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Lactarius subg. *Lactarius* (Russulaceae) in Indian Himalaya: two new species with morphology and phylogenetic inferences

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Abstract – The present paper deals with two novel species in *Lactarius* subg. *Lactarius* collected from western Himalaya (India): *Lactarius indozonarius* sp. nov. and *Lactarius thindii* sp. nov. Morphological descriptions, illustrations and nrITS-based phylogenetic analyses of these species are presented.

Milkcaps / Macrofungi / nrITS / phylogeny / Russulales / taxonomy / western Himalaya

INTRODUCTION

Lactarius Pers. is a large ectomycorrhizal genus playing a significant role as a mycobiont in different ecosystems, from tropical to temperate and arctic-alpine regions (Verbeken & Nuytinck 2013, Leonardi *et al.* 2016). Species traditionally placed in *L.* subg. *Lactarius* (one of the three subgenera) are characterized in the field by a slimy to viscid or shiny, rarely dry, zonate to azonate pileus, with or without a hairy margin; zonate to azonate pileus context; a dry or sticky stipe which is often scrobiculate and variable latex colour. Microscopically, they typically have an ixocutis to ixotrichoderm (more rarely a cutis to a trichoderm) type of pileipellis (Le *et al.* 2007, Verbeken & Nuytinck 2013). This subgenus is very well represented in all Northern hemisphere continents (Le *et al.* 2007).

In Indian Himalaya, macrofungal explorations by various workers, especially in the past 25 years, reported 29 species so far. These are *Lactarius abbotanus* K. Das & J. R. Sharma, *L. alnicola* A. H. Sm., *L. byssaceus* K. Das & Verbeken, *L. controversus* Pers., *L. dafianus* K. Das *et al.*, *L. deliciosus* (L.) Gray, *L. deterrimus* Gröger, *L. dhakurianus* K. Das *et al.*, *L. elaioviscidus* K Das & Verbeken, *L. fennoscandicus* Verbeken & Vesterh., *L. indigo* (Schwein.) Fr.,

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L. kumaonensis Uniyal *et al.*, *L. maitlyensis* K. Das *et al.*, *L. mayawatianus* K. Das & J. R. Sharma, *L. olivaceoglutinus* K. Das & Verbeken, *L. olivaceoumbrinus* Hesler & A. H. Sm., *L. paradoxus* Beardslee & Burl., *L. proximellus* Beardslee & Burl., *L. pseudoaspideus* Hesler & A. H. Sm., *L. pubescens* Fr., *L. pyriodorus* K. Das & Verbeken, *L. rubrifluus* Gillet, *L. sanguifluus* (Paulet) Fr., *L. scrobiculatus* (Scop.) Fr., *L. subindigo* Verbeken & E. Horak, *L. subpurpureus* Peck, *L. yazooensis* Hesler & A. H. Sm., *L. yumthangensis* K. Das & Verbeken and *L. zonarius* (Bull.) Fr. (Atri *et al.* 1994, Das & Sharma 2005, Das & Verbeken 2011, Joshi *et al.* 2012, Das 2013, Das *et al.* 2015, Uniyal *et al.* 2017). Among these reported species, several are European and American representatives of *L.* subg. *Lactarius* that are reported from India based on morphological similarity. DNA based studies are needed to confirm species delimitation and intercontinental conspecificity for a large number of these species (*L. alnicola*, *L. deliciosus*, *L. deterrimus*, *L. fennoscandicus*, *L. indigo*, *L. olivaceoumbrinus*, *L. paradoxus*, *L. proximellus*, *L. pseudoaspideus*, *L. pubescens*, *L. rubrifluus*, *L. sanguifluus*, *L. scrobiculatus*, *L. subpurpureus*, *L. yazooensis* and *L. zonarius*). Therefore, collection of more samples and a thorough revision of this group from Indian Himalaya with the support of molecular phylogeny is needed. Unfortunately, macrofungal surveys in Russulaceae have nearly all been undertaken

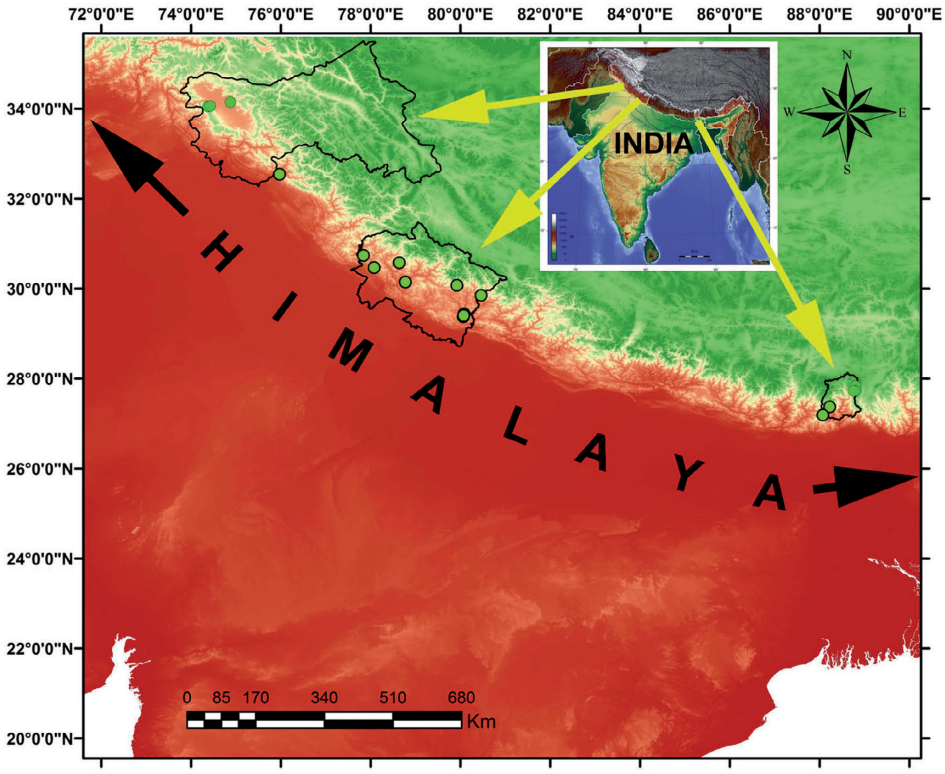


Fig 1. Map of Indian Himalayan region showing sites for the occurrences (only small patches in three states) of *Lactarius* subg. *Lactarius* members with green dots.

in Uttarakhand, Sikkim and Himachal Pradesh (Fig. 1) while the rest of Indian Himalaya remains unexplored.

While undertaking routine macrofungal surveys in temperate forests of Uttarakhand (Figs. 3-6), two interesting taxa were encountered by one (PU) of us. Thorough morphological examination and nrITS-based phylogenetic data of these taxa revealed two novel species within *Lactarius* subg. *Lactarius* and we describe them here as *Lactarius indozonarius* (*L.* sect. *Zonarii*) and *Lactarius thindii* (*L.* sect. *Colorati*).

MATERIAL AND METHODS

Collecting and morphology

Macromorphological characters and field data were recorded in the forest or basecamp from the fresh and dissected young to mature basidiomata. Macrochemical colour reactions on pileus, stipe surface, context and latex were also recorded. Images of the fresh basidiocarps were captured with the help of Canon Power Shot SX 50 HS and Sony Cyber Shot W730 cameras. Color codes and terms follow Methuen Handbook of Color (Kornerup & Wanscher 1978). Micromorphological characters were observed with the help of a light microscope (Olympus CH20i) from dry material mounted in a mixture of 5% KOH, 1% Phloxin and 1% Congo red. Drawings of micromorphological elements were made with a camera lucida at 2000 × magnification. Microphotographs were captured with a digital camera attached to the Olympus CH20i and Olympus-CX21iLED light microscopes. Basidiospores were mounted in Melzer's reagent and measured in lateral view excluding the height of ornamentation and apiculus. Basidiospore measurements are presented as minimum-*mean*-maximum length × minimum-*mean*-maximum width and Q = length/width ratio.

Scanning Electron Microscope (SEM) images of basidiospores were obtained from dry basidiospores that were directly mounted on a double-sided adhesive tape pasted on a metallic specimen-stub and then scanned with silver coating at different magnifications in high vacuum mode (20 KV). SEM-studies were carried out with a ZEISS EVO 18 SPECIAL EDITION model installed at USIC Dept., HNBGU Srinagar (Garhwal), India. Herbarium codes follow Thiers (continuously updated).

DNA isolation, amplification and sequencing

Genomic DNA was isolated from 100 mg of (dry) tissue of the basidiomata using the XcelGen Plant Fungal gDNA kit (XG2416-01) following the manufacturer's instructions. The nrITS region was amplified with primer pairs ITS1-F and ITS4-B (White *et al.* 1990). PCR amplification was performed using a thermocycler (ABI, Veriti) programmed for 3 min at 95°C, followed by 1 min at 94°C, 30 cycles of 45 sec at 48°C, 45 seconds at 72°C and a final stage of 10 min at 72°C. The PCR amplicon was purified with exosap enzymatic purification as per the manufacturer instruction (ABI). After the purification the products were subjected to Sanger sequencing using an ABI 3730XL DNA analyzer. Forward and reverse strands were

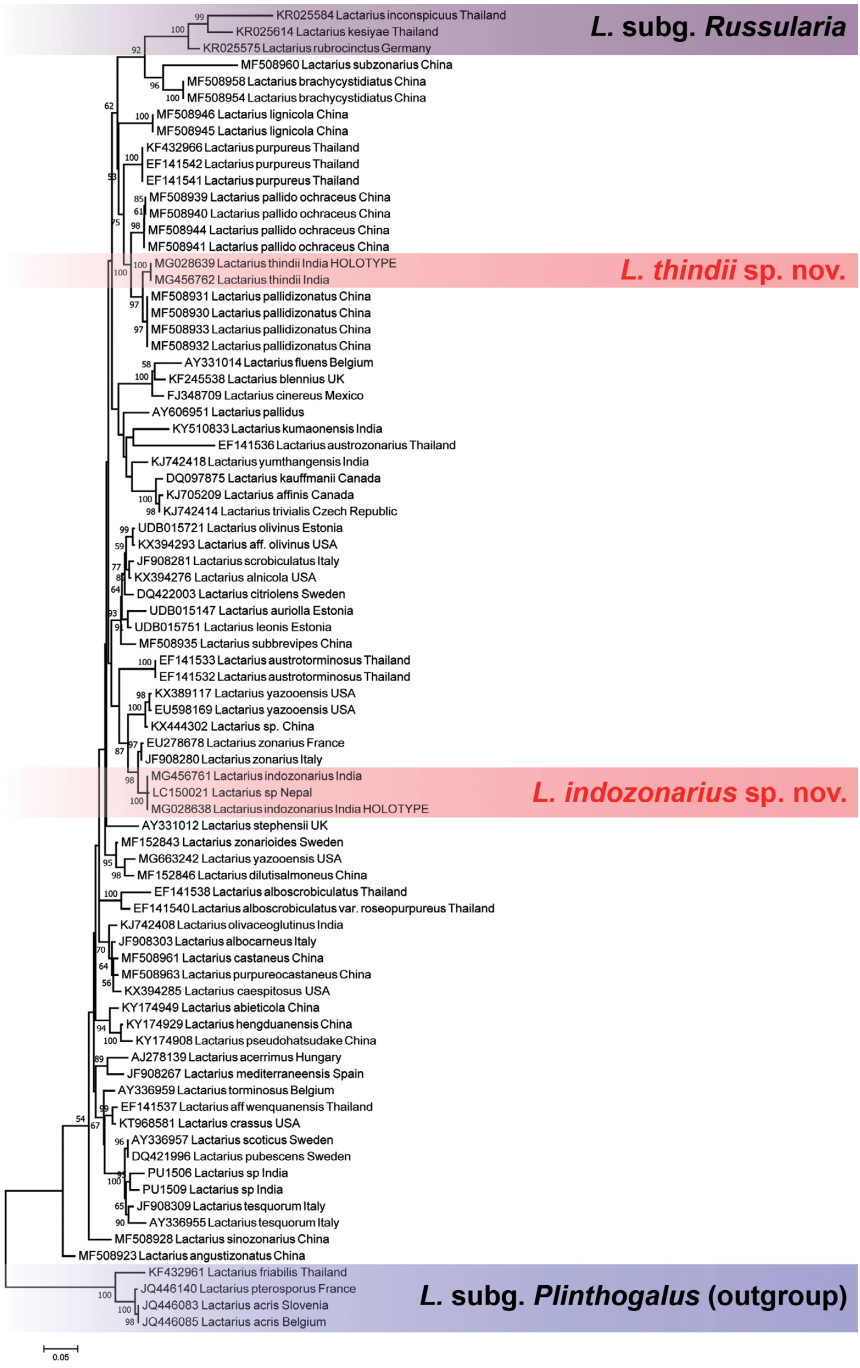


Fig 2. Phylogram generated from ITS-rDNA sequences: The evolutionary history was inferred by using the Maximum Likelihood method in RAxML v. 8.0.24. Bootstrap support values (>50%) obtained from the ML analysis are shown above or below the branches at nodes.

sequenced separately with the ITS1 and ITS4 primers using BDT v3.1 Cycle sequencing kit. Sequences generated in this study are deposited in GenBank.

Phylogenetic analysis

A dataset with reference nrITS sequences was assembled by considering the sequences from studies on *L.* subg. *Lactarius* (Le *et al.* 2007, Nuytinck *et al.* 2007, Das *et al.* 2015, Uniyal *et al.* 2017, Wang 2017, Shi *et al.* 2018), and a BLAST (Altschul *et al.* 1997) search in GenBank (Clark *et al.* 2016) and UNITE (Kõljalg *et al.* 2013). We aimed for the inclusion of as many Asian representatives as possible. Phylogenetic analyses were carried out to establish the relationships of our new taxa. Species of *L.* subg *Plinhogalus* were selected as outgroup. Multiple sequence alignment was performed using MAFFT v.7 (Katoh & Standley 2013), applying the E-INS-I strategy. Alignments were manually edited in Bioedit v 7.2.5 (Hall *et al.* 1999). Maximum Likelihood (ML) analyses were conducted in RAxML v. 8.0.24 (Stamatakis 2014) on the CIPRES Science Gateway (Miller *et al.* 2010).

RESULTS

Phylogenetic inference

Our ITS-based phylogenetic analysis being conducted with 109 nucleotide sequences (Fig. 2) supports the placement of *L. indozonarius* sp. nov. and *L. thindii* sp. nov. in *L.* subg. *Lactarius.* Although this subgenus is paraphyletic in our analysis with *L.* subg. *Russularia* nested inside, all close relatives of the newly described species are traditionally considered to be members of *L.* subg. *Lactarius.*

Delimiting sections and subsections in *Lactarius* is impossible based on ITS sequences only, but the two new species described here fall in well-supported species groups that also make sense morphologically. This is discussed in more detail in the taxonomy section of this manuscript.

Taxonomy

Lactarius indozonarius Uniyal, K. Das & Nuytinck, **sp. nov.** **Figs 7-20**

MycoBank: MB823734

Genbank: MG028638 (holotype), MG456761 (paratype)

Diagnosis: Differs from *L. zonarius* by its zoned context and smaller basidiospores with higher (up to 1.5 µm) ornamentations and by its nrITS data.

Holotype: INDIA: **Uttarakhand**, Pauri Garhwal, Chaubatta, N30º 09.697' E078º 51.195', 1913 m asl., growing in a mixed temperate forest dominated by *Quercus*, *Rhododendron*, *Myrica*, *Cedrus* and *Pinus* sp., 16th July 2016, *P. Uniyal*, PU-1087 (CAL;).

Etymology: Referring to morphological resemblance and close affinity with *L. zonarius*, a European species.

Pileus 60-122 mm diam., convex to plano-convex, shallowly depressed, finally infundibuliform; surface viscid to glutinous, zonate, increasingly matted-

Figs 3-6. Habitats. **3-4.** Mixed forest of Chopta-Baniyakund; collection site of *Lactarius thindii*. **5-6.** Mixed forest of Chaubatta and Chaurikhal dominated by *Quercus leucotrichophora*, collection site of *Lactarius indozonarius*.

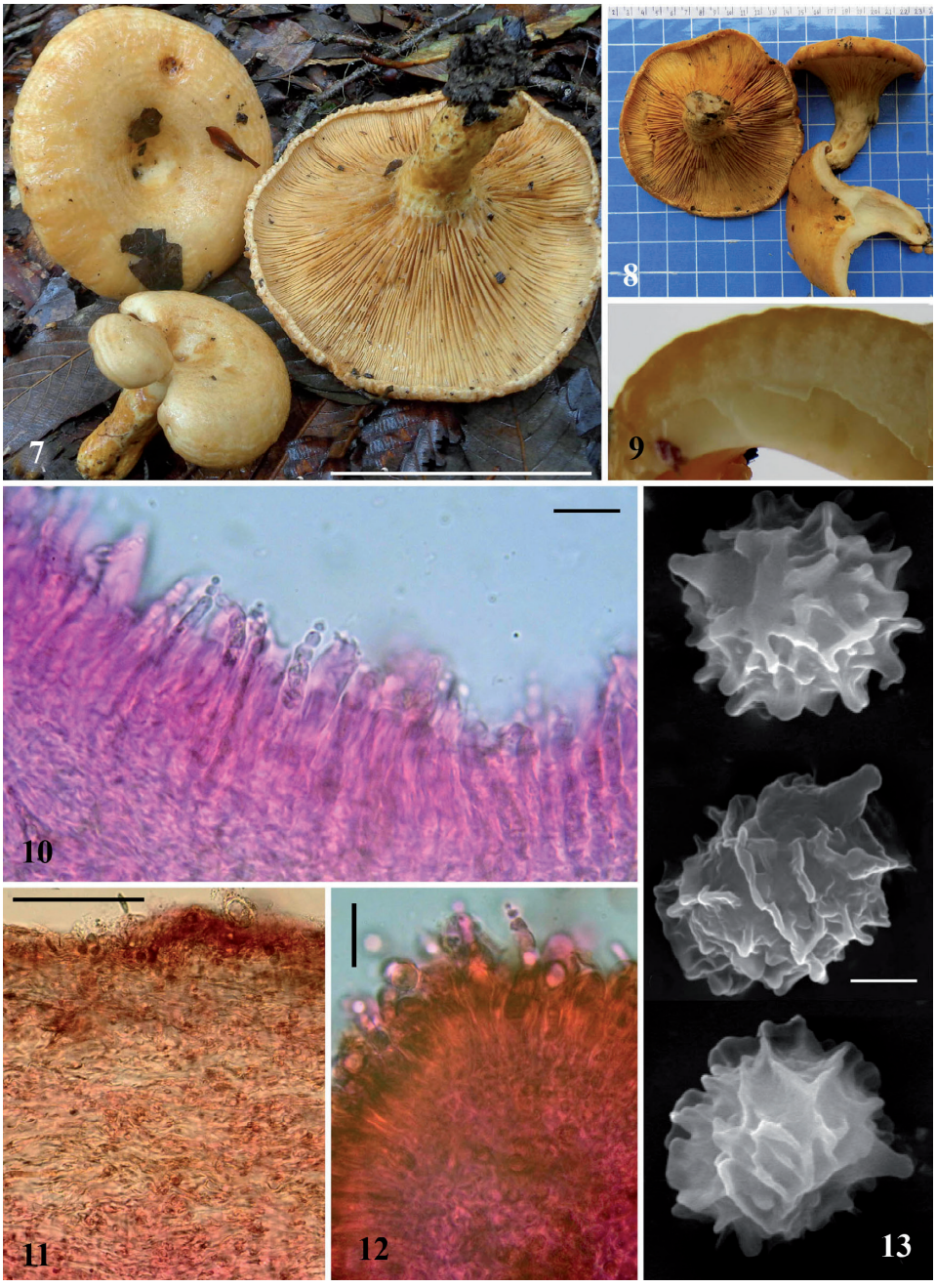
fibrillose towards margin, straw yellow to wax yellow (3B4-5) when young, light yellow (4A4-5) to greyish yellow (4B3) or corn yellow (4B5) with age, finally brownish yellow (5C6-8), sometimes paler near margin, hairs up to 2 mm long, turning brownish yellow (5C7); zonations greyish orange (5B3-4); margin inrolled to decurved, undulate to entire, radially ridged when young, hairy. **Lamellae** subdecurrent, very crowded (15-17 L+l/cm), pale yellow to pastel yellow (3A3-4) when young, greyish yellow (4B4-5) with age, brownish orange (5C5) where damaged, some forked near attachment; lamellulae numerous. **Stipe** 45-72 × 13-29 mm, cylindrical, equal, scrobiculated, pale yellow (3A3) to greyish yellow (3B4-5), yellowish white (3A2) near attachment; scrobicules watery or yellowish white (3A2), becoming greyish yellow to yellowish orange (4B5–7) on handling or with age. **Context** 7–10 mm thick, white to yellowish white (2A2), zonate, zonations watery, continuations in zones of pileus surface, gradually disappearing toward centre; unchanging with FeSO4 and KOH, turning pastel red (8A4–5) at first with guaiac, then brownish red (8C8); taste mild to slightly acrid; stuffed to hollow in stipe. **Latex** scarce, white, unchanging; taste acrid on tissue and in isolation. **Odor** pleasant, fruity. **Spore deposit** yellowish white (1A2).

Basidiospores 7-*7.5*-8.5 × 6.5-*6.9*-7.5 µm, subglobose to broadly ellipsoid, (n = 20, Q = 1.07-*1.13*-1.23), ornamentations ≤1.5 µm high, rounded to triangular warts and connecting ridges never forming a complete reticulum; plage inamyloid. **Basidia** 40-51 × 9-12 µm, subclavate, 2-, 4-spored; sterigmata 4-5 µm long. **Pleuromacrocystidia** abundant, 30-63 × 4-7.5 µm, cylindric to subfusiform, apices capitate to mucronate and constricted, mostly moniliform; contents dense, small crystal-like. **Pleuropseudocystidia** up to 5.5 µm thick, nonemergent to slightly emergent, cylindric, with a round apex and often forked near apex. **Lamellae edge** sterile. **Cheilomacrocystidia** 36-42 × 4-5.5 µm, subcylindric to subfusiform, apex moniliform to constricted; contents dense. **Lactifers in hymenophoral trama** up to 10 µm thick. **Pileipellis** an ixocutis, 80-137 µm thick, composed of densely packed parallel, often shrivelled hyphae; hyphae 1-2.5 µm wide. **Lactifers in pilear trama** up to 9 µm thick.

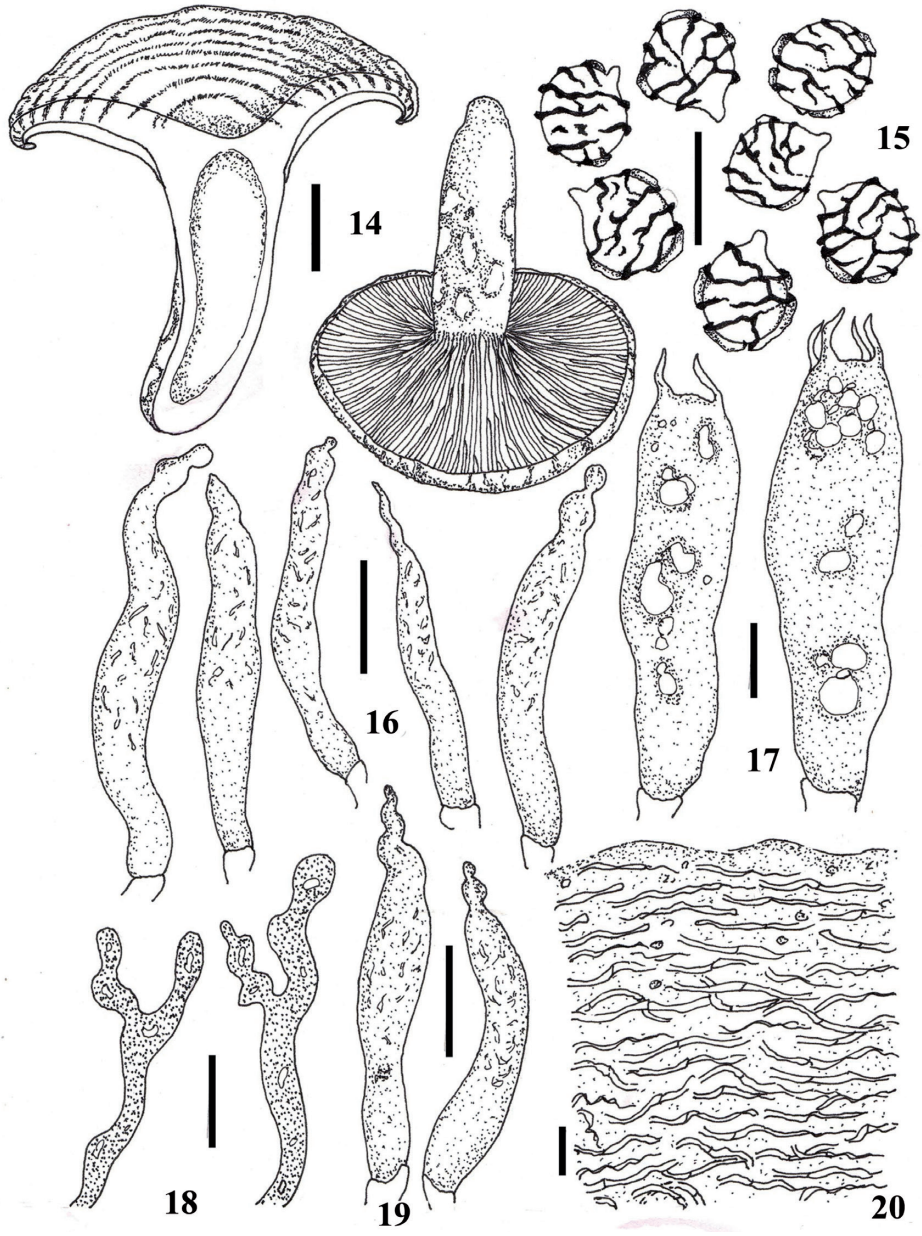
Ecology: Growing in association with *Quercus leucotrichophora* in mixed temperate forest dominated by *Quercus*, *Rhododendron*, *Myrica*, *Cedrus* and *Pinus* sp.

Other collection examined: INDIA: **Uttarakhand**, Pauri Garhwal, Chaurikhal, N30º 05.681' E078º 43.890', 1989 m asl., 21st Aug. 2014, *P. Uniyal*, PU-439 (GUH).

Comments: The viscid to glutinous, zonate, yellowish pileus with hairy margin, and the white, unchanging latex, scrobiculate stipe and fruity odour undoubtedly place the present taxon in *Lactarius* sect. *Zonarii*. This is also confirmed in the molecular phylogeny by the placement of *L. indozonarius* as the sister species of *L. zonarius,* although the monophyly of *L.* sect. *Zonarii* in its traditional morphological sense cannot be confirmed. A Nepalese sample (LC150021) is clustered with *L. indozonarius* but lacks any morphological description. *Lactarius indozonarius* is quite distinct due to the zonations in the pileus context. This character has only been reported in Thai species of *L.* sect. *Zonarii*: *L. alboscrobiculatus* var. *roseopurpureus* H.T. Le & A. Verbeken, *L. austrotorminosus* H.T. Le & A. Verbeken and *L. austrozonarius* H.T. Le & A. Verbeken (Le *et al.* 2007), but is a generic character for its sister genus *Multifurca* (Wang *et al.* 2018). Microscopically, *L. indozonarius* is characterized by subglobose to broadly ellipsoid basidiospores, abundant macrocystidia and an ixocutis pattern of the pileipellis.



Figs. 7-13. *Lactarius indozonarius* sp. nov. (PU-1087, holotype). **7-8.** Fresh basidiomata in field and basecamp. **9.** Zonations in context. **10.** Pleuromacrocystidia. **11.** Transverse section through pileipellis. **12.** Cheilomacrocystidia. **13.** SEM image of basidiospores. Scale bars **7** = 100 mm; 10 & 12 = 25 µm; 11 = 100 µm; 13 = 2 µm.



Figs. 14-20. *Lactarius indozonarius* sp. nov. (drawings from holotype: PU-1087). **14.** Fresh/dissected basidiomata. **15.** Basidiospores. **16.** Pleuromacrocystidia. **17.** Basidia. **18.** Pleuropseudocystidia. **19.** Cheilomacrocystidia. **20.** Pileipellis. Scale bars 14 = 10 mm; 15-19 = 10 µm; 20 = 25 µm.

Lactarius indozonarius is morphologically similar to *L. zonarius* by the presence of a strongly zonate, yellowish pileus, brownish discoloration in lamellae on damage, burning acrid taste, pleasant odour and abundant pleurocystidia. Yet, our

new species is clearly distinct from it due to its hairy pileus and zoned context. Microscopically, *L. zonarius* differs because of its smaller (6.9-7.7 × 5.8-6.2 µm) basidiospores with lower (0.7 µm) ornamentation (Basso 1999; Heilmann-Clausen *et al.* 1998).

L. alboscrobiculatus var. *roseopurpureus* (95% similarity for 100% query coverage in BLAST search) is distinct by its white to cream-coloured pileus, distant lamellae and very low (0.5-0.8 µm) ornamentations on the basidiospores. *L. austrozonarius* differs by its subdistant lamellae, very abundant, white to watery cream-coloured latex and distinctively larger (7.2-12.2 ×7-10.2 µm) basidiospores with very high ridges (≤2.5 µm). *Lactarius indozonarius* shares with *L. austrotorminosus* a hairy cap margin, dense lamellae with brownish orange discoloration and ≤1.5 µm high ornamentations on the basidiospores, but the latter species is still recognizable by its pinkish orange basidiomes and smaller (30-80 mm diam.), papillate pileus. Micromorphologically, *L. austrotorminosus* is quite distinct from *L. indozonarius* due to the structure of the pileipellis being a cutis or trichoderm, and the zebroid ornamentation of the basidiospores (Le *et al.* 2007).

Lactarius thindii Uniyal, K. Das & Nuytinck, **sp. nov.** **Figs 21-33**

MycoBank: MB823735

Genbank: MG028639 (holotype), MG456762 (paratype)

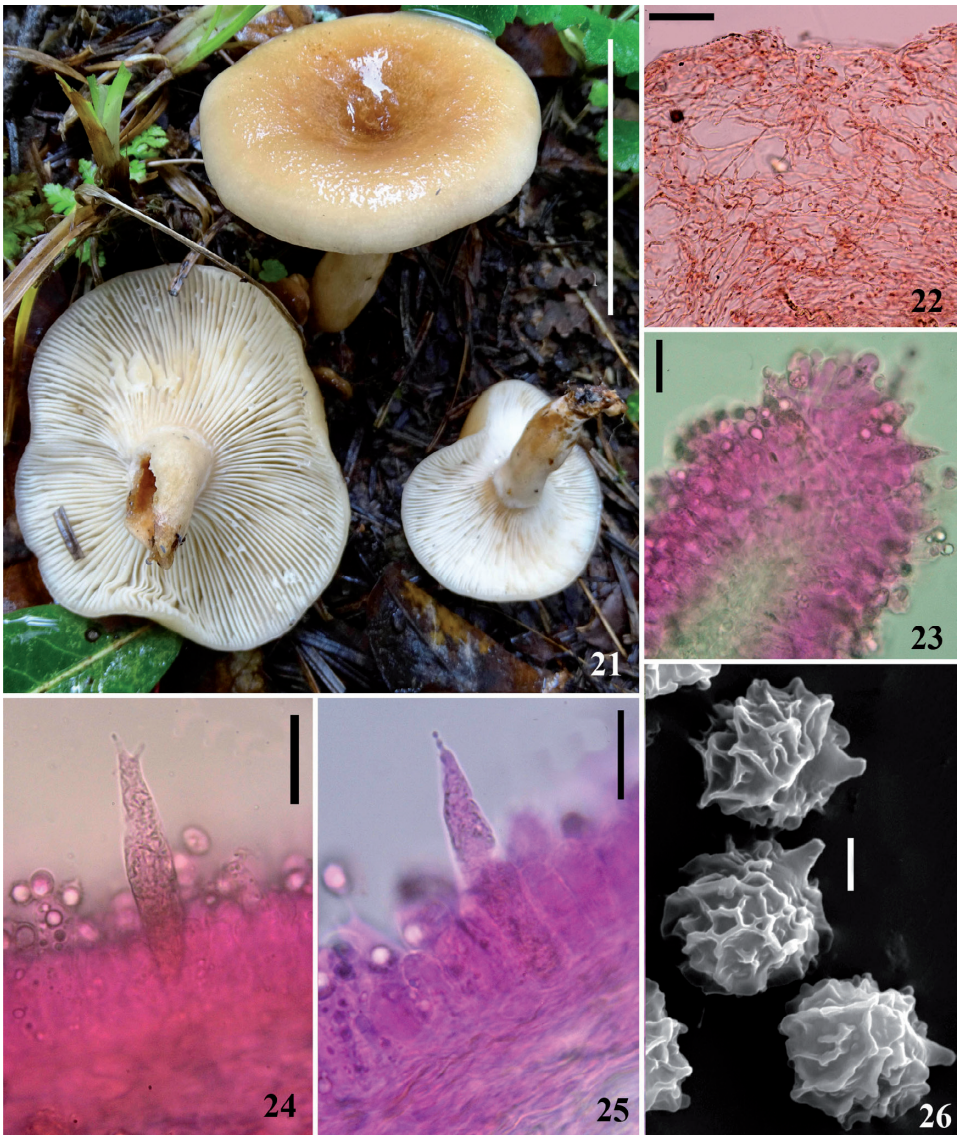
Diagnosis: Differs from *Lactarius pallidizonatus* by the presence of an azonate to faintly zonate pileus, non striate pileus margin, unchanging latex, smaller (6.0-7.0 × 5.0-6.0 µm) basidiospores and nrITS sequence data.

Holotype: INDIA: **Uttarakhand**: Rudraprayag, Chopta-Baniyakund, N30º 28.914' E079º 10.854', 2630 m asl., growing in mixed subalpine forest dominated by *Quercus*, *Rhododendron*, *Lyonia*, *Myrica* and *Abies* spp., 7th Aug. 2017, *P. Uniyal*, PU-1526 (CAL).

Etymology: in **commemoration** of Prof. K. S. Thind for his contributions to the study of Indian mycobiota.

Pileus 24-37 mm diam., convex to plano-convex with depressed center, surface smooth, sticky to slightly glutinous, azonate to faintly zonate near margin, light orange (5A4-5) to greyish orange (5B3-4), brownish yellow (5C7-8) at centre, pale yellow (4A3) near margin; margin undulate, decurved. **Lamellae** subdecurrent, rather close (6-7 L/cm), white to yellowish white (2A2), unchanging when damaged; lamellulae 1-2 between two lamellae. **Stipe** 25-36 × 6-11 mm, brownish orange (5C4-5), whitish toward apex. **Context** white to orange white (5A2), greyish orange (5B4) in stipe when mature, stuffed to hollow, unchanging on exposure and with FeSO4 and KOH; taste faintly acrid; odour insignificant. **Latex** scarce, white, unchanging; taste acrid. **Spore deposit** yellowish white (2A2).

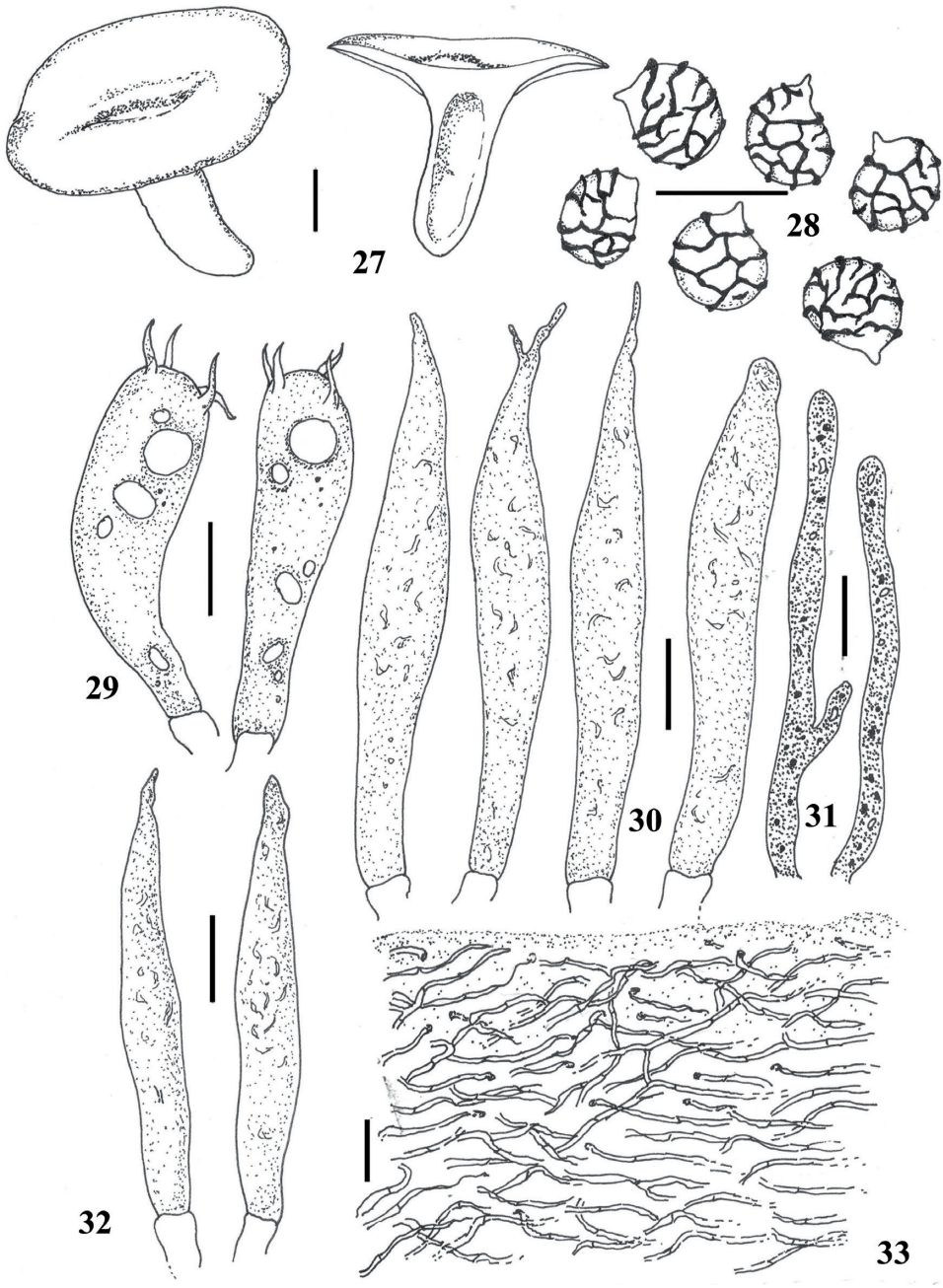
Basidiospores 6-*6.3*-7 × 5-*5.2*-6 µm, (n = 20, Q = (1) 1.10–*1.20*–1.27); broadly ellipsoid to ellipsoid, ornamentations composed of some small round to conical warts and ridges (≤1.2 µm high) that form a close incomplete reticulum; plage inamyloid. **Basidia** 33-45 × 9-11 µm, subclavate, 4-spored; sterigmata 3-5 µm long. **Pleuromacrocystidia** 54-82 × 6.5-12 µm, fusiform to subfusiform, often forked near apex; apices acute, capitate and mucronate to moniliform, contents dense, needle shaped. **Pleuropseudocystidia** up to 6.5 µm thick, cylindrical, sometimes forked. **Cheilomacrocystidia** 45-58 × 6.5-8 µm; apex acute to mucronate. **Lactifers in hymenophoral trama** up to 9 µm thick. **Pileipellis** an ixocutis, 85-165 µm thick; hyphae densely packed, septate, repent to slightly ascending, interwoven in the form of a reticulum, 1-4 µm thick.



Figs. 21-26. *Lactarius thindii* sp. nov. (PU-1526, holotype). **21.** Fresh basidiomata in field. **22.** Transverse section through pileipellis. **23.** Cheilomacrocystidia. **24-25.** Pleuromacrocystidia. **26.** SEM image of basidiospores. Scale bars 21 = 50 mm; 22-25 = 25 µm; 26 = 2 µm.

Ecology: Growing in association with *Quercus semecarpifolia* in a mixed subalpine forest dominated by *Quercus*, *Rhododendron*, *Lyonia*, *Myrica* and *Abies* spp.

Other collection examined: INDIA: **Uttarakhand**, Rudraprayag, Chopta-Baniyakund, N30º 28.998' E079º 10.658', 2653 m asl., 19th July 2015, *P. Uniyal*, PU-705 (GUH).



Figs. 27-33. *Lactarius thindii* sp. nov. (drawings from holotype: PU-1526). **27.** Fresh/dissected basidiomata. **28.** Basidiospores. **29.** Basidia. **30.** Pleuromacrocystidia. **31.** Pleuropseudocystidia **32.** Cheilomacrocystidia. **33.** Pileipellis. Scale bars 27 = 10 mm; 28-32 = 10 µm; 33 = 25 µm.

Comments: *Lactarius thindii* is morphologically characterized by its small sized basidiomes, its sticky to slightly glutinous, greyish orange to brownish yellow pileus that is almost white towards the margin; unchanging, white latex; subglobose to broadly ellipsoid basidiospores with a dense, incomplete reticulum; often forked pleurocystidia and ixocutis type of pileipellis. Molecular data suggest its close relation with *L. purpureus* R. Heim ex R. Heim, *L. pallidizonatus* X.H. Wang and *L. pallido-ochraceus* X.H. Wang. The Asian species *L. purpureus* is unmistakably different from *L. thindii* by its wine red to pink, scaly pileus surface; larger (5.2-8.6 × 4.5-7.9 µm) basidiospores and a cutis to trichoderm type of pileipellis (Verbeken & Horak 2000; Le *et al.* 2007). *Lactarius pallidizonatus* and *L. pallido-ochraceus* share similarities with *L. thindii* in having a faintly zonate to zonate, smooth pileus surface, acrid tasting white latex, ixocutis type of pileipellis and occurrence under fagaceous trees. However, both species are different from *L. thindii* due to presence of hygrophanous pileus surface with sub-transparently striate margin. In addition, *L. pallidizonatus* is distinct by latex changing to watery, larger (7.5-9.0 × 6.0-7.5 µm) basidiospores with lower (0.4-0.6 µm) ornamentations and very thick (200-500 µm) pileipellis. *Lactarius pallido-ochraceus* is different from *L. thindii* due to presence of brownish to greyish ochraceous discoloration in lamellae on bruising and unchanging to glaucous green discolouring latex (Wang 2017).

Lactarius fraxineus Romagn. is remarkably similar to *L. thindii* in having crowded, cream-coloured lamellae, white latex, basidiospores (6-7 × 5-6 µm) with incomplete reticulation and an ixocutis type of pileipellis. However, this European species differs from the present taxon by its larger (≤ 85 mm) pileus with scaly surface, scrobiculate stipe and greyish-olive latex discoloration (Basso 1999).

In India, *Lactarius dafianus* is the sole representative of *L.* sect. *Colorati* and can be confused with *L. thindii* due to its reddish orange pileus with darker centre, dense lamellae and unchanging latex. The former is different on the basis of its watery latex, white spore deposit, abundant isolated warts on the basidiospores and trichodermal pileipellis (Das & Sharma 2005).

A provisional key to the known species of Lactarius subg. Lactarius from Indian Himalaya

1a. Latex strikingly coloured, presence of greenish discoloration in tissue 2
1b. Latex white to watery, absence of greenish discoloration in tissue 10
2a. Pileus greyish blue to blue with silvery lusture 3
2b. Pileus pinkish, brownish or orange 5
3a. Latex vinaceous red, occurrence under *Pinus* ..... *L. paradoxus*
3b. Latex blue 4
4a. Latex turning green on exposure, basidiospores 7–9.5 × 6–7.5 µm, occurrence under *Pinus* and *Quercus* ..... *L. indigo*
4b. Latex unchanging on exposure, basidiospores 6.6–8.3 × 5.4–6.5 µm, occurrence under *Castanopsis* and *Lithocarpus* ..... *L. subindigo*
5a. Lamellae subdistant to distant (3-4/cm) 6
5b. Lamellae crowded (12-18/cm) 7
6a. Pileus brownish orange to brown, pleuromacrocystidia scarce, occurrence under *Pinus* ..... *L. rubrifluus*
6b. Pileus dirty pinkish, pleuromacrocystidia abundant, occurrence under *Tsuga* ..... *L. subpurpureus*
7a. Pileus distinctly or faintly zonate 8
7b. Pileus azonate, occurrence under *Pinus* ..... *L. sanguifluus*

8a. Stipe nonscrobiculate, basidiospore ornamentation consisting of isolated warts and short ridges, never forming reticulum 9
8b. Stipe scrobiculate, basidiospores ornamentation forming an incomplete reticulum, occurrence under *Pinus* ..... *L. deliciosus*
9a. Pileus typically azonate or with a few zones near the margin, with mainly bright orange colours and green tinges, occurrence under *Picea* ..... *L. deterrimus*
9b. Pileus clearly zonate and brown-orange with sometimes lilac-grey tinges, occurrence under *Picea* ..... *L. fennoscandicus*
10a. Pileus distinctly to faintly zonate 11
10b. Pileus azonate 23
11a. Pileus pubescent to fibrillose 12
11b. Pileus neither pubescent nor fibrillose 15
12a. Pileus large (≥120 mm diam.) 13
12b. Pileus smaller (≤ 60 mm) 14
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