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ORIGINAL ARTICLE

Two new species in the *Lulesia fallax* complex (*Entolomataceae*, *Agaricales*) from Europe (Fennoscandia and Switzerland), *Lulesia neofallax* comb. nov., and new records of recently described or poorly known species of *Lulesia*

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Abstract
Lulesia fallacioides (from Finland) and *L. parvifallax* (from Switzerland) are described as new species, based on both a morphological and molecular approach, in the *L. fallax* complex (*Lulesia* subgen. *Paraclitopilus*), a morphology-delimited aggregate of species sharing white basidiomes and a bitter context. Compared to *L. fallax*, the former differs mainly by wider spores and a gelatinized pileipellis and the latter by smaller basidiomes and shorter spores. The recently described *Clitocella neofallax* from China is here combined in *Lulesia*. New collections of *L. colorata* and *L. solaris* made in Italy and Finland have allowed us to better understand the distinctive features and/or to extend the distribution area of these recently established species. The presence of *L. fallax*, *L. mundula*, and *L. obscura* in Finland is here molecularly confirmed for the first time. Finally, a full morphological description of *L. alachuana*, a North American species so far described from Florida, is provided based on ancient (holotype included) and recent collections.

Keywords *Basidiomycota* · *Agaricomycetes* · *Tricholomatineae* · *Clitocella* · *Rhodocybe* · Cryptic species · Multigene analysis · Taxonomy

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Introduction

The genus *Lulesia* Singer was established (Singer 1970) for accommodating two species previously considered part of *Armillariella* Singer (Singer 1951; Singer and Digilio 1951), viz. *A. densifolia* Singer (type of *Lulesia*, from Tucumán, Argentina) and *A. alachuana* (Murrill) Singer (≡ *Clitocybe alachuana* Murrill) (from Florida, USA), due to their clitocyboid habit, adnato-decurrent to decurrent lamellae, pale spore-print, inamyloid basidiospores and tissues, basidia without carminophilous granulation, and clampless hyphae. Singer (1970) differentiated *Lulesia* from *Armillariella* by having a zonate pileus, very narrow lamellae, a bitter taste, smaller spores, a trichodermic pileus covering, and a terricolous/humicolous habitat. *Lulesia densifolia* (Singer) Singer spores were described as smooth in some mounting media (methylene blue, carmine-acetic acid, and Melzer's reagent) but appearing slightly rounded-angular and nodulose in aqueous NH_3 and KOH in light microscopy (Singer and Digilio 1951; Singer 1970, 1986). According to Singer and Digilio (1951) and Singer (1986), this slight irregularity of the spore surface would be reminiscent of the spores of the species in genus *Rhodocybe* Maire.

Baroni (1981) and Bigelow (1982, 1985), after studying the holotype collection of *Clitocybe alachuana*, considered it a later synonym of *Rhodocybe mundula* (Lasch) Singer, and this conclusion was also followed by Singer (1986). The species recognized in *Lulesia* were recently supplemented by Lechner et al. (2006) with another new species from Argentina, *L. lignicola* B.E. Lechner & J.E. Wright. No further collections of *L. densifolia* apart from the original ones were reported until recent findings in the Dominican Republic (Angelini and Contu 2012).

Based only on morphological data, *Lulesia* was placed by Singer (1970, 1986) in subtribe *Omphalineae* Singer (tribe *Clitocybeae* Fayod, family *Tricholomataceae* R. Heim ex Pouzar), by Lechner et al. (2006) and Agerer (2018) in *Tricholomataceae* s.l., and by He et al. (2019) in *incertae sedis Agaricales* Underw. In the supplementary materials of the first molecular study including a sequence (nrLSU) obtained from a collection of *Lulesia* (Varga et al. 2019), viz. *L. densifolia*, it clustered within *Clitocella* Kluting, T.J. Baroni & Bergemann [type *C. popinalis* (Fr.) Kluting, T.J. Baroni & Bergemann], a genus segregated from *Rhodocybe* s.l. (*Entolomataceae* Kotl. & Pouzar) by Kluting et al. (2014) and monographed at European level by Vizzini et al. (2023). Based on this preliminary molecular indication, Kalichman et al. (2020) and He et al. (2024) included *Lulesia* in the *Entolomataceae*.

Recently, based on multigene analyses and large taxon sampling, Vizzini et al. (2024) confirmed that *L. densifolia* is part of the *Clitocella* clade. This indicated *Lulesia* as a priority synonym of *Clitocella*. Three distinct subgenera are currently recognized in *Lulesia* relied on types of hymenophoral trama, basidiome colours, and reactions of basidiome surface to KOH solution: subgen. *Lulesia*, *Paraclitopilus* (Vizzini & Cons.) Vizzini & Cons., and *Rhodopleurella* (Vizzini & Cons.) Vizzini & Cons. (Vizzini et al. 2024).

Lulesia species typically produce a gymnocarpic centrally stipitate to pleuropodal [(*L. termitophila* (T.J. Baroni & Angelini) T.J. Baroni & Angelini], clitocyboid basidiome, which exhibits a small to large (≤ 120 mm) pileus that can range from white to greyish, grey-brown, or purplish grey in colour, usually covered with a white bloom, long-decurrent narrow lamellae with pinkish tinges at maturity, a cylindrical glabrous to pubescent, floccose or fibrillose stipe usually with white rhizomorphs at the base, context usually with farinaceous to cucumber-like smell and bitter taste, surfaces of the dried basidiomes reddening or not in KOH, spore-print incarnate-pink, hymenophoral trama regular (consisting of parallel cylindrical hyphae) or irregular (composed of interwoven hyphae), hymenial cystidia usually lacking, and cyanophilic, inamyloid, non-dextrinoid, thin-walled basidiospores with obscure or distinct undulating pustules or minute bumps (Kluting et al. 2014; Vizzini et al. 2023, 2024). To date, a total of 17 species of *Lulesia* and two uncombined *Clitocella* species have been validly published based on the records from the Index Fungorum database (www.indexfungorum.org, accessed 21 January 2025). *Lulesia* has been reported in Asia, Europe, North, South, and Central America, and can be observed in various ecosystems, including forested and grassland systems, as well as on dunes or in association with hind dune trees, from temperate to subtropical/tropical areas (Angelini and Contu 2012; Kluting et al. 2014; Baroni et al. 2020; Jian et al. 2020a; Mao et al. 2022; Vizzini et al. 2023, 2024; Liu et al. 2025; Xiao et al. 2024). Its species are presumably saprotrophic (Vizzini et al. 2023, 2024), usually terrestrial but *C. lignicola* is reported on dead wood of dicotyledonous trees (Lechner et al. 2006), and *C. termitophila* grows on arboreal nests of neotropical termites (Baroni et al. 2020).

The aim of the present work was to describe two new *Lulesia* species from Europe (Fennoscandia and Switzerland) morphologically closely related to *L. fallax* (Quél.) T.J. Baroni, Niveiro & B.E. Lechner because of their white, non-staining black pileus and bitter taste, by using both a traditional (morphological) and multilocus molecular approach. Additionally, a full morphological description of the north American species *L. alachuana* (Murrill) Singer based on ancient and modern collections as well as notes on the recently established species *L. colorata* (L. Fan & N. Mao) T.J. Baroni, Niveiro & B.E. Lechner and *L. solaris* (Musumeci, Cons. & Vizzini) Musumeci, Cons. & Vizzini (Mao et al. 2022; Vizzini et al. 2023), are provided.

Materials and methods

Morphological studies

Macroscopic morphological features were studied in fresh specimens. Codes for colours follow the Methuen Handbook of Colour (Kornerup and Wanscher 1984). 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, 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 optical microscope, using immersion oil at × 1000 magnification. Basidiospore measurements were made by capturing images of a single visual field with multiple spores (taken from lamellar squashes of exsiccated material of mature specimens) which were then measured using the DS-L1 Nikon camera control unit. Basidiospore dimensions excluded the hilar appendix and are given as (*a*)*b*–*c*–*d*(*e*), where (*a*) = minimum value, *b* = (average minus standard deviation), *c* = *average*, *d* = (average plus standard deviation), and (*e*) = maximum value; *Q* = (minimum –) average minus standard deviation – *average* – average plus standard deviation (– maximum) of ratio length/width; *V* = (minimum –) average minus standard deviation – *average* – average plus standard deviation (– maximum) of the volume. 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. A minimum of 30 spores were measured for each collection. *Q* indicates the quotient of length and width of the spores in side view. 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. Photographs of microscopic features were taken using a Nikon DS 5 M digital camera with a preset resolution of 2560 × 1980 pixels connected to a Nikon Eclipse 80i optical microscope with both brightfield and interferential contrast optics and saved in TIFF format. They were then cleaned using Adobe Photoshop CC 2019 version 20.0.10, in some cases replacing, through the Magic Wand Tool and with the appropriate tolerances, the background colour of the photograph with an alternative uniform background to highlight the morphology of the microscopic characters, which maintained their original size and hue. In other cases, the best individual spores from microscopy photos were copied using the Polygonal Lasso Tool or alternatively the Magnetic Lasso Tool of Adobe Photoshop CC 2019 version 20.0.10, onto a new monochrome sheet, with the same resolution (2560 × 1980 pixels) to maintain the spore size and original colours as previously acquired.

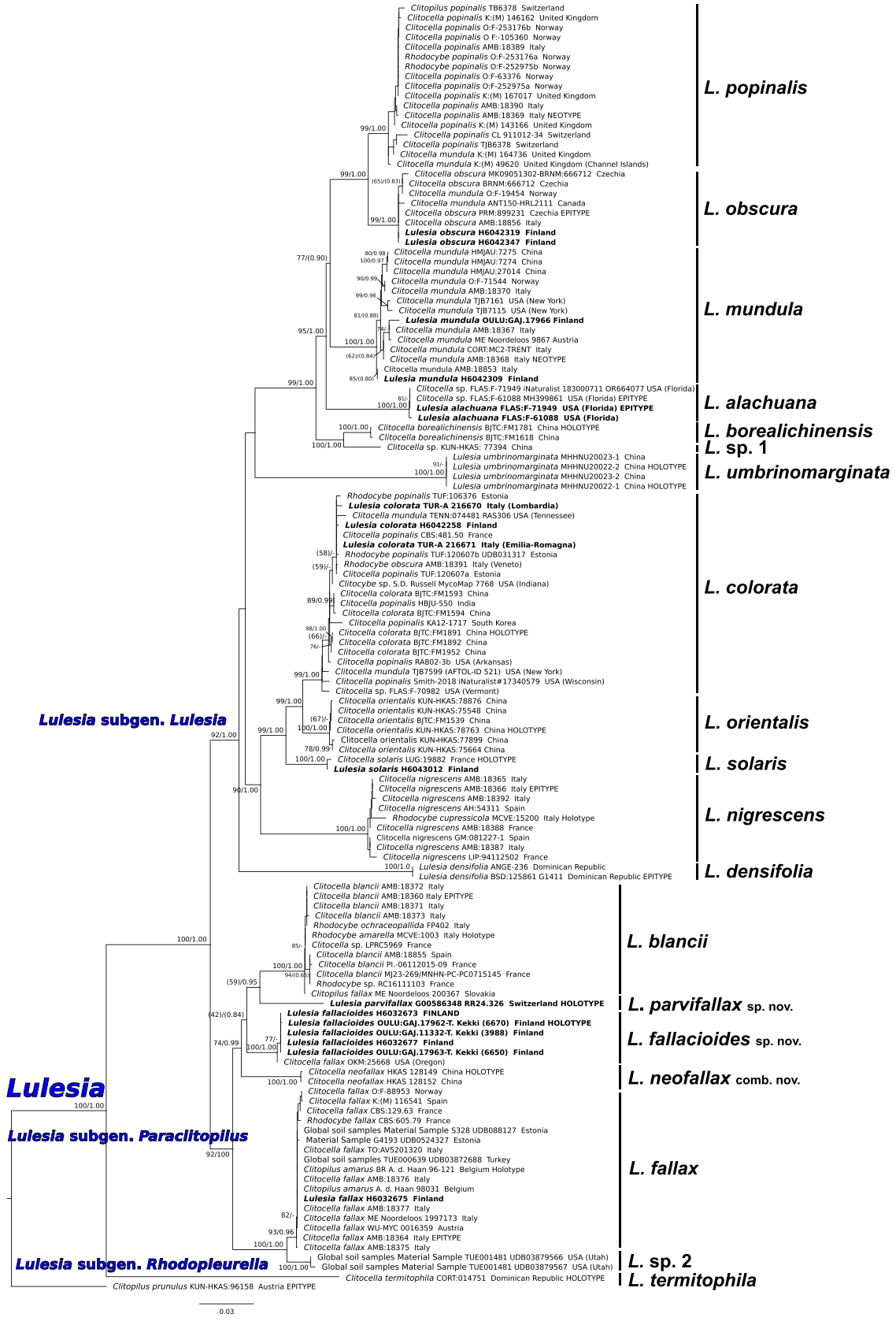
Macro- and microchemical testing of pigments were performed using basic solutions (5% KOH and 10% ammonia, separately). Chemical spot tests were performed on the pileus surface, lamellae, and stipe of fresh and/or dried basidiomes using 3% and 10% KOH, following Baroni (1978, 1981). Fungarium acronyms follow Thiers (2025) except that ANGE and T. Kekki refer to the personal herbarium of Claudio Angelini and Tapio Kekki, respectively.

DNA extraction, amplification, and sequencing

Total DNA was extracted from seventeen dry specimens (Fig. 1, Table 1) employing a modified protocol based on Murray and Thompson (1980). PCR (Mullis and Faloona 1987) reaction conditions (cycles and annealing temperature) follow Alvarado et al. (2010, 2012). The primers ITS1F and ITS4 (White et al. 1990; Gardes and Bruns 1993) were used to amplify the ITS rDNA nuclear region, LR0R and LR5 (Vilgalys and Hester 1990; Cubeta et al. 1991) for the LSU rDNA nuclear region, EF1-983F, EF1-1567R, and EF1-2218R (Rehner and Buckley 2005) for the translation elongation factor 1-alpha (*TEF1-1α*) gene, and bRPB2-6F2 (reverse of bRPB2-6R2) and bRPB2-7R2 for the RNA polymerase II second largest subunit (*RPB2*) gene (Matheny et al. 2007). PCR products were checked in 1% agarose gels, and amplicons were sequenced with one or both PCR primers. Sequences were corrected to remove reading errors in chromatograms.

Phylogenetic analyses

Two different dataset/alignments were built. (1) A *Lulesia* dataset aimed to provide an accurate view of the position of the newly sequenced collections within this genus was prepared. It included sequences of five different loci (nrITS, nrLSU, *RPB2*-exons, *TEF-1α* -exons, and *ATP6*) from all the species recognized in Vizzini et al. (2023, 2024) supplemented with those present in Xiao et al. (2024) and Liu et al. (2025), and the most closely related sequences selected from public databases such as the International Nucleotide Sequence Database Collaboration public database (INSDC/GenBank https://www.ncbi.nlm.nih.gov/genbank/, Arita et al. 2021), UNITE (https://unite.ut.ee/), and BOLDSYSTEMS (http://www.boldsystems.org/), via the BLASTn algorithm (Altschul et al. 1990). *Clitopilus prunulus* was employed as an outgroup taxon following Baroni et al. (2020), Mao et al.


Clitopilus popinalis TB6378 Switzerland
Clitocella popinalis K:(M) 146162 United Kingdom
Clitocella popinalis O:F-253176b Norway
Clitocella popinalis O F:-105360 Norway
Clitocella popinalis AMB:18389 Italy
Rhodocybe popinalis O:F-253176a Norway
Rhodocybe popinalis O:F-252975b Norway
Clitocella popinalis O:F-63376 Norway
Clitocella popinalis O:F-252975a Norway
Clitocella popinalis K:(M) 167017 United Kingdom
Clitocella popinalis AMB:18390 Italy
Clitocella popinalis AMB:18369 Italy NEOTYPE
Clitocella popinalis K:(M) 143166 United Kingdom
Clitocella popinalis CL 911012-34 Switzerland
Clitocella popinalis TJB6378 Switzerland
Clitocella mundula K:(M) 164736 United Kingdom
Clitocella mundula K:(M) 49620 United Kingdom (Channel Islands)
L. popinalis
Clitocella obscura MK09051302-BRNM:666712 Czechia
Clitocella obscura BRNM:666712 Czechia
Clitocella mundula O:F-19454 Norway
Clitocella mundula ANT150-HRL2111 Canada
Clitocella obscura PRM:899231 Czechia EPITYPE
Clitocella obscura AMB:18856 Italy
Lulesia obscura H6042319 Finland
Lulesia obscura H6042347 Finland
L. obscura
Clitocella mundula HMJAU:7275 China
Clitocella mundula HMJAU:7274 China
Clitocella mundula HMJAU:27014 China
Clitocella mundula O:F-71544 Norway
Clitocella mundula AMB:18370 Italy
Clitocella mundula TJB7161 USA (New York)
Clitocella mundula TJB7115 USA (New York)
Lulesia mundula OULU:GAJ.17966 Finland
Clitocella mundula AMB:18367 Italy
Clitocella mundula ME Noordeloos 9867 Austria
Clitocella mundula CORT:MC2-TRENT Italy
Clitocella mundula AMB:18368 Italy NEOTYPE
Clitocella mundula AMB:18853 Italy
Lulesia mundula H6042309 Finland
L. mundula
Clitocella sp. FLAS:F-71949 iNaturalist 183000711 OR664077 USA (Florida)
Clitocella sp. FLAS:F-61088 MH399861 USA (Florida) EPITYPE
Lulesia alachuana FLAS:F-71949 USA (Florida) EPITYPE
Lulesia alachuana FLAS:F-61088 USA (Florida)
L. alachuana
Clitocella borealichinensis BJTC:FM1781 China HOLOTYPE
Clitocella borealichinensis BJTC:FM1618 China
L. borealichinensis
Clitocella sp. KUN-HKAS: 77394 China
L. sp. 1
Lulesia umbrinomarginata MHHNU20023-1 China
Lulesia umbrinomarginata MHHNU20022-2 China HOLOTYPE
Lulesia umbrinomarginata MHHNU20023-2 China
Lulesia umbrinomarginata MHHNU20022-1 China HOLOTYPE
L. umbrinomarginata
Rhodocybe popinalis TUF:106376 Estonia
Lulesia colorata TUR-A 216670 Italy (Lombardia)
Clitocella mundula TENN:074481 RAS306 USA (Tennessee)
Lulesia colorata H6042258 Finland
Clitocella popinalis CBS:481.50 France
Lulesia colorata TUR-A 216671 Italy (Emilia-Romagna)
Rhodocybe popinalis TUF:120607b UDB031317 Estonia
Rhodocybe obscura AMB:18391 Italy (Veneto)
Clitocella popinalis TUF:120607a Estonia
Clitocybe sp. S.D. Russell MycoMap 7768 USA (Indiana)
Clitocella colorata BJTC:FM1593 China
Clitocella popinalis HBJU-550 India
Clitocella colorata BJTC:FM1594 China
Clitocella popinalis KA12-1717 South Korea
Clitocella colorata BJTC:FM1891 China HOLOTYPE
Clitocella colorata BJTC:FM1892 China
Clitocella colorata BJTC:FM1952 China
Clitocella popinalis RA802-3b USA (Arkansas)
Clitocella mundula TJB7599 (AFTOL-ID 521) USA (New York)
Clitocella popinalis Smith-2018 iNaturalist#17340579 USA (Wisconsin)
Clitocella sp. FLAS:F-70982 USA (Vermont)
L. colorata
Clitocella orientalis KUN-HKAS:78876 China
Clitocella orientalis KUN-HKAS:75548 China
Clitocella orientalis BJTC:FM1539 China
Clitocella orientalis KUN-HKAS:78763 China HOLOTYPE
Clitocella orientalis KUN-HKAS:77899 China
Clitocella orientalis KUN-HKAS:75664 China
L. orientalis
Clitocella solaris LUG:19882 France HOLOTYPE
Lulesia solaris H6043012 Finland
L. solaris
Clitocella nigrescens AMB:18365 Italy
Clitocella nigrescens AMB:18366 Italy EPITYPE
Clitocella nigrescens AMB:18392 Italy
Clitocella nigrescens AH:54311 Spain
Rhodocybe cupressicola MCVE:15200 Italy Holotype
Clitocella nigrescens AMB:18388 France
Clitocella nigrescens GM:081227-1 Spain
Clitocella nigrescens AMB:18387 Italy
Clitocella nigrescens LIP:94112502 France
L. nigrescens
Lulesia densifolia ANGE-236 Dominican Republic
Lulesia densifolia BSD:125861 G1411 Dominican Republic EPITYPE
L. densifolia
Lulesia subgen. Lulesia
Clitocella blancii AMB:18372 Italy
Clitocella blancii AMB:18360 Italy EPITYPE
Clitocella blancii AMB:18371 Italy
Clitocella blancii AMB:18373 Italy
Rhodocybe ochraceopallida FP402 Italy
Rhodocybe amarella MCVE:1003 Italy Holotype
Clitocella sp. LPRC5969 France
Clitocella blancii AMB:18855 Spain
Clitocella blancii PI.-06112015-09 France
Clitocella blancii MJ23-269/MNHN-PC-PC0715145 France
Rhodocybe sp. RC16111103 France
Clitopilus fallax ME Noordeloos 200367 Slovakia
L. blancii
Lulesia parvifallax G00586348 RR24.326 Switzerland HOLOTYPE
L. parvifallax sp. nov.
Lulesia fallacioides H6032673 FINLAND
Lulesia fallacioides OULU:GAJ.17962-T. Kekki (6670) Finland HOLOTYPE
Lulesia fallacioides OULU:GAJ.11332-T. Kekki (3988) Finland
Lulesia fallacioides H6032677 Finland
Lulesia fallacioides OULU:GAJ.17963-T. Kekki (6650) Finland
Clitocella fallax OKM:25668 USA (Oregon)
L. fallacioides sp. nov.
Clitocella neofallax HKAS 128149 China HOLOTYPE
Clitocella neofallax HKAS 128152 China
L. neofallax comb. nov.
Lulesia
Clitocella fallax O:F-88953 Norway
Clitocella fallax K:(M) 116541 Spain
Clitocella fallax CBS:129.63 France
Rhodocybe fallax CBS:605.79 France
Global soil samples Material Sample S328 UDB088127 Estonia
Material Sample G4193 UDB0524327 Estonia
Clitocella fallax TO:AV5201320 Italy
Global soil samples TUE000639 UDB03872688 Turkey
Clitopilus amarus BR A. d. Haan 96-121 Belgium Holotype
Clitocella fallax AMB:18376 Italy
Clitopilus amarus A. d. Haan 98031 Belgium
Lulesia fallax H6032675 Finland
Clitocella fallax AMB:18377 Italy
Clitocella fallax ME Noordeloos 1997173 Italy
Clitocella fallax WU-MYC 0016359 Austria
Clitocella fallax AMB:18364 Italy EPITYPE
Clitocella fallax AMB:18375 Italy
L. fallax
Lulesia subgen. Paraclitopilus
Lulesia subgen. Rhodopleurella
Global soil samples Material Sample TUE001481 UDB03879566 USA (Utah)
Global soil samples Material Sample TUE001481 UDB03879567 USA (Utah)
L. sp. 2
Clitocella termitophila CORT:014751 Dominican Republic HOLOTYPE
L. termitophila
Clitopilus prunulus KUN-HKAS:96158 Austria EPITYPE
0.03

◂**Fig. 1** Maximum likelihood phylogram built with nucleotide sequence data of the nrITS/nrLSU/*RPB2*/*TEF-1α*/*ATP6* dataset of *Lulesia*, rooted with *Clitopilus prunulus* (*Entolomataceae*). Nodes were annotated on or below the branches with BP ≥ 70% (left) and PP ≥ 0.95 (right). Subsignificant support values were annotated in parentheses. Newly sequenced collections are in bold. The lengths of the branches were estimated as average values on the sampled trees

(2022), and Vizzini et al. (2023, 2024). 2) A nrITS dataset focused on *Lulesia* subgen. *Paraclitopilus* and including also all environmental sequences was prepared, with *L. popinalis* as outgroup taxon. All the sequences employed are listed in Table 1. The combined and ITS alignments used for the phylogenetic analyses are deposited in Figshare (https://doi.org/10.6084/m9.figshare.29654816).

Sequences first were aligned in MEGA 6.0 (Tamura et al. 2013) with its MUSCLE (Edgar 2004) applications and then realigned manually as needed to establish positional homology. The matrices were analysed by using the Bayesian Inference (BI) and the Maximum Likelihood (ML) criteria through the MESQUITE 3.81 (Maddison and Maddison 2023) software by which were obtained the.nex and.phy files.

The.nex files were loaded into MrBayes v. 3.2.7a (Ronquist et al. 2012) of the CIPRES Science Gateway v. 3.3 platform (Miller et al. 2010) and Bayesian analyses were performed with the nrITS–nrLSU–*RPB2*–*TEF-1α*-*ATP6* partitioned alignment and the ITS alignment (GTR + G + I model, two simultaneous runs, six chains, temperature set at 0.2, sampling every 1000 generations) until reaching convergence parameters (standard deviation less than 0.01 and PSRF (Potential Scale Reduction Factor) (Gelman and Rubin 1992) equal to 1), after 3.17 M generations and 13.45 M generations, respectively. As required from the procedure, 25% of the trees, those of the initial stretch and those of the final tail, were 'burned'.

A full search for the best-scoring maximum likelihood tree was performed loading the.phy files of the multilocus alignment and ITS alignment into the RAxML v. 8.2.12 program (Stamatakis 2014) using the standard search algorithm with the same partitions and 1000 bootstrap cycles according to the GTR + GAMMA model. The trees in.tre format were read with the software SEAVIEW v. 4 (Gouy et al. 2010) and saved in a vector format for printing.

The significance threshold was set ≥ 70% for bootstrap proportions (BP) and ≥ 0.95 for posterior probabilities (PP).

Results

Molecular data

The topology of the best tree from the ML analysis and 50% majority-rule consensus tree from the BI analysis are essentially identical, so only the ML tree is presented here, with support values from both analyses (Bootstrap (BS) ≥ 70% and/or Posterior Probabilities (PP) ≥ 0.95) (Figs. 1 and 2).

The final combined multigene nrITS–nrLSU–*RPB2*–*TEF-1α*–*ATP6 Lulesia* data matrix encompassed a total of 339 sequences (including 27 newly generated, 303 from INSDC/GenBank, and 9 from UNITE) (100 ITS, 66 LSU, 84 *RPB2*, 51 *TEF-1α*, 38 *ATP6*) from 132 samples of 21 taxa. The alignment is 3387 bp long (gaps included).

The nrITS *Lulesia* subgen. *Paraclitopilus* data matrix encompassed a total of 34 sequences (including 7 newly generated, 22 from INSDC/GenBank, and 5 from UNITE) from 34 samples of 8 taxa. The alignment is 604 bp long (gaps included).

Except for *L. termitophila*, all the other species of *Lulesia* included in the present multigene analysis clustered together forming a monophyletic lineage (BP = 100%, PP = 1.00). *Lulesia termitophila* was sister to all the other species of *Lulesia* (BP = 100%, PP = 1.00) (Fig. 1). Three major clades are recognized in *Lulesia*, corresponding to *Lulesia* subgen. *Lulesia* (BP = 92%, PP = 1.0), subgen. *Paraclitopilus* (BP = 92%, PP = 1.00), and subgen. *Rhodopleurella*, as previously highlighted by Vizzini et al. (2023, 2024).

Lulesia encompasses nineteen monophyletic species-rank clades corresponding to fifteen already described species, two new species, and two *Lulesia* sp. (*Lulesia* sp. 1 and *Lulesia* sp. 2) (Fig. 1). All these species clades with more than one sequence were strongly supported. The two new species (described here as *L. fallacioides* and *L. parvifallax*) and *Lulesia* sp. 2 belong to *Lulesia* subgen. *Paraclitopilus* which also includes *L. blancii*, *L. fallax*, and *L. neofallax* (Fig. 1). *Lulesia fallacioides*, *L. parvifallax*, and *Lulesia* sp. 2 (as *Lulesia* sp.) are clearly supported as distinct taxa also in the nrITS analysis focused on *Lulesia* subgen. *Paraclitopilus* (Fig. 2). *Lulesia* sp. 2 consists of two environmental sequences from the USA (Utah) and two basidiomatal sequences (China-Xizang and USA-California). Morphological data will be needed to formally describe the clade as a new species.

Taxonomy

Lulesia* subgen. *Paraclitopilus (Vizzini & Cons.) Vizzini & Cons., in Vizzini et al., Boll. Assoc. Micol. Ecol. Romana 39(3): 8 (2024) [2023].

Basionym: *Clitocella* subgen. *Paraclitopilus* Vizzini & Cons., Persoonia 50: 146 (2023).

Type: *Omphalia fallax* Quél., Compt. Rend. Assoc. Franç. Avancem. Sci. 24 (2): 617 (1896).

Habit like that of the centrally stipitate *Clitopilus* species, pileus white to cream coloured under a white pruinose covering, surfaces of both fresh and dried basidiomes not staining grey or black when bruised or in age and with a

Table 1 Taxa, vouchers, locations, GenBank and UNITE accessions numbers of the DNA sequences used in the phylogenetic molecular analyses. Sequences in bold were generated in this study

Species (revised name)	Label	Voucher	State	GenBank Accession No.					Reference
				nrITS	nrLSU	*RPB2*	*TEF-1α*	*ATP6*	
Clitopilus prunulus	*Clitopilus prunulus*	KUN-HKAS: 96158 EPITYPE	Austria	NR_172770	MN065691	MN148129	MN166240	MN133745	Jian et al. (2020)
Lulesia alachuana	*Clitocella* sp.	FLAS:F-61088	USA: Florida	MH399861	–	–	–	–	Kaminsky B, Smith ME, Healy R, Spakes-Richter B 2019, direct submission, unpublished
Lulesia alachuana	***Clitocella* sp.**	**FLAS:F-61088, EPITYPE**	**USA: Florida**	**PV780532**	**PV780530**	**PV786165**	**PV819100**		**This study**
Lulesia alachuana	*Clitocella* sp.	FLAS:F-71949-iNaturalist-183000711	USA: Florida	OR664077	–	–	–	–	Sheffer FLP and Smith ME 2023, Biodiversity of Florida Fungi, direct submission, unpublished
Lulesia alachuana	***Clitocella* sp.**	**FLAS:F-71949-iNaturalist-183000711**	**USA: Florida**	**PV780533**	**PV780531**	**PV786166**	–	–	**This study**
Lulesia blancii	*Clitocella blancii*	AMB:18360 EPITYPE	Italy	ON502686	ON502626	ON524537	ON524566	–	Vizzini et al. (2023)
Lulesia blancii	*Clitocella blancii*	AMB:18371	Italy	ON502687	ON502627	ON524538	ON524567	–	Vizzini et al. (2023)
Lulesia blancii	*Clitocella blancii*	AMB:18372	Italy	ON502688	ON502628	ON524539	ON524568	–	Vizzini et al. (2023)
Lulesia blancii	*Clitocella blancii*	AMB:18373	Italy	–	–	ON524540	ON524569	–	Vizzini et al. (2023)
Lulesia blancii	*Clitocella blancii*	AMB:18855	Spain	ON502689	ON502629	–	–	–	Vizzini et al. (2023)
Lulesia blancii	*Rhodocybe ochraceopallida*	FP402	Italy	ON502691	–	–	–	–	Vizzini et al. (2023)
Lulesia blancii	*Clitocella* sp.	LPRC5969	France	OQ843195	–	–	–	–	Ivaldi et al. (2023)
Lulesia blancii	*Rhodocybe amarella*	MCVE:1003 HOLOTYPE of *Rhodocybe amarella*	Italy	ON502690	–	–	–	–	Vizzini et al. (2023)
Lulesia blancii	*Clitopilus fallax*	ME Noordeloos 200367	Slovakia	–	GQ289210	GQ289276	–	–	Co-David et al. (2009)
Lulesia blancii	*Clitocella blancii*	MJ23-269/MNHN-PC-PC0715145	France	PV121761	PV122064	–	–	–	Jerusalem M, Funif-Col and FUNDIVE project, fungal biodiversity, survey of France, 19-FEB-2025, unpublished
Lulesia blancii	*Clitocella blancii*	PI.-06112015-09	France	OQ819029	–	–	–	–	Ivaldi et al. (2023)
Lulesia blancii	*Rhodocybe* sp.	RC16111103	France	OM397450	–	–	–	–	Chalange R, Mycoseq sequences for R. Chalange Jan 2022, unpublished
Lulesia borealichinensis	*Clitocella borealichinensis*	BJTC:FM1618	China	OL966942	OL966946	OL989912	–	OL989922	Mao et al. (2022)
Lulesia borealichinensis	*Clitocella borealichinensis*	BJTC:FM1781 HOLOTYPE	China	OL966943	OL966957	OL989913	OL989917	OL989923	Mao et al. (2022)
Lulesia colorata	*Rhodocybe obscura*	AMB:18391	Italy	ON502692	ON502630	ON524541	–	–	Vizzini et al. (2023)
Lulesia colorata	*Clitocella colorata*	BJTC:FM1593	China	OL966940	–	–	–	–	Mao et al. (2022)
Lulesia colorata	*Clitocella colorata*	BJTC:FM1594	China	OL966941	–	–	–	–	Mao et al. (2022)
Lulesia colorata	*Clitocella colorata*	BJTC:FM1891 HOLOTYPE	China	OL966944	OL966955	OL989914	OL989918	OL989924	Mao et al. (2022)
Lulesia colorata	*Clitocella colorata*	BJTC:FM1892	China	OL966945	OL966956	OL989915	OL989919	OL989925	Mao et al. (2022)
Lulesia colorata	*Clitocella colorata*	BJTC:FM1952	China	–	OL966958	OL989916	OL989920	OL989926	Mao et al. (2022)
Lulesia colorata	***Clitocella colorata***	**TUR-A 216670**	**Italy (Lombardia)**	**PV780534**	–	**PV819098**	–	–	**This study**
Lulesia colorata	***Clitocella mundula***	**TUR-A 216671**	**Italy (Emilia-Romagna)**	**PV780535**	–	–	–	–	**This study**
Lulesia colorata	*Clitocella popinalis*	CBS:481.50	France	FJ770397	–	–	–	–	Hartley et al. (2009)
Lulesia colorata	*Clitocella* sp.	FLAS:F-70982	USA: Vermont	OP932049	OP932040	–	–	–	**This study**
Lulesia colorata	***Rhodocybe* cf. *mundula***	**H6042258**	**Finland**	**PV815355**	–	–	–	–	**This study**
Lulesia colorata	*Clitocella popinalis*	HBJU-550	India	KU561066	–	–	–	–	Kour et al. (2016)
Lulesia colorata	*Clitocella popinalis*	KA12-1717	South Korea	KR673647	–	–	–	–	Kim et al. (2015)
Lulesia colorata	*Clitocella popinalis*	RA802-3b	USA: Arkansas	MK217434	–	–	–	–	Alanbagi RA, Alshuwaili FE and Stephenson SL 2020, Fungi associated with forest floor litter in northwest Arkansas, unpublished
Lulesia colorata	*Clitocybe* sp.	S.D. Russell MycoMap 7768	USA: Indiana	MK532767	–	–	–	–	Russell 2019, Mycoflora of Indiana, direct submission, unpublished
Lulesia colorata	*Clitocella popinalis*	Smith-2018 iNaturalist # 17340579	USA: Wisconsin	MK573922	–	–	–	–	Russell 2019, Mycoflora of Indiana, direct submission, unpublished
Lulesia colorata	*Clitocella mundula*	TENN:074481 RAS306	USA: Tennessee	MT237519	–	–	–	–	Matheny PB, Swenie RA and Hughes KW 2020, Mushrooms of the Smokies and the Southern Appalachians, direct submission, unpublished
Lulesia colorata	*Clitocella mundula*	TJB7599 (AFTOL-ID 521)	USA: New York	–	–	KC816953	KC816863	KC816783	Kluting et al. (2014)
Lulesia colorata	*Rhodocybe popinalis*	TUF:106376	Estonia	UDB011645	–	–	–	–	UNITE, Vello Liiv TUF seened
Lulesia colorata	*Clitocella popinalis*	TUF:120607a	Estonia	ON502693	ON502631	ON524542	–	–	Vizzini et al. (2023)
Lulesia colorata	*Rhodocybe popinalis*	TUF:120607b	Estonia	UDB031317	–	–	–	–	UNITE, Vello Liiv TUF seened
Lulesia densifolia	*Lulesia densifolia*	ANGE-236	Dominican Republic	OR994620	OR994669	PP001698	PP001699	–	Vizzini et al. (2024)
Lulesia densifolia	*Lulesia densifolia*	BSD 125861 G1411 EPITYPE	Dominican Republic	–	MK278305	–	–	–	Vizzini et al. (2024)
Lulesia fallacioides	***Clitocella* aff. *fallax***	**OULU:GAJ.11332-T. Kekki (3988)**	**Finland**	**PV815356**	–	–	–	–	**This study**
Lulesia fallacioides	***Rhodocybe fallax***	**H6032673**	**Finland**	**PV815354**	–	–	–	–	**This study**
Lulesia fallacioides	***Rhodocybe fallax***	**H6032677**	**Finland**	**PV815361**	–	–	–	–	**This study**
Lulesia fallacioides	***Lulesia fallacioides***	**OULU:GAJ.17963-T. Kekki (6650)**	**Finland**	**PV815365**	**PV815353**	**PV866981**	–	–	**This study**
Lulesia fallacioides	***Lulesia fallacioides***	**OULU:GAJ.17962-T. Kekki (6670), HOLOTYPE**	**Finland**	**PV815362**	**PV815352**	**PV866982**	–	–	**This study**
Lulesia fallacioides	*Clitocella fallax*	OKM:25668	USA: Oregon	–	–	KC816937	KC816846	KC816768	Kluting et al. (2014)
Lulesia fallax	*Clitopilus amarus*	A. d. Haan 98031	Belgium	KC885963	–	–	–	–	Morgado et al. (2016)
Lulesia fallax	*Clitocella fallax*	AMB:18364 EPITYPE	Italy	ON502696	ON502634	ON524546	ON524573	ON934200	Vizzini et al. (2023)
Lulesia fallax	*Clitocella fallax*	AMB:18375	Italy	ON502694	ON502632	ON524543	ON524570	–	Vizzini et al. (2023)
Lulesia fallax	*Clitocella fallax*	AMB:18376	Italy	ON502695	ON502633	ON524544	ON524571	ON934199	Vizzini et al. (2023)
Lulesia fallax	*Clitocella fallax*	AMB:18377	Italy	–	–	ON524545	ON524572	ON934198	Vizzini et al. (2023)
Lulesia fallax	*Clitopilus amarus*	BR A. d. Haan 96-121 HOLOTYPE	Belgium	OP002024	OP002025	OP021856	–	–	Vizzini et al. (2023)
Lulesia fallax	*Rhodocybe fallax*	CBS:129.63	France	AF357017	AF223166	EF421018	–	–	Hofstetter et al. (2002)
Lulesia fallax	*Rhodocybe fallax*	CBS:605.79	France	AF357018	–	–	–	–	Hofstetter et al. (2002)
Lulesia fallax	*Clitopilus* sp.	G4193 (Material Sample)	Estonia	UDB0524327	–	–	–	–	UNITE,Tedersoo L et al. Global soil samples
Lulesia fallax	***Rhodocybe fallax***	**H6032675**	**Finland**	**PV815359**	–	–	–	–	**This study**
Lulesia fallax	*Clitocella fallax*	K:(M) 116541	Spain	–	–	KC816938	KC816847	KC816769	Kluting et al. (2014)
Lulesia fallax	*Clitopilus fallax*	ME Noordeloos 1997173	Italy	–	GQ289209	GQ289275	–	–	Co-David et al. (2009)
Lulesia fallax	*Clitocella fallax*	O:F-88953	Norway	–	–	KC816936	KC816845	KC816767	Kluting et al. (2014)
Lulesia fallax	*Clitopilus* sp.	S328 (Material Sample)	Estonia	UDB088127	–	–	–	–	UNITE, Tedersoo L et al. Global soil samples
Lulesia fallax	*Clitocella fallax*	TO:AV5201320	Italy	ON502697	–	–	–	–	Vizzini et al. (2023)
Lulesia fallax	*Clitopilus* sp.	TUE000639 (Material sample)	Turkey	UDB03872688	–	–	–	–	UNITE, Tedersoo L et al. Global soil samples
Lulesia fallax	*Clitocella fallax*	WU-MYC 0016359	Austria	ON922913	–	ON934196	–	–	Vizzini et al. (2023)
Lulesia mundula	*Clitocella mundula*	AMB:18367	Italy	ON502698	ON502635	ON524547	–	–	Vizzini et al. (2023)
Lulesia mundula	*Clitocella mundula*	AMB:18368 NEOTYPE	Italy	ON502699	ON502636	ON524548	–	–	Vizzini et al. (2023)
Lulesia mundula	*Clitocella mundula*	AMB:18370	Italy	ON502700	ON502637	ON524549	–	–	Vizzini et al. (2023)
Lulesia mundula	*Clitocella mundula*	AMB:18853	Italy	ON502701	ON502638	ON524550	ON524574	–	Vizzini et al. (2023)
Lulesia mundula	*Clitocella popinalis*	CORT:MC2-TRENT	Italy	–	–	KC816973	–	KC816798	Kluting et al. (2014)
Lulesia mundula	***Clitocella mundula***	**OULU:GAJ.17966**	**Finland**	**PV815358**	–	–	–	–	**This study**
Lulesia mundula	***Rhodocybe* cf. *popinalis***	**H6042309**	**Finland**	**PV815363**	–	–	–	–	**This study**
Lulesia mundula	*Clitocella mundula*	HMJAU:27014	China	–	MN065722	MN148159	MN166270	MN133779	Jian et al. (2020a)
Lulesia mundula	*Clitocella mundula*	HMJAU:7274	China	–	MN065724	MN148161	MN166272	MN133781	Jian et al. (2020a)
Lulesia mundula	*Clitocella mundula*	HMJAU:7275	China	–	MN065723	MN148160	MN166271	MN133780	Jian et al. (2020a)
Lulesia mundula	*Clitopilus popinalis*	ME Noordeloos 9867	Austria	–	GQ289213	GQ289280	–	–	Co-David et al. (2009)
Lulesia mundula	*Clitocella mundula*	O:F-71544	Norway	–	–	KC816950	KC816860	KC816780	Kluting et al. (2014)
Lulesia mundula	*Clitocella mundula*	TJB7115	USA: New York	–	–	KC816951	KC816861	KC816781	Kluting et al. (2014)
Lulesia mundula	*Clitocella mundula*	TJB7161	USA: New York	–	–	KC816952	KC816862	KC816782	Kluting et al. (2014)
Lulesia neofallax	*Clitocella neofallax*	HKAS 128149 HOLOTYPE	China	OQ755418	OR067882	OR077303	OR091165	–	Liu et al. (2025)
Lulesia neofallax	*Clitocella neofallax*	HKAS 128152	China	OQ755417	OR067883	OR077302	OR091166	–	Liu et al. (2025)
Lulesia nigrescens	*Clitocella nigrescens*	AH:54311	Spain	ON502703	ON502639	ON524551	–	–	Vizzini et al. (2023)
Lulesia nigrescens	*Clitocella nigrescens*	AMB:18365	Italy	–	–	ON524552	ON524575	–	Vizzini et al. (2023)
Lulesia nigrescens	*Clitocella nigrescens*	AMB:18366 EPITYPE	Italy	ON502704		ON524553	ON524576	–	Vizzini et al. (2023)
Lulesia nigrescens	*Clitocella nigrescens*	AMB:18387	Italy	ON502705	ON502640	ON524554	–	–	Vizzini et al. (2023)
Lulesia nigrescens	*Clitocella nigrescens*	AMB:18388	France	ON502707	ON502642	ON524556	–	–	Vizzini et al. (2023)
Lulesia nigrescens	*Clitocella nigrescens*	AMB:18392	Italy	ON502709	ON502643	ON524557	–	–	Vizzini et al. (2023)
Lulesia nigrescens	*Clitocella nigrescens*	GM:081227-1	Spain	ON502706	ON502641	ON524555	–	–	Vizzini et al. (2023)
Lulesia nigrescens	*Clitocella nigrescens*	LIP:94112502	France	ON502702	–	–	–	–	Vizzini et al. (2023)
Lulesia nigrescens	*Rhodocybe cupressicola*	MCVE:15200 HOLOTYPE of *Rhodocybe cupressicola*	Italy	ON502708	–	–	–	–	Vizzini et al. (2023)
Lulesia obscura	*Clitocella obscura*	AMB:18856	Italy	ON502712	ON502646	ON524560	ON524577	–	Vizzini et al. (2023)
Lulesia obscura	*Clitocella mundula*	ANT150-HRL2111	Canada	MN992316	ON923665	ON934195	–	–	Vizzini et al. (2023)
Lulesia obscura	*Clitocella obscura*	BRNM:666712	Czechia	ON502710	ON502644	ON524558	–	–	Vizzini et al. (2023)
Lulesia obscura	***Rhodocybe* cf. *popinalis***	**H6042319**	**Finland**	**PV815357**	–	–	–	–	**This study**
Lulesia obscura	***Rhodocybe* cf. *popinalis***	**H6042347**	**Finland**	**PV815364**	–	–	–	–	**This study**
Lulesia obscura	*Clitocella obscura*	MK09051302 -BRNM:666712	Czechia	KX271753	–	–	–	–	Vizzini A, Sesli E and Ercole E 2016, The genus *Rhodocybe* in Turkey, direct submission, unpublished
Lulesia obscura	*Clitocella mundula*	O:F-19454	Norway	–	–	KC816954	KC816864	KC816784	Kluting et al. (2014)
Lulesia obscura	*Clitocella obscura*	PRM:899231 EPITYPE	Czechia	ON502711	ON502645	ON524559	–	–	Vizzini et al. (2023)
Lulesia orientalis	*Clitocella orientalis*	BJTC:FM1539	China	–	OL966947	OL989911	OL989921	–	Mao et al. (2022)
Lulesia orientalis	*Clitocella orientalis*	KUN-HKAS:75548	China	MN061333	MN065727	MN148164	MN166275	MN133784	Jian et al. (2020a)
Lulesia orientalis	*Clitocella orientalis*	KUN-HKAS:75664	China	MN061332	MN065726	MN148163	MN166274	MN133783	Jian et al. (2020a)
Lulesia orientalis	*Clitocella orientalis*	KUN-HKAS:77899	China	–	MN065725	MN148162	MN166273	MN133782	Jian et al. (2020a)
Lulesia orientalis	*Clitocella orientalis*	KUN-HKAS:78763 HOLOTYPE	China	–	MN065728	MN148165	MN166276	MN133785	Jian et al. (2020a)
Lulesia orientalis	*Clitocella orientalis*	KUN-HKAS:78876	China	MN061334	MN065729	MN148166	MN166277	MN133786	Jian et al. (2020a)

Table 1 (continued)

Lulesia parvifallax	***Lulesia parvifallax***	**G00586348 RR24.326 HOLOTYPE**	**Switzerland**	**PV780536**	–	–	–	–	**This study**
Lulesia popinalis	*Clitocella popinalis*	AMB:18369 NEOTYPE	Italy	ON502715	ON502649	ON524563	–	–	Vizzini et al. (2023)
Lulesia popinalis	*Clitocella popinalis*	AMB:18389	Italy	ON502716	ON502650	ON524564	–	–	Vizzini et al. (2023)
Lulesia popinalis	*Clitocella popinalis*	AMB:18390	Italy	ON502717	ON502651	–	–	–	Vizzini et al. (2023)
Lulesia popinalis	*Clitocella popinalis*	CL 911012-34	Switzerland	ON502718	ON502652	ON524565	–	–	Vizzini et al. (2023)
Lulesia popinalis	*Clitocella popinalis*	K:(M) 143166	United Kingdom	–	–	KC816971	KC816878	KC816796	Kluting et al. (2014)
Lulesia popinalis	*Clitocella popinalis*	K:(M) 146162	United Kingdom	–	–	KC816970	KC816877	KC816795	Kluting et al. (2014)
Lulesia popinalis	*Clitocella mundula*	K:(M) 164736	United Kingdom	–	–	KC816949	KC816859	KC816779	Kluting et al. (2014)
Lulesia popinalis	*Clitocella popinalis*	K:(M) 167017	United Kingdom	–	–	KC816972	KC816879	KC816797	Kluting et al. (2014)
Lulesia popinalis	*Clitocella mundula*	K:(M) 49620	United Kingdom (Channel Islands)	–	–	KC816948	KC816858	KC816778	Kluting et al. (2014)
Lulesia popinalis	*Clitocella popinalis*	O:F-105360	Norway	–	–	KC816975	KC816881	KC816800	Kluting et al. (2014)
Lulesia popinalis	*Clitocella popinalis*	O:F-252975a	Norway	ON502713	ON502647	ON524561	–	–	Vizzini et al. (2023)
Lulesia popinalis	*Rhodocybe popinalis*	O:F-252975b	Norway	UDB037336	–	–	–	–	UNITE, Norwegian fungi from BOLD to UNITE
Lulesia popinalis	*Rhodocybe popinalis*	O:F-253176a	Norway	UDB017726	–	–	–	–	UNITE, Klaus Høiland 2012, unpublished
Lulesia popinalis	*Clitocella popinalis*	O:F-253176b	Norway	ON502714	ON502648	ON524562	–	–	Consiglio G, Vizzini A and Marchetti M 2014, direct submission, unpublished
Lulesia popinalis	*Clitocella popinalis*	O:F-63376	Norway	–	–	KC816974	KC816880	KC816799	Kluting et al. (2014)
Lulesia popinalis	*Clitocella popinalis*	TB6378	Switzerland	–	AF261285	GU384654	–	–	Moncalvo et al. (2002), Baroni et al. (2011)
Lulesia popinalis	*Clitocella popinalis*	TJB6378	Switzerland	–	–	KC816976	KC816882	KC816801	Kluting et al. (2014)
Lulesia solaris	***Rhodocybe caelata***	**H6043012**	**Finland**	**PV815360**	–	–	–	–	**This study**
Lulesia solaris	*Clitocella solaris*	LUG:19882 HOLOTYPE	France	ON922914	ON923666	ON934197	–	–	Vizzini et al. (2023)
Lulesia sp.	*Clitocella* sp.	KUN-HKAS: 77394	China	MZ675558	MZ675569	MZ681891	MZ681869	–	He and Yang (2022)
Lulesia sp.	*Clitopilus* sp.	TUE001481 (Material Sample)	United States: Utah	UDB03879567	–	–	–	–	UNITE, Tedersoo L et al. Global soil samples
Lulesia sp.	*Clitopilus* sp.	TUE001481 (Material Sample)	United States: Utah	UDB03879566	–	–	–	–	UNITE, Tedersoo L et al. Global soil samples
Lulesia sp.	*Clitocella* sp.	CA02' voucher HAY-F-005753 iNaturalist # 182882379	United States: California	PP594830	–	–	–	–	D'Elia G, Singer H, Schwarz C, Lema F, Ospina S 2024, California Fungal Diversity Survey (CA FUNDIS) 2022-2023, direct submission, unpublished
Lulesia sp.	*Clitocella* sp.	HKAS:133585	China: Xizang Autonomous Region, Zayu County	PV124053	–	–	–	–	Lu JR and Zhao Q 2025, direct submission, unpublished
Lulesia termitophila	*Clitocella termitophila*	CORT:014751 HOLOTYPE	Dominican Republic	PP028782	PP028781	MN893319	–	–	Baroni et al. (2020), Vizzini et al. (2024)
Lulesia umbrinomarginata	*Lulesia umbrinomarginata*	MHHNU20022-1 HOLOTYPE	China: Guangdong Province, Huidong County	PP060629	PP059604	PP158701	PP158693	PP158697	Xiao et al. (2024)
Lulesia umbrinomarginata	*Lulesia umbrinomarginata*	MHHNU20022-2 HOLOTYPE	China: Guangdong Province, Huidong County	PP060630	PP059605	PP158702	PP158694	PP158698	Xiao et al. (2024)
Lulesia umbrinomarginata	*Lulesia umbrinomarginata*	MHHNU20023-1	China: Guangdong Province, Huidong County	PP060631	PP059606	PP158703	PP158695	PP158699	Xiao et al. (2024)
Lulesia umbrinomarginata	*Lulesia umbrinomarginata*	MHHNU20023-2	China: Guangdong Province, Huidong County	PP060632	PP059607	PP158704	PP158696	PP158700	Xiao et al. (2024)

negative KOH reaction, hymenophoral trama regular, basidiospores broadly ellipsoid, ellipsoid to oblong, amygdaliform, obscurely angular, often adhering (grouping) in tetrads, and sporal Q on average usually exceeding (1.20–)1.30.

Lulesia fallacioides Kekki, Vizzini, Cons., M. Marchetti & Kytöv., **sp. nov.** Figs. 3a–c and 5

MycoBank MB860683.

Etymology: fallacioìdes = from the root fallac- of fallax (fallac-is) (Latin) and the suffix -ìdes relating to Greek ειδος (éidos), which means 'external aspect, form, semblance', therefore indicating resemblance to *Lulesia fallax.*

Diagnosis: It differs from *L. fallax* by an ixocutis type of pileipellis, wider basidiospores (4.7 µm on average), and association with *Picea abies* forests.

Holotype (here designated): **Finland**, Tervola, Raemäki, calciferous *Picea abies* forest, on needle litter, 04 October 2023, leg. T. Kekki (6670), OULU:GAJ.17962 (**Holotype**, Isotype AMB 20536). GenBank: nrITS, PV815362; nrLSU, PV815352; *RPB2*, PV866982.

Description: *Pileus* 10–50(–80) mm diam., convex, then applanate and usually depressed in the centre, often irregular when old. Margin involute when young, then straight, usually strongly wavy and undulating; surface dry, smooth to slightly tomentose, not hygrophanous, not translucently striate, white, sometimes with slight cream (4A3–4) or ochre (4B4–5) tinges in the centre when old. *Lamellae* L = 20–45, l = (2–) 3–5, crowded, arcuate-decurrent, 2–4 mm broad, sordid white, finally tinged with pink (5A2), pinkish buff (5A3–4) to clay-buff (5B2–3) tinges when dry, with a smooth concolorous edge. *Stipe* 8–26 × 2–7 mm, cylindrical, often tapering downwards, subclavate at the base, solid, white, usually with white rhizomorphs at the base. *Contex* solid, white. *Smell* not distinctive, *taste* bitter. No part of the basidiome staining black. *Spore-print* pale cream pink (6A2). *Chemical spot-test reactions* KOH on dried basidiomes surfaces (pileus, lamellae, and stipe) produces no reaction (negative). *Basidiospores* (4.81–)5.9–*6.5*–7.2(–8.45) × (3.59–)4.4–*4.7*–5.1(–5.70) µm [175/3/3], *Q* = (1.10–)1.27–*1.38*–1.50(–1.79), *V* = (37.9–)59.2–*76.8*–94.5(–138) µm^3, subamygdaliform in side view, ovoid-ellipsoid in frontal view, minutely angular in polar view (7–10 facets), weakly nodulose-pustulate to verrucose in all views, rounded to slightly attenuated apically, often adhering in tetrads, thin-walled (no sclerospores), hilar appendage evident, up to 1 µm long, contents smooth, uni- to pluriguttulate (guttulae greenish in water), wall cyanophilic, pale yellow in water, yellow in Melzer's. *Basidia* 18–30 × 7–10 µm, cylindrical to clavate-cylindrical, usually with guttulate contents, mainly tetrasporic, rarely bisporic, sterigmata up to 4 µm long. *Subhymenium* 20–30 µm thick, consisting of *textura intricata* short elements, 2.5–5 µm wide. *Hymenophoral trama* regular to subregular of parallel to slightly intervowen cylindrical, thin-walled hyphae, hyaline, 3–10 µm wide, sometimes inflated at septa. *Hymenial cystidia* absent. *Pileipellis* an ixocutis of thin-walled, 3–8 µm wide, subparallel to loosely intertwined cylindrical hyphae, sometimes inflated at septa, faintly yellowish; terminal ascending (erect) elements rare to frequent, immersed in a gelled matrix, mostly in clusters, sinuous, subcylindrical with rounded apex, 2–4 µm wide, often multi-articulated into multiple segments; pigment absent to pale yellow, parietal or rarely minutely incrusting some hyphae. *Subpellis* of subparallel to loosely intertwined 3–10 µm wide hyaline hyphae. *Thromboplerous hyphae* not observed. *Stipitipellis* consisting of parallel,

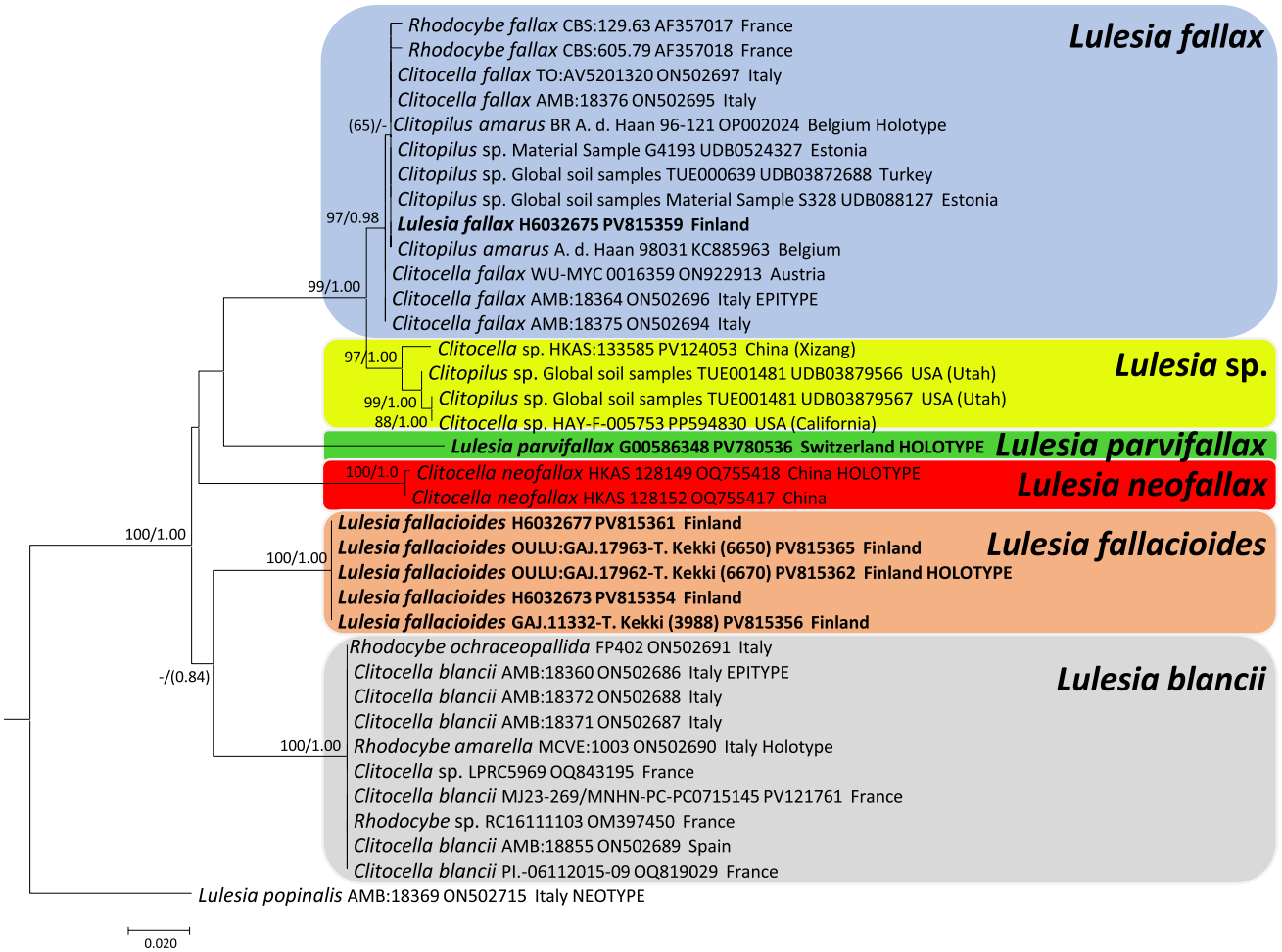


Fig. 2 Maximum likelihood phylogram built with nucleotide sequence data of the nrITS dataset of *Lulesia* subgen. *Paraclitopilus*, rooted with *L. popinalis* (*Lulesia* subgen. *Lulesia*). Nodes were annotated on or below the branches with BP ≥ 70% (left) and PP ≥ 0.95 (right). Subsignificant support values were annotated in parentheses. Newly sequenced collections are in bold

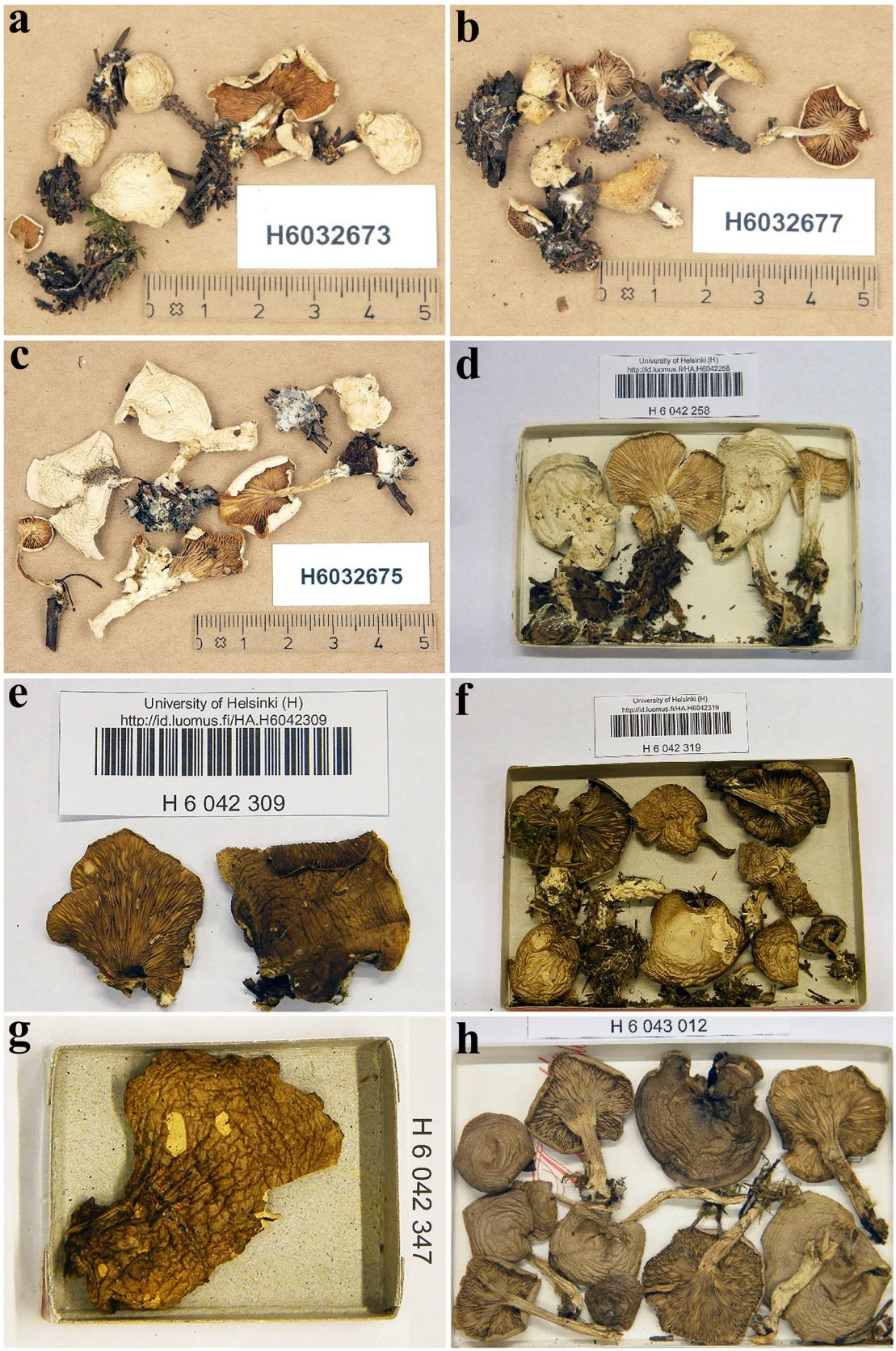
faintly yellowish, 2–4 µm wide cylindrical repent hyphae, occasionally producing clusters of erect, clavate, subglobose to cylindrical (and then multi-articulate) 4–8 µm wide hyaline caulocystidioid hyphae (elements). *Stipititrama* of hyaline, short cylindrical, slightly thick-walled (wall up to 0.5 µm thick), 3–7 µm wide hyphae. *Clamp connections* absent.

Habitat and distribution: Boreal forests of *Picea abies*, gregarious on needle litter, August–October (European collections), so far known from Finland, Sweden, and North America (USA, Oregon).

Material examined: **Finland**, Kainuu, Paltamo, Kontiomäki, mesic *Picea abies* forest, 14 September 2008, leg. I. Kytövuori, H6032677 (H); Suomussalmi, Lohivaara, herb-rich *Picea abies* forest on needle litter, 29 August 2019, leg. T. Kekki (3988) & T. Helo, OULU:GAJ.11332; Koillismaa, Taivalkoski, Katajavaara, old mesic *Picea abies* forest with damp grass-herb depressions, on needle litter, 02 September 2008, leg. I. Kytövuori, H6082249 (H); Perä-Pohjanmaa, Kemijärvi, Pyhätunturi, fairly old *Picea abies* forest, 27 August 2008, leg. I. Kytövuori, H6032673 (H); Rovaniemi, Kylmäoja, mesic *Picea abies* forest by a stream, on needle litter, 04 October 2023, leg. T. Kekki (6650), OULU:GAJ.17963; Tervola, Raemäki, calciferous *Picea abies* forest, on needle litter, 04 October 2023, leg. T. Kekki (6670), OULU:GAJ.17962 (**Holotype**, Isotype AMB 20536); ibid. 04 October 2023, leg. T. Kekki (6666), OULU:GAJ.17965; ibid. 04 October 2023, leg. T. Kekki (6668), OULU:GAJ.17964. **Sweden**, Jämtland, Åre, mesic *Picea abies* forest, 23 August 2006, leg. M. Toivonen & I. Kytövuori, H7001634 (H).

Notes – The species grows gregarious, in autumn, in the thick needle litter under *Picea abies*. It is probably circumpolar as there are collections from Finland, Sweden, and North America. It is rare and prefers old-growth *Picea* forests. *Lulesia fallacioides* can be confused with *Leucopaxillus*

Fig. 3 Fresh basidiomes of sequenced collections. **a**–**c** *Lulesia fallacioides* [OULU:GAJ.17963-T. Kekki (6650), OULU:GAJ.17962-T. Kekki (6670) Holotype, OULU:GAJ.11332-T. Kekki (3988)]. **d**, **e** *L. parvifallax* (G00586348, Holotype). **f** *L. mundula* (OULU:GAJ.17966). **g**, **h** *L. colorata* (TUR-A 216670, TUR-A 216671). **i**, **j** *L. alachuana* (FLAS-F-71949-iNaturalist-183000711). Photos: **a**–**c**, **f** by T. Kekki; **d**, **e** by R. Rickmann; **g**, **h** by M. Carbone; **i**, **j** by L.P. Sheffer


a
H6032673
b
H6032677
c
H6032675
d
University of Helsinki (H)
http://id.luomus.fi/HA.H6042258
H 6 042 258
e
University of Helsinki (H)
http://id.luomus.fi/HA.H6042309
H 6 042 309
f
University of Helsinki (H)
http://id.luomus.fi/HA.H6042319
H 6 042 319
g
H 6 042 347
h
H 6 043 012

◂**Fig. 4** Dried basidiomes of sequenced collections. **a**, **b** *Lulesia fallacioides* (H6032673, H6032677). **c** *L. fallax* (H6032675). **d** *L. colorata* (H6042258). **e** *L. mundula* (H6042309). **f**, **g** *L. obscura* (H6042319, H6042347). **h** *L. solaris* (H6043012). Photos: **a**–**c** by D. Weckman; **d**–**h** by B. Dima

alboalutaceus (F.H. Møller & Jul. Schäff.) F.H. Møller, *Ripartites* P. Karst. spp. and centrally stipitate *Clitopilus* (Fr. ex Rabenh.) P. Kumm. species due to its white pileus and pinkish buff decurrent lamellae, but its basidiospore structure is diagnostic. *Lulesia fallax* is morphologically very similar, but it grows usually in deciduous forests and grasslands, has a xerocutis (versus an ixocutis), and narrower oblong basidiospores (4.1 µm and $Q = 1.60$ versus 4.7 µm and $Q = 1.38$, on average) (Vizzini et al. 2023). The Swedish collection named *Rhodocybe fallax* in von Bonsdorff et al. (2014), due to its habitat, viscid pileus, and basidiospore shape, is surely attributable to *L. fallacioides*. The short description of *R. fallax* included in Funga Nordica by Noordeloos (2012), with basidiospores 5–7 × 3–4 µm, pileus 10–40 mm, stipe 2–7 mm wide, in deciduous woods, scrubs, calcareous sand dunes, in litter under *Syringa*, *Alnus*, indicates that the true *L. fallax* is present in Scandinavia. Our analyses (Figs. 1 and 2) show that based on molecularly confirmed collections, *L. fallax* is present in Nordic areas such as Finland (H6032675, Fig. 4a) and Estonia. The Chinese *L. neofallax* (see below) and the Swiss *L. parvifallax* (see below) are mainly distinguished from *L. fallacioides* by smaller basidiomes, a xerocutis as pileipellis, smaller basidiospores, and different habitat (Table 2, Liu et al. 2025).

Lulesia blancii (Maire) Vizzini, Cons., P. Alvarado, Angelini & M. Marchetti is a xerophilic species from the Mediterranean basin distinguished by a dry alutaceous ochre, chamois, grey-brown pileus, lamellae with evident yellow-ochre tinges, and shorter basidiospores (5.5 µm long on average) (Contu 1999; Eyssartier and Roux 2011; Ivaldi et al. 2023; Vizzini et al. 2023) (Fig. 5).

Lulesia parvifallax Rickmann, Vizzini, Cons. & A. Gross, **sp. nov.** Figs. 3d and e and 6

MycoBank MB860684.

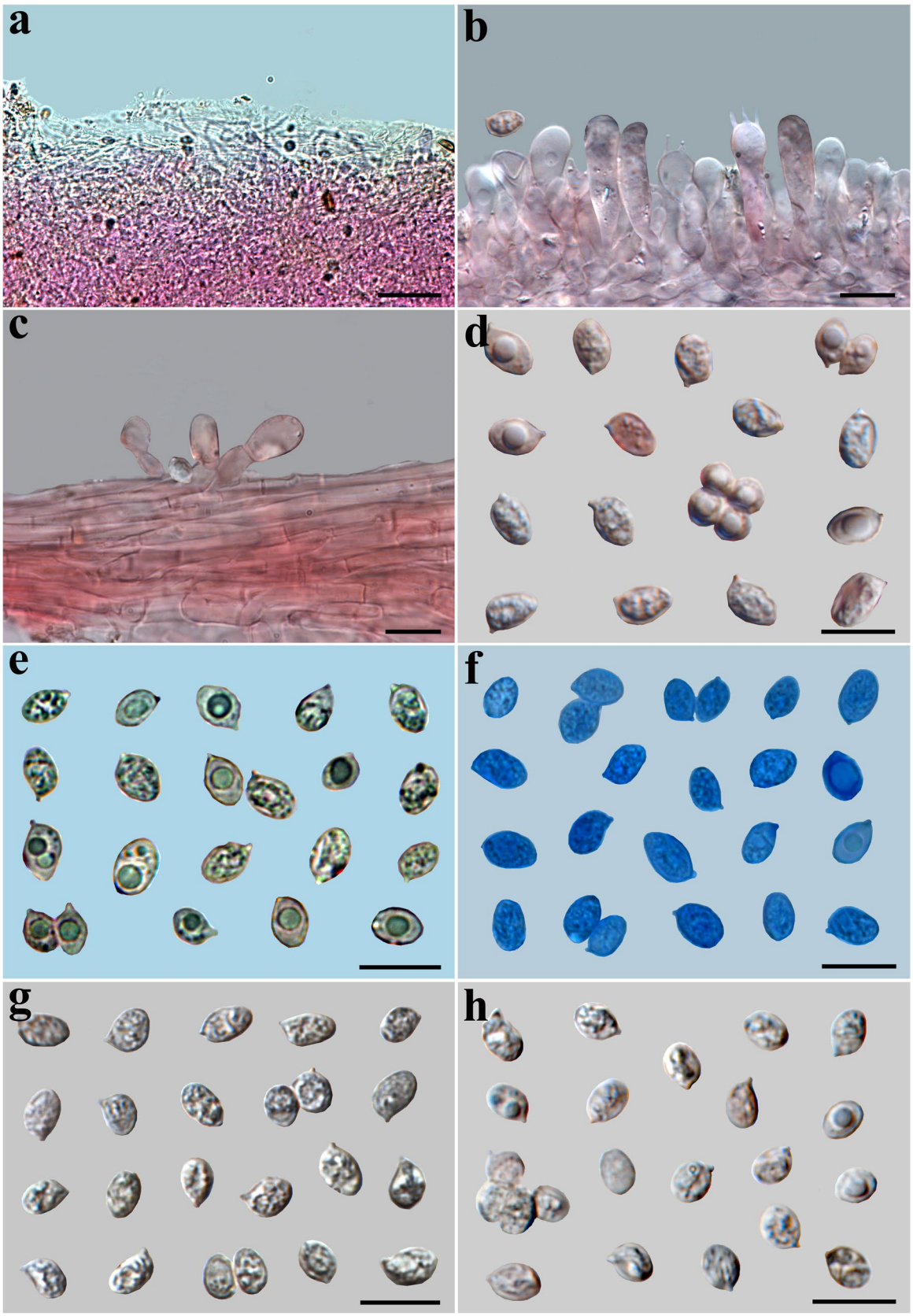
Etymology: from the Latin adjectives *parvus* (small) and *fallax* (false, fallacious), due to its similarity to *Lulesia fallax*, from which it differs especially by having smaller basidiomes and smaller basidiospores.

Diagnosis: It differs from *L. fallax* by smaller basidiomes and smaller basidiospores.

Holotype (here designated): **Switzerland**, Canton of Valais, municipality of Leuk, 572 m a.s.l., sunny, dry area on sandy, calcareous soil; the ground covered with mosses and lichens; nearby vegetation includes *Pinus sylvestris*, *Quercus pubescens*, and numerous bushes of *Berberis vulgaris*, 19 October 2024, leg. R. Rickmann, G00586348 (**Holotype**). GenBank: nrITS, PV780536; nrLSU, PX285936; *RPB2*, PX310534.

Description: *Pileus* 15–35(–45) mm diam., convex, soon applanate or depressed at centre, getting irregular when old. Margin involute when young, later more or less undulating, often crenulate, not striate. Surface smooth or slightly pruinose, dry, white, sometimes with cream (6A3–4) tinges, not hygrophanous, often concentrically cracking and showing a darker buff (6A5–6) context. *Lamellae* L = 25–40, l = 1–3, moderately crowded, decurrent, anastomosing, 1.5–3 mm broad, whitish, later tinged pinkish cream (5A2–4), edge smooth, concolorous. *Stipe* 10–35 × 2–5 mm, central or slightly eccentric attached, cylindrical, usually tapering downwards, smooth, solid, ivory white (4A1–2) to pale ochre beige (4A5–7), often with a tinge of pink (5A2–3) towards the base, with white rhizomorphs at the base. *Context* whitish. Smell not distinctive, taste strongly bitter. No part of the basidiome staining black. KOH on dried basidiome surfaces negative. *Spore-print* cream pink (6A2–3). *Basidiospores* (4.7–)5.0–*5.5*–5.9(–6.2) × (3.2–)3.5–*3.9*–4.3(–4.6) µm [60/2/1], Q = (1.26–)1.34–*1.43*–1.55(–1.63), V = (25.7–)34.3–*43.9*–57.9(–66.5), subamygdaliform in side view, ovoid-ellipsoid in frontal view, angular in polar view (5–7 facets), weakly nodulose-pustulate to verrucose in all views, rounded to slightly attenuated or subconical apically, often adhering in tetrads, usually thin-walled, rarely somewhat thick-walled, hilar appendage evident, up to 1 µm long, contents smooth, uni- to pluriguttulate (guttulae greenish in water), wall cyanophilic, pale yellow in water, yellow in Melzer's. *Basidia* 22–30 × 6–8 µm, cylindrical to clavate-cylindrical, usually with guttulate contents, mainly tetrasporic, rarely bisporic, sterigmata up to 6 µm long. *Subhymenium* 30–50 µm thick, consisting of irregular elements, up to 12 µm wide. *Hymenophoral trama* regular to subregular of parallel to slightly interwoven, cylindrical or inflated, thin-walled, hyaline, 4–14 µm wide hyphae. *Hymenial cystidia* absent. *Pileipellis* a xerocutis of thin-walled, 3–6 µm wide, subparallel to loosely intertwined cylindrical hyphae, sometimes inflated at septa, terminal elements inconspicuous, cylindrical, subclavate or subfusiform, with rounded apex, pigment absent or parietal, not incrusting, pale yellow. *Subpellis* poorly differentiated, of subparallel to loosely intertwined 3–6 µm wide hyaline hyphae. *Thromboplerous hyphae* not observed. *Stipitipellis* consisting of parallel, faintly yellowish, 3–5 µm wide cylindrical repent hyphae, terminal elements hardly differentiated. *Stipititrama* of hyaline, cylindrical, thin-walled, 5–9 µm wide hyphae. *Clamp connections* absent.

Habitat and distribution: Dry grassland on sandy, calcareous soil, accompanied by *Pinus sylvestris* and *Quercus pubescens*. So far only known from the type locality.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◂**Fig. 5** *Lulesia fallacioides*. Microscopic characters. **a** Pileipellis. **b** Hymenium (basidia). **c** Caulocystidia. **d–h** Basidiospores. **a–f** from OULU:GAJ.17962-T. Kekki (6670) Holotype, **g** from OULU:GAJ.17963-T. Kekki (6650), **h** from OULU:GAJ.11332-T. Kekki (3988). **a** in phloxine, **b–e**, **g**, **h** in Congo Red, **f** in Cotton Blue. **a–c**, **e–f** Bright-field microscopy, **d**, **g–h** interference contrast microscopy. Scale bars: **a** = 30 µm, **b–h** = 10 µm. Photos by M. Marchetti

Material examined: **Switzerland**, Canton of Valais, municipality of Leuk, 572 m a.s.l., sunny, dry area on sandy, calcareous soil; the ground covered with mosses and lichens; nearby vegetation includes *Pinus sylvestris*, *Quercus pubescens*, and numerous bushes of *Berberis vulgaris*; other fungal species observed in the vicinity were *Calocybe carnea* (Bull.) Donk, *Clitocybe barbularum* (Romagn.) P.D. Orton, *Entoloma coracis* Brandrud, Dima, Noordel., G.M. Jansen & Vila, *Infundibulicybe glareosa* (Röllin & Monthoux) Harmaja, *Lepiota pseudolilacea* Huijsman, *Lichenomphalia ericetorum* (Pers.) Voitk, Thorn & I. Saar and *Tulostoma melanocyclum* Bres.; 19 October 2024, leg. R. Rickmann (private herbarium no. RR24.326), G00586348 (**Holotype**).

Notes – *Lulesia parvifallax* is so far only known from the type locality in Switzerland. Its precise habitat requirements still need to be clarified through additional collections.

In the field, reliable distinction from closely related species is hardly possible. Apart from the habitat, only the rather small basidiomes with slender stipes may serve as an indication of *L. parvifallax*. However, microscopic differentiation is possible; see also Table 2.

Lulesia fallax and *L. fallacioides* differ by having slightly larger basidiospores, usually longer than 6 µm (Vizzini et al. 2023 and Table 2). Furthermore, *L. fallacioides* has an ixocutis. The recently described *L. neofallax* from China can be distinguished by very minute stipes (only 1–2 mm wide) and a lower spore quotient (Q = 1.2). So far, this species has not been recorded in Europe (Liu et al. 2025).

Despite the morphological similarity of *L. parvifallax* with the other white-capped species, it is molecularly quite distant from these in the multigene analysis (Fig. 1) while its closest relative is *L. blancii* (with an ITS sequence similarity of approximately 91%). *Lulesia blancii* shares with *L. parvifallax* similar basidiospore dimensions but it has usually significantly larger basidiomes (pileus up to 70(–100) mm broad), darker pileus colours, and is so far only known from Mediterranean regions (Ivaldi et al. 2023; Vizzini et al. 2023).

Lulesia neofallax (W.H. Lu, Karun. & Tibpromma) Vizzini & Cons., **comb. nov.**

MycoBank MB860685.

Basionym: *Clitocella neofallax* W.H. Lu, Karun. & Tibpromma, in Liu et al., Mycology 16(1): 26. (2025) [2024] [MB#571612].

In our analysis, *Clitocella neofallax* is phylogenetically part of *Lulesia* subgen. *Paraclitopilus* (Figs. 1 and 2) and it is combined above in *Lulesia* accordingly. The species is distinguished among the others within the *L. fallax* complex by gracile basidiomes, pileus 10–30 mm wide, dry, low convex, sometimes infundibuliform, with a shallow depression at the centre, stipe 10−25 × 1−2 mm, lamellae with evident yellowish hues even when young, basidiospores (4.0–)4.8–6.3 × (3.5–)4–5 µm, *Q* = 1.2 and very short basidia, 15−23.5 × 6−9 µm (Liu et al. 2025). It is so far known only from China (Yunnan Province, Qujing City, Qujing Normal University) on soil associated with bamboo roots.

Lulesia* subgen. *Lulesia Singer, Fl. Neotrop., Monogr. 3: 16 (1970).

Autonym.

Type: *Armillariella densifolia* Singer, in Singer & Digilio, Lilloa 25: 72 (1952) [1951].

Pileus usually pale grey, grey, dark grey, brown, violaceous black, basidiome surfaces unchanging or turning grey or black when bruised or with age, usually with a positive, reddish, KOH reaction, hymenophoral trama usually irregular (intertwined hyphae), and basidiospores globose, subglobose, broadly ellipsoid to ellipsoid, which are obscurely to clearly angular, and weakly to clearly pustulate.

Lulesia alachuana (Murrill) Singer, Fl. Neotrop., Monogr. 3: 17 (1970) Figs. 3i and j, 7, and 8

Basionym: *Clitocybe alachuana* Murrill, Proc. Florida Acad. Sci. 7 (2–3): 107 (1945).

Holotype: FLAS-F-17903, USA, Florida, Alachua, Prairie Creek Hammock, on dead leaves, 15 July 1938, leg. West, Arnold, and Murrill, det. Murrill.

Epitype: FLAS-F-61088 (Designated by Vizzini et al., Boll. Assoc. Micol. Ecol. Romana 39(3): 5. 2024). MycoBank MBT10017392.

Description: *Pileus* 20–80 mm diam., at first convex, soon depressed; surface hygrophanous, dry, subglabrous, at first covered with a minute white soon disappearing pruina (which often fragments concentrically) that persists on the margin, grey avellaneous, tan (5C5–7), brown (4E6–7), dark brown (1F5–7, 3F4–8, 4F6–7), sometimes with purplish-grey tones (7F2–5), margin incurved, uneven, undulate, lobed. *Lamellae* long decurrent, narrow, very close (crowded) L = 40–70, l = 1–3, some forked halfway, at the base and at the apex, entire, at first white, pale yellowish (3A7–8) when old, with pinkish tones (5A3–4), never turning grey black on handling or bruising, with an even, sinuous, concolorous or paler edge. *Stipe* 15–30 × 5–8 (–10) mm, usually equal, solitary, often flared at the apex, rarely attenuated at the base, at first white, then beige (5A3), cream avellaneous (6A3–4), white tomentose, especially at the base, with white rhizomorphs at the base. *Context* very thin, white, unchanging; *smell* not recorded

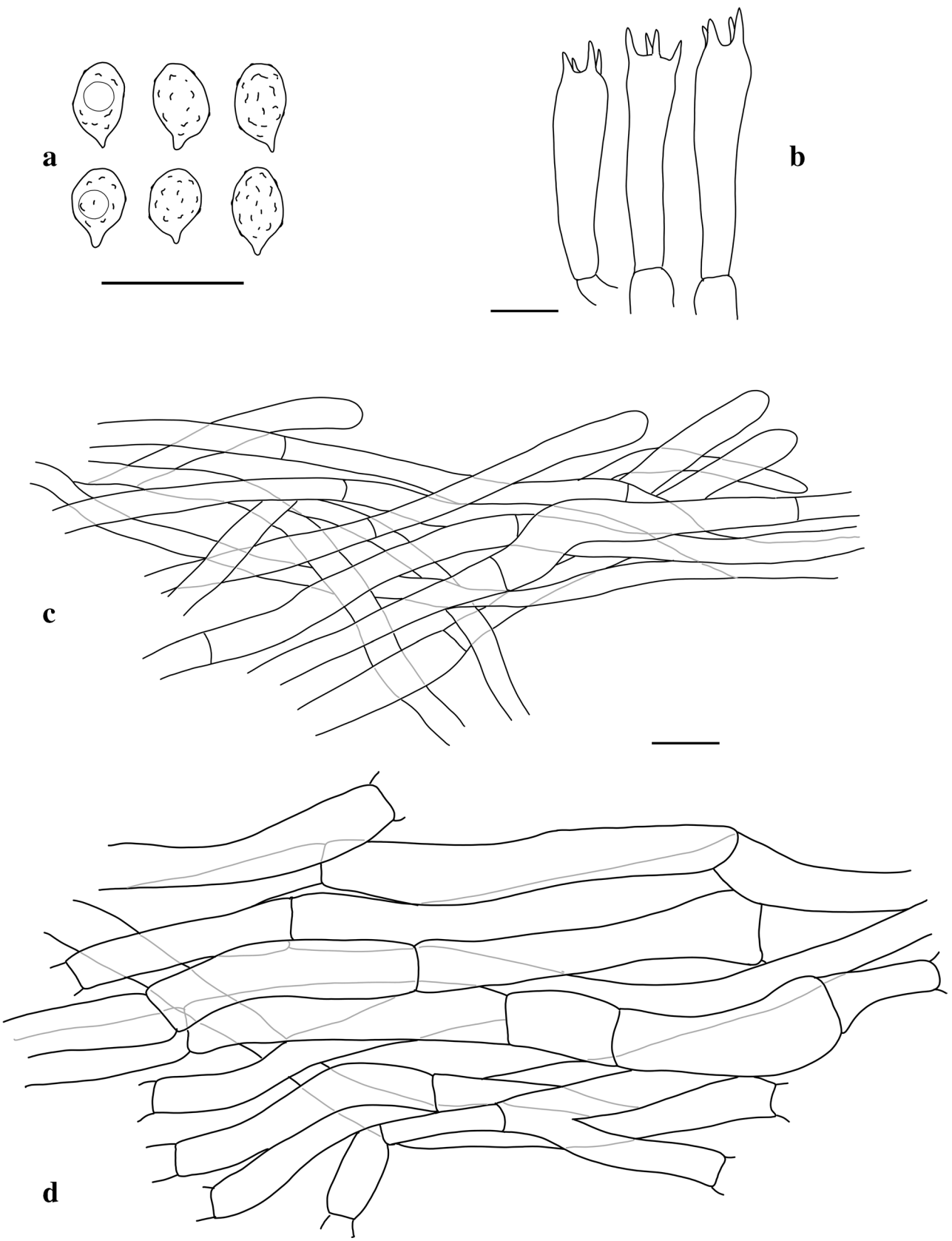
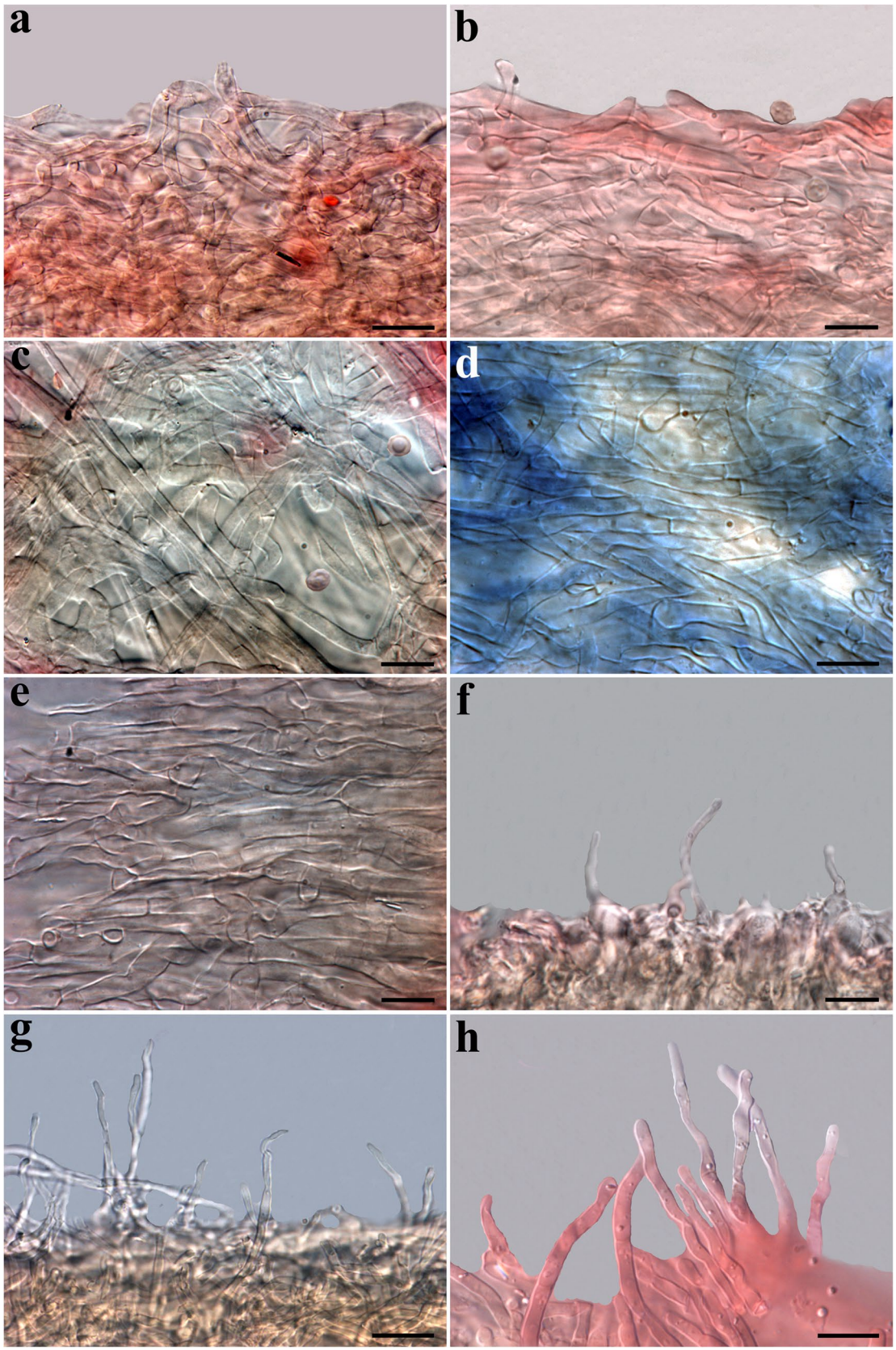


Fig. 6 *Lulesia parvifallax*. Microscopic characters (G00586348, Holotype). **a** Basidiospores. **b** Basidia. **c** Pileipellis. **d** Elements of the hymenophoral trama. Scale bars = 10 µm. Drawings by R. Rickmann

Table 2 Main distinguishing characters of the *Lulesia* subg. *Paraclitopilus* species

Character	*L. blancii* (data from Vizzini et al. 2023)	*L. fallax* (data from Vizzini et al. 2023)	*L. fallacioides* (this study)	*L. neofallax* (data from Liu et al. 2025)	*L. parvifallax* (this study)
Pileus colour	Alutaceous ochre, chamois to grey-brown,	White, sometimes with cream tinges	White, sometimes with cream tinges	White to greyish white	White, sometimes with cream tinges
Pileus size (mm)	20–70(–100)	10–50	10–50(–80)	10–30	15–35(–45)
Stipe width (mm)	2–8	2–7(–10)	2–7	1–2	2–5
Lamellae colour	Pale, yellowish cream, very late with pink tinges	Pale, then yellowish, finally tinged with pink	Sordid white, finally tinged with pink	Yellowish white to pale yellow	Whitish, later tinged pinkish cream
Average spore size (µm), Qm, Vm (µm^3)	5.0–*5.5*–6.1 × 3.6–*4.0*–4.4 µm *Q* = 1.24–*1.38*–1.51 *V* = 35.7–*47.4*–59.1	5.8–*6.6*–7.3 × 3.7–*4.1*–4.6 µm *Q* = 1.44–*1.60*–1.75 *V* = 42.1–*59.8*–77.4	5.9–*6.5*–7.2 × 4.4–*4.7*–5.1 µm *Q* = 1.27–*1.38*–1.50 *V* = 59.2–*76.8*–94.5	4.8–*5.3*–6.3 × 3.5–*4.1*–5 µm *Q* = 1.2	5.0–*5.5*–5.9 × 3.5–*3.9*–4.3 µm *Q* = 1.34–*1.43*–1.55 *V* = 34.3–*43.9*–57.9
Basidia size (µm)	18–30(–40) × 5.5–7(–7.5)	18–30 × (5–)6–11	18–30 × 7–10	15–23.5 × 6–9	22–30 × 6–8
Pileipellis type	Xerocutis	Xerocutis	Ixocutis	Xerocutis	Xerocutis
Habitat	Xerophilic species growing in the litter of coniferous and deciduous trees present in the Mediterranean basin	In deciduous forests and in grasslands, prefers nitrophilous, man-disturbed areas	In the thick needle litter under *Picea abies*	On the soil associated with bamboo roots	Dry grassland on sandy, calcareous soil, accompanied by *Pinus sylvestris* and *Quercus pubescens*
Distribution	North Africa and South Europe (Algeria, France, Italy and Spain)	Europe (widespread)	Europe (Fennoscandia) and North America (USA, Oregon)	Asia (China)	Europe (Switzerland)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◂**Fig. 7** *Lulesia alachuana*. **a**, **b** Pileipellis (FLAS-F-71949-iNaturalist-183000711, FLAS-F-61088, Epitype). **c** Pileipellis scalp (FLAS-F-71949-iNaturalist-183000711). **d**, **e** Hymenophoral trama (FLAS-F-71949-iNaturalist-183000711, FLAS-F-61088, Epitype). **f** Cystidioid (rare) hyphoid elements on the lamellar edge (FLAS-F-61088, Epitype). **g**, **h** Caulocystidia (FLAS-F-61088, Epitype, FLAS-F-71949-iNaturalist-183000711). **a**–**c**, **e**–**h** in Congo Red, **d** in Cotton Blue. **a**–**g** Bright-field microscopy, **h** interference contrast microscopy. Scale bars: **a** = 20 µm, **b**–**f**, **h** = 10 µm, **g** = 30 µm. Photos by M. Marchetti

(of light anise in FLAS-F-71949-iNaturalist-183000711), *taste* very bitter. *Spore-print* not obtained. Chemical spot-test reactions: KOH on pileus surface negative.

Basidiospores (4.3–)4.8–*5.1*–5.4(–6.0) × (3.6–)4.2–*4.5*–4.7(–5.2) µm [192/4/4], *Q* = (1.00–)1.06–*1.14*–1.21(–1.36), *V* = (33.3–)45.8–*54.0*–62.3(–75.6) µm^3, globose, subglobose up to broadly ellipsoid in side and frontal view, clearly angular (9–12 facets) especially when young, obscurely angular when mature, with small pustules or bumps, hilar appendage up to 1 µm long, contents smooth, uni- to pluriguttulate (guttulae greenish in water), wall cianophilic, faintly congophilic, hyaline to pale yellow in water, yellow in Melzer's (inamyloid). *Basidia* 18–30(–35) × 6.5–8 µm, cylindrical-clavate, tetrasporic, rarely bisporic, sterigmata up to 5 µm long, usually with guttulate greenish contents. *Subhymenium* 20–40 µm thick, consisting of textura intricata type short elements, 2–5 µm wide. *Hymenophoral trama* subregular, hyphae subparallel to intertwined, cylindrical, 2–8 µm wide, thick-walled (wall up to 0.6 µm thick), hyaline to faintly cream. *Hymenial cystidia* usually absent. In the collection FLAS-F-61088, cystidioid hyaline and thin-walled elements, subcylindrical, sinuous, 20–50 × 2–4 µm, are occasionally present on the lamellar edge (Fig. 7f). *Pileipellis* as a xerocutis with cylindrical, mostly intertwined hyphae, 2.5–6(–7) µm wide, thick-walled (wall up to 0.6 µm thick), hyaline, smooth, the more superficial ones reclined to ascendant, hyaline or with a pale yellow cytoplasmatic pigment, pileocystidia not observed; *thromboplerous hyphae* absent. *Subpellis* of subparallel to loosely intertwined 3–8 µm wide hyaline hyphae. *Stipitipellis* as a cutis consisting of subparallel to intertwined loose hyphae, 2–5 µm wide, faintly yellowish; *caulocystidia* as dense tufts of reclining to erect hyphoid elements, often multiseptate, straight to wavy, short to long, 30–100(–150) × 2–4 µm, with an obtuse to acute apex, sometimes also subcapitate, smooth or with an epiparietal pigment in patches. *Stipititrama* made up of parallel subcylindrical, 3–7 µm wide, hyaline hyphae, thin- to thick-walled (wall up to 0.5 µm thick). *Clamp connections* absent.

Material examined: **USA**, Florida, Alachua, Prairie Creek Hammock, 29.598463 −82.247989 ± 1600 m, on dead leaves, 15 July 1938, leg. West, Arnold & Murrill, FLAS-F-17903 (**Holotype**, as *Clitocybe alachuana*); Florida, Alachua, Gainesville, 29.66636 −82.32993 ± 8000 m, trash in rich hammock, 08 August 1939, leg. E. West, det. WA Murrill, FLAS-F-19879 (as *C. alachuana*); Florida, Putnam County, Ordway-Swisher Biological Station, Mill Creek Swamp Bridge, 30.80138 −86.292863, on decorticate wood, *Quercus* and palm tree dominated swamp, 06 July 2017, leg. D. Borland & B. Kaminsky, det. ME Smith (as cf. *Clitocella*), FLAS-F-61088 (**Epitype**), duplo in CORT014753, det. TJ Baroni (as *Lulesia alachuana*); Florida, Melrose, Putnam County, Ordway-Swisher Biological Station, 29.71900833 −81.97166333, on the ground in highly decayed litter and also very decayed wood of hardwoods, 12 September 2023, leg. F. Sheffer, FLAS-F-71949-iNaturalist-183000711(https://www.inaturalist.org/observations/183000711) (as *Clitocella* sp.).

Notes – *Lulesia alachuana*, originally described from Florida (Murrill 1944, Alachua County, *inde nomen*, from which the species name derives), is so far known only from Florida (Table 1 and Fig. 1). The present full description of the species is the first to be provided after the original one by Murrill (1944). Due to its greyish brown pileus, pileipellis as a cutis, subglobose, slightly angular, undulate pustulate or nearly smooth spores, a hymenophoral trama of interwoven hyphae, and bitter taste (Murrill 1944; Bigelow 1982; our observations), *L. alachuana* is also morphologically a good member of *Lulesia* subgen. *Lulesia*, as molecularly supported in the multigene analysis (Fig. 1) where it is sister to a strongly supported clade (BP = 95%, PP = 1.00) consisting of *L. mundula*, *L. obscura*, and *L. popinalis* (all with greyish colours, irregular hymenophoral trama, and red reaction to KOH). Because of its subglobose spores 5.1 × 4.5 µm, Q = 1.14 on average, and growth on forest (hardwood) litter, *L. alachuana* seems quite close to *L. mundula* and in fact it was considered a later synonym of the latter by some authors [e.g. T. Baroni's handwritten notes (1978) accompanying the holotype collection of *Clitocybe alachuana* (FLAS-F-17903), https://www.mycoportal.org/portal/collections/individual/index.php?occid=604249&clid=0; Baroni (1981); Bigelow (1982, 1985); Singer (1986)]. It morphologically seems to differ from *L. mundula* mainly by a darker and hygrophanous pileus (brown, dark brown versus white, pale cream, beige-ochraceous), a non-blackening context, a pileus surface with negative KOH reaction (greyish brown versus red), and different nrDNA sequences (Fig. 1; Vizzini et al. 2024 and our observations).

Lulesia colorata (L. Fan & N. Mao) T.J. Baroni, N. Niveiro & B.E. Lechner, in Baroni, Lechner & Niveiro, Index Fungorum 566: 1 (2023) Figs. 3g and h and 4b

Basionym: *Clitocella colorata* L. Fan & N. Mao, in Mao, Lv, Xu, Zhao & Fan, MycoKeys 88: 161 (2022).

Holotype: BJTC FM1891.

For full descriptions (as *Clitocella colorata*) see Mao et al. (2022) and Vizzini et al. (2023)

Material examined: **Finland**, Etelä-Karjala, Kouvola, somewhat springfed spruce-hardwood swamp, 19 September 1994, leg. I. Kytövuori (as *Rhodocybe* cf. *mundula*), det. T. Kekki, H6042258 (H). **Italy**. Lombardia, Pavia, Brallo di Pregola, under *Fagus sylvatica*, 15 October 2022, leg. M. Carbone, TUR-A 216670; Emilia-Romagna, Piacenza, Ferriere, Loc. Le Moline, mixed forest with *Quercus cerris*, *Q. pubescens*, and *Ostrya carpinifolia*, 12 October 2019, leg. et det. M. Carbone & F. Calledda (as *Clitocella mundula*), TUR-A 216671.

Notes – *Lulesia colorata* (as *Clitocella colorata*) has recently been described from China (Shanxi province, North China or Huabei) on soil or rotten wood in coniferous (*Pinus*) or broad-leaved (*Quercus*) forest (Mao et al. 2022). The Chinese authors highlighted that also a North American collection named as *C. mundula* (TJB7599 (AFTOL-ID 521) USA, NY) clustered within the *C. colorata* clade. In the original description, no reference is made to a possible colour change of the basidiome surfaces, its smell and taste are not reported, and the hymenophoral trama is indicated as regular (Mao et al. 2022). In their monographic work on the genus *Clitocella* in Europe, Vizzini et al. (2023), based on molecular data and new collections (from Italy-Veneto and Estonia in mixed coniferous forests) highlighted that *C. colorata* has (1) a wider geographical distribution, and it is also present in India, South Korea, USA (Arkansas, Indiana, New York, Tennessee, Wisconsin), and in Europe (France, Italy–Veneto, and Estonia) (Fig. 1); (2) pileus, lamellae, and stipe surface stain strongly black when bruised or in age, smell is farinaceous, taste is bitter, and the hymenophoral trama is subregular at first but then irregular and composed of interwoven hyphae. Our present analysis allows to extend the geographical distribution of this species to Finland and the Italian regions of Lombardy and Emilia-Romagna and to confirm the additional features provided by Vizzini et al. (2023), including also the blackening of basidioma surfaces. Consequently, an emended combination of characters circumscribes *L. colorata* such as clitocyboid basidiomes (strongly depressed pileus), a usually pale-coloured pileus surface (white to yellowish white, greyish white to greyish brown, pink-white), the surfaces of the basidiome turning black when old or on handling and showing no reddish reaction in KOH, farinaceous smell and bitter taste, (4.7–)5.1–*5.5*–5.9(–6.8) × (3.7–)4.1–*4.3*–4.6(–5.0) µm, (globose) subglobose to broadly ellipsoid basidiospores slightly angular and with minute pustules or bumps, hyphae of pileipellis with pale yellow to yellowish brown intracellular and/or parietal pigment, and growth in coniferous or angiospermous forests (Mao et al. 2022; Vizzini et al. 2023; our observations).

Morphologically, *C. colorata* can be easily confused with *C. mundula* and *C. popinalis* which, however, have dried basidiome surfaces producing a reddish reaction with KOH (Baroni 1981; Moreau 1997; Kluting et al. 2014; Vizzini et al. 2023). Indeed, many collections that clustered in the *L. colorata* clade (Fig. 1) were originally identified as *C. mundula* or *C. popinalis* (Fig. 1 and Tab. 1). Additionally, *C. mundula* differs in the obscurely angular basidiospores with indistinct pustules or bumps (Baroni 1981; Neukom 1994; Moreau 1997) and *C. popinalis* in basidiome surfaces usually unchanging on handling, a dark-coloured pileus slightly depressed only in senescing basidiomes, its association with grasses, and slightly broader and longer basidiospores (Baroni 1981; Moreau 1997; Overall 2011; Kluting et al. 2014; Jian et al. 2020a).

Lulesia solaris (Musumeci, Cons. & Vizzini) Musumeci, Cons. & Vizzini, in Vizzini, Alvarado, Cons., Angelini & Marchetti, Boll. Assoc. Micol. Ecol. Romana 39(3): 8. (2024) [2023]. Fig. 4f

Basionym: *Clitocella solaris* Musumeci, Cons. & Vizzini, in Vizzini et al., Persoonia 50: 144 (2023).

Holotype: LUG 19882.

For a full description (as *C. solaris*) see Vizzini et al. (2023).

Material examined: **Finland**, Kittilän Lappi, Kolari, *Pinus sylvestris* forest near limestone quarry, 16 August 2001, leg. I. Kytövuori (as *Rhodocybe caelata*), det. T. Kekki (H6043012).

Notes – The species was recently described from France (Département Haut-Rhin, Alsace) as gregarious on moss pads (*Rhacomitrium canescens*) in open and sunny areas (with seedlings of *Betula pubescens* and at some distance (at least 30 m) two *Pinus sylvestris* trees, on sandy-pebbly, alluvial soil, silty substrate rich in woody debris and carbonate). Until the present work, it was so far known only from the *locus typicus* (Vizzini et al. 2023). *Lulesia solaris* is distinguished by a unique combination of characters such as the small-sized basidiomes (pileus not exceeding 10 mm diam), a whitish cream pileus surface with a positive (red) KOH reaction, distant (spaced) lamellae, an unchanging, not staining black context, subfarinaceous smell and taste, absence of hymenial cystidia, and clearly angular, subglobose, broadly ellipsoid to ellipsoid basidiospores with evident bumps in Cotton Blue. In the present work, a Finnish 24-year-old collection misidentified as *Rhodocybe caelata* (H6043012, see above) turned out to be conspecific with *L. solaris* (Fig. 1). It was found on calcareous soil and close to *Pinus sylvestris* trees as the holotype collection. Molecularly, *L. solaris* is sister (BP = 99%, PP = 1.00) to a clade formed by *L. colorata* and *L. orientalis* (Fig. 1), species which show larger basidiomes, a negative KOH reaction, crowded lamellae, and differently shaped basidiospores (Jian et al. 2020a; Mao et al. 2022; Vizzini et al. 2023 and our observations). *Lulesia popinalis* has a larger pileus and stipe, a usually dark-coloured pileus surface (purplish grey, brownish

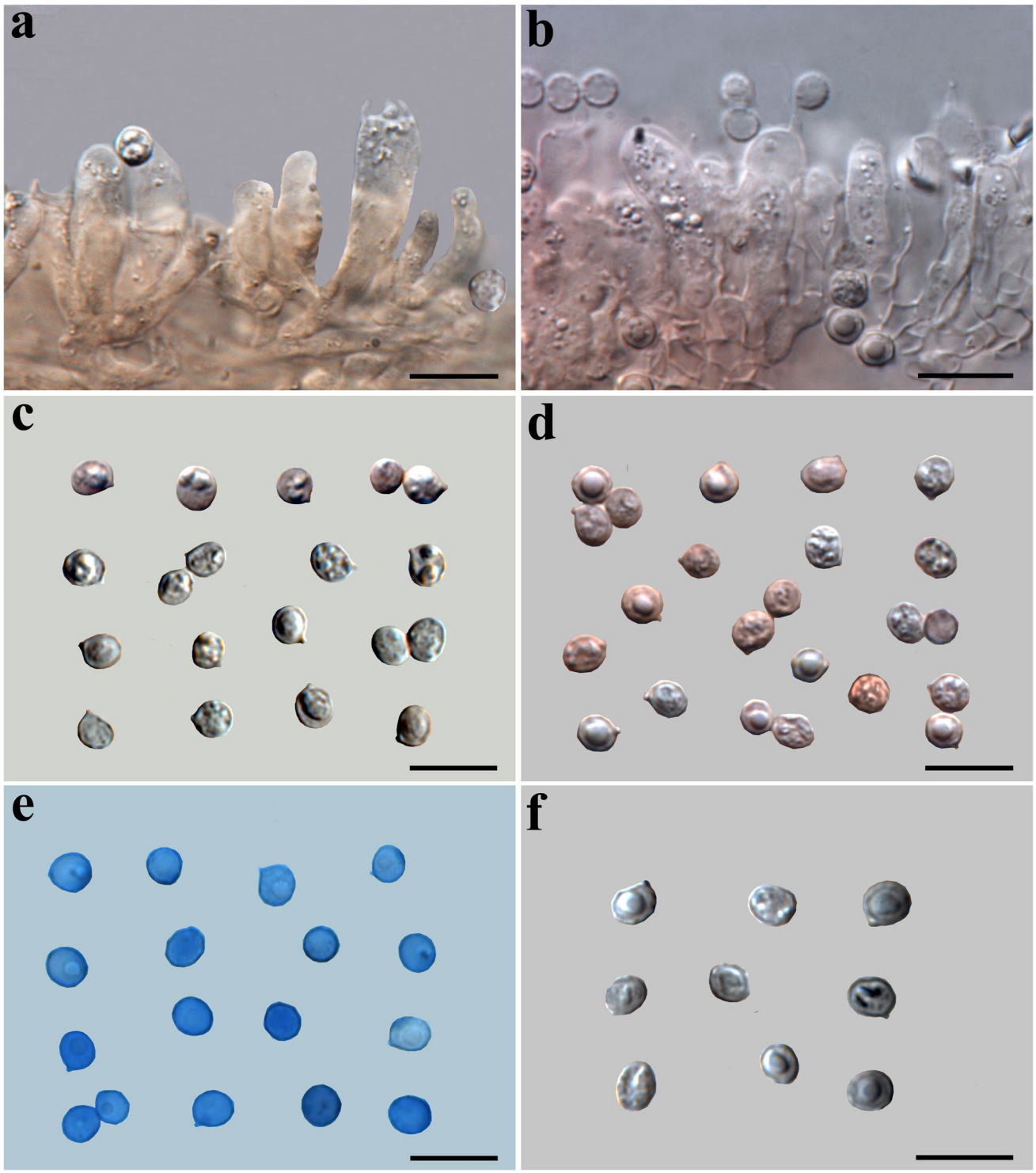

Fig. 8 *Lulesia alachuana*. **a**, **b** Hymenium (basidia and developing spores) (FLAS-F-61088, Epitype, FLAS-F-71949-iNaturalist-183000711). **c**–**f** Basidiospores (FLAS-F-19879, FLAS-F-71949-iNaturalist-183000711, FLAS-F-71949-iNaturalist-183000711, FLAS-F-61088, Epitype). **a**–**d**, **f** in Congo Red, **e** in Cotton Blue. Scale bars = 10 µm. All photos in interference contrast microscopy. Photos by M. Marchetti

grey, blackish grey), crowded lamellae, and subglobose to broadly ellipsoid wider basidiospores (5.1 µm on average) (Vizzini et al. 2023).

Discussion

The morphological delimited *L. fallax* species complex is part of *Lulesia* subgen. *Paraclitopilus* (pallid *Clitopilus*-like coloured basidiomes, regular to subregular hymenophoral trama made up of parallel to slightly intertwined cylindrical hyphae, negative KOH reaction, and often adhering in tetrads spores; Vizzini et al. 2023). The *L. fallax* complex consists of species sharing a bitter taste, a white-pruinose pileus reminding *Clitocybe* sect. *Candicantes* (Quél.) Singer & Digilio species and often in association with coniferous trees. This species complex encompasses *L. fallax*, *L. neofallax*, and the two new species *L. fallacioides* and *L. parvifallax*, which are all very similar taxa morphologically differentiated almost only based on the size of the basidiomes and the basidiospores (Table 2). These species, together with those gravitating around *L. mundula* of *Lulesia* subgen. *Paraclitopilus*, viz. *L. popinalis*, *L. solaris*, and *L. colorata*, could be considered cryptic taxa, namely species exhibiting shallow morphological differences (morphological stasis, deceleration of morphological evolution), but considerable genetic disparity (Bickford et al. 2007; Grebenc et al. 2009; Korhonen et al. 2018; Struck et al. 2018a, b; Korshunova et al. 2019; Peintner et al. 2019; Cerca et al. 2020; Struck and Cerca 2019, 2022; Ekanayaka et al. 2025). Cryptic species could be considered the opposite of adaptive radiation (pronounced morphological differences, shallow genetic divergence) (Cerca et al. 2020; Struck and Cerca 2019, 2022) and, a priori, they could result from recent speciation, parallelism, convergence, or stasis (Struck and Cerca 2019, 2022). Molecular analyses (Vizzini et al. 2023, 2024; Figs. 1 and 2 in the present paper) would indicate that the phenomena of evolutionary convergence and parallelism should be excluded for the appearance of cryptospecies in *Lulesia*.

Examples of morphological stasis are commonplace in other rhodocyboid fungi, viz. the *Rhodophana nitellina* complex (Anil Raj et al. 2016; Dima et al. 2018; Buyck et al. 2021; Papetti 2023), and the *Rhodocybe gemina* complex (Crous et al. 2017; Sesli and Vizzini 2017; Vizzini et al. 2018; Silva-Filho et al. 2020; Dutta et al. 2021; Sun and Bau 2023).

As all the species covered in the present paper show difficulty in morphological distinction, these may have been misdetermined in the past, and a greater scrutiny and increased sequencing of historical and modern collections are now imperative before any conclusions can be drawn regarding more precise distribution and rarity data for each of these species in the world.

The occurrence of *L. fallax* in North America (Baroni 1981) and The Netherlands (Noordeloos 1988) is based on presumably heterogeneous collections and thus gives rise to collective descriptions (basidiospores 6.5–8 × 4–5(–6.5) µm and 5.0–8.5 × 3.5–5.0 µm-Q 1.4–2.0, respectively). So, the presence of the true *L. fallax* in North America and The Netherlands is still questionable. No sequences in the public databases obtained by Dutch fungal collections clustered within *Lulesia* subg. *Paraclitopilus* and the *L. fallax* complex (Figs. 1 and 2). The only sequences from an American collection named *C. fallax* (OKM:25668, USA-Oregon) represent the new species *L. fallacioides* (Fig. 1). Two ITS environmental sequences from USA (Utah) (UDB03879566 and UDB03879567) and two basidiomatal sequences (USA-California and China-Xizang) (PP594830 and PV124053) clustered in a clade (*Lulesia* sp. 2) within *Lulesia* subg. *Paraclitopilus* (Fig. 2) which probably represents a distinct not yet described species.

Swiss specimens growing on bare soil of a riparian forest named *Rhodocybe fallax* (Breitenbach & Kränzlin 1995), characterized by gracile, diminutive omphaloid basidiomes (pileus 10–20 mm wide, infundibuliform, stipe 10–30 × 1.5–3 mm) with basidiospores 7–8.6 × 3.8–4.8 (Q = 1.7–1.9, V = 76) and resembling *Clitopilus* sect. *Scyphoides* Singer (Singer 1986; Jian et al. 2020b), are macromorphologically similar to those cited in Baroni (1981). They will have to be further studied and molecularly checked to ascertain their taxonomic status.

Finally, the presence of *L. fallax*, *L. mundula*, and *L. obscura* in Finland is here molecularly confirmed for the first time (Figs. 1 and 2 and see Fig. 4 and Table 1).

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Author contribution AV and GC conceived the study, IK, TK, and RR conducted sampling and provided materials, MM and RR performed all microscopy analyses mentioned in this study, AV performed the laboratory experiments and prepared all figures and tables, and GC analysed the sequence data. AV wrote the manuscript with contributions from all authors. All authors agreed with the submission of the manuscript.

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Data availability Sequence data have been deposited in GenBank as given in Table 1 and alignments in Figshare (https://doi.org/10.6084/m9.figshare.29654816).

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interests The authors declare no competing interests.

References

Agerer R (2018) Subphylum *Agaricomycotina* Doweld. In: Frey W (ed) Begerow D, Agerer R, McTaggart A, *Basidiomycota* and *Entorhizomycota*. A. Engler's Syllabus of Plant Families, part 1/3. Borntraeger, Stuttgart, pp 130–444

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. J Mol Biol 215(3):403–410

Alvarado P, Manjón JL, Matheny PB, Esteve-Raventós F (2010) *Tubariomyces*, a new genus of *Inocybaceae* from the Mediterranean region. Mycologia 102(6):1389–1397. https://doi.org/10.3852/10-041

Alvarado P, Moreno G, Manjón JL (2012) Comparison between *Tuber gennadii* and *T. oligospermum* lineages reveals the existence of the new species *T. cistophilum* (*Tuberaceae*, *Pezizales*). Mycologia 104(4):894–910. https://doi.org/10.3852/11-254

Angelini C, Contu M (2012) *Lulesia densifolia* (*Basidiomycota, Agaricomycetes*) rinvenuta nella Repubblica Dominicana (Caraibi). Boll Assoc Micol Ecol Romana 86(2):20–24

Anil Raj KN, Deepna Latha KP, Iyyappan R, Manimohan P (2016) *Rhodophana squamulosa* - a new species of *Entolomataceae* from India. Mycoscience 57(2):90–95. https://doi.org/10.1016/j.myc.2015.10.001

Arita M, Karsch-Mizrachi I, Cochrane G (2021) The international nucleotide sequence database collaboration. Nucleic Acids Res 49:D121–D124. https://doi.org/10.1093/nar/gkaa967

Baroni TJ (1978) Chemical spot-test reactions – boletes. Mycologia 70(5):1064–1076

Baroni TJ (1981) A revision of the genus *Rhodocybe* Maire (*Agaricales*). Nova Hedwigia Beih 67:1–194

Baroni TJ, Hofstetter V, Largent DL, Vilgalys R (2011) *Entocybe* is proposed as a new genus in the *Entolomataceae* (*Agaricomycetes, Basidiomycota*) based on morphological and molecular evidence. N Am Fungi 6(12):1–19

Baroni TJ, Angelini C, Bergemann SE, Lodge DJ, Lacey L, Curtis TA, Cantrell SA (2020) *Rhodocybe-Clitopilus* clade (*Entolomataceae, Basidiomycota*) in the Dominican Republic: new taxa and first reports of *Clitocella, Clitopilus,* and *Rhodocybe* for Hispaniola. Mycol Progr 19:1083–1099. https://doi.org/10.1007/s11557-020-01619-y

Bickford D, Lohman DJ, Sodhi NS, Ng PK, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends Ecol Evol 22(3):148–155. https://doi.org/10.1016/j.tree.2006.11.004

Bigelow HE (1982) Species described in *Clitocybe* by C.H. Peck and W.A. Murrill. Sydowia 35:37–74

Bigelow HE (1985) North American species of *Clitocybe*. Part II. Nova Hedwig Beih 81:281–471

Breitenbach J, Kränzlin F (1995) Champignons de Suisse. Tome 4. Champignons à lames, 2ème partie. Ed Mykologia, Luzern

Buyck B, Eyssartier G, Dima B, Consiglio G, Noordeloos ME, Papp V, Bera I, Ghosh A, Rossi W, Leonardi M, Das K (2021) Fungal biodiversity profiles 101–110. Cryptogam Mycol 20(5):63–89. https://doi.org/10.5252/cryptogamie-mycologie2021v42a5

Cerca J, Meyer C, Stateczny D, Siemon D, Wegbrod J, Purschke G, Dimitrov D, Struck TH (2020) Deceleration of morphological evolution in a cryptic species complex and its link to paleontological stasis. Evolution 74(1):116–131. https://doi.org/10.1111/evo.13884

Clémençon H (1972) Zwei verbesserte Präparierlösungen für die microskopische Untersuchung von Pilzen. Z Pilzkd 38:49–53

Co-David D, Langeveld D, Noordeloos ME (2009) Molecular phylogeny and spore evolution of *Entolomataceae*. Persoonia 23:147–176

Contu M (1999) Ecologia e tassonomia del genere *Rhodocybe* R. Maire (*Basidiomycetes*, *Entolomataceae*) in Sardegna. Rev Catalana Micol 22:5–14

Crous PW, Wingfield MJ, Burgess TI, Hardy GESJ, Barber PA, Alvarado P, Barnes CW, Buchanan PK, Heykoop M, Moreno G, Thangavel R, van der Spuy S, Barili A, Barrett S, Cacciola SO, Cano-Lira JF, Crane C, Decock C, Gibertoni TB, Guarro J, Guevara-Suarez M, Hubka V, Kolařík M, Lira CRS, Ordoñez ME, Padamsee M, Ryvarden L, Soares AM, Stchigel AM, Sutton DA, Vizzini A, Weir BS, Acharya K, Aloi F, Baseia IG, Blanchette RA, Bordallo JJ, Bratek Z, Butler T, Cano-Canals J, Carlavilla JR, Chander J, Cheewangkoon R, Cruz RHSF, da Silva M, Dutta AK, Ercole E, Escobio V, Esteve-Raventós F, Flores JA, Gené J, Góis JS, Haines L, Held BW, Jung MH, Hosaka K, Jung T, Jurjević Ž, Kautman V, Kautmanova I, Kiyashko AA, Kozanek M, Kubátová A, Lafourcade M, La Spada F, Latha KPD, Madrid H, Malysheva EF, Manimohan P, Manjón JL, Martín MP, Mata M, Merényi Z, Morte A, Nagy I, Normand AC, Paloi S, Pattison N, Pawłowska J, Pereira OL, Petterson ME, Picillo B, Raj KNA, Roberts A, Rodríguez A, Rodríguez-Campo FJ, Romański M, Ruszkiewicz-Michalska M, Scanu B, Schena L, Semelbauer M, Sharma R, Shouche YS, Silva V, Staniaszek-Kik M, Stielow JB, Tapia C, Taylor PWJ, Toome-Heller M, Vabeikhokhei JMC, van Diepeningen AD, Van Hoa N, M VT, Wiederhold NP, Wrzosek M, Zothanzama J, Groenewald JZ (2017). Fungal Planet description sheets: 558–624. Persoonia 38:240–384 https://doi.org/10.3767/003158517X698941

Cubeta MA, Echandi E, Abernethy T, Vilgalys R (1991) Characterization of anastomosis groups of binucleate *Rhizoctonia* species using restriction analysis of an amplified ribosomal RNA gene. Phytopathology 81:1395–1400

Dima B, Papp V, Szabó E, Brandrud TE, Noordeloos ME, Kovács GM (2018) Revealing the phylogenetic relationship in the *Rhodophana nitellina* complex. Poster abstract. State of the World's Fungi Symposium, 13–14 Sept 2018, Royal Botanic Gardens Kew, London p. 41

Dutta AK, Gates GM, Rakshit S, Acharya K (2021) *Rhodocybe brunneoaurantiaca* (sect. *Rufrobrunnea*, *Entolomataceae*): a new species from India. Nord J Bot 39(6):e03061 https://doi.org/10.1111/njb.03061

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32(5):1792–1797

Ekanayaka AH, Karunarathna SC, Tibpromma S, Dutta AK, Tennakoon DS, Karunarathna A, Chukeatirote E, Dai D-Q, Stephenson SL, Maharachchikumbura SSN, Liu C, Phillips AJL (2025) Species evolution: cryptic species and phenotypic noise with a particular focus on fungal systematics. Front Cell Infect Microbiol 15:1497085. https://doi.org/10.3389/fcimb.2025.1497085

Eyssartier G, Roux P (2011) Le guide des champignons France et Europe. Belin, Paris, p 1120

Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rusts. Mol Ecol 2(2):113–118. https://doi.org/10.1111/j.1365-294x.1993.tb00005.x

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences (with discussion). Statist Sci 7(4):457–472

Gouy M, Guindon S, Gascuel O (2010) Seaview version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Mol Biol Evol 27(2):221–224. https://doi.org/10.1093/molbev/msp259

Grebenc T, Martín MP, Kraigher H (2009) Ribosomal ITS diversity in the European species of the genus *Hydnum* (*Hydnaceae*). Anales Jard Bot Madrid 66S1:121–132

Gross G (1972) Kernzahl und Sporenvolumen bei einigen Hymenogasterarten. Z Pilzkd 38:109–158

Hartley AJ, de Mattos-Shipley K, Collins CM, Kilaru S, Foster GD, Bailey AM (2009) Investigating pleuromutilin-producing *Clitopilus* species and related basidiomycetes. FEMS Microbiol Lett 297(1):24–30

He M-Q, Zhao R-L, Hyde KD, Begerow D, Kemler M, Yurkov A, McKenzie EHC, Raspé O, Kakishima M, Sánchez-Ramírez S, Vellinga EC, Halling R, Papp V, Zmitrovich IV, Buyck B, Ertz D, Wijayawardene NN, Cui B-K, Schoutteten N, Liu X-Z, Li T-H, Yao Y-J, Zhu X-Y, Liu A-Q, Li G-J, Zhang M-Z, Ling Z-L, Cao B, Antonín V, Boekhout T, da Silva BDB, De Crop E, Decock C, Dima B, Dutta AK, Fell JW, Geml J, Ghobad-Nejhad M, Giachini AJ, Gibertoni TB, Gorjón SP, Haelewaters D, He S-H, Hodkinson BP, Horak E, Hoshino T, Justo A, Lim YW, Menolli N, Mešić A, Moncalvo J-M, Mueller GM, Nagy LG, Nilsson RH, Noordeloos M, Nuytinck J, Orihara T, Ratchadawan C, Rajchenberg M, Silva-Filho AGS, Sulzbacher MA, Tkalčec Z, Valenzuela R, Verbeken A, Vizzini A, Wartchow F, Wei T-Z, Weiß M, Zhao C-L, Kirk PM (2019) Notes, outline and divergence times of *Basidiomycota*. Fungal Divers 99(1):105–367. https://doi.org/10.1007/s13225-019-00435-4

He M-Q, Cao B, Liu F, Boekhout T, Denchev TT, Schoutteten N, Denchev CM, Kemler M, Gorjón SP, Begerow D, Valenzuela R, Davoodian N, Niskanen T, Vizzini A, Redhead SA, Ramírez-Cruz V, Papp V, Dudka VA, Dutta AK, García-Sandoval R, Liu X-Z, Kijpornyongpan T, Savchenko A, Tedersoo L, Theelen B, Trierveiler-Pereira L, Wu F, Zamora JC, Zeng X-Y, Zhou L-W, Liu S-L, Ghobad-Nejhad M, Giachini AJ, Li G-J, Kakishima M, Olariaga I, Haelewaters D, Sulistyo B, Sugiyama J, Svantesson S, Yurkov A, Alvarado P, Antonín V, da Silva AF, Druzhinina I, Gibertoni TB, Guzmán-Dávalos L, Justo A, Karunarathna SC, Galappaththi MCA, Toome-Heller M, Hosoya T, Liimatainen K, Márquez R, Mešić A, Moncalvo J-M, Nagy LG, Varga T, Orihara T, Raymundo T, Salcedo I, Silva-Filho AGS, Tkalčec Z, Wartchow F, Zhao C-L, Bau T, Cabarroi-Hernández M, Cortés-Pérez A, Decock C, De Lange R, Weiss M, Menolli N, Nilsson RH, Fan Y-G, Verbeken A, Gafforov Y, Meiras-Ottoni A, Mendes-Alvarenga RL, Zeng N-K, Wu Q, Hyde KD, Kirk PM, Zhao R-L (2024) Phylogenomics, divergence times and notes of orders in *Basidiomycota*. Fungal Divers 126(1):127–406. https://doi.org/10.1007/s13225-024-00535-w

He Z-M, Yang ZL (2022) The genera *Bonomyces*, *Harmajaea* and *Notholepista* from Northwestern China: two new species and a new record. Mycol Progress 21(2):26. https://doi.org/10.1007/s11557-022-01786-0

Hofstetter V, Clémençon H, Vilgalys R, Moncalvo J-M (2002) Phylogenetic analyses of the *Lyophylleae* (*Agaricales, Basidiomycota*) based on nuclear and mitochondrial rDNA sequences. Mycol Res 106(9):1043–1059. https://doi.org/10.1017/S095375620200641X

Ivaldi P, Maurice JP, Suberbielle N, Domergue P, Normand A-C (2023) *Clitocella blancii*, un champignon méditerranéen. Bull Fed Assoc Mycol Mediterr 64:17–31

Jian S-P, Bau T, Zhu X-T, Deng W-Q, Yang Z-L, Zhao Z-W (2020a) *Clitopilus, Clitocella,* and *Clitopilopsis* in China. Mycologia 112(2):371–399. https://doi.org/10.1080/00275514.2019.1703089

Jian S-P, Karadelev M, Wang P-M, Deng W-Q, Yang Z-L (2020b) *Clitopilus abprunulus*, a new species from North Macedonia with notes on *C. ravus* and pleuromutilin producing taxa. Mycol Prog 19:805–816. https://doi.org/10.1007/s11557-020-01603-6

Kalichman J, Kirk PM, Matheny PB (2020) A compendium of generic names of agarics and *Agaricales*. Taxon 69(3):425–447. https://doi.org/10.1002/tax.12240

Kim CS, Jo JW, Kwag YN, Sung GH, Lee SG, Kim SY, Shin CH, Han SK (2015) Mushroom flora of Ulleung-gun and a newly recorded *Bovista* species in the Republic of Korea. Mycobiology 43(3):239–257. https://doi.org/10.5941/MYCO.2015.43.3.239

Kluting KL, Baroni TJ, Bergemann SE (2014) Toward a stable classification of genera within the *Entolomataceae*: a phylogenetic re-evaluation of the *Rhodocybe-Clitopilus* clade. Mycologia 106(6):1127–1142. https://doi.org/10.3852/13-270

Korhonen A, Seelan JSS, Miettinen O (2018) Cryptic species diversity in polypores: the *Skeletocutis nivea* species complex. MycoKeys 36:45–82. https://doi.org/10.3897/mycokeys.36.27002

Kornerup JH, Wanscher A (1984) Methuen handbook of colour, 3rd edn. Eyre Methuen, London, p 252

Korshunova T, Picton B, Furfaro G, Mariottini P, Pontes M, Prkić J, Fletcher K, Malmberg K, Lundin K, Martynov A (2019) Multilevel fine-scale diversity challenges the 'cryptic species' concept. Sci Rep 9(1):6732. https://doi.org/10.1038/s41598-019-42297-5

Kour H, Kumar S, Sharma YP, Nandi S, Acharya K (2016) *Clitocella* (*Entolomataceae*) - a new genus record for India. Stud Fungi 1(3):130–134. https://doi.org/10.5943/sif/1/1/13

Lechner BE, Wright JE, Popoff O (2006) New taxa and new records for Argentina from Iguazú National Park, Misiones. Fungal Divers 21:131–139

Liu S-L, Zhao P, Cai L, Shen S, Wei H-W, Na Q, Han M, Wei R, Ge Y, Ma H, Karunarathna SC, Tibprommab S, Zhang B, Dai D, Lin L, Fan X-L, Luo Z-L, Shen H-W, Lu L, Lu W, Xu RF, Tohtirjap A, Wu F, Zhou L-W (2025) Catalogue of fungi in China 1. New taxa of plant-inhabiting fungi. Mycology 16(1):1–58. https://doi.org/10.1080/21501203.2024.2316066

Maddison WP, Maddison DR (2023) Mesquite: a modular system for evolutionary analysis. Version 3.81. http://www.mesquiteproject.org. Accessed 20 May 2025

Mao N, Lv J-C, Xu Y-Y, Zhao T-Y, Fan L (2022) Two new *Clitocella* species from North China revealed by phylogenetic analyses and morphological characters. MycoKeys 88:151–170

Matheny PB, Wang Z, Binder M, Curtis JM, Lim YW, Nilsson RH, Hughes KW, Hofstetter V, Ammirati JF, Schoch CL, Langer E, Langer G, McLaughlin DJ, Wilson AW, Frøslev T, Ge ZW, Kerrigan RW, Slot JC, Yang ZL, Baroni TJ, Fischer M, Hosaka K, Matsuura K, Seidl MT, Vauras J, Hibbett DS (2007) Contributions of rpb2 and tef1 to the phylogeny of mushrooms and allies (*Basidiomycota, Fungi*). Mol Phylogenet Evol 43(2):430–451. https://doi.org/10.1016/j.ympev.2006.08.024

Meerts P (1999) The evolution of spores in agarics: do big mushrooms have big spores? J Evol Biol 12:161–165. https://doi.org/10.1046/j.1420-9101.1999.00020.x

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA, pp 1–8. https://doi.org/10.1109/GCE.2010.5676129

Moncalvo JM, Vilgalys R, Redhead SA, Johnson JE, James TY, Catherine Aime M, Hofstetter V, Verduin SJ, Larsson E, Baroni TJ, Greg Thorn R, Jacobsson S, Clémençon H, Miller OK Jr (2002) One hundred and seventeen clades of euagarics. Mol Phylogenet Evol 23(3):357–400. https://doi.org/10.1016/S1055-7903(02)00027-1

Moreau PA (1997) Le genre *Rhodocybe* Maire: quelques observations sur le groupe *R. mundula-R. popinalis*. Bull Soc mycol Fr 113(4):343–354 + atlas pl. 336–339

Morgado LN, Noordeloos ME, Hausknecht A (2016) *Clitopilus reticulosporus*, a new species with unique spore ornamentation, its phylogenetic affinities and implications on the spore evolution theory. Mycol Prog 15(3):26. https://doi.org/10.1007/s11557-016-1165-0

Mullis K, Faloona FA (1987) Specific synthesis of DNA *in vitro* via a polymerase-catalyzed chain reaction. Methods Enzymol 155:335–350. https://doi.org/10.1016/0076-6879(87)55023-6

Murray MG, Thompson WF (1980) Rapid isolation of high molecular weight plant DNA. Nucleic Acids Res 8(19):4321–4325. https://doi.org/10.1093/nar/8.19.4321

Murrill WA (1944) New Florida fungi. Proc Fla Acad Sci 7(2/3):107–127

Neukom H-P (1994) Pilz des Monats. *Rhodocybe mundula* (Lasch: Fr.) Sing. im Vergleich mit *Rhodocybe popinalis* (Fr.) Sing. Ein Beitrag zur Klärung zweier kritischer Arten. Schweiz Z Pilzkd 5–6:113–122

Noordeloos ME (1988) Rhodocybe Maire. In: Bas C, Kuyper TW, Noordeloos ME, Vellinga EC (eds) Flora Agaricina Neerlandica, vol I. Balkema, Rotterdam, pp 77–82

Noordeloos ME (2012) *Rhodocybe* Maire. In: Knudsen H, Vesterholt J (eds) Funga Nordica, vol 2, 2nd edn. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera. Nordsvamp, Copenhagen, pp 576–579

Overall A (2011) Fungi royale. Some interesting larger fungi of the Royal Parks – Part 2 saprobes. Field Mycol 12(1):26–30. https://doi.org/10.1016/j.fldmyc.2010.12.008

Papetti C (2023) *Rhodophana almae-lunae* una nuova specie del gruppo di *Rhodophana nitellina*. Riv Micol 66(3):195–208

Peintner U, Kuhnert-Finkernagel R, Wille V, Biasioli F, Shiryaev A, Perini C (2019) How to resolve cryptic species of polypores: an example in *Fomes*. IMA Fungus 10:1–21. https://doi.org/10.1186/s43008-019-0016-4

Rehner SA, Buckley E (2005) A *Beauveria* phylogeny inferred from nuclear ITS and EF1-a sequences: evidence for cryptic diversification and links to *Cordyceps* teleomorphs. Mycologia 97(1):84–98. https://doi.org/10.3852/mycologia.97.1.84

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61(3):539–542. https://doi.org/10.1093/sysbio/sys029

Sesli E, Vizzini A (2017) Two new *Rhodocybe* species (sect. *Rufobrunnea*, *Entolomataceae*) from the East Black Sea coast of Turkey. Turk J Bot 41:200–210. https://doi.org/10.3906/bot-1607-1

Silva-Filho AGS, Baroni TJ, Komura DL, Moncalvo JM, Baseia IG, Wartchow F (2020) *Rhodocybe fusipes* (*Entolomataceae*), a new species from amazonian 'terra-firme' forest of Brazil. Sydowia 72:163–170 https://doi.org/10.12905/0380.sydowia72-2020-0163

Singer R (1951) The A*garicales* in modern taxonomy. Lilloa 22:5–832

Singer R (1970) *Omphalineae* (*Clitocybeae-Tricholomataceae, Agaricales*). Fl Neotrop Monogr 3:1–80

Singer R (1986) The *Agaricales* in modern taxonomy, 4th rev ed. Koeltz, Koenigstein, p 981

Singer R, Digilio APL (1951) Pròdromo de la flora agaricina argentina. Lilloa 25:5–461

Stamatakis A (2014) RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9):1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Struck TH, Feder JL, Bendiksby M, Birkeland S, Cerca J, Gusarov VI, Kistenich S, Larsson KH, Liow LH, Nowak MD, Stedje B, Bachmann L, Dimitrov D (2018a) Finding evolutionary processes hidden in cryptic species. Trends Ecol Evol 33(3):153–163. https://doi.org/10.1016/j.tree.2017.11.007

Struck TH, Feder JL, Bendiksby M, Birkeland S, Cerca J, Gusarov VI, Kistenich S, Larsson KH, Liow LH, Nowak MD, Stedje B, Bachmann L, Dimitrov D (2018b) Cryptic species - more than terminological chaos: a reply to Heethoff. Trends Ecol Evol 33(5):310–312. https://doi.org/10.1016/j.tree.2018.02.008

Struck TH, Cerca J (2019) Cryptic species and their evolutionary significance. Encyclopaedia of life sciences. Wiley, Chichester pp 1–9. https://doi.org/10.1002/9780470015902.a0028292

Struck TH, Cerca J (2022) Connecting micro- and macro-evolutionary research: extant cryptic species as systems to understand macro-evolutionary stasis. In Monro AK & Mayo S J (eds) Cryptic species. Morphological stasis, circumscription, and hidden diversity. Systematics Association Special Volume 89, Cambridge University Press, pp 143–168 https://doi.org/10.1017/9781009070553.006

Sun Y-L, Bau T (2023) *Rhodocybe subasyae*, a new species of *Rhodocybe* sect. *Rufobrunnea* (*Entolomataceae*, *Agaricales*) from northeast China. Mycoscience 64(3):96–100. https://doi.org/10.47371/mycosci.2023.03.001

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. Mol Biol Evol 30(12):2725–2729. https://doi.org/10.1093/molbev/mst197

Thiers BM (2025). Index Herbariorum. https://sweetgum.nybg.org/science/ih/. Accessed 22 Sept 2025

Varga T, Krizsán K, Földi C, Dima B, Sánchez-García M, Sánchez-Ramírez S, Szöllősi GJ, Szarkándi JG, Papp V, Albert L, Andreopoulos W, Angelini C, Antonín V, Barry KW, Bougher NL, Buchanan P, Buyck B, Bense V, Catcheside P, Chovatia M, Cooper J, Dämon W, Desjardin D, Finy P, Geml J, Haridas S, Hughes K, Justo A, Karasiński D, Kautmanova I, Kiss B, Kocsubé S, Kotiranta H, LaButti KM, Lechner BE, Liimatainen K, Lipzen A, Lukács Z, Mihaltcheva S, Morgado LN, Niskanen T, Noordeloos ME, Ohm RA, Ortiz-Santana B, Ovrebo C, Rácz N, Riley R, Savchenko A, Shiryaev A, Soop K, Spirin V, Szebenyi C, Tomšovský M, Tulloss RE, Uehling J, Grigoriev IV, Vágvölgyi C, Papp T, Martin FM, Miettinen O, Hibbett DS, Nagy LG (2019) Megaphylogeny resolves global patterns of mushroom evolution. Nat Ecol Evol 3(4):668–678. https://doi.org/10.1038/s41559-019-0834-1

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. J Bacteriol 172(8):4238–4246. https://doi.org/10.1128/jb.172.8.4238-4246.1990

Vizzini A, Ferrari RJ, Ercole E, Fellin A (2018) A new species of *Rhodocybe* sect. *Rufobrunnea* (*Entolomataceae*, *Agaricales*) from Italy. MycoKeys 36:21–33. https://doi.org/10.3897/mycokeys.36.27094

Vizzini A, Consiglio G, Marchetti M (2023) Overview of the European species of the genus *Clitocella* (*Entolomataceae, Agaricales*) with notes on extralimital taxa. Persoonia 50:123–157. https://doi.org/10.3767/persoonia.2023.50.04

Vizzini A, Alvarado P, Consiglio G, Angelini C, Marchetti M (2024) [2023] *Lulesia* Singer (1970), an older name for *Clitocella* Kluting, T.J. Baroni & Bergemann (2014, *Entolomataceae*). RMR, Boll Assoc Micol Ecol Romana numero speciale (fuori serie) 2023 (3):3–23 https://doi.org/10.57624/AMER.2023.18

von Bonsdorff T, Kytövuori I, Vauras J, Huhtinen S, Halme P, Rämä T, Kosonen L, Jakobsson S (2014) Sienet ja metsien luontoarvot 27:1–272

White TJ, Bruns TD, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky J, White TJ (eds) PCR protocols: a guide to methods and applications. Academic Press, London, pp 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1

Xiao Y-Q, Xu Y-D, Chen Z-H, He Z-M (2024) *Lulesia umbrinomarginata* (*Entolomataceae*, *Agaricales*), a newly discovered species from Southern China. Phytotaxa 650(1):060–072 https://doi.org/10.11646/phytotaxa.650.1.5