former must be considered

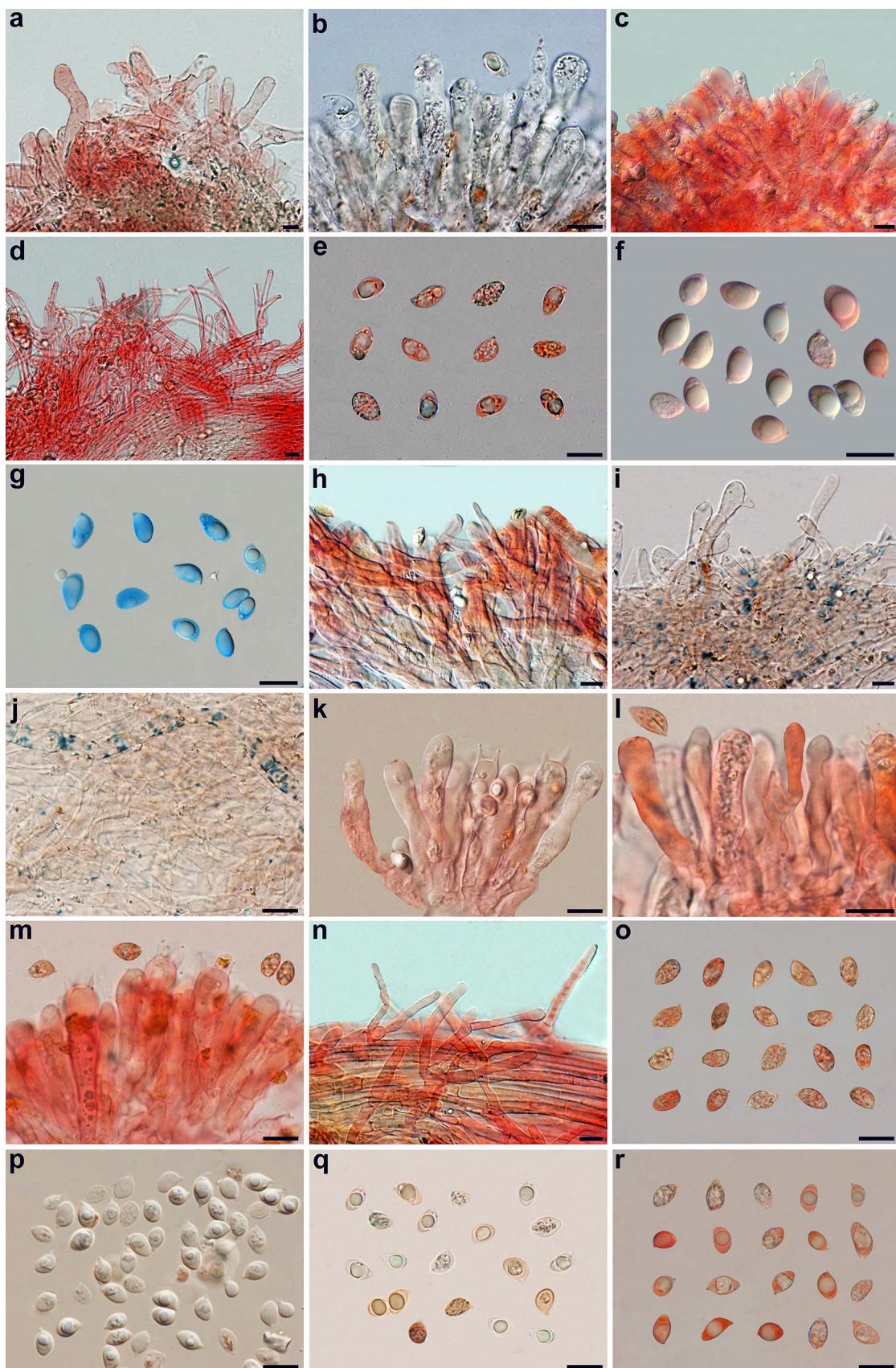
the priority name. The protologue and the drawings of *Collybia aerina* provided by Quélet (1884) fit well with those of *Tricholoma olivascens* (Boudier 1917; Josserand 1943; Bon 1984, 1991; Picciola and Zugna 2017) except for the spores which are described as ovoid and depicted (Quélet 1884, plate VI, fig. 2) without the apical papilla so typical in those of *T. olivascens*.

Xerophorus donadinii (Bon) Vizzini, Consiglio & M. Marchetti, comb. nov. Figs. 10e–g, 11h–r
MycoBank MB 831419

Basionym: *Callistosporium olivascens* var. *donadinii* Bon, Docums Mycol. 20 (79): 57 (1990)
≡ *Callistosporium donadinii* (Bon) Contu, Micol. Ital. 22(1): 55 (1993)

Description: Habit collybioid. *Pileus* 10–30 mm broad, convex first then flat-convex, without an evident umbo; margin exceeding the lamellae, often sinuous, undulate, sometimes fissured; surface dry, smooth, pruinose, not hygrophanous, yellow-orange to reddish or vinous-purple. *Lamellae* distant, spaced, $L = 15\text{--}20$, $l = 1\text{--}4$, adnate-emarginated to slightly decurrent, ventricose, 5–6 mm broad, thick, whitish-yellow to lemon yellow, with a paler edge. *Stipe* 20–60 \times 3–7 mm, cylindrical, sinuose, sometimes grooved, first fistulose and later hollow, surface dry, entirely pruinose, longitudinally fibrillose below the bloom, first lemon yellow and then yellow-brown, with abundant white rhizomorphs at the base. *Context* fragile, whitish to pale lemon yellow, turning slightly vinaceous when cut. *Smell* and *taste* recalling camphor-menthol or not remarkable. *Spore print* white. *Macrochemical reactions*: the surface of the whole basidioma (both fresh and dried) turns bluish green in basic solutions; the individual lamellae turn vinous-red in basic solutions.

Spores [391, 4, 4] $7.1\text{--}9.1 \times 4.8\text{--}5.6$ μm (on average $8.1\text{--}5.2$ μm), $Q = 1.32\text{--}1.81$ ($Q_m = 1.57$), $V = 86\text{--}145$ μm^3 ($V_m = 115$ μm^3), amygdaliform with an apex often ogival to papillate in side view and ovoid-ellipsoid in front view, with an evident apicule up to 1.0 (–1.2) μm long, smooth, hyaline, with one or more pale greenish drops, inamyloid, cyanophilous. *Basidia* 30–40(–50) \times (7.5–)8–9.5(–10) μm , cylindraceous to cylindric-clavate, tetrasporic, with up to 7(–8) μm long sterigmata, rarely also bisporic or monosporic, and then with up to 9(–10) μm long sterigmata, sometimes with a greenish granulose cytoplasmatic content. *Cheilocystidia* 30–40 \times 8–12 μm , not well differentiated, similar to basidia and basidioles, cylindraceous to flexuose, often constricted in the middle, and sometimes subcapitate or weakly mucronate. *Pleurocystidia* absent. *Subhymenium* well differentiated, thick, mostly composed of short elements 3–6 μm wide. *Hymenophoral trama* composed of rather regular hyaline hyphae 4–12(–14) μm wide, cylindrical to rounded at



◀Fig. 11 Microscopical features of *Xerophorus* spp. *Xerophorus olivascens*. **a** Pileipellis (pileocystidia, 18224 AMB). **b** Hymenial elements (18224 AMB). **c** Cheilocystidia (18227 AMB). **d** Stipitipellis (caulocystidia, 18224 AMB). **e** Spores (18224 AMB). **f** Spores (18227 AMB). **g** Spores (18229 AMB). *X. donadini*. **h** Pileipellis (Donadini 338-78 LIP, holotype). **i** Pileipellis (18223 AMB). **j** Elements of subpellis (18223 AMB). **k** Hymenial elements (18223 AMB). **l** Hymenial elements (Donadini 338-78 LIP, holotype). **m** Hymenial elements and spores (18222 AMB). **n** Caulocystidia (18223 AMB). **o** Spores (Donadini 338-78 LIP, holotype). **p** Spores (18223 AMB). **q** Spores (18223 AMB). **r** Spores (CA 20181110.02). **a, c–e, h, k–o, r** in ammoniacal Congo red; **b, i–j, q** in 10% ammonia; **f–p** in ammoniacal Congo red-interferential contrast; **g** in Cotton blue in Lactic acid. Bars = 10 µm. Photographs by M. Marchetti

septa, mostly thin-walled and only rarely with walls up to 1.2 µm thick. *Pileipellis* a cutis of intertwined hyphae 3–10 µm wide occasionally with the cytoplasmatic pigment staining vinous red in basic solutions, and an epiparietal encrusting pigment in small plates staining blue-green in basic solutions. Some scattered terminal elements emerge isolated or in tufts, subglobose to subclavate or cylindrical-clavate (pileocystidoid), measuring 15–35 × 8–10 µm. *Subpellis* consisting of hyphae 4–12(–15) µm wide, with walls up to 1(–1.2) µm thick, sometimes with parietal and epiparietal pigment in small plates staining blue-green in basic solutions. *Stipitipellis* composed of cylindraceous to claviform hyphae sometimes rounded at septa, 2–10(–12) µm wide and variable in length, with walls up to 1.2 µm thick, with epiparietal brown pigment in small plates, as well as intracellular pigment consisting of scattered clusters of red-vinous to reddish-brown or greenish-brown material, and polymorphic formations of refractive crystals. *Caulocystidia* consisting of cylindrical to claviform elements, sometimes flexuose, lageniform, or bilobed, with rounded to subcapitate apex, 30–50(–70) × 5–10(–14) µm. *Clamp connections* absent.

Ecology: gregarious or subcespitosse, growing in different Mediterranean forests (*Quercus suber*, *Pinus*, *Cupressus*, *Acer*, *Prunus*) often among fallen kernels and walnuts.

Specimens examined: FRANCE: Porquerolles, under *Cupressus* and *Pinus*, leg. J.C. Donadini, XI-1978, Donadini 338-78 (LIP) (**holotype**). ITALY: Marche, Pesaro-Urbino, Villa Ceccolini, F. Foglia, broadleaved trees, leg. M. Maletti, 22-V-2010, 18223 (AMB); Piandimeleto, mixed broadleaved wood, leg. M. Maletti & L. Polidori, 11-XI-2015, 18222 (AMB); Puglia, Brindisi, Bosco dei Lucci, under *Quercus suber*, calcareous soil, leg. C. Agnello & A. De Marco, 10-XI-2018, CA 20181110.02.

Comments: This species was first proposed by Bon (1990) as a variety of *C. olivascens*, but later raised to the rank of species by Contu (1993). However, this decision was not accepted by some authors (Picciola and Zugna 2017). The phylogenetic analyses conducted in the present work suggest that this

taxon is an independent species (Fig. 3). Unfortunately, the repeated attempts to produce genetic data from the French type collection failed, but the three modern Italian collections sequenced show macro- and microscopic characters perfectly matching those of the typus. *Callistosporium donadini* seems to be restricted to the Mediterranean coastal regions of Europe. Basidiomes have a more or less vinaceous to dark red-brown pileus, a usually camphor-menthol odour, amygdaliform spores measuring 6–9 × 4.0–5.0 µm, and more or less cylindrical scattered marginal cheilocystidia (Bon 1984, 1990, 1991; Neville 1992; Contu 1993, 1998; Ludwig 2001; Damiani 2005; Horak 2005; Angeli and Tullii 2010, 2011; Tanchaud 2018). The variability of spore dimensions observed in the present work is likely due to the different contribution of mono- and trisporic basidia present in each basidiome.

Xerophorus dominicanus Angelini, Vizzini & Bazzi, sp. nov. Figs. 10h, 12
Mycobank MB 831420

Etymology: The specific epithet refers to the country, Dominican Republic, where the type collection was made.
Type specimen: DOMINICAN REPUBLIC: Sosua (Puerto Plata), 6 specimens collected on the ground of a garden, leg. C. Angelini, 04-12-2013, 127428 (JBSD) (**holotype**); 46117 (AH) (**isotype**).

Diagnosis: Habit collybioid. Development gymnocarpic. *Pileus* 12–16 mm broad, hemispherical to convex, flat at maturity, with a broad obtuse umbo; margin at first inflexed then straight, irregularly undulate or sometimes lobate, not translucently striate; surface dry, mat, not hygrophanous, fibrillose to minutely felty-tomentose, wrinkled, sometimes tuberculated, uniformly light cyclamen pink, at first entirely covered with a white pruina that persists even in mature specimens at the margin of the pileus. *Lamellae* thick, distant, L = 15–25, l = 1–3, up to 2 mm broad, adnexed to emarginate, often with a decurrent tooth or sometimes subdecurrent, light cream with pink hues, with a slightly irregular to eroded concolorous edge. *Stipe* 20–25 × 2–4 mm, central, cylindrical, generally curved towards the base, sinuose; surface dry, mat, fibrillose to finely scurfy-flocculent, concolorous with the pileus, covered with a white pruina towards the base. *Context* thin, pinkish-white, up to 1–2 mm thick at the centre of the pileus. *Smell* and *taste* indistinct. *Spore print* white.

Spores [45, 2, 1] 7.6–8.9 × 5.7–6.5 µm (on average 8.3 × 6.1 µm), Q = 1.27–146 ($Q_m = 1.36$), V = 130–190 µm³ ($V_m = 160 \mu\text{m}^3$), amygdaliform in side view and rounded in front view, usually with an apical papilla, smooth, thin-walled, hyaline in water, inamyloid, cyanophilous, always containing one large central yellowish droplet (resembling an egg yolk) that turns emerald green with basic solutions, with an evident apicule up to 1.0 µm long. *Basidia* 38–42 ×

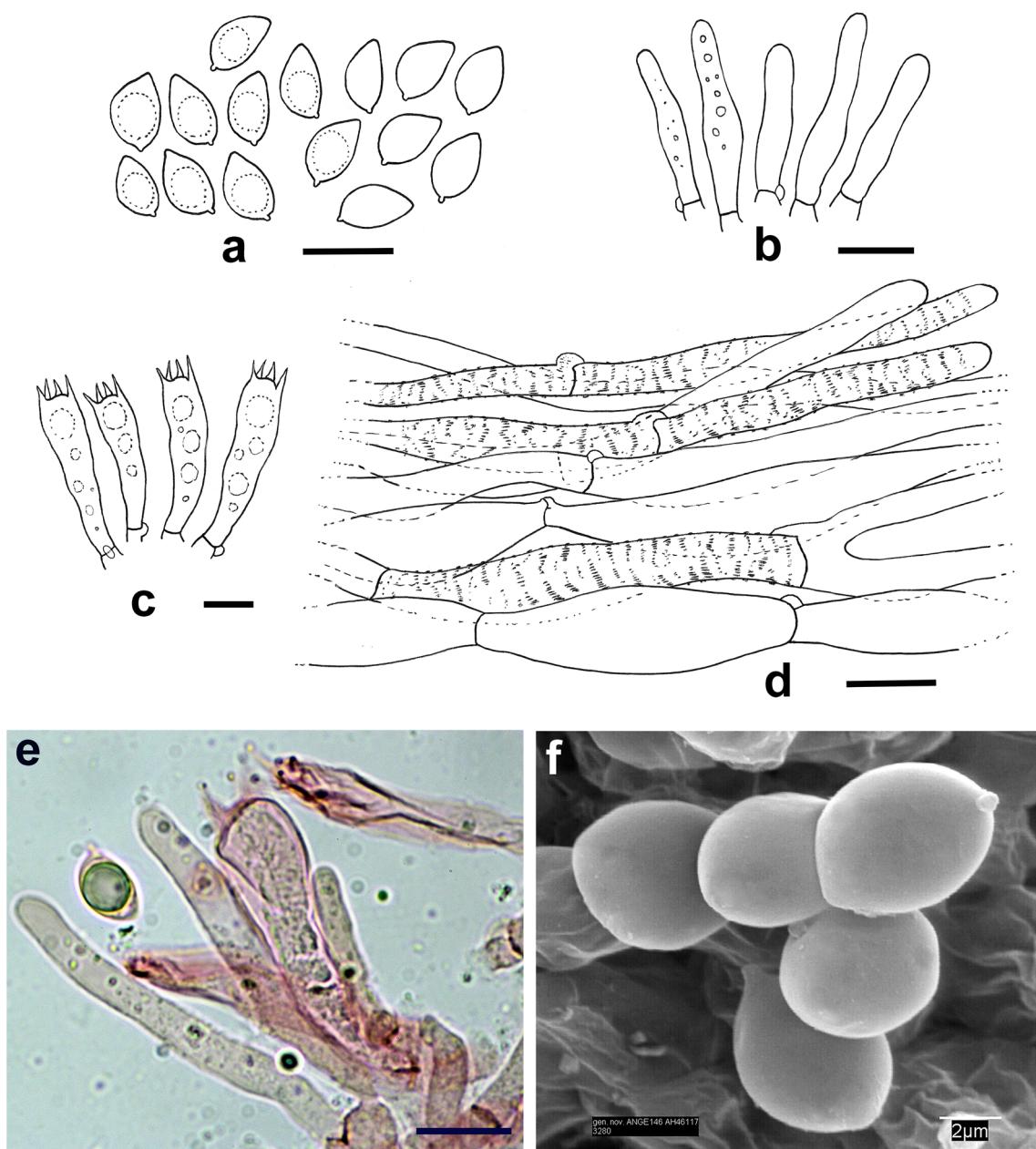


Fig. 12 Microscopical features of *Xerophorus dominicanus* (127428 JBSD, holotype). **a** Spores. **b** Cheilocystidia. **c** basidia. **d** Pileipellis. **e** Basidia and cheilocystidia. **f** Spores (SEM). **e** In ammoniacal Congo

red. Bars: **a–e** = 10 μm . Drawings by F. Boccardo. Photographs: **e** by C. Angelini, **f** by G. Moreno

7–11 μm , clavate, tetrasporic, with basal clamp-connections, sterigmata up to 3–5 μm long. *Cheilocystidia* 21–44 \times 3–5 μm , cylindrical to slightly clavate, sinuose. *Pleurocystidia* absent. *Hymenophoral trama* more or less divergent when young, but then regular, subparallel or somewhat divergent in the compact subhymenium, made of cylindrical to undulating hyaline hyphae up to 7 μm wide. *Pileipellis* a cutis with some ascending hyphae and cylindrical to slightly clavate terminal elements measuring 48–120 \times 7–15 μm . *Subpellis* consisting of intertwined hyphae up to 20 μm wide; pigment

brown, parietal to minutely incrusting and extracellular, turning bright green in basic solutions. *Stipitipellis*: similar to the pileipellis but hyphae only up to 5 μm wide. *Caulocystidia* absent. *Clamp connections* present everywhere.

Ecology: gregarious, terricolous, in grass areas. So far known only from the type locality in the Dominican Republic.

Comments: This striking species is characterized by basidiomes with cyclamen pink tinges, and above all the presence

of clamp connections in the pileipellis elements and at the base of basidia. It is the only species among the callistosporioid fungi to have clamp connections (with the exception of a single African collection of *C. imbricatum* where clamps were observed at the base of the basidia by Desjardin and Perry 2017). *Xerophorus dominicanus* is the only non-European species of this genus known so far.

Macrocybe Pegler & Lodge, in Pegler, Lodge, Nakasone, Mycologia 90(3): 496 (1998)

Type species: *Macrocybe titans* (H.E. Bigelow & Kimbr.) Pegler, Lodge & Nakasone, Mycologia 90(3): 500 (1998)

Description: Habit tricholomatoid, basidiomata large, fleshy, often connate or forming caespitose clusters, gymnocarpic. *Pileus* convex, umbonate to depressed, surface white, cream to greyish ochre, smooth, dry, margin incurved when young. *Lamellae* sinuate, pale, crowded, with multiple lamellulae. *Stipe* cylindrical to obclavate, often with a distinctly inflated base, solid, surface smooth and fibrillose or squarrose; arising from a cottony mycelium or a pseudosclerotium. *Context* white, unchanging after cutting. *Spore print* white to cream. *Spores* < 10 µm long, subglobose to broadly ellipsoid, hyaline, cyanophilous, inamyloid, thin-walled, smooth, often containing one or more droplets. *Basidia* clavate, tetrasporic, lacking siderophilic granules. *Hymenial cystidia* absent or present as gloeocystidoid pseudocystidia (with refractive contents and arising deep in the hymenium). *Hymenophoral trama* regular; subhymenial layer narrow. *Pileipellis* a well developed and repent cutis, made of narrow but slightly inflated thin-walled hyphae, sometimes with gloeo-hyphae. *Clamp connections* always present.

Ecology: in grasslands or associated with decaying wood, non-mycorrhizal. Tropical.

Comments: *Macrocybe* is represented by 7 species of pantropical distribution (Pegler et al. 1998, see comments below). They were previously classified within *Tricholoma* sect. *Leucorigida* Singer by Singer (1986) because of the presence of clamp connections, an interwoven cutis, whitish basidiomes, and a non-mycorrhizal lifestyle. However, *Tricholoma mongolicum* S. Imai, the type species of section *Leucorigida*, was suggested to be a species of *Calocybe* Kühner ex Donk by Pegler et al. (1998), and later accommodated into the new genus *Leucocalocybe* X.D. Yu & Y.J. Yao by Yu et al. (2011). Pegler et al. (1998) provided genetic support to combine species of *Tricholoma* sect. *Leucorigida* with massive basidiomes, saprotrophic habit and growing in subtropical to tropical areas into the new genus *Macrocybe*. Moncalvo et al. (2002), found that 28S/LSU rDNA sequences of *Macrocybe* were significantly related with those of the callistosporioid clade, and Ammirati et al. (2007) and Sánchez-García et al.

(2016) linked it with the *Catathelasma* clade and the *Catathelasmataceae*, respectively.

Macrocybe titans (H.E. Bigelow & Kimbr.) Pegler, Lodge & Nakasone, Mycologia 90(3): 500 (1998) Fig. 13

Basionym: *Tricholoma titans* H.E. Bigelow & Kimbr., Mycotaxon 11(2): 426 (1980)

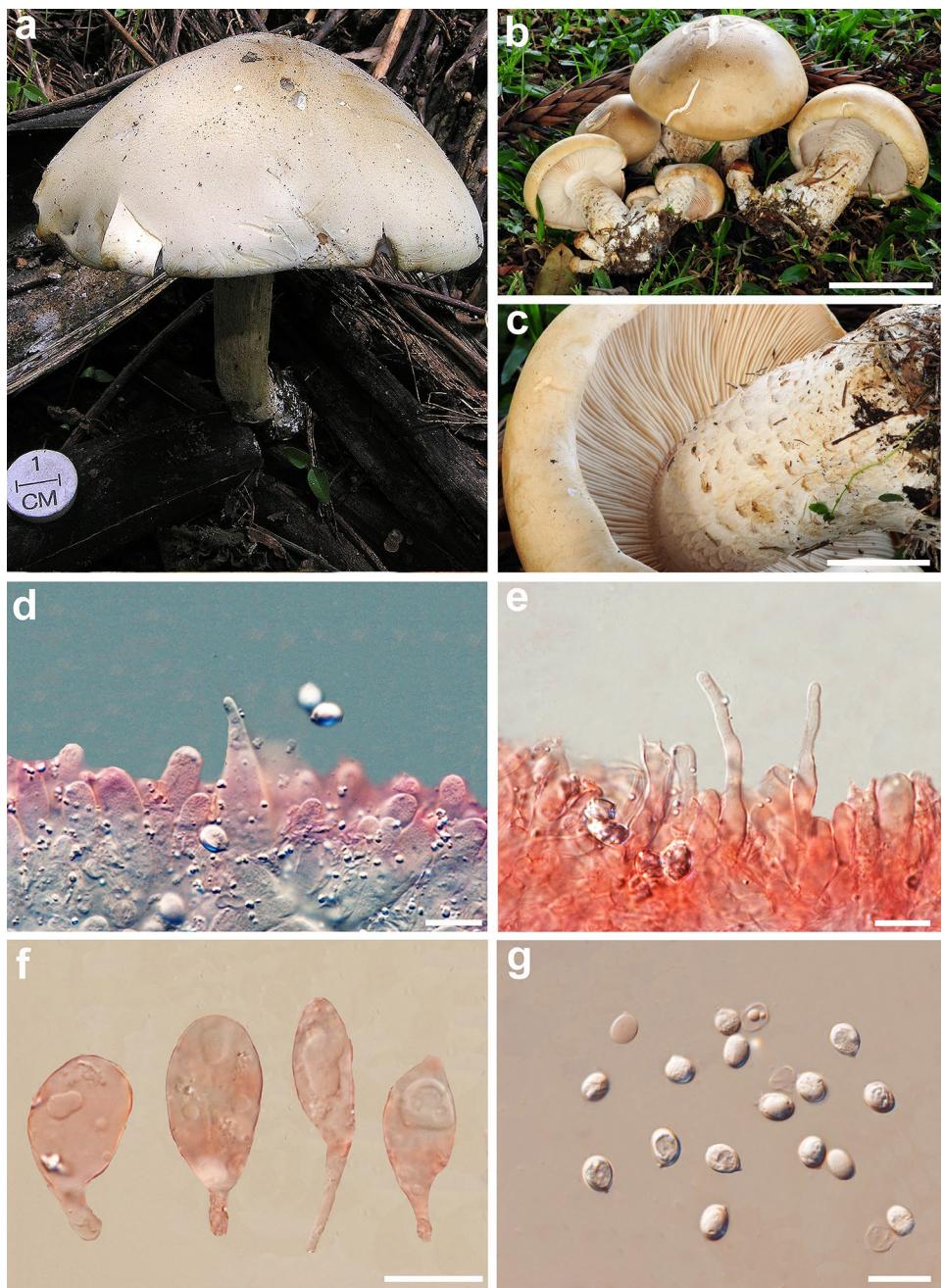
= *Tricholoma cystidiosum* Cifuentes & Guzmán [as ‘cystidiosa’], Boln. Soc. mex. Microl. 16: 38 (1981), nom. illegit., Art. 53.1, preoccupied by *Tricholoma cystidiosum* A.H. Sm., Mycologia 33(1): 14 (1941)

= *Tricholoma cifuentesii* Courtec., Docums Mycol. 16(61): 49 (1985) (replacement name for *Tricholoma cystidiosum* Cifuentes & Guzmán) fide Singer (1990)

Description: Habit tricholomatoid, caespitose. *Pileus* 40–500(–1000) mm broad, hemispherical, convex at first but soon becoming broadly convex or flattened, centre somewhat depressed with age, margin incurved at first and later uplifted, slightly undulate or lobate; surface dry, smooth, not hygrophanous, cracking into small adpressed squamules, cream to pale yellow, pale ochraceous, lighter at margin. *Lamellae* crowded, sinuate to adnate with a decurrent tooth, with lamellulae of four different lengths, up to 10(–15) mm broad, whitish to cream, with a concolorous entire edge. *Stipe* 60–150(–380) × 15–50(–120) mm, cylindrical to clavate, up to 120 mm at the base, central, solid, fleshy; surface at first white to pale yellow, later ochraceous, with numerous and reflexed darker squamules. *Context* compact, 15–40 mm thick at pileus centre, thinner towards the margin, whitish, unchanging. *Smell* strong fungic, *taste* slightly bitter. *Spore print* cream.

Spores [148, 3, 3] 5.8–6.8 × 4.4–5.1 µm (on average 6.3 × 4.7 µm), Q = 1.2–1.4 ($Q_m = 1.33$), V = 59–90 µm³ ($V_m = 75 \mu\text{m}^3$), subglobose to ovoid or broadly ellipsoid, with an evident apicule up to 1(–1.2) µm long, smooth, thin-walled, often with a big refractive greenish drop, cyanophilous, inamylod. *Basidia* 25–38 × 6–9(–10) µm, subcylindraceous to cylindrical-clavate, tetrasporic, with basal clamp connections. *Pseudeocheilocystidia* 35–50(–80) × 5–10 µm, isolated or in clusters, fusoid, with subacute to rostrate or rounded apices, lanceolate to lageniform with a long filiform neck, often emerging from the edge, originating below the basidia and connected to conducting elements, gloeocystidiod, containing amorphous refractive material. *Pseudopleurocystidia* absent. *Hymenophoral trama* regular, composed of cylindraceous hyphae 3–7 µm wide, enlarged at septa up to 15 µm wide, thin-walled. *Subhymenium* differentiated, composed of short subintertwined hyaline elements 3–8 µm wide. *Pileipellis* a cutis, composed of mostly intertwined or at times emerging to erected hyphae 2–6 µm wide, non gelatinose, thin-walled, with refractive content. *Stipitipellis*

Fig. 13 *Macrocybe titans*. **a** Basidioma (127429 JBSD). **b** Basidiomata (28653 MCVE). **c** Stipe and squamules (28653 MCVE). **d–f** Pseudocheilocystidia. **g** Spores. **d** in Phloxine; **e** in ammoniacal Congo red; **g** in ammoniacal Congo red-interferential contrast. Bars: **b** = 100 mm; **c** = 20 mm; **d–g** = 10 µm. Photographs: **a** by C. Angelini; **b, c** by P. Picciola; **d–f** by M. Marchetti



consisting of thin-walled hyphae 2–6 µm wide. *Caulocystidia* absent. *Clamp connections* present.

Specimens examined: **BRAZIL:** Paraná, Curitiba, Campina Grande do Sul, in a wood of broadleaved trees and *Araucaria angustifolia*, 980 m asl, leg. P. Picciola, 04-IV-2015, 28653 (MCVE). **DOMINICAN REPUBLIC:** Sosua (P.to Plata), Loc. Puerto Chiquito, 1 specimen growing among the arboreal roots of *Roystonea regia*, leg. C. Angelini, 20-IV-2013, 127429 (JBSD). **PUERTO RICO:** unknown locality, on soil in a garage, near *Spondias dulcis*, leg. C. Laboy, 1997, 55023 (K-M). **USA:** Florida, Lake, Tavares, on leaves

beneath oaks, leg. Haddox, 19-VIII-1978, 51990 (FLAS-F) (**holotype**); in grass, Coniferae, leg. S.E. Evans, 2002, 127842 (K-M); Florida, Alachua, Gainesville, University of Florida Campus; Entomology building, altered ground next to parking lot, on the ground, big fruiting body growing in clusters, leg. D. Mancero, 02-X-2012, 58974 (FLAS-F); Florida, Alachua, Gainesville, The Laurels Apartments, 4455 SW, 34th St, mulch bed, in clusters in disturbed area, leg. C.G. Ferguson, 19-IX-2014, 59217 (FLAS-F).

Comments: Originally proposed to accomodate collections from Florida (southern USA) by Bigelow and Kimbrough

(1980), *Macrocybe titans* shows an apparently pantropical distribution. In America, it has been found in Mexico (Cifuentes and Guzmán 1981; Singer 1990; Armando López and Juventino García 2018), Costa Rica (Pegler et al. 1998; Corrales and López-Quintero 2005; Calonge et al. 2007), Colombia (Corrales and López-Quintero 2005), Panamá (Piepenbring 2008), Ecuador, Martinique, Puerto Rico, Trinidad and Tobago and Venezuela (Pegler et al. 1998). In Asia, it has been reported from Taiwan (Chen and Chen 1999) and India (Vrinda et al. 1997; Farook et al. 2013). It has been also recently reported from southern USA (DeLong and Talbot Brewer 2013), southern Brazil (Battistin and Picciola 2015), and Argentina (Ramirez et al. 2017). The collection 127429 (JBSD) studied in the present work represents the first report of *Macrocybe titans* from the Dominican Republic. *Macrocybe titans* shows a unique combination of characters, namely

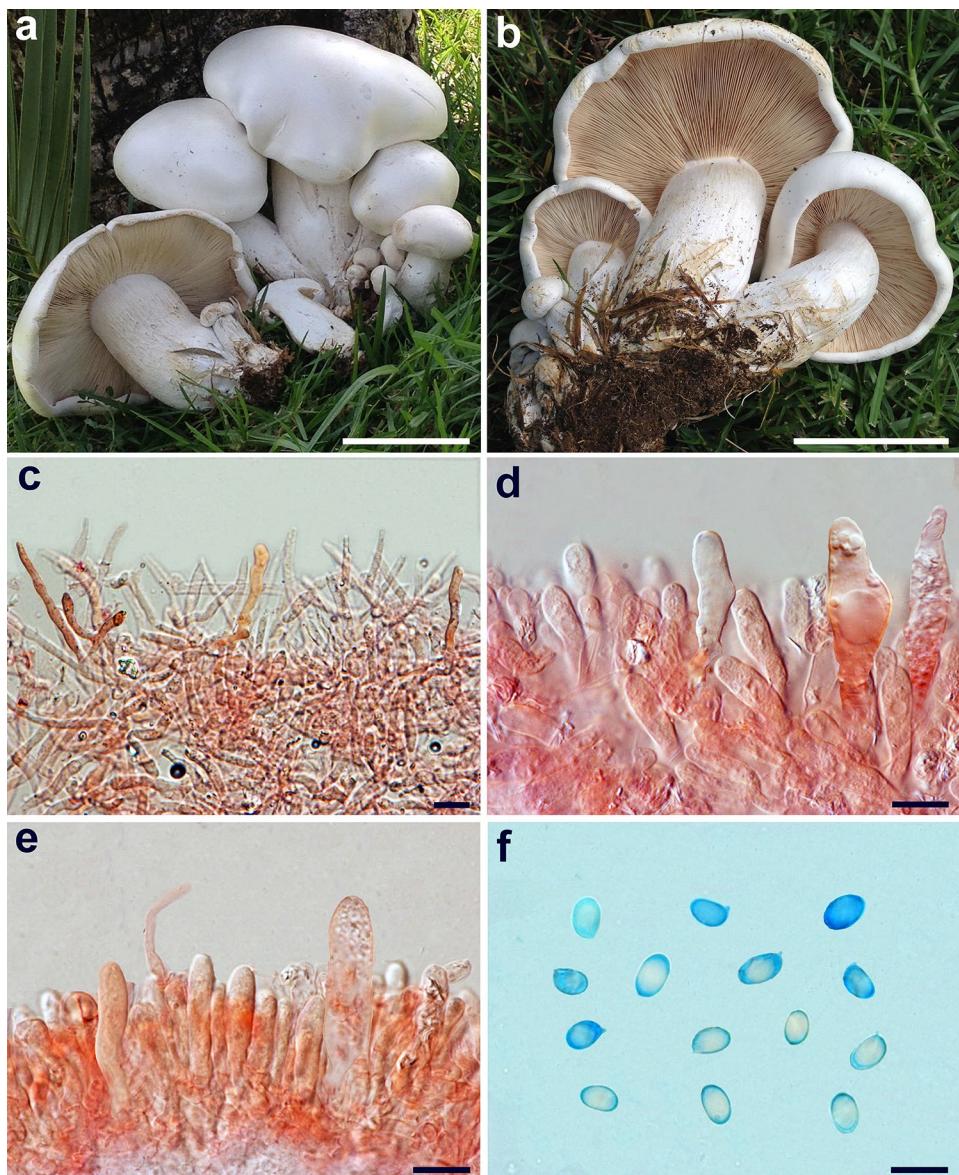
its large pileus (up to 1000 mm broad) with ochre-yellow surface tending to crack when old), a stipe with conspicuous uplifted scales, and voluminous pseudocheilocystidia (Bigelow and Kimbrough 1980; Pegler et al. 1998; Battistin and Picciola 2015; Ramirez et al. 2017). Finally, *Macrocybe pachymeres* (Berk. & Broome) Pegler & Lodge from Sri Lanka and India is considered by Pegler et al. (1998) the species resembling most *M. titans* morphologically, but it differs only for the uncertain presence of pseudocystidia.

Macrocybe sardoa Vizzini, Consiglio & M. Marchetti, sp. nov. Fig. 14

MycoBank MB 831403

Etymology: the specific epithet refers to Sardinia, the Italian island where the type collection was made.

Fig. 14 *Macrocybe sardoa* (29083 MCVE, holotype). **a** Basidiomes. **b** Basidiomes (lamellae and stipes). **c** Pileipellis. **d** Pseudocheilocystidia. **e** Pseudoplectrocystidia. **f** Spores. **c–e** in ammoniacal Congo red; **f** in Cotton blue in Lactic acid. Bars: **a, b** = 100 mm; **c–f** = 10 µm. Photographs: **a, b** by L. Cappai; **c–f** by M. Marchetti



Type specimen: ITALY: Sardinia, Cagliari, Quartu S. Elena, loc. Marina di Capitana, under *Phoenix dactylifera*, leg. L. Cappai, 02-IX-2015, 29083 (MCVE) (**holotype**)

Diagnosis: Habit tricholomatoid, caespitose. *Pileus* 150–250(–350) mm broad, at first hemispherical then convex, flat-convex sometimes with a broad low umbo; margin incurved at first and then decurved, sinuous, lobed, slightly exceeding the lamellae; surface first pure white but turning cream-ochre with time or when handled, dry, not hygrophanous, finely tomentose when young and then glabrous, not peelable, smooth but slightly cracking into minute squamules arranged radially to concentrically (larger and more sparse in the pileus centre, denser and smaller towards the margin), showing the underlying white context. *Lamellae* crowded with numerous lamellulae, thin, sinuate to adnate with a decurrent tooth or subdecurrent, 8–12 mm broad, first whitish, then cream with pale greyish hues, and finally cream with pink tinges, with a paler crenulated edge. *Stipe* 100–150(–200) × 40–60(–80) mm, concolorous with the pileus, compact and solid, usually cylindrical, sometimes slightly clavate, tapering and flattened (compressed) towards the base due to the caespitose growth, longitudinally fibrillose and wrinkled, finely velvety to minutely squamulose at the top, base wrapped in a white and cottony mycelium layer, incorporating soil particles. *Context* firm, compact, never colonized by insect larvae, pure white, not changing on exposure, 15–25(–40) mm thick at pileus centre, thinner towards the margin. *Smell* pleasant and sweetish in the young basidiomes, but unpleasant and nauseating (compost-like) in the old ones; *taste* mild. *Spore print* white. *Macrochemical reactions:* 20% KOH at first chrome yellow then orange on pileus surface and lamellae, no reaction on the context; FeSO₄ slightly and slowly pinkish on pileus surface and context, slowly orange on lamellae.

Spores [33, 1, 1] 6.3–7.5 × 4.5–4.9 µm (on average 6.9 × 4.7 µm), Q = 1.34–1.62 (Q_m = 1.48), V = 69–90 µm³ (V_m = 79 µm³), ellipsoid to broadly ellipsoid, smooth, hyaline, inamyloid, cyanophilous, sometimes with a lateral apicule, with a big drop. *Basidia* 32–39 × 6.6–7.7 µm, clavate, usually tetrasporic or rarely monosporic, with sterigmata about 5.6–8.6 µm long, with an ochraceous granulous cytoplasmatic content, not siderophilous. *Pseudocheilocystidia* 18–30 × 3.8–5.5 µm, more or less fusiform to lageniform or sometimes claviform, often sinuose. *Pseudopleurocystidia* scattered among basidioles, 40–52 × 7.2–14 µm, fusiform, rostrate, sometimes mucronate, occasionally with a long basal neck, smooth, sometimes septate, with several refractive yellow drops in basic solutions, sometimes presenting a dark blue content when observed in Brilliant Cresyl blue. *Hymenophoral trama* subregular composed of cylindrical hyphae 1.7–5.3 µm wide, narrower (1.5–2.8 µm) and more regular near the hymenopode. *Pileipellis* a trichoderm with hyphae 34–50 × 3.1–3.9

µm in young basidiomes, but apparently a cutis with loosely intertwined hyphae in old specimens and exsiccata, probably due to the collapse of tissues, with parietal encrusting ochraceous brown pigment. *Subcutis* consisting of hyphae 2.2–5.8 µm wide. *Pileitrama* consisting of 2.4–11 µm wide hyphae. *Stipitipellis* with numerous filiform emerging elements about 34–74 × 3.1–3.7 µm at the top of the stipe, often irregularly sinuose, but sometimes biforked or constricted, occasionally septate, supported by intertwined hyphae 2.4–3.4 µm wide, with intracellular and slightly encrusting ochraceous pigment. *Clamp connections* frequent everywhere.

Ecology: caespitose, growing under a *Phoenix dactylifera* tree imported from Kuwait, in a grassy lawn of a flower bed. So far known only for the type locality in Sardinia (Italy).

Specimens examined: **ITALY:** Sardinia, Cagliari, Quartu S. Elena, loc. Marina di Capitana, under *Phoenix dactylifera*, leg. L. Cappai, 02-IX-2015, 29083 (MCVE) (**holotype**) (as *Macrocybe titans*).

Comments: The collection 29083 (MCVE) was claimed as the first Italian (and European) report of *Macrocybe titans* by Cappai et al. (2016). However, phylogenetic analyses (Fig. 3) suggest it represents a different species with distinct morphological features, namely a pure white pileus when young, a stipe without uplifted (reflexed) scales, larger spores (up to 7.5 long), a pileipellis arranged as a trichoderm or a transition to a cutis, and the presence of pseudocystidia on the edge and face of lamellae. *Macrocybe sardoa* and *M. titans* are the only species of this genus with pseudocystidia (but see below), but they are only subsignificantly related (PP = 0.87, BP = 56%). Further sampling is needed to ascertain whether *M. sardoa* is actually a native Mediterranean species or it was imported there from other biogeographical regions.

Macrocybe crassa (Berk.) Pegler & Lodge, in Pegler, Lodge & Nakasone, Mycologia 90(3): 497 (1998) Fig. 15

Basionym: *Agaricus crassus* Berk. in Hooker, Lond. J. Bot. 6: 483 bis (1847)

≡ *Tricholoma crassum* (Berk.) Sacc., Syll. fung. (Abellini) 5: 109 (1887)

= (?) *Tricholoma giganteum* Massee, Bull. Misc. Inf., Kew: 254 (1912)

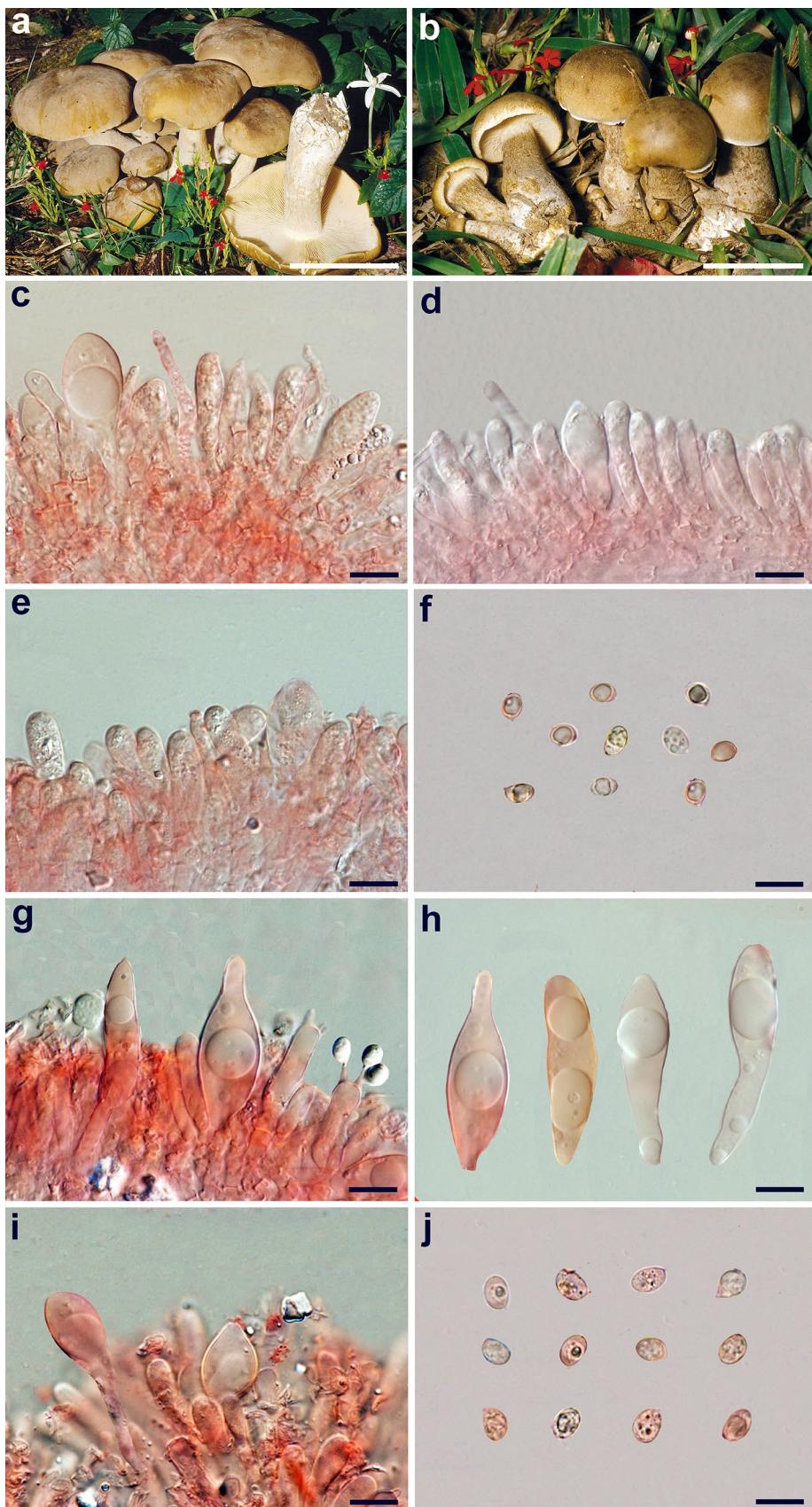
≡ (?) *Macrocybe gigantea* (Massee) Pegler & Lodge, in Pegler, Lodge & Nakasone, Mycologia 90(3): 497 (1998)

= (?) *Agaricus pachymeres* Berk. & Broome, J. Linn. Soc., Bot. 11(56): 515 (1871)

≡ (?) *Macrocybe pachymeres* (Berk. & Broome) Pegler & Lodge, in Pegler, Lodge & Nakasone, Mycologia 90(3): 498 (1998)

= *Lyophyllum prasinense* Colucci & Galli, Riv. Micol. 53(1): 45 (2010)

Fig. 15 *Lyophyllum praslinense* (10295 AMB, holotype). **a** Basidiomata. **b** Basidiomata. **c** Pseudocheilocystidia. **d**, **e** Pseudopleurocystidia. **f** Spores. *Macrocybe crassa* (141390 K). **g** Pseudocheilocystidia. **h** Pseudocheilocystidia. **i** Pseudopleurocystidia. **j** Spores. **c–j** in ammoniacal Congo red. Bars: **a**, **b** = 50 mm; **c–j** = 10 µm. Photographs: **a** by R. Galli; **b** by E. Colucci; **c–j** by M. Marchetti



Description: Spores [55, 2, 2] 5.8–6.9 × 4.3–5.0 µm (on average 6.3 × 4.7 µm), Q = 1.25–1.48, $Q_m = 1.36$, $V = 57\text{--}89 \mu\text{m}^3$ ($V_m = 73 \mu\text{m}^3$), ovoid to broadly ellipsoid, smooth, with an evident apicule and a large drop, inamyloid, cyanophilous. Basidia 25–35 × 6–7 µm, tetrasporic, but sometimes also mono-, bi- or trisporic, long clavate, often with more or less numerous greenish droplets, with basal clamp connections, not siderophilous. Hymenophoral trama regular. Pseudocheilocystidia 25–40(–60) × 7–13 µm, subfusiform to clavate with a long peduncle, sometimes with a rostrate apex to narrowly lageniform with acute to rounded apex, thin-walled, with one or two big greyish drops. Pseudopleurocystidia present but scattered, 20–25(–30) × 7–12 µm, pyriform to claviform or lageniform. Pileipellis a cutis with intertwined hyphae 3–8 µm wide, with epiparietal encrusting pigment. Subpellis and hypoderm regular, with parallel hyaline hyphae 4–12 µm wide.

Specimens examined: INDIA: unknown locality, on soil, leg. C.P. Rao, 1980, 37717 (K-M) (as *Macrocybe gigantea*). SEYCHELLES: Praslin Island, in the park of the golf course of “Lemuria Resort”, leg. E. Colucci & R. Galli, 08-VII-2007, 10295 (AMB) (holotype of *Lyophyllum praslinense*). THAILAND: unknown locality, leg. D. Arora, 1999, 141390 (K-M) (as *Macrocybe titans*); Nakhon Phanom, Nakhon Phanom market, leg. D. Arora, 27-VIII-1999, 024256 (SFSU-F) (as *Macrocybe crassa*).

Comments: *Macrocybe crassa* and *M. gigantea* are the two largest tricholomatoid agarics of southeast Asia (large basidiomata can weigh up to 1.25 kg), both forming dense clusters of several basidiomes, and both are edible and largely cultivated in Asia (Razaq et al. 2016; Inyod et al. 2017; Verma et al. 2017). According to the monographic work on the genus *Macrocybe* by Pegler et al. (1998), both species present expanded pilei exceeding 200 mm in diam., and lack hymenial pseudocystidia and pseudosclerotia, but they can be mainly discriminated because (i) the lamellae of *M. crassa* are white, but straw yellow in *M. gigantea*, (ii) the stipe of *M. crassa* is inflated at the base, while it is sub-equal-cylindrical in *M. gigantea*, (iii) the stipe is off-white with brown fibrillose streaks in *M. crassa*, but concolorous with the pileus and fibrillose-striate in *M. gigantea*, and (iv) *M. gigantea* often displays glaucous tinges on the surface of the pileus that are lacking in *M. crassa*. To date, *M. crassa* and *M. gigantea* have been exclusively found in Asia (Pegler et al. 1998; Razaq et al. 2016; Inyod et al. 2017). Before the publication of the critical work of Pegler et al. (1998), both species were considered conspecific (Corner 1994, as *Tricholoma crassum* and *T. giganteum*) or else *M. crassa* (as *T. crassum*) was thought to be conspecific with the later name *T. pachymeres* (Berk. & Broome) Sacc. (Pegler 1983, 1988), while *T. giganteum* was considered a priority

synonym over *T. lobayense* Heim, a species from Central Africa, and/or *T. spectabile* Peerally & Sutra from Mauritius (Nagasawa and Hongo 1981). According to Pegler et al. (1998), *T. lobayense* and *T. spectabile* have obvious morphological differences with *M. crassa*/*M. gigantea*, while the delimitation of the species concept of *M. pachymeres* (Berk. & Broome) Pegler & Lodge is rather problematic. The basionym *Agaricus pachymeres* Berk. & Broome (Berkeley and Broome 1871) was proposed for a collection from Sri Lanka, the same country where the original material of *A. crassus* Berk. was found. *Agaricus pachymeres* was reported to differ from *A. crassus* “in the even not sinuato-plicate margin, the scaly stem and other characters” (Berkeley and Broome 1871). *Agaricus pachymeres* was later combined into *Tricholoma* by Saccardo (1887), then considered a synonym of *Tricholoma crassum* by Pegler (1986, 1988), and finally combined as an independent species into *Macrocybe* by Pegler et al. (1998). The latter authors, highlighted that the scaly stipe of *M. pachymeres* suggested that this species is phylogenetically closer to *M. titans* than to *M. crassa*, although no hymenial pseudocystidia were found in the type, probably due to the poor condition of the type, which was even contaminated with molds. After the type collection, the species was never reported again with certainty.

In the present phylogenetic analysis of the *Callistosporiaceae* (Fig. 3), the new collections of *Macrocybe* and those present in GenBank seem to constitute three significantly distinct clades, one of them matching the species concept of *M. titans*, another containing samples identified either as *M. crassa* or *M. gigantea* (and the holotype collection of *Lyophyllum praslinense* Colucci & Galli), and finally a third lineage putatively representing a new species, which is here proposed as *M. sardoa*. Two Asiatic collections identified as *M. titans* (141390 K from Thailand and VQGCT19092014 from Vietnam) were found to belong to the clade of *M. crassa* and *M. gigantea*, but they probably represent incorrect identifications. *Lyophyllum praslinense* was recently proposed for collections found in the Seychelles islands (Colucci and Galli 2010), and it is characterized by growing in clusters, a stipe covered with brown-ochre fibrils-squamules all over its surface, siderophilous basidia, and presence of cheilo- and pleurocystidia. However, non-siderophilus basidia have been found in the type collection in the present work (see above), in agreement with other species of *Macrocybe*. In addition, the present studies revealed that the hymenial cystidia reported in the protologue are actually pseudocystidia (Fig. 15c–e). Macroscopically, *L. praslinense* (Fig. 15a, b) seems very similar to the Malaysian collections of *Tricholoma crassum* depicted by Corner (1994, Plate 7), who reported the presence of subhymenial pleurocystidia. According to Pegler et al. (1998), Corner’s collection could represent the original concept of *M. pachymeres*, but similar sterile elements were also observed in the present work in the *M.*

crassa collection K 141390 from Thailand (Fig. 15g–i), and previously also by Cléménçon (in Pegler et al. 1998) in Japanese collections identified as *T. giganteum*, where no cystidia were reported by Nagasawa and Hongo (1981).

Therefore, considering that (i) *M. crassa*, *M. pachymeres* and *M. gigantea* are strictly Asiatic and respectively described from Sri Lanka (Berkeley 1847; Berkeley and Broome 1871) and India (Massee 1912); (ii) the present phylogenetic analyses suggest the existence of a genetically independent and internally more or less homogeneous clade formed by collections identified as *M. crassa*, *M. gigantea* and *L. praslinense*; and (iii) pseudocystidia are present in at least some of the specimens analysed, and they can be easily go unnoticed in some others because of their deep subhymenial origin and because they only rarely reach the height of the tips of the basidia; it is here hypothesized the existence of a single species, to be called *M. crassa* (the older name), characterized by a sub-smooth to fibrillose-squamulose stipe surface, and the presence of hymenial pseudocystidia. The collections from Seychelles (type of *L. praslinense*) extend the geographical range of this species. However, we cannot reject the possibility that it was introduced here from south India with the French trade. In this view, it is probable that the collections of *M. titans* reported from Taiwan (Chen and Chen 1999) and the Indian state of Kerala (Vrinda et al. 1997; Farook et al. 2013) actually represent *M. crassa*.

Guyanagarika Sánchez-García, T.W. Henkel & Aime, in Sánchez-García, Henkel, Aime, Smith & Matheny, Fungal Biology 120(12): 1544 (2016)

Type species: *Guyanagarika aurantia* Sánchez-García, T.W. Henkel & Aime, in Sánchez-García, Henkel, Aime, Smith & Matheny, Fungal Biology 120(12): 1546 (2016)

Description: Habit tricholomatoid. Pileus dark orange becoming lighter towards the margin, broadly convex to broadly subconic to plano-convex with prominent broad umbo with age. Surface glabrous to minutely tomentose. Lamellae sub-thick to thick, initially adnate to adnexed, sinuate with age, brittle. Stipe equal, tapering evenly from apex to base, solid. Spores hyaline, smooth, inamyloid, acyanophilous. Spore print white. Hymenial cystidia absent. Pileipellis initially a cutis becoming a trichoderm with age. Clamp connections present in all tissues. Thromboplerous hyphae (oleiferous hyphae sensu Cléménçon 2004) present in all tissues. Ectomycorrhizal. Three species recognized, so far known only from Guyana.

Comments: *Guyanagarika* is the only genus in the *Callistosporiaceae* with a verified ectomycorrhizal (ECM) lifestyle (Sánchez-García et al. 2016). Some putatively ECM lineages have been found among sequences generated from ECM

roots collected in various tropical areas (Tedersoo and Smith 2013). Moreover, *Guyanagarika* is, so far, the only known ECM genus among the Agaricales endemic to the Neotropics (more specifically to Guyana), although some endemic Neotropical ECM genera have recently been described in the Boletaceae (Smith et al. 2015; Henkel et al. 2016; Farid et al. 2018). According to Sánchez-García et al. (2016), *Guyanagarika* is characterized by its medium to large tricholomatoid basidiomata with a conspicuously umbonate pileus that are entirely bright orange in colour, as well as by their relatively thick and sinuate lamellae, lack of veins, spores hyaline, smooth and inamyloid, hymenial cystidia absent, pileipellis initially a cutis but becoming a trichoderm with age, clamp connections present everywhere, and always fruiting on soil in association with ECM trees, such as *Pakaraimaea dipterocarpacea* (Dipterocarpaceae subfamily *Pakaraimoideae*), *Dicymbium corymbosum*, or *D. jenmanii* (Fabaceae subfamily *Caesalpiniaceae*) (Moyersoen 2006; Smith et al. 2013). Macroscopically, species of *Guyanagarika* can be confused with the north temperate ECM genera *Tricholoma* (*Tricholomataceae*, *Tricholomatinae*) or *Hygrophorus* Fr. (*Hygrophorineae*, *Hygrophoraceae*), or with the saprotrophic genus *Gerhardtia* (*Tricholomataceae*, *Lyophyllaceae*).

Anupama K.N.A. Raj, K.P.D. Latha & Manim., Mycol. Progr. 18: 661 (2019).

Type species: *Anupama indica* K.N.A. Raj, K.P.D. Latha & Manim.

Description: Habit tricholomatoid. Pileus surface brownish, glabrous, and somewhat waxy. Lamellae sinuate, crowded, with concolorous edges. Stipe central or slightly eccentric, solid, with white rhizomorphs at the base; surface densely appressed-fibrillose all over. Spore print greyish white. Spores subglobose, ovoid or somewhat lacrymoid, smooth, inamyloid, acyanophilous. Cheilocystidia abundant. Pleurocystidia scarce. Pileipellis a cutis. Clamp connections present on all hyphae. In small groups, occasionally scattered singly on the soil under bamboo (*Bambusa striata*). So far known only from India.

Comments: Since no ectomycorrhizal symbiosis is known among monocotyledons (Hyde et al. 2002; Smith and Read 2008), the monospecific genus *Anupama* is probably a saprotroph associated with bamboo. According to Raj et al. (2019), it could be related with the genus *Guyanagarika*, although the present results (Fig. 3) suggest a nearly significant relationship with *Macrocybe* (PP = 0.93, BP = 68%). *Anupama indica* recalls macroscopically *Rhodocybe gemina* (Paulet) Kuyper & Noordel. or species of *Lepista* (Fr.) W.G. Sm., and differs from *Guyanagarika* because of

the subglobose, obovoid to lacrymoid spores and the presence of cheilocystidia.

Discussion

In the present work, a new phylogenetic concept of the family *Biannulariaceae* is discussed, and the new family *Callistosporiaceae* is proposed to classify most genera previously associated with *Catathelasma*. The *Callistosporiaceae* are sister to the *Tricholomataceae* s.s. while the *Biannulariaceae* are basal to a major clade consisting of *Callistosporiaceae*, *Clitocybeae*, *Entolomataceae*, *Lyophyllaceae* s.l., *Pseudoomphalina*, and *Tricholomataceae* s.s. (Fig. 1). This taxonomic arrangement differs from those of Sánchez-García et al. (2014, 2016), Sánchez-García (2016), Alvarado et al. (2018a, b) and Raj et al. (2019), probably because of an improved taxon sampling within *Catathelasma*, *Callistosporium* and *Macrocybe*. Similar efforts already proved to have a significant effect on the accuracy of the phylogenetic support in other studies (Rydin and Källersjö 2002; Zwickl and Hillis 2002; Nabhan and Sarkar 2011). In addition, *tef1* and *rpb2* sequences were obtained from several species previously represented by ribosomal markers only, increasing the number of informative positions in the analyses (Matheny et al. 2007; Frøslev et al. 2005; Schoch et al. 2009). Finally, a putative error in the *rpb2* sequences DQ470830 (obtained from AFTOL-ID 1488, 45682 WTU-F, PBM 2403) and KP255469 (obtained from 221514 DAOM) was detected, since both sequences match the genetic identity of *Callistosporium graminicolor* instead of the expected *Catathelasma*. Consequently, these sequences were pruned from the dataset. The specimens were asked on loan and new correct sequences were obtained from them and used in the analyses.

The genus *Catathelasma*: new phylogenetic affinities and revision of the *Biannulariaceae*

The genus *Catathelasma* was proposed by Lovejoy (1910) for *C. evanescens*, a remarkable agaric with fleshy and stout basidiomes, distant and long decurrent lamellae, a delicate and evanescent annulus; a large white volva opening around its top and leaving a thick even white margin, persistent and closely embracing the large, white, bulbous base of the stipe; spores white, smooth, ellipsoid to fusiform, measuring 14–17.5 × 3–5 µm; and growing under *Abies* and *Picea* in Wyoming (USA). Unfortunately, this species has been never reported again with certainty from other localities until the present work. *Catathelasma* was later included together with another monospecific genus, *Biannularia* Beck (type species *Armillaria imperialis* P. Karst.) in the tribus *Biannularieae* Singer of the *Tricholomataceae* (Singer 1936), characterized

by the tricholomatoid fleshy basidiomes with double veil, amyloid spores, and bilateral hymenoporal trama of their species. Since *Biannulariaceae* was a *nomen invalidum* (no Latin diagnosis was provided by Singer), the name was validated by Bas (1990). *Biannularia* was subsequently considered a later synonym of *Catathelasma* by Singer (1940), who formally combined *Armillaria imperialis* and *Lentinus ventricosus* Peck into the genus *Catathelasma*, and later, a third species, *C. singeri* was added by Mitchel and Smith (1978) to accommodate some American collections. Over the years, most mycological works accepted the synonymy between *Biannularia* and *Catathelasma* (e.g. Singer 1986; Bas 1990; Vesterholt 2012a), even though Jülich (1981) proposed the family *Biannulariaceae* for *Biannularia*, which was later considered a synonym of Singer's broad concept of the *Tricholomataceae* (1986). Four years after the publication of Jülich's work, the Ukrainian mycologist Wasser (1985), who was probably unaware of the existence of *Biannulariaceae*, introduced the name *Catathelasmataceae* based on *Catathelasma*.

As initially established by Jülich (1981) and Wasser (1985), the *Biannulariaceae* and *Catathelasmataceae* were monogeneric. The first comprehensive phylogenetic analysis of the Agaricales by Moncalvo et al. (2002) was based on 28S/LSU rDNA sequences alone, but revealed that *Catathelasma* constituted an independent monogeneric clade (named as Catathelasma clade, consisting of *C. imperiale* and *C. ventricosum*) maybe sister (but lacking significant support) to some species of *Rhodocybe*. Matheny et al. (2006) employed a six-gene dataset (28S/LSU, 18S/SSU and 5.8S rDNA, *rpb1* exonic regions, *rpb1* intronic regions, and *rpb2*), and found that *Callistosporium*, *Catathelasma* and *Clitocybe subvelosa* (combined into *Cleistocybe* by Ammirati et al. 2007) formed a significantly monophyletic lineage (the Catathelasma clade) within the so-called Tricholomatoid clade (later formally named suborder *Tricholomataceae* by Dentinger et al. 2016). A similar result was obtained by Binder et al. (2010) using the same sequences. In the seminal paper of Sánchez-García et al. (2014) *Cleistocybe* did not belong in the Catathelasma clade, which consisted of *Callistosporium*, *Catathelasma* and *Clitocybe* aff. *fellea*. Later, Sánchez-García et al. (2016) and Sánchez-García & Matheny (2017), readded *Pleurocollybia*, *Pseudolaccaria*, *Macrocybe* and *Clitocybe fellea* to this clade, which they named *Catathelasmataceae*, unaware at the time that *Biannulariaceae* had priority. Alvarado et al. (2018a, b) obtained similar results, but employed the earlier name *Biannulariaceae* following the advice of Sánchez-García et al. (pers. comm.). Finally, Raj et al. (2019) added the new genus *Anupama* to this clade. As pointed out by Sánchez-García et al. (2016), the clade is morphologically very heterogeneous and encompasses fungi with very different ecological and morphological traits, habit ranging from clitocyboid,

collybioid to tricholomatoid, lamellae adnate to decurrent, spores amyloid or not, hymenophoral trama divergent to parallel, saprotrophic (on soil, on wood) to ectomycorrhizal.

The present analyses (Figs. 1, 2) based on a larger number of species of *Catathelasma* and *Callistosporium*, and employing newly generated *rpb2* sequences to replace those putatively compromised (see Supplementary Material Figs. 1–3), evidence that *Catathelasma* has not a direct phylogenetic relationship with *Anupama*, *Callistosporium*, *Guyanagarika*, *Macrocybe*, *Pleurocollybia* or *Pseudolaccaria*, but seems to integrate a monophyletic lineage with *Cleistocybe* and *Bonomyces*. It is therefore proposed to employ the name *Biannulariaceae* for this clade. This new concept of the *Biannulariaceae* is much more homogeneous because of a number of shared morphological features: dry, often cracking pileus surface, the presence of a partial veil (simple in *Cleistocybe*, double in *Catathelasma*, reduced to a pseudo-annular granulose zone in *Bonomyces*), decurrent lamellae, confluent pileus and stipe, firm context, and growth on soil (mainly under ectomycorrhizal *Pinaceae*), divergent hymenophoral trama, stipititrama formed by densely arranged slender hyphae which give a dry and fibrous consistency, presence of clamp connections, and a farinaceous smell (Ammirati et al. 2007; Alvarado et al. 2018b; Wu et al. 2018). *Catathelasma* differs from *Bonomyces* and *Cleistocybe* because of its amyloid and cyanophilous spores and the double annulus, while *Bonomyces* species differ from *Cleistocybe* species because of the salmon to reddish pigment (absent in *Cleistocybe*), the white to pale, or at most yellow lamellae (pinkish gray to vinaceous buff in *Cleistocybe*), the non-rooting stipe, and the ellipsoid spores with obtuse base (amygdaliform to fusiform with acute base in *Cleistocybe*) (Alvarado et al. 2018b). *Bonomyces* basidiomata are usually terrestrial and often occur close to ectomycorrhizal plants (*Pinaceae*), but it has not been confirmed if they are ectomycorrhizal or saprotrophic, whereas *Catathelasma* is surely ectomycorrhizal (Hutchison 1992; Rinaldi et al. 2008; Tedersoo et al. 2010; Tedersoo and Smith 2013) and *Cleistocybe* is supposed to be saprotrophic (Sánchez-García and Matheny 2017). According to the last statement, the recently described species *Cleistocybe vernaloides* H.M. Wu, J.Q. Luo, Ke Wang & Y.J. Yao seems to be strictly associated with *Platycladus orientalis* (*Cupressaceae*) (Wu et al. 2018), a plant that is considered endomycorrhizal (Smith and Read 2008).

The *Callistosporiaceae*, the polyphyletic nature of *Callistosporium* and the status of *Pleurocollybia*

The significantly supported clade including *Anupama*, *Callistosporium*, *Guyanagarika*, *Macrocybe*, *Pseudolaccaria* and *Xerophorus* (Figs. 1–3) is also morphologically more homogeneous, although it still lacks evident synapomorphic features, and is here given the family name

Callistosporiaceae. Most members of the *Callistosporiaceae* are putative saprotrophs (excepting for the ectomycorrhizal *Guyanagarika*), gymnocarpic (they lack a partial veil), have adnate to adnexed or emarginate-adnexed lamellae, regular to subregular hymenophoral trama, and have inamyloid spores (except in *Pseudolaccaria*).

The present results suggest also that the traditional concept of *Callistosporium* (Singer 1986; Bon 1984, 1991) actually includes two distinct genera, *Callistosporium* s.s. and *Xerophorus*. The type species of the genus *Pleurocollybia* (*P. praemultifolia*) and related species, as well as two American clitocyboid taxa, *C. hesleri* and *C. aff. fellea*, are also embedded within *Callistosporium* s.s., suggesting that the habit (pleurotoid vs. collybioid, type of insertion of the stipe), or the presence of brightly coloured necropigments in the spores, basidia and trmal hyphae, could not have a phylogenetic meaning at the genus level.

Clamp connections are absent (or at most they can be present at the base of the basidia in *C. imbricatum*) in both *Callistosporium* and *Xerophorus*, with the exception of *Xerophorus dominicanus* that seems to be the only callistosporioid species described so far in the genus outside Europe contrary to what is known for *Callistosporium*, whose biodiversity is higher in the extra-European areas (Singer 1986). Several non-European genetic lineages lack a suitable name, and probably represent new species (Fig. 3), such as *Callistosporium* sp. ECV5506 (Tennessee, USA, Sánchez-García & Matheny 2017), *Clitocybe* sp. G4345 (Guyana, Roy et al., unpublished), uncultured soil fungus clones NCD LSU otu2501, otu2536 and otu896 (North Carolina, USA, Mueller et al. 2014), *Pleurocollybia* sp. Mel-2363162 (Australia) and *Pleurocollybia* sp. Mes-920 (Chile).

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