



A novel species of *Lepiota* sect. *Lepiota* (Agaricaceae) from Jammu and Kashmir, India

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ABSTRACT: *Lepiota rufobrunnea* is proposed as a new species from Jammu and Kashmir, India based on morphological characteristics and phylogenetic analyses of the internal transcribed spacer (ITS) nrDNA region. *Lepiota rufobrunnea* was found on dead and decayed debris of needles of *Cedrus deodara*. It is characterized by light brown to brownish orange pileus with obtuse reddish-brown umbo covered with scales in concentric fashion, with snow white, hairy cortinate appendages, pileus covering a trichoderm type composed of elongate thick-walled elements with granular contents. A comprehensive description, illustrations, and comparisons with morphologically similar and related taxa are provided.

KEY WORDS: *Cedrus deodara*, ITS-rDNA, *Lepiota oreadiformis*, *Lepiota rufobrunnea*, mushrooms, phylogeny, taxonomy.

INTRODUCTION

Lepiota (Pers.) S.F. Gray is a saprophytic genus in the Agaricaceae, with over 500 species recorded from tropical to temperate regions of the world (Vellinga, 2004; Kirk *et al.*, 2008; Asif *et al.*, 2022; Ahamed *et al.*, 2023). Until now, around 37 distinct *Lepiota* species have been described from India; however, the majority of species were described based only on morphology and lack molecular data support (Kumar and Manimohan, 2009; Kumari *et al.*, 2012; Ahamed *et al.*, 2023). *Lepiota* species have varied types of pileus shapes (convex to applanate or campanulate) with squamulose pileus surfaces, mostly with light to white spore print (occasionally pinkish). Microscopically, this genus exhibits a variety of basidiospore shapes ranging from broadly ellipsoid, ellipsoid, spurred to fusiform with a smooth surface and a dextrinoid, non-metachromatic nature; more frequent presence of cheilocystidia than pleurocystidia; and the presence of clamp connections in all tissues (Vellinga, 2003; Sysouphanthong *et al.*, 2016; Kaygusuz, 2022); the presence of several forms of pileal covering, including hymeniderm, cutis, trichoderm, epithelium, and a normal regular hymenophoral trama. The pileipellis and the shape of the basidiospores are the primary characteristics that allow dividing the genus *Lepiota* further into multiple sections (Vellinga, 2001a; Niazi *et al.*, 2021; Asif *et al.*, 2022). Molecular evidence has shown that the genus *Lepiota* is polyphyletic. Through extensive multigene phylogenetic analyses, members of the genus have been categorized into different sections (Sysouphanthong *et al.*, 2011).

The genus *Lepiota* consists of six sections, namely sect. *Lilaceae* M. Bon., sect. *Stenosporae* J.E. Lange, sect.

Lepiota (Pers.) Gray, sect. *Echinatae* Fay., sect. *Fuscovinaceae* Bon & Candusso, and sect. *Ovisporae* (J.E. Lange) Kühner, (Kirk *et al.*, 2008; Sysouphanthong *et al.*, 2011; Niazi *et al.*, 2021; Asif *et al.*, 2022). The section *Echinatae* has even been regarded as a section of *Cystolepiota* by Knudsen (1978), but was later removed from both *Lepiota* and *Cystolepiota* (Knudsen 1980) and treated as a separate genus, *Echinoderma* (Locq. ex Bon) Bon. However, Vellinga (2003) regarded this genus as *L. sect. Echinatae*. Some other mycologists have also adopted *L. sect. Echinatae* (Liang 2007; Sysouphanthong *et al.*, 2011; Razaq *et al.*, 2013). At present members of sect. *Echinatae* now placed partly within *Lepiota*, and partly in its own genus i.e. *Echinoderma* (Maruyama *et al.*, 2017; Hou and Ge, 2020).

The fusiform to amygdaliform basidiospores with convex abaxial and convex adaxial sides, or a straight abaxial side, the pileus covering composed of long cylindrical elements with or without short clavate elements at the base, and the presence of clamp connections are the characteristics that define the members of section *Lepiota* (Vellinga, 2001a). Unfortunately, physical differences alone were used to classify many species into many sections, which was far from sufficient to differentiate between species within various sections (Vellinga and Huijser, 1998). Consequently, the accurate delineation of taxa has been aided by the development of molecular phylogeny based on multigene sequence data (Asif *et al.*, 2022).

Various systematic studies were carried out to investigate and inventory the lepiotaceous fungal diversity in the understudied areas of the Union Territory of Jammu and Kashmir, India. In the course of these investigations, a fascinating and unidentified species of *Lepiota* was found.



Based on morphological and molecular data, this species is here proposed as new to science and with detailed phylogeny and comprehensive macro- and micro-morphological descriptions along with drawings.

MATERIALS AND METHODS

Site description

The Jammu and Kashmir, India, extends from 32° 17' N to 37° 05' N latitude and from 72° 31' E to 80° 20' E longitude, covering a total area of 42, 241 km² and receiving an average rainfall of 1030 mm per year. This vast geographical area rich in forests, has a varied topography, and various climatic regimes. The present new species was collected from the Bhandarwah forest division (Jai Valley) of the district of Doda in Jammu and Kashmir in a coniferous forest dominated by *Cedrus deodara*.

Macro- and micromorphology

Fresh basidiomata were collected and photographed in the field using a Nikon D5300 camera. Macro-morphological characteristics, habit, habitat, and soil type were also noted. The samples were carefully dug out of the soil and dried. The terminology of macro-morphology is in accordance with Vellinga (1988). Colour codes were designated according to Kornerup and Wanscher (1978). All anatomical details were observed from dried samples by making freehand sections that were mounted in either 5% KOH, 1% phloxine or 1% Congo red (Largent *et al.*, 1977) and examined under an Olympus CH20i compound microscope. Micromorphological features such as shape and size of basidiospores, cheilocystidia, basidia, and elements of pileipellis and stiptipellis covering were observed using a light microscope and were drawn with a camera lucida at 2000× magnification. Photomicrographs of the various elements were captured with a digital camera attached to an Olympus CX33 compound microscope. Seventy-five basidiospores were measured from each of the three specimens and two different collections in 10% ammonia and amyloidity was checked in Melzer's reagent (Largent *et al.*, 1977). Basidiospore measurements are represented as minimum-mean-maximum length × minimum-mean-maximum width and $Q = \text{length}/\text{width}$ ratio, with Q_m the average Q of all basidiospores. Twenty-five measurements were made of basidia and cheilocystidia. Basidium length excludes the length of the sterigmata. The terminologies used for descriptions follow Vellinga (2001b). The dried specimens were deposited in the HBJU Herbarium, Department of Botany, University of Jammu, Jammu & Kashmir, India.

DNA extraction, PCR amplification, and sequencing

A Plant II Kit (Macherey-Nagel) was used to isolate nuclear genomic DNA from 100 mg of dried basidiomata. The ITS-rDNA regions were amplified following Verma

et al. (2023). The universal primer pairs ITS1F (5'-TCCGTAGGTGAACCTGCGG-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') were used to amplify the entire ITS-rDNA region of the nuclear ribosomal DNA (White *et al.*, 1990; Gardes and Bruns, 1993). PCR amplification reactions were carried out in a 20 µl reaction volume that contained 1X Phire PCR buffer (mixed with 1.5 mM MgCl₂), 0.2 mM each of dNTPs, 1 µl DNA, 0.2 µl Phire Hotstart II DNA polymerase enzyme, 0.1 mg/ml BSA, 3% DMSO, 0.5M betaine, and 5 pM of forward and reverse primers. The thermal profile of PCR for ITS-rDNA was carried out in a PCR thermal cycler (Gene Amp PCR System 9700, Applied Biosystems). The thermal cycler protocol used in the amplification of nrITS regions involved: an initial denature step of 94 °C for 4 min., then a repeat of 35 cycles that included a denaturation step of 94 °C for 1 min., an annealing step of 52 °C (ITS-rDNA). The PCR products were purified with the QIAquick Gel Extraction Kit (QIAGEN, Germany) and then subjected to Sanger sequencing in an automated DNA sequencer (ABI3730xl DNA Analyzer, Applied Biosystems, USA). The newly generated ITS-rDNA sequence was deposited in GenBank (PP331855).

Dataset representation

The initial BLASTn search results with the newly amplified sequence of the collected *Lepiota* species in the GenBank database revealed the best matches with species in *Lepiota* sect. *Lepiota* viz., *Lepiota elseae* A. Caball., Vizzini, G. Muñoz & Contu, *L. erminea* (Fr.) P. Kumm., *Lepiota cremea* Kaygusuz, and *L. clypeolaria* (Bull.) P. Kumm. Thus, ITS-rDNA sequences from species belonging to *Lepiota* sect. *Lepiota* were included in the phylogenetic analyses based on the BLAST search result and previous published phylogenetic studies (Ahamed *et al.*, 2023). The sequences of *Chlorophyllum molybdites* (G. Mey.) Masee, *Leucoagaricus infuscatus* Vellinga and *Leucocoprinus cretaceus* (Bull.) Locq. were included in the dataset as outgroup taxa based on earlier studies by Zhang *et al.* (2019) and Roy *et al.* (2023). The details of the all the sequences used in the phylogenetic analyses are presented in Table 1.

Sequence alignment

The ITS-rDNA sequences were aligned using MAFFT v.7.427 (Katoh & Standley, 2013) with default settings. The alignment was checked and trimmed manually with BioEdit v.7.0.9 (Hall, 1999). Statistical selection for the best fit models of nucleotide substitution for the dataset was performed by jModelTest 2.1.10 v. 20160303 (Darriba *et al.*, 2012) on XSEDE using CIPRES web portal (Miller *et al.*, 2011). The GTR+G model was chosen as the most suitable for performing the phylogenetic analyses due to its lowest BIC values of 12950.284113.

**Table 1.** Information of nrITS sequences retrieved for phylogenetic purpose, their sequence accession number, country of origin and reference to published work from which they were obtained. The bold text denotes present study.

Taxon	GenBank Accession number	Country of origin	Reference
<i>Chlorophyllum molybdites</i>	AY081243	USA	Unpublished
<i>Lepiota alba</i>	MN810115	China	Hou and Ge, 2020.
<i>Lepiota albofloccosa</i>	OP954870	India	Ahamed <i>et al.</i> , 2023.
<i>Lepiota angusticystidiata</i>	KP177192	China	Liang <i>et al.</i> , 2018.
<i>Lepiota attenuata</i>	EU681776	China	Liang <i>et al.</i> , 2011.
<i>Lepiota clypeolaria</i>	MN810127	China	Hou and Ge, 2020.
<i>Lepiota cortinarius</i>	EU416306	China	Liang <i>et al.</i> , 2010
<i>Lepiota cremea</i>	OL630458	Turkey	Kaygusuz, 2022.
<i>Lepiota cremea</i>	OL630459	Turkey	Kaygusuz, 2022.
<i>Lepiota cf. erminea</i>	MK651624	China	Unpublished
<i>Lepiota cf. erminea</i>	MK651626	China	Unpublished
<i>Lepiota echinella</i>	AY176366	Belgium	Vellinga, 2004.
<i>Lepiota elseae</i>	KP640556	Spain	Caballero <i>et al.</i> , 2015.
<i>Lepiota erminea</i>	OL527680	Germany	Sarawi <i>et al.</i> , 2022
<i>Lepiota erminea</i>	AY176470	Netherlands	Vellinga, 2003.
<i>Lepiota eurysperma</i>	HQ718462	Thailand	Sysouphanthong <i>et al.</i> , 2011
<i>Lepiota eurysperma</i>	MW054212	Loas	Unpublished
<i>Lepiota felina</i>	EU416286	China	Liang <i>et al.</i> , 2010.
<i>Lepiota forquignonii</i>	AY176370	Netherlands	Vellinga, 2004.
<i>Lepiota ignivolva</i>	AY176473	France	Vellinga, 2003.
<i>Leucoagaricus infuscatus</i>	EU141943	USA	Vellinga, 2007.
<i>Lepiota kuehneriana</i>	GU199360	China	Liang <i>et al.</i> , 2011
<i>Lepiota kuehneriana</i>	MK651627	China	Unpublished
<i>Lepiota magnispora</i>	MN810126	China	Hou and Ge, 2020.
<i>Lepiota mengei</i>	MN810131	China	Hou and Ge, 2020.
<i>Lepiota metulispora</i>	MK651632	China	Liang <i>et al.</i> , 2011.
<i>Lepiota oreadiformis</i>	MW554391	China	Unpublished
<i>Lepiota oreadiformis</i>	GU199361	China	Liang <i>et al.</i> , 2011
<i>Lepiota pseudolilacea</i>	EU416304	China	Liang <i>et al.</i> , 2011.
<i>Lepiota rufobrunnea</i>	PP331855	India	Present study
<i>Lepiota sp.</i>	MN810129	China	Hou and Ge, 2020.
<i>Lepiota spheniscispora</i>	AF391001	USA	Vellinga, 2001a.
<i>Lepiota subgracilis</i>	EU416290	China	Liang <i>et al.</i> , 2010.
<i>Lepiota thrombophora</i>	MK651651	China	Liang <i>et al.</i> , 2011.
<i>Lepiota xanthophylla</i>	AY176405	Netherlands	Vellinga, 2004.
<i>Leucocoprinus cretaceus</i>	AY176447	Malaysia	Vellinga, 2004.

Phylogenetic analyses

The ITS dataset was analysed by Maximum Likelihood (ML) and Bayesian Inference (BI) methods utilizing the best fit model (GTR+G). RAXMLHPC2 v.8.2.12 (Stamatakis, 2014) was used to conduct an ML analysis on the CIPRES NSF XSEDE resource. The quick bootstrap approach with 1000 replicates was applied to calculate nodal support values. A BI analysis was carried out with MrBayes v. 3.2.2 (Ronquist *et al.*, 2012) using MCMC methods (Geyer, 1991) under the GTR+G model. Markov chains were iterated 1,000,000 times until the standard deviation of split frequencies decreased below the threshold of 0.01. Trees were sampled every 100th generation. The first 25% of trees were removed as burn-in, and the remaining trees were utilized to determine group posterior probabilities (PP). The phylogenetic trees generated were visualized in FigTree v.1.4.4. (Rambaut,

2018). Values of at least 50% for Maximum Likelihood Bootstrap (MLBS) and at least 0.50 for Bayesian Posterior Probabilities (BPP) are displayed in the phylogenetic tree (Figure 1).

RESULTS

Phylogenetic inferences: The relationships among the species of *Lepiota* were determined through ML and BA analyses based on ITS-rDNA region sequence data (Figure 1). The alignments consisted of a total of 753 characters, with gaps included. There are 463 unique alignment patterns with 20.17% gaps and characters that are completely undetermined. The estimated base frequencies were as follows: A = 0.229473, C = 0.215007, G = 0.230859, T = 0.324661; substitution rates: AC = 1.288494, AG = 3.997761, AT = 1.338164, CG = 0.603028, CT =

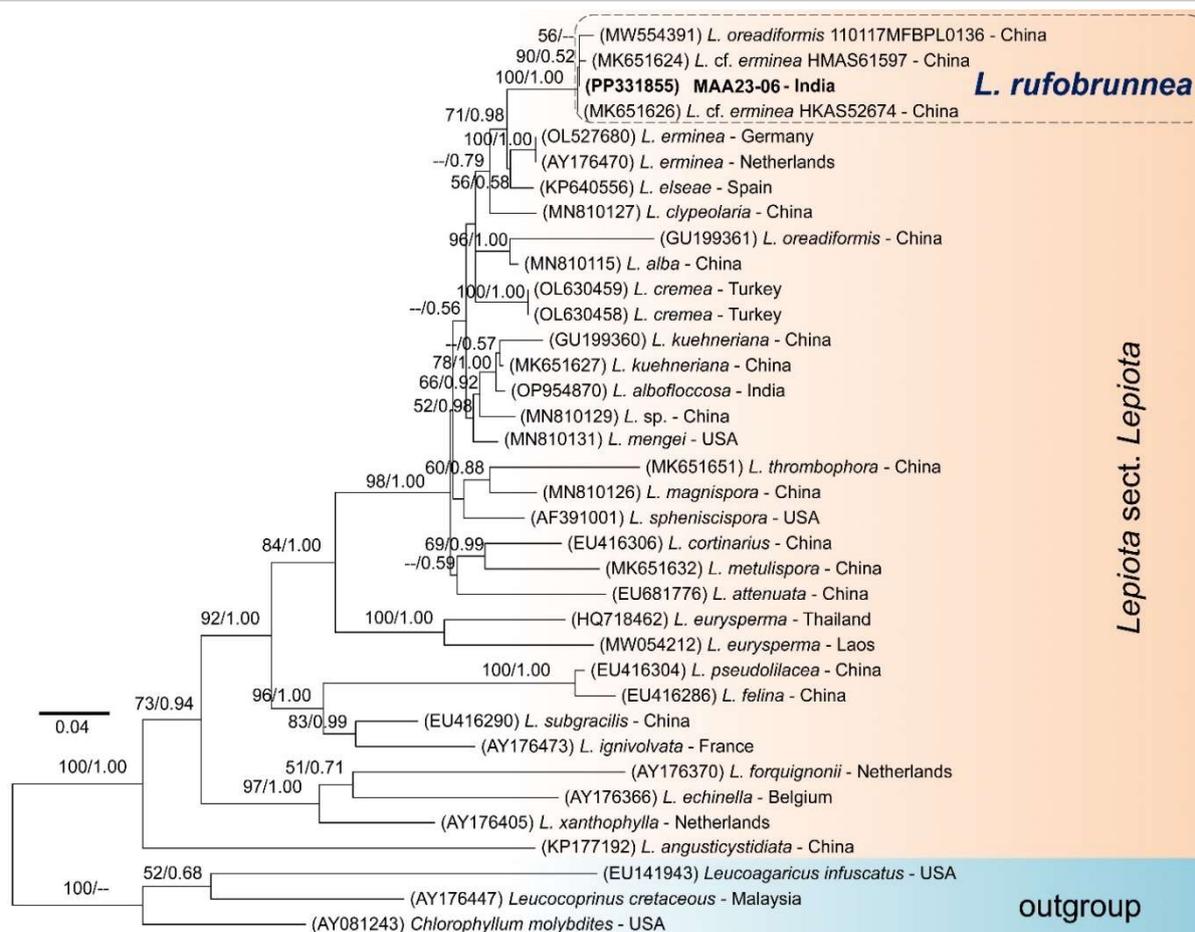


Fig.1. Maximum Likelihood phylogenetic tree ($-\ln L = 6214.286422$) inferred from ITS-rDNA sequence data using the GTR+G model of nucleotide evolution. Branches are labeled with ML bootstrap support values ($\geq 50\%$, left of '/'). Sequence derived from the holotype of *Lepiota rufobrunnea* sp. nov. is shown in blue bold.

4.462083, $GT = 1.000000$; $\alpha = 0.424934$, and tree-length = 2.709553. Based on the ITS-rDNA dataset, the phylograms obtained from the ML analyses were identical with the phylograms obtained in the BA analyses. Therefore, only the ML tree with the log likelihood values of -6214.286422 (Figure 1) is presented with the branch support values recovered from the ML and BA analyses. In the phylogenetic tree, the sequence of newly described *L. rufobrunnea* clusters together with three Chinese sequences (100% MLBS, 1.00 PP) earlier deposited in GenBank under the names *L. oreadiformis* (GenBank MW554391) and *L. cf. erminea* (GenBank MK651624 and MK651626). Basal to this cluster is a small clade comprising of two sequences of *L. erminea*, one from Germany (GenBank OL527680) the other from the Netherlands (GenBank AY176470), and one sequence of *L. elseae* (GenBank KP640556) from Spain.

TAXONOMIC TREATMENT

Lepiota rufobrunnea M. Ahamed, A.K. Dutta, K. Verma & Y.P. Sharma, *sp. nov.* **Figs. 2 & 3**

MycoBank: MB852520. **GenBank:** PP331855 (nrITS).

Type: India, Jammu and Kashmir: Doda District, Bhaderwah, Jai Valley, in coniferous forest dominated by *Cedrus deodara*, 33°1'23.62"N, 75°46'16.06"E, alt. 2442 m, 16 August 2023, Masood Ahamed and Yash Pal Sharma - MAA23-06-M168 (Holotype: HBJU!; Isotype: M)

Diagnosis: *Lepiota rufobrunnea* differs from *L. oreadiformis* by its brownish orange pileus with obtuse reddish-brown umbo covered with scales in concentric fashion, with snow white, hairy cortinate appendages, pileus covering a trichoderm type, elongate to cylindrical basidiospores ($14.35\text{--}18.22 \times 6.12\text{--}7.69 \mu\text{m}$), and its occurrence on the debris of the *Cedrus deodara*.

Etymology: The epithet '*rufobrunnea*' (red-brown) refers to the colouration of the pileus umbo.

Description: Basidiomata small to medium sized. Pileus 30–65 mm diam., hemispherical when young, later becoming convex to planoconvex on maturity, distinctly with reddish brown (9D6–8) broad umbo, pileus surface light brown (7D6) to brownish orange (7C6) with fibrillose squamulose structures covering entire pileus; margin splitting, with snow white (1A1), hairy cortinate appendages

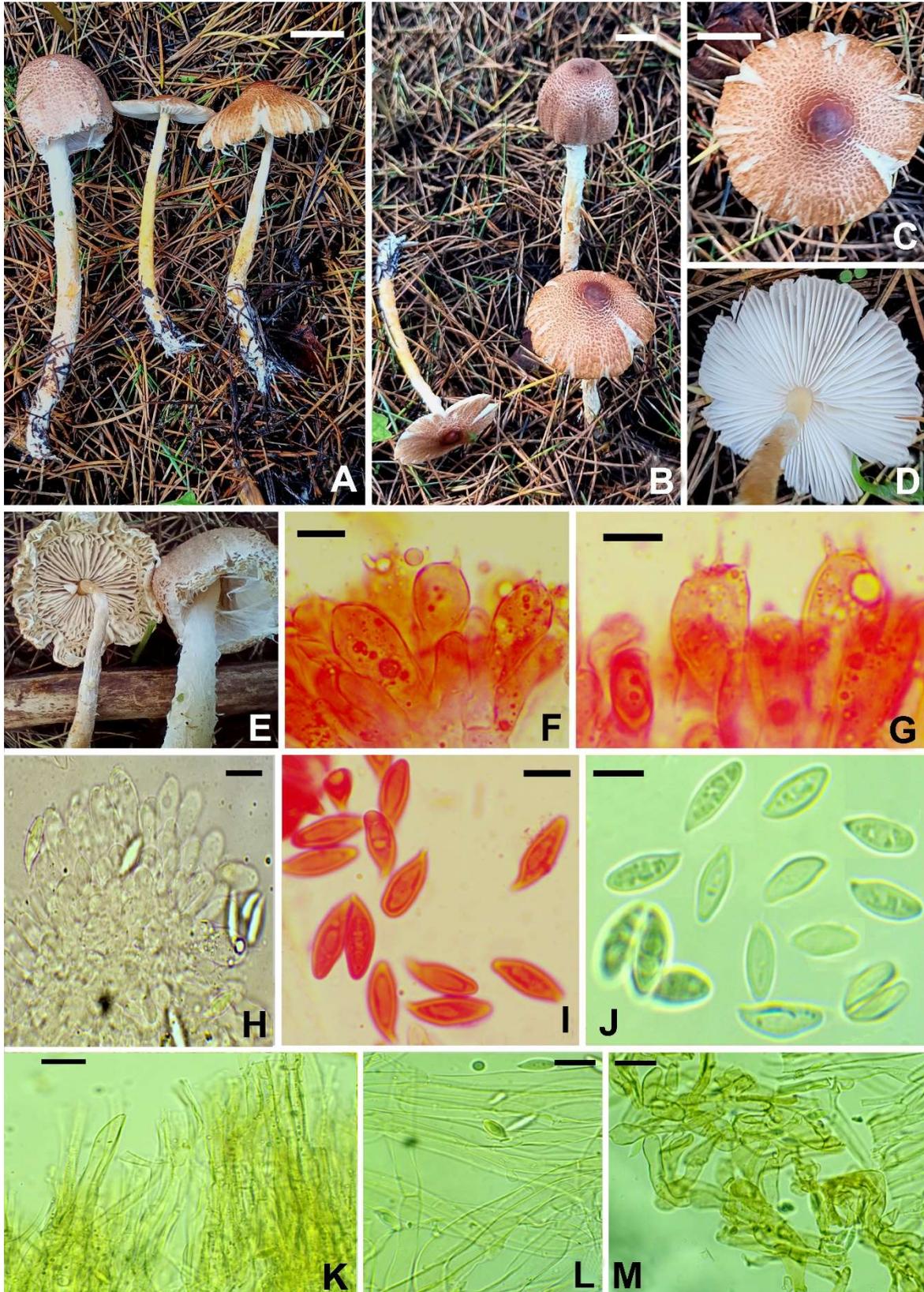


Fig. 2. *Lepiota rufobrunnea* sp. nov. (MAA23-06) A–C. Basidiomata in the field; D–E. Basidiomata showing gill portion; F–G. Basidia; H. Cheilocystidia; I–J. Basidiospores; K. Pileipellis hyphae; L. Pileipellis hyphae showing clamp-connections; M. Elements of pileus fibrillose scales. Scale bars: A–C = 20 mm, F–M = 10 μ m.

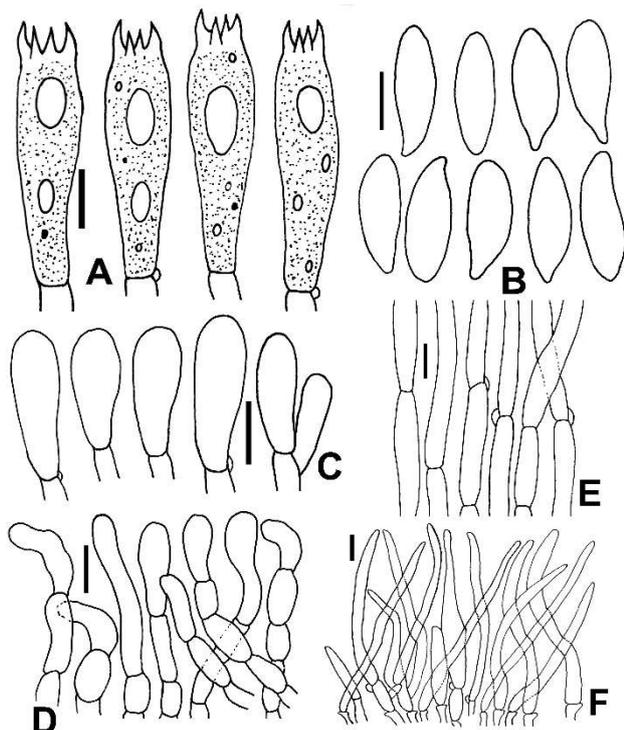


Fig. 3. *Lepiota rufobrunnea* sp. nov. (MAA23-06) **A.** Basidia; **B.** Basidiospores; **C.** Cheilocystidia; **D.** Elements of pileus fibrillose scales; **E.** Stiptipellis; **F.** Pileipellis. Scale bar: **A-F** = 10 μ m

(remnants of the floccose velum partiale); surface gradually cracking from centre toward margin. Lamellae 3.5–7 mm wide, free, even, crowded 15/1cm, creamy white (1A1–A2), with concolorous, even margin, with two–three tiers of lamellulae. Stipe 80–125 \times 5–7 mm, central, cylindrical, slightly tapered towards the apex; surface dry, light yellow (4A5) to pale yellow (2A3), becoming light orange when bruised, covered with snow-white (1A1) hairy squamules; hollow; context white. Annulus simple, rudimentary, white floccose. Odor pleasant; taste not recorded. Spore-print whitish.

Basidiospores (12.8–)14.3–18.2(–19.1) \times (5.0–)6.1–7.7(–7.9) μ m in side view, $av_l \times av_w = 16.2 \times 6.9$ μ m, $Q = 1.8–2.7$, $Q_{av} = 2.3$, elongate to cylindrical with suprahilar depression in abaxial view, ellipsoid to oblong with acute apex side view, ellipsoid-ovoid in frontal view, smooth, hyaline, slightly thick-walled, dextrinoid, with granular contents. Basidia (30–)31–35(–38) \times (11–)12–13(–14.8) μ m, subclavate to broadly clavate, hyaline in KOH, thin-walled, 2–4 spored. Lamella edge sterile. Cheilocystidia (18–)19–26.5(–28) \times (10–)11–11.3(–12.7) μ m, clavate to broadly clavate, colourless, thin-walled. Pleurocystidia absent. Pileus covering a trichoderm, composed of elongate, subcylindrical terminal elements measuring (31.0–) 42.0–155.0 (–190.0) \times (7.5–)9.6–10.6(–12.3) μ m with rounded apex or tapering apex, sometimes more or less erect, frequently septate, hyaline, thick-walled; with short narrowly clavate elements, 15–

35 \times 11–25 μ m. Stiptipellis hyphae numerous, in clusters, (30.0–)35.0–65.5(–85.0) \times (4.0–)5.0–11.0(–14.0) μ m, present only at base of stipe, absent above the annular zone, variable in shape, usually narrow, cylindrical, oblong, hyaline, thin-walled. Clamp connections present in all examined tissues.

Habit and habitat: Solitary to scattered, on humus-rich soil in coniferous forests on the debris of needles of *Cedrus deodara*.

Geographical distribution range: Known only from Jammu and Kashmir in Bhaderwah Forest Division of district Doda, and Nathatop region of district Udhampur.

Additional specimens examined: INDIA. India, Jammu and Kashmir: Doda District, Bhaderwah, Jai Valley, 33° 1'43.27"N, 75°46'17.05"E, alt. 2385 m, 23 August 2023, Masood Ahamed - MAA23-22-M169 (HBJU/M, paratype).

DISCUSSION

Based on phylogenetic analyses of ITS sequences (fig. 1), our new taxon, *Lepiota rufobrunnea*, shows close relationship with *Lepiota* cf. *erminea* (MK651624 and MK651626), *L. erminea* (AY176470, OL527680), *L. elseae* (KP640556), *L. clypeolaria* (MN810127) and *L. cremea* (OL630458, OL630459). The sequences of *Lepiota* cf. *erminea* (MK651624 and MK651626) may be the sequences of *L. erminea*, and we have compared the same with our species and it is quite distinct. *Lepiota erminea*, a European grassland species, is distinguished from *Lepiota rufobrunnea* by its pale ochre or yellowish-brown pileus with white to whitish or yellowish woolly-fibrillose stipe, slightly longer basidiospores (10.0–23.0 \times 5.0–8.0 μ m) and longer pileus elements (up to 400 μ m) (Candusso and Lanzoni, 1990; Vellinga, 2001a). *Lepiota elseae* can be segregated from *L. rufobrunnea* by its reddish chestnut to ochre-brown pileus surface with whitish to ivory background, fibrillose towards margin and its occurrence under *Quercus ilex* litter in the Mediterranean region (Caballero *et al.*, 2015). *Lepiota cremea*, another Mediterranean species, differs from the present species by its small basidiomata with whitish to pale beige pileus, the absence of an annulus on the stipe, smaller basidiospores (12.0–17.0 \times 5.4–6.8 μ m), a trichodermal pileus covering made up of elements with often nodulose or horn-like bumps and mostly narrowly clavate to narrowly utriform stiptipellis elements.

Lepiota oreadiformis Velen. can be distinguished from *L. rufobrunnea* by its pale pileal surface without distinct and contrasting squamules, unpleasant odour like rubber, smaller (11.6–15 \times 4.1–5.5 μ m), fusiform amygdaliform basidiospores, non-septate pileipellis hyphae and its solitary occurrence in grasslands (Vellinga, 2001a; Ćetković *et al.*, 2021). *Lepiota attenuata* J.F. Liang & Zhu L. Yang, a species reported from China, differs from *L. rufobrunnea* by its yellowish-brown disk at center and with yellow to yellowish brown pileus squamules on whitish background and radially sulcate



striate margin with penguin-shaped to fusiform basidiospores (Liang *et al.*, 2011). *Lepiota magnispora* Murrill differs from *L. rufobrunnea* in having a dark brown disk at the center which breaks into dark brown squamules toward the margin on whitish background (Vellinga, 2000). *Lepiota thrombophora* (Berk. & Broome) Sacc. differs from *L. rufobrunnea* by its pileus with red-brown to fuscous brown squamules and a radially sulcate striate margin with penguin-shaped basidiospores (Liang *et al.*, 2011). *Lepiota metulispora* (Berk. & Broome) Sacc. differs from *L. rufobrunnea* in having small basidiomata (20–30mm), radially sulcate striate pileus with brownish yellow to ochraceous-buff squamules and penguin shaped basidiospores (Liang *et al.*, 2011).

Recently, the newly discovered *Lepiota albofloccosa* M. Ahamed *et al.* (2023) reported from a similar habitat differs from *Lepiota rufobrunnea* by its snow-white pileus with smooth brownish yellow umbo and scaly to cottony surface covered with floccose velar remnants, pale yellowish stipe covered by floccose to fibrillose scales and its occurrence on debris of *Picea smithiana* needles (Ahamed *et al.*, 2023).

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