Fundación Miguel Lillo
Tucumán
Argentina

Collybiopsis himalayensis sp. nov. (Omphalotaceae), a new white-spored agaric from the Indian Himalaya

Collybiopsis himalayensis sp. nov. (Omphalotaceae), un nuevo agárico de esporas blancas del Himalaya de la India

Shikha Choudhary[1]; Yash Pal Sharma[1]; Priyanka Uniyal[2*]

[1] Department of Botany, University of Jammu, 180006, Jammu and Kashmir, India.
[2] Government PG College, Gopeshwar, Chamoli 246401, Uttarakhand, India.
* Corresponding author: <pugpc90@gmail.com>

Abstract

A new species, *Collybiopsis himalayensis*, from the Uttarakhand Himalaya, India, is described based on micro-morphological and molecular phylogenetic analyses. This species is characterized by its convex to campanulate pileus with a slight umbo, margins uplifted, minutely pruniose surface, pale brown, sub-decurrent lamellae, sub-ellipsoidal basidiospores, large basidia (36-51.5 × 6.6-7.9 μm), and presence of pleurocystidia and large hyphae like pileocystidia and cheilocystidia. Phylogenetic analyses of nrITS sequences confirm its categorization as a new taxon of *Collybiopsis*.

Keywords: Basidiomycota; nrITS; phylogeny; taxonomy.

Resumen

Se describe una nueva especie, *Collybiopsis himalayensis,* del Himalaya de Uttarakhand, India, basada en análisis micromorfológicos y filogenéticos moleculares. Esta especie se caracteriza por su píleo convexo a campanulado con un pequeño umbo, márgenes elevados, superficie finamente pruinosa, de color marrón claro, láminas subdecurrentes, basidiosporas subelipsoidales, basidios grandes (36-51,5 × 6,6-7,9 μm) y la

➤ Ref. bibliográfica: Choudhary, S.; Sharma, Y. P.; Uniyal, P. 2025. *Collybiopsis himalayensis* sp. nov. (Omphalotaceae), a new white-spored agaric from the Indian Himalaya. *Lilloa 62* (2): 425-436. doi: https://doi.org/10.30550/j.lil/2003
➤ Recibido: 31 de marzo 2025 – Aceptado: 18 de julio 2025 – Publicado: 8 de agosto 2025.
➤ URL de la revista: http://lilloa.lillo.org.ar
➤ Esta obra está bajo una Licencia Creative Commons Atribución – No Comercial – Sin Obra Derivada 4.0 Internacional.

presencia de pleurocistidios e hifas grandes, similares a los pileocistidios y queilocistidios. Su clasificación como un nuevo taxón de *Collybiopsis* se confirma mediante análisis filogenéticos de secuencias nrITS.

Palabras clave: Basidiomycota; filogenia; nrITS; taxonomía.

INTRODUCTION

Collybiopsis, established by Earle in 1909, is a genus of mushrooms with gymnopoid and marasmioid characteristics, classified under the family Omphalotaceae (Earle 1909; Petersen & Hughes 2021). These fungi typically exhibit fruiting bodies that resemble forms such as collybioid, gymnopoid, marasmielloid, omphalioid, or pleurotoid. Their gills range from free to decurrent, and their stipes can be centrally to eccentrically attached, sometimes embedded in the substrate. The spores are ellipsoid to oblong, do not react to iodine (inamyloid), are translucent (hyaline), and leave white spore prints. Additional features include the presence of caulocystidia and a pileipellis with coral-like or branched (diverticulate) terminal elements (Murrill, 1915; Singer, 1973; Antonín & Noordeloos, 1993; Retnowati, 2018; Oliveira *et al*., 2019). Due to their relatively unspecialized fruiting body structures and limited morphological diversity, many species with gymnopoid or marasmioid traits were initially grouped under *Collybia* (Staude, 1857) or *Marasmius* (Fries, 1835), prior to the widespread use of molecular tools in fungal classification. Recent phylogenetic analyses, however, have clarified the evolutionary relationships among gymnopoid/marasmioid fungi within the Omphalotaceae and Marasmiaceae families (Wilson & Desjardin, 2005; Oliveira *et al*., 2019).

Collybiopsis shares both morphological features and a close evolutionary relationship with the genus *Gymnopus* (Desjardin *et al*., 1999; Dutta *et al*., 2015). The two genera can generally be differentiated based on characteristics such as the structure of the terminal elements in the pileipellis, how the gills attach, features of the stipe, the shape and nature of basidiospores, and the presence or form of cheilocystidia. However, these distinguishing traits are not always definitive, as overlaps and exceptions occur, making it challenging to rely solely on morphology for accurate identification. Additionally, the fruiting body traits of these fungi can vary significantly with environmental conditions and growth stages. As a result, molecular analyses have become essential for reliably distinguishing between these genera (Antonín & Herink 1999; Hughes *et al*. 2014; Hughes & Petersen 2015).

In this study, a new species of *Collybiopsis* is described based on morphological and phylogenetic analysis. Detailed morphological descriptions, colour photos, illustrations, morphological comparison with similar taxa and molecular-phylogenetic analyses of combined nuclear ribosomal internal transcribed spacer (nrITS) data is presented.

MATERIAL AND METHODS

Macro- and Micromorphology

Fresh basidiomata were gathered and photographed on-site using a Nikon D5300 camera. Different macroscopic features were documented directly from the fresh fruiting bodies in their natural environment, including details about the habitat and the host plants they were associated with (Vellinga, 1988). The color standards utilized were in accordance with Kornerup & Wanscher (1978). Microscopic details were examined from hand-cut sections of dried specimens (Largent *et al*., 1977). These sections were prepared by mounting them in a solution composed of 5% KOH, 1% Phloxine, and 1% Congo red, then observed using a compound microscope (Olympus CH20i). Line sketches were produced utilizing a Camera Lucida connected to a microscope magnified at 1000 times. Photographs of the different components were captured using a digital camera affixed to an Olympus BX43 compound microscope. Measurements of 60 basidiospores from each sample were recorded (60/3/2 means 60 readings of basidiospores from 3 different fruiting bodies of 2 different sites), presenting the basidiospore dimensions as a range of minimum to maximum length and width, with the quotient (Q) calculated as the length divided by the width of the basidiospores.

DNA Extraction, PCR Amplification, and Sequencing

Fungal genomic DNA was extracted from 100 mg of dried fruit bodies using a fungal genomic DNA Mini Kit (RGCB, Thiruvananthapuram). The ITS region of the nuclear ribosomal DNA gene was amplified using primer pairs ITS1 and ITS4 (White *et al*., 1990). PCR amplification was conducted in a 20 μL reaction volume containing Phire PCR buffer, dNTPs, DNA template, Phire Hotstart II DNA polymerase enzyme, BSA, DMSO, Betaine, and forward and reverse primers. The PCR program included initial denaturation at 96°C for 2 minutes, followed by 30 cycles of denaturation at 96°C for 30 seconds, annealing at 50°C for 40 seconds, and extension at 60°C for 4 minutes. Purification of PCR products was done using the QIAquick Gel Extraction Kit (QIAGEN, Germany), followed by Sanger sequencing using the same primers in an automated DNA sequencer. The obtained sequences were submitted to GenBank (http://www.ncbi.nlm.nih.gov), and accession numbers for two collections are provided in Fig. 1.

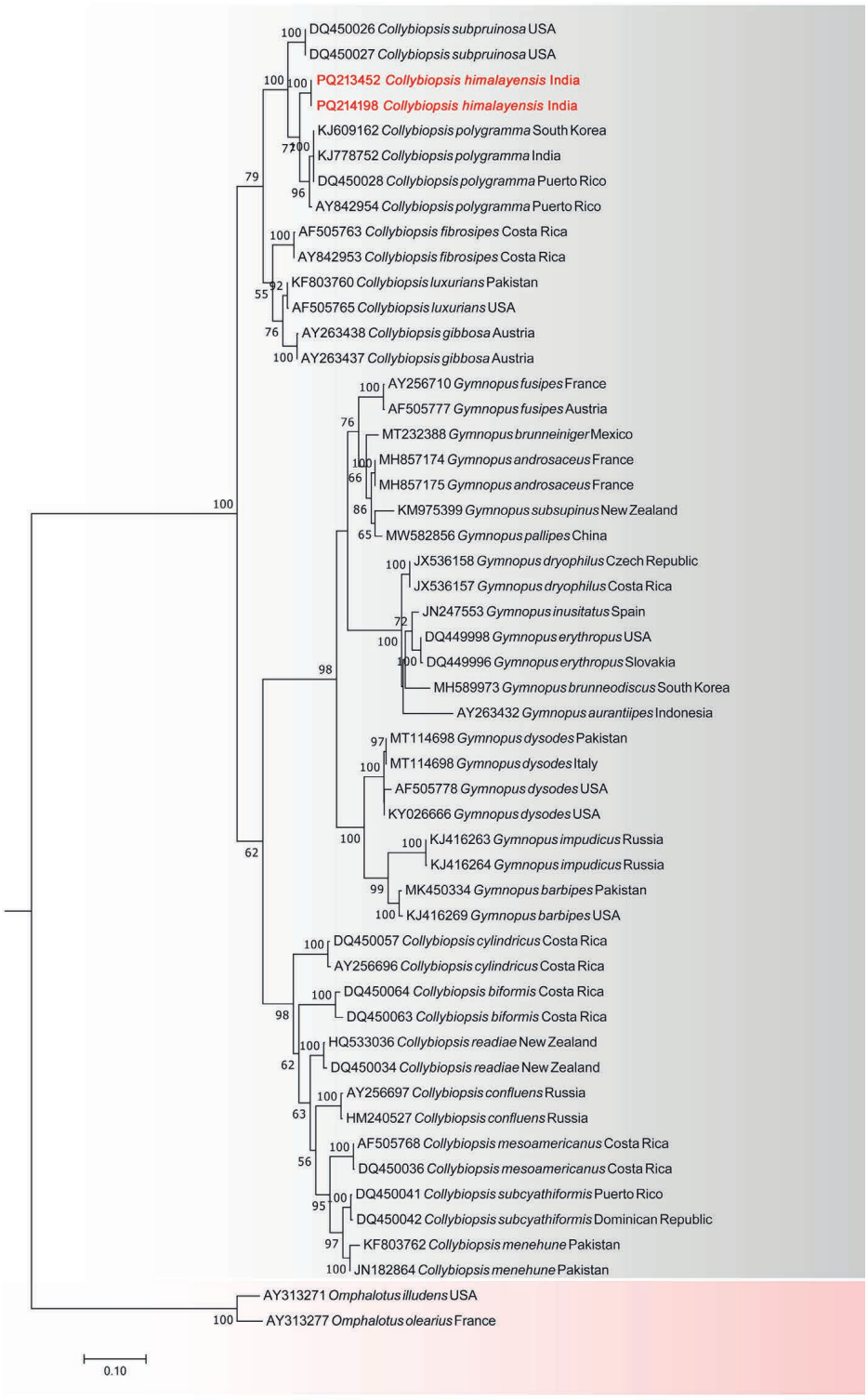

Fig. 1. Maximum Likelihood phylogenetic tree inferred from ITS-rDNA sequence data using the GTR+GAMMA model of nucleotide evolution constructed in RAxML v.2.0.10. Branches are labelled with ML bootstrap support values (≥70 %). Sequence derived from *Collybiopsis himalayensis* is shown in bold in the tree.

Fig. 1. Árbol filogenético de máxima verosimilitud inferido a partir de datos de secuencias de ADNr ITS utilizando el modelo GTR+GAMMA de evolución nucleotídica construido en RAxML v.2.0.10. Las ramas están etiquetadas con valores de soporte bootstrap ML (≥70 %). La secuencia derivada de *Collybiopsis himalayensis* se muestra en negrita en el árbol.

Phylogenetic Analysis

Phylogenetic analysis was conducted utilizing the nrITS dataset, which included the newly obtained sequence, sequences identified through BLAST searches (Altschul *et al*., 1997) in GenBank (Clark *et al*., 2016), and previously published phylogenies (Peterson & Hughes, 2021; Li *et al*., 2022; Kim *et al*., 2022). For this study, a dataset consisting of 48 nrITS sequences of *Collybiopsis* species, including the newly acquired sequence, was employed. The alignment of the nrITS dataset was performed using MAFFT v.7 (Katoh & Standley, 2013). Maximum likelihood (ML) phylogenetic analysis of nrITS sequences was executed using RaxML GUI software (Edler *et al*., 2021), with 1000 bootstrap (BS) replicates analyzed to ascertain nodal support values. Bootstrap support values (>50%) obtained from the ML analysis are presented above or below the branches at nodes. Species of *Omphalotus* Fayod were utilized as an outgroup for the current phylogenetic analysis (GenBank no. AY313271, and AY313277) (Table 1).

RESULTS

Phylogenetic Inferences

The nrITS dataset was made for investigating the phylogenetic relationships of the proposed new species. In nrITS analysis *Collybiopsis himalayensis* (GenBank PQ213452, PQ214198) is clustered within a clade formed by a species including *C. polygramma* (Mont.) J. L. Mata (GenBank AY842954, KJ778752, KJ609162, DQ450028) and *C. subpruinosa* (Murrill) Desjardin, Halling & Hemmes (GenBank DQ450026, DQ450027). Within the clade, *Collybiopsis* is closest to *C. polygramma* (97% identity with 100% query cover) and *C. subpruinosa* (93% identity with 100% query cover) supported by a 100 % bootstrap value (Fig. 1).

Taxonomy

Collybiopsis himalayensis Choudhary, Uniyal and Y.P. Sharma sp. nov. (Fig. 2, 3)
MycoBank No MB855521
GenBank No nrITS (PQ213452, PQ214198)

Diagnosis.— It is distinguished from phylogenetically closest species, *C. polygramma* by its convex to campanulate pileus with a slight umbo, margins uplifted, minutely pruniose surface, pale brown, sub-decurrent lamellae, large basidia (36-51.5 × 6.6-7.9 μm) and presence of pleurocystidia and large hyphae like pileocystidia and cheilocystidia.

Table 1. Sequences used in ML analysis of the study. Newly sequenced collections are in red.

Tabla 1. Secuencias utilizadas en el análisis ML del estudio. Las nuevas colecciones secuenciadas se muestran en rojo.

Species name	Specimen Voucher	Country	GenBank Accession Number (nrITS)
Collybiopsis biformis	TFB7820	Costa Rica	DQ450063
Collybiopsis biformis	TFB7843	Costa Rica	DQ450064
Collybiopsis confluens	TENN58242	Russia	AY256697
Collybiopsis confluens	UBC F19677	Russia	HM240527
Collybiopsis cylindricus	TFB10091	Costa Rica	DQ450057
Collybiopsis cylindricus	TENN58024	Costa Rica	AY256696
Collybiopsis fibrosipes	FB9699	Costa Rica	AF505763
Collybiopsis fibrosipes	PR23TN	Costa Rica	AY842953
Collybiopsis gibbosa	AWW95	Austria	AY263438
Collybiopsis gibbosa	AWW66	Austria	AY263437
Collybiopsis himalayensis	**SC/PU/24/03**	**India**	**PQ213452**
Collybiopsis himalayensis	**SC/PU/24/04**	**India**	**PQ214198**
Collybiopsis luxurians	M39	Pakistan	KF803760
Collybiopsis luxurians	FB10350	USA	AF505765
Collybiopsis menehune	MSM#003	Pakistan	KF803762
Collybiopsis menehune	isolate 3	Pakistan	JN182864
Collybiopsis mesoamericanus	REH7379	Costa Rica	AF505768
Collybiopsis mesoamericanus	TFB10411	Costa Rica	DQ450036
Collybiopsis polygramma	SFC20120821-64	South Korea	KJ609162
Collybiopsis polygramma	CUH:AM082	India	KJ778752
Collybiopsis polygramma	TFB9628	Puerto Rico	DQ450028
Collybiopsis polygramma	PR2542TN	Puerto Rico	AY842954
Collybiopsis readiae	PDD:95844	New Zealand	HQ533036
Collybiopsis readiae	TFB7571	New Zealand	DQ450034
Collybiopsis subcyathiformis	TFB9629	Puerto Rico	DQ450041
Collybiopsis subcyathiformis	TFB11714	Dominican Republic	DQ450042
Collybiopsis subpruinosa	TFB9529	USA	DQ450026
Collybiopsis subpruinosa	TFB11066	USA	DQ450027
Gymnopus androsaceus	CBS 239.53	France	MH857174
Gymnopus androsaceus	CBS 240.53	France	MH857175
Gymnopus aurantiipes	AWW118	Indonesia	AY263432
Gymnopus barbipes	MSM#0034	Pakistan	MK450334
Gymnopus barbipes	TFB14110	USA	KJ416269
Gymnopus brunneiniger	Cesar50	Mexico	MT232388
Gymnopus brunneodiscus	BRNM 714974	South Korea	MH589973
Gymnopus dryophilus	BRNM 707149	Czech Republic	JX536157
Gymnopus dryophilus	BRNM 712600	Costa Rica	JX536158
Gymnopus dysodes	SWAT 01	Pakistan	MT114698
Gymnopus dysodes	SWAT 02	Pakistan	MT114699
Gymnopus dysodes	FB11040	USA	AF505778
Gymnopus dysodes	TFB12563	USA	KY026666
Gymnopus erythropus	SAV XI 2002	USA	DQ449996
Gymnopus erythropus	TFB11911	Slovakia	DQ449998
Gymnopus fusipes	TENN59217	France	AY256710
Gymnopus fusipes	FB11439	Austria	AF505777
Gymnopus impudicus	TFB12155	Russia	KJ416263
Gymnopus impudicus	LE(BIN) 147-2004	Russia	KJ416264
Gymnopus inusitatus	BCN:SCM B-4058	Spain	JN247553
Gymnopus pallipes	GDGM 81513	China	MW582856
Gymnopus subsupinus	PDD:96595	New Zealand	KM975399
Omphalotus illudens	TENN54507	USA	AY313271
Omphalotus olearius	9061b	France	AY313277

Type.— INDIA. Uttarakhand: district Chamoli, Gopeshwar, Mandal 30°27'20.84"N 79°16'38.24"E, 1900 m asl, 14 July 2024, *Shikha Choudhary, Priyanka Uniyal and Yash Pal Sharma*, SC/PU/24/03 (CAL 2140). Holotype.

Etymology.— The specific epithet "*himalayanensis*" (Latin) refers to the geographical origin of the studied collection in the Northwestern Himalayan range.

Description.— Pileus 48-95 mm diam, convex to broadly convex, campanulate, soon becoming broadly campanulate to plano-convex, with or without a small central papilla or umbo; margin decurved to horizontal, uplifted at maturity, even to wavy, conspicuously rugulose- striate or corrugate-sulcate to the disc; surface dull, moist to dry, hygrophanous, minutely pruinose; when young pale brown (5A2-5A3) to buff brown (5B2) at the centre to pale cream (5A2) at the margins, and fading elsewhere to buff brown (5B2), becoming pale brownish (5B2) to greyish brown (5C3) overall on drying. Context very thin (<1 mm), dingy buff (5A2). Lamellae subdecuurent, subdistant to crowded with alternate of lamellulae, narrowly broad (1-2 mm), straight to slightly concave or convex, sometimes intervenose, buff or pale (5A3) to white (1A1) when young, becoming pale yellow (5A3) in age, finely pruinose when dried. Stipe 80–105 mm, central to slightly eccentric, terete, apex equal or slightly flared, base enlarged, equal centrally tough, fistulose, dull, dry, pubescent to tomentose overall, vestiture dark brown to greyish brown; apex concolorous with the lamellae, base greyish brown (5D2-5D3), dark greyish brown (5E3), or dark brown (5E4); sometime with coarse white (1A1) rhizomorphs attached. Odor mild. Basidiospores (60/3/2) 6.8-7.76-9.4 × 4.4-5.1-5.9 (1.25-1.48-1.78) ellipsoid to amygdaliform smooth, hyaline, inamyloid, acyanophilous. Basidia 36-51.5 × 6.6-7.9 μm clavate. Basidioles 37-45 × 5.8-7.2 μm subclavate. Cheilocystidia abundant, lamellar edge sterile, 23.7-46.7 × 5.2-9 μm, versiform, ranging from irregularly cylindrical or sinuous to clavate, cylindrical-capitate ventricose or sphaeropedunculate, rarely knob like outgrowth often in chains of 2-3 cells, hyaline, thin-walled. Pleurocystidia 37-50 × 5.3-6.5 μm and same in shapes as cheilocystidia. Pileipellis a cutis with hyphae 3.9-6.1 μm diam, cylindrical subparallel to slightly interwoven, radially arranged, non diverticulate, smooth or more commonly heavily incrusted with annular to zebroid, yellowish brown to brown pigment deposits, nongelatinous; Pileocystidia 32.5-88.5 × 4.9-6.7 μm; long swollen hyphae with mucorate apex; Pileus trama interwoven; hyphae 5-10 μm, cylindrical, smooth, hyaline, inamyloid, nongelatinous, thick-walled (1 μm). Hymenophoral trama regular; hyphae similar to those of pileus trama. Stipitipellis cutis type 4.9-9 μm diam, cylindrical to slightly in flated, hyaline to pale; Caulocystidia 45-71 × 5.3-8 μm, abundant in number same in shape as pileocysitidia; arranged in cluster. Clamp connection present.

Fig. 2. *Collybiopsis himalayensis*. A-C) Fresh basidiomata in the field and basecamp. D) Basidiospores. E-F) Basidia. G-H) Pleurocystidia. I-J) Cheilocystidia. K) Transverse section through pileipellis. L) Hyphae showing clamp connections. M) Caulocystidia. Scale: A-B = 20 mm, D-M = 10 μm.

Fig. 2. *Collybiopsis himalayensis*. A-C) Basidiomas frescos en el campo y en el campamento base. D) Basidiosporas. E-F) Basidios. G-H) Pleurocistidios. I-J) Queilocistidios. K) Sección transversal del pileipelis. L) Hifas con conexiones en pinza. M) Caulocistidios. Escala: A-B = 20 mm, D-M = 10 μm.

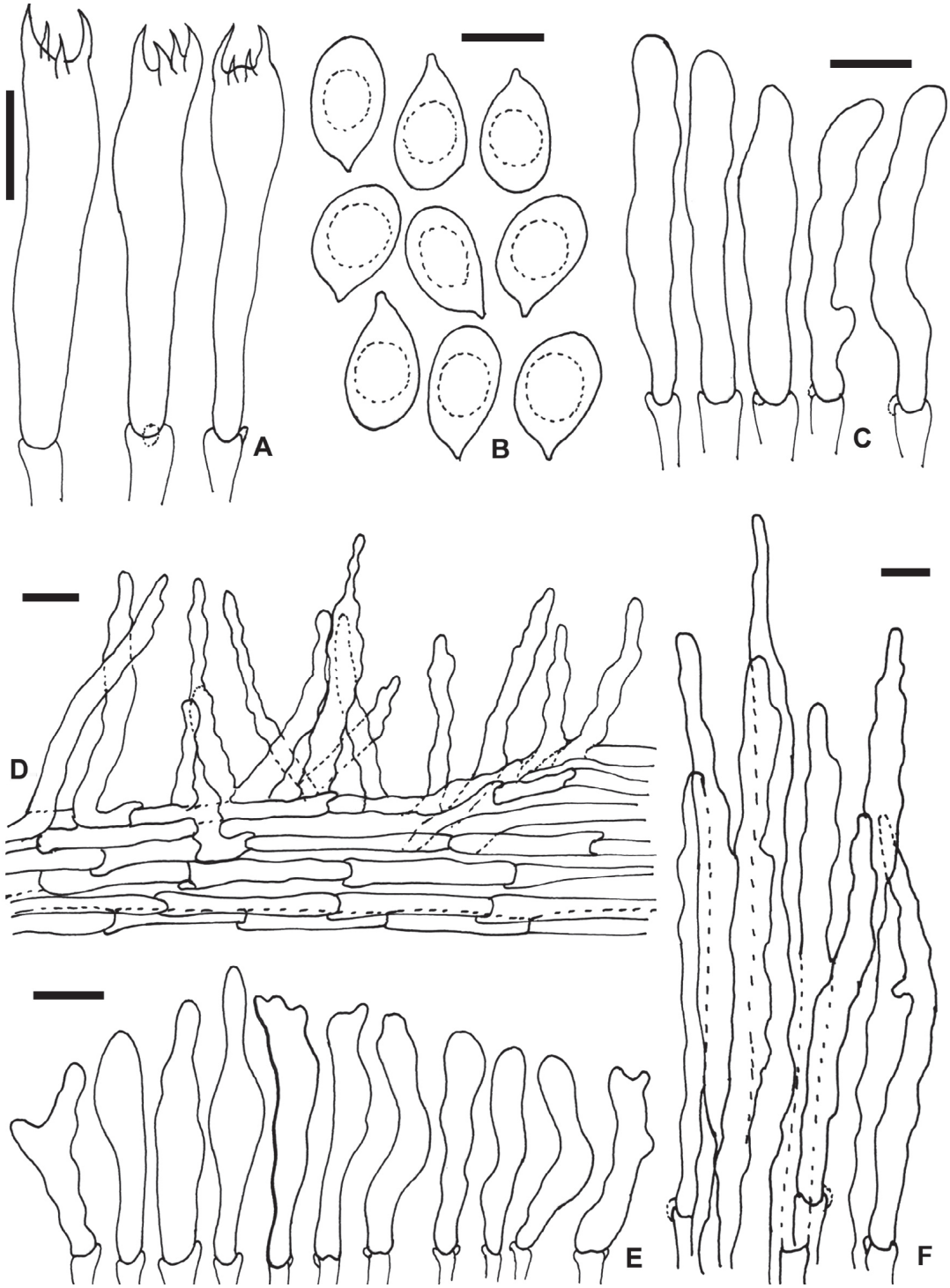

Fig. 3. *Collybiopsis himalayensis*. A) Basidia. B) Basidiospores. C) Pleurocystidia. D) Transverse section through pileipellis. E) Cheilocystidia. F) Caulocystidia. Scale: A-F= 10 μm.

Fig. 3. *Collybiopsis himalayensis*. A) Basidios. B) Basidiosporas. C) Pleurocistidios. D) Sección transversal del pileipelis. E) Queilocistidios. F) Caulocistidios. Escala: A-F= 10 μm.

Habit and Habitat.— Terrestrial, solitary to gregarious under mixed forest of *Quercus leucotrichophora* A. Camus and *Rhododendron arboreum* Sm.

Additional Specimen.— INDIA. Uttarakhand: district Chamoli, Deval, Lohajung, Didna trek, Bedni-bugyal, 30°10'02.49"N 79°38'05.98"E, 2499 m asl, 19 August 2024, *Shikha Choudhary, Priyanka Uniyal* and *Yash Pal Sharma*, SC/PU/24/04 (HBJU/M/182) Paratype.

DISCUSSION

Field identification of the novel species was initially challenging due to its close morphological resemblance to *Gymnopus rodhallii* Desjardin & B.A. Perry and *G. melanopus* A.W. Wilson, Desjardin & E. Horak. However, upon detailed examination, it was distinguished from *G. rodhallii* by several micro-morphological traits, despite sharing a similar pileal surface and stipe coloration. The novel species differs by possessing adnate lamellae that are concolorous with the edge, a densely white pruinose stipe, presence of pleurocystidia, and subclavate to clavate caulocystidia. In comparison, *G. melanopus* also exhibits adnate lamellae but can be differentiated by its dark brown to black stipe, absence of pleurocystidia and pileocystidia, and presence of exclusively clavate caulocystidia.

Morphologically, our species resembles *Collybiopsis confluens* (Pers.) R.H. Petersen and *Gymnopus allegreti* (De Seynes) A.W. Wilson, Desjardin & E. Horak, but can be distinguished from *C. confluens* by its smaller basidiocarps (14-37 mm in diameter), which arise from a common base; the lamellae are densely packed with pruinose edges; the stipe is fibrillose-striate; and the basidiospores measure 7.2–11 μm in length. It also differs from *G. allegreti* by having an umbonate, often campanulate pileus that is yellowish grey to pinkish-cinnamon in color and marked with sulcate-striate features (Dutta *et al*., 2015).

Phylogenetically, the new taxon is close to *C. polygramma* and *C. subpruinosa*. However, *C. polygramma* can be easily segregated from *C. himalayanensis* on the basis of characters such as convex to plano-convex pileus with silky fibrillose, lamellae adnexed, distant, often with light brown to vinaceous brown patches, stipe creamy white to creamy vinaceous; smaller basidia (20-25 × 3-7 μm) and absence of pleurocystidia (Dutta *et al*., 2015). Similarly our novel species differs from *C. subpruinosa* on the basis of smaller pileus (up to 30 mm) reddish brown to greyish brown or dingy orange, lamellae are adnate to adnexed and range from somewhat spaced to widely spaced; they exhibit a pale orange to buff-orange hue with pinkish-tan tones, often mottled with reddish-brown spots. The gill edges are finely pruinose, and the stipe is pale greyish-orange. The basidia are relatively small, measuring 30-36 × 7-8 μm, and pleurocystidia are absent. (Desjardin & Perry, 2017).

In our phylogenetic analysis, *Gymnopus* and *Collybiopsis* are not completely segregated and there is a clade of gymnopoid taxa within *Collybiopsis* in the phylogenetic tree as Family Omphalotaceae is still under continuous taxonomic changes and need more studies which is beyond scope of present work.

AKNOWLEDGEMENT

The authors are grateful to the Head, Department of Botany, University of Jammu and Principal, Govt. P.G. College, Gopeshwar, Chamoli for providing the necessary laboratory facilities. Financial assistance received from the DST-SERB (SPG/2021/003424) is gratefully acknowledged. Field assistance rendered by Dr. Ravi Shankar Kuniyal and Khyati Kuniyal is duly acknowledged.

CONFLICTS OF INTEREST

Authors declare that there is no conflict of interest.

REFERENCES

Altschul, S. F., Madden T. L., Schaffer, A. A., *et al*. (1997). Gapped BLAST and PSI-BLAST: a new generation of protein database search programs. *Nucleic Acids Research* 25: 3389-3402.

Antonín, V. & Herink, J. (1999). Notes on the variability of *Gymnopus luxurians* (Tricholomataceae). *Czech Mycology* 52 (1): 41-49.

Antonín, V. & Noordeloos, M. E. (1993). A Monograph of *Marasmius*, *Collybia*, and Related Genera in Europe: *Marasmius, Setulipes*, and *Marasmiellus*. *Libri botanici* 8: 1-229.

Clark, K., Karsch-Mizrachi, I. & Lipman, D. J. (2016). GenBank. (Database issue) *Nucleic Acids Research* 44 (1): D67-D72.

Desjardin, D. E., Halling, R. E. & Hemmes, D. E. (1999). Agaricales of the Hawaiian Islands. 5. The genera *Rhodocollybia* and *Gymnopus*. *Mycologia* 91 (1): 166-176.

Desjardin, D. E. & Perry, B. A. (2017). The gymnopoid fungi (Basidiomycota, Agaricales) from the Republic of São Tomé and Príncipe, West Africa. *Mycosphere* 8: 1317-1391.

Dutta, A. K., Wilson, A. W., Antonín, V. & Acharya, K. (2015). Taxonomic and phylogenetic study on gymnopoid fungi from Eastern India. I. *Mycological Progress* 14 (10): 1-18.

Earle, F. S. (1909). The genera of the North American gill fungi. *Bulletin of the New York Botanical Garden* 5: 373-451.

Edler, D., Klein, J. & Antonelli, A. (2021). raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. *Methods in Ecology and Evolution* 12: 373-377.

Fries, E. (1835). Corpus florarum provincialium Sueciae: I. Floram scanicam (Vol. 1). Typis Palmblad, Sebell & Company.

Hughes, K. W. & Petersen, R. H. (2015), Transatlantic disjunction in fleshy fungi III: *Gymnopus confluens*. *MycoKeys* 9: 37-63.

Hughes, K. W., Segovia, A. R. & Petersen, R. H. (2014). Transatlantic disjunction in fleshy fungi. I. The *Sparassis crispa* complex. *Mycological Progress* 13 (2): 407-427.

Katoh, K. & Standley, D. M. (2013). MAFFT multiple sequence alignment software ver. 7: improvement in performance and usability. *Molecular Biology and Evolution* 30: 772780.

Kim, J. S., Cho, Y., Park, K. H., Park, J. H., Kim, M., Kim, C. S. & Lim, Y. W. (2022). Taxonomic study of *Collybiopsis* (Omphalotaceae, Agaricales) in the Republic of Korea with seven new species. *MycoKeys* 88: 79-108.

Kornerup, A. & Wanscher, J. H. (1978). Methuen handbook of colour, 3rd edn. Reprinted. – Eyre Methuen.

Largent, D., Johnson, D. & Watling, R. (1977). How to identify mushrooms to genus III: microscopic features. Mad River Press Inc., Eureka, California.

Li, J. P., Pan, M. C., Li, Y., Deng, C. Y., Wang, X. M., Zhang, B. X., Li, C. T. & Li, Y. (2022). Morpho-Molecular Evidence Reveals Four Novel Species of *Gymnopus* (Agaricales, Omphalotaceae) from China. *Journal of Fungi* 8 (4): 398.

Murrill, W. (1915). Agaricaceae (pars). *Flora of North America* 9: 286-296.

Oliveira, J. J., Vargas-Isla, R., Cabral, T. S., Rodrigues, D. P. & Ishikawa, N. K. (2019). Progress on the phylogeny of the Omphalotaceae: *Gymnopus* s. str., *Marasmiellus* s. str., *Paragymnopus* gen. nov. and *Pusillomyces* gen. nov. *Mycological Progress* 18 (5): 713-739.

Petersen, R. H. & Hughes, K. W. (2021). *Collybiopsis* and its type species, Co. ramealis. *Mycotaxon* 136 (2): 263-349.

Retnowati, A. (2018). The species of *Marasmiellus* (Agaricales: Omphalotaceae) from Java and Bali. *Gardens' Bulletin Singapore* 70 (1): 191-258.

Singer, R. (1973). The genera *Marasmiellus*, *Crepidotus* and *Simocybe* in the neotropics. *Nova Beih Nova Hedwigia* 44: 1-517.

Staude, F. (1857). Die Schwämme Mitteldeutschlands, insbesondere des Herzogthums Coburg. Dietz, Coburg.

Vellinga, E. C. (1988). Glossary. In C Bas, Th W Kuyper, ME Noordeloos, EC Vellinga (eds.). *Flora Agaricina Neerlandica* 1: 54-64.

Wilson, A. W. & Desjardin, D. E. (2005). Phylogenetic relationships in the gymnopoid and marasmioid fungi (Basidiomycetes, euagarics clade). *Mycologia* 97 (3): 667-679.