International Journal of Plant & Soil Science

Volume 37, Issue 2, Page 180-187, 2025; Article no.IJPSS.131419
ISSN: 2320-7035

One New Species of *Thaxterogaster* Subgenus *Riederorum* (Agaricales) from India

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Authors' contributions

This work was carried out in collaboration among all authors. Author AB has designed the study and wrote the first draft of the manuscript. Author DC has undertaken the survey tour, collected the specimens and has checked the manuscript. Authors SD and KD managed the analyses of the study and revised the manuscript. All authors read and approved the final manuscript.

Article Information

DOI: https://doi.org/10.9734/ijpss/2025/v37i25317

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://pr.sdiarticle5.com/review-history/131419

Original Research Article

Received: 10/12/2024
Accepted: 12/02/2025
Published: 15/02/2025

ABSTRACT

The family Cortinariaceae is one of the dominant groups of mushrooms in the Indian Himalayas. Currently, this family includes ten genera, with *Thaxterogaster* being one of them. This study introduces a new species, *T. thindii*, collected from the state of Meghalaya, and provides an overview of its morphology along with molecular phylogenetic analysis.

Keywords: Agaricales; Basidiomycota; Macrofungi; morphology; phylogenetic inferences.

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Cite as: *Bose, Arunima, Dyutiparna Chakraborty, Sudeshna Datta, and Kanad Das. 2025. "One New Species of Thaxterogaster Subgenus Riederorum (Agaricales) from India". International Journal of Plant & Soil Science 37 (2):180-87. https://doi.org/10.9734/ijpss/2025/v37i25317.*

1. INTRODUCTION

The Cortinariaceae R. Heim ex Pouzar *emend*. Niskanen & Liimat., remains largely understudied in India, with only 36 species of Cortinariaceae identified to date (Bose et al*.,* 2024a; Bose et al*.,* 2024b). In contrast, more than 3,157 species have been documented worldwide, with many yet to be discovered (Soop et al*.,* 2019; Kalichman et al*.,* 2020; Liimatainen et al*.,* 2022). Recently, this family has been classified into ten genera: *Cortinarius* (Pers.) Gray, *Phlegmacium* (Fr.) Wünsche, *Thaxterogaster* Singer, *Calonarius* Niskanen & Liimat., *Aureonarius* Niskanen & Liimat., *Cystinarius* Niskanen & Liimat., *Volvanarius* Niskanen & Liimat., *Hygronarius* Niskanen & Liimat., *Mystinarius* Niskanen & Liimat., and *Austrocortinarius* Niskanen & Liimat. (Liimatainen et al*.,* 2022). Among these, *Thaxterogaster* includes over 170 species, with major research focused in Australasia, Europe, and North and South America (Xie et al*.,* 2024). For the past 50 years, *Thaxterogaster* was regarded as an independent genus (Xie et al*.,* 2024), until ITS- and LSU-based phylogenetic analyses led to its recognition as a synonym of *Cortinarius* (Peintner et al*.,* 2002). Recently, the genus *Thaxterogaster* has divided into six subgenera: *Thaxterogaster* Niskanen & Liimatainen, *Cretaces* Niskanen & Liimatainen, *Multiformes* Niskanen & Liimatainen, *Riederorum* Niskanen & Liimatainen, *Scauri* Niskanen & Liimatainen, and *Variegati* Niskanen & Liimatainen (Liimatainen et al*.,* 2023; Ghosh et al*.,* 2023). However, very little work has been done on Indian *Thaxterogaster* species, with only four species reported: *Tcarneus* S.S. Ahmed & Z.A. Reshi, *Thaxterogaster indopurpurascens* Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt ex A. Ghosh, D. Chakr., K. Das & Vizzini (*nom. Inval.*) Art. 35.1 (Shenzhen), *T. purpurascens* (Fr.) Niskanen & Liimat., and *T. shoreae* A. Ghosh, D. Chakr., K. Das & Vizzini (Bose et al*.,* 2024a).

The genus was dedicated to Roland Thaxter (1905-1906) who was the first to collect sequestrate taxa of this genus in Patagonia, South America, with subsequent descriptions by Dodge and Zeller (1934), Singer (1951, 1960), Singer and Smith (1963), Horak and Moser (1965), and Horak (1979). For example, *T. magellanicum* is a sequestrate species, confirming that the Cortinariaceae family, particularly the genus *Thaxterogaster*, includes sequestrate members (Nouhra et al*.,* 2021; Singer, 1951; Liimatainen et al*.,* 2022).

Cortinariaceae species are important ectomycorrhizal fungi in India's forest ecosystems, ranging from temperate to tropical regions (Liimatainen et al., 2020). The primary host trees belong to families such as Caesalpiniaceae, Cistaceae, Dipterocarpaceae, Fagaceae, Myrtaceae, Nothofagaceae, Pinaceae, Rhamnaceae, Rosaceae, and Salicaceae, with some herbaceous plants from the Cyperaceae family (Ghosh et al*.,* 2023). These fungi are, therefore, essential components of tropical to subalpine terrestrial ecosystems (Bose et al*.,* 2024b).

In terms of economic value, *T. multiformis* (Fr.) Niskanen & Liimat. and *T. purpurascens* (Fr.) Niskanen & Liimat. are highly valued as edible species in China (Dai et al*.,* 2010), while *T. turmalis* (Fr.) Niskanen & Liimat. is recognized for its antitumoral properties (Dai et al*.,* 2008).

During extensive macrofungal surveys in Sohra, Meghalaya, India, several intriguing specimens of *Thaxterogaster* were collected. In-depth morphological studies and molecular phylogenetic analyses, based on nrITS sequences of these recent specimens, revealed an undescribed species from the subgenus *Riederorum*, section *Riederorum*. Previously referred to as *Riederi*, this section was renamed to *Riederorum* following the application of Article 21.2 of the current version of the Code of Nomenclature (“Code Shenzhen” Turland., et al*.,* 2018). *Thaxterogaster thindii* sp. nov. is proposed in the present study. This study presents detailed macro- and micromorphological descriptions, and illustrations of the new species, and comparisons with closely related taxa. Molecular phylogenetic estimation in support of the novel species is also given.

2. MATERIALS AND METHODS

2.1 Morphological Studies

A comprehensive macrofungal survey was carried out in Sohra, Meghalaya, India, during the rainy season of April, 2024. This led to the collection of fresh basidiomata from the Cortinariaceae family. Macromorphological traits were examined directly in the field using fresh specimens, with photographs of the samples taken in both the field and at the basecamp using Samsung S23 and OnePlus Nord CE. The color codes followed the Methuen Handbook of Color (Kornerup & Wanscher, 1978). After recording all

macromorphological details, the samples were dissected and dried using an electric dryer. Micromorphological analysis involved preparing freehand sections from the dried specimens, which were then mounted in a solution containing 5% KOH, 1% Phloxin, and 1% ammoniacal Congo red. These sections were observed under an Olympus CX 41 compound microscope. Anatomical features were illustrated with a drawing tube attached to the same microscope at 1000× magnification, and microphotographs were taken using a camera mounted on an Olympus BX 53 microscope. Basidiospores were examined in Melzer's reagent, and their measurements (excluding ornamentations) were taken in side view. Measurements for basidiospores and other micromorphological structures, including basidia, followed a standard protocol, with thirty (30) measurements for basidiospores and twenty (20) for other structures. The specimens were deposited in the Central National Herbarium (CAL), Howrah.

2.2 DNA Extraction, PCR Amplification and Sequencing

Genomic DNA was extracted from 100 mg of dried basidioma using the HiPurA Fungal DNA Purification Kit (HIMEDIA), in accordance with the manufacturer's instructions. The nrITS gene region was amplified with the primer pair ITS1-F and ITS4 (White et al., 1990; Gardes & Bruns, 1993). The PCR conditions were as follows:

Table 1. A list of species, specimen voucher and GenBank accession no. of species used in this study

Species name (as reported in GenBank)	Voucher/strain no.	Country	GenBank accession no. (nrITS)
Phlegmacium boreicyanites Type	S:CFP931	Sweden	KF732296
Phlegmacium cyanites Type	UPS:A. Taylor 2005069	Sweden	KF732355
Thaxterogaster argyrionus Type	MEL:2331642	Australia	NR_152999
Thaxterogaster borealicremeolinus Type	HMAS:287398	China	NR_198606
Thaxterogaster borealicremeolinus	LY418	China	OR395363
Thaxterogaster cremeolina Type	PDD:70506	New Zealand	NR_157889
Thaxterogaster cremeorufus Type	PDD:94056	New Zealand	NR_153064
Thaxterogaster cremeorufus	PDD:72649	New Zealand	KT833622
Thaxterogaster dulciorum Type	PDD:78797	New Zealand	NR_157898
Thaxterogaster dulciorum	PDD:107708	New Zealand	KT875195
Thaxterogaster dovrensisType	NR_160640	Norway	NR_160640
Thaxterogaster glaucocyanopus Type	G:5034	France	MH846274
Thaxterogaster Iringa Type	PDD:73135	New Zealand	NR_120131
Thaxterogaster kaimanawa Type	PDD:73133	New Zealand	NR_157891
Thaxterogaster mendax Type	PC:A. Bidaud 07-10-162	France	NR_153019
Thaxterogaster melleicarneus Type	H:I. Kytovuori 01-053	Estonia	KF732577
Thaxterogaster natarajanii Type	AP23-63	India	PP892258
Thaxterogaster natarajanii	AP23-64	India	PP892259
Thaxterogaster nebulobrunneus Type	MEL:2331648	Australia	NR_152995
Thaxterogaster occidentalis Type	MICH:10382	USA	NR_130234
Thaxterogaster porphyropusType	S:F47381	Sweden	NR_130246
Thaxterogaster pallidoriederi Type	BOZ:Bellu 30-09-2011	Italy	NR_160639
Thaxterogaster pallidirimosus Type	H:6035694	Finland	KF732578
Thaxterogaster rhipiduranus	PDD:72617	New Zealand	MH101624
Thaxterogaster rhipiduranus Type	PDD:88269	New Zealand	NR_157902
Thaxterogaster riederi	TEB141-10	Sweden	MH923056
Thaxterogaster riederi	Bellu 12-08-2012	Italy	MH923057
Thaxterogaster rufoallutus Type	PC:P. Moenne-Loccoz 635	France	KF732413
Thaxterogaster rufopurpureus Type	HMAS287399	China	OR395229
Thaterogaster shoreae Type	AGDC 21-04	New Zealand	OP473976
Thaxterogaster sinopurpurascens Type	HMAS287400	China	OR395230
Thaxterogaster thindii Type	**DCM-1**	**India**	**PQ686617**
Thaxterogaster thindii	**DCM-3**	**India**	**PQ686634**

initial denaturation at 94 °C for 3 minutes, followed by 35 cycles of denaturation at 94 °C for 1 minute, annealing at 50 °C for 30 seconds, and extension at 72°C for 1 minute. The final extension step was at 72°C for 7 minutes. The PCR products were purified using the QIAquick PCR Purification Kit. Both strands of the amplified fragments were sequenced using the same primers on a 3730xl DNA Analyzer. Sequence quality was assessed using Sequence Scanner Software version 1. Sequence alignment, editing, and contig assembly were performed with Geneious version 5.1 (Drummond et al*.,* 2010) as well as manually. Two sequences were obtained in this study, one for each species: *Thaxterogaster thindii* (DCM-1 and DCM-3). These sequences were subsequently submitted to GenBank (Table 1).

2.3 Phylogenetic Analysis

The nrITS sequences for the newly identified *Thaxterogaster thindii* and its close relatives were retrieved from GenBank (https://www.ncbi.nlm.nih.gov/genbank) as well as from relevant published phylogenies (Xie et al*.,* 2023; Xie et al*.,* 2024). The raw nrITS dataset was compiled independently. Sequence alignment was carried out using the online version of the MAFFT v. 7 program (https://mafft.cbrc.jp/alignment/software/), applying the L-INS-i algorithm, a 200PAM/k = 2 scoring matrix, a gap open penalty of 1.53, and an offset value of 0.123. The alignment was manually inspected and trimmed in MEGA v. 7 (Kumar et al*.,* 2016) to ensure the preservation of conserved motifs. Both forward and reverse reads were manually corrected when necessary. Phylogenetic analysis was performed using the maximum likelihood (ML) method with RAxMLGUI version 2.0, employing the GTRGAMMA model. To evaluate nodal support, an ultrafast bootstrap with 1,000 replicates was conducted. Maximum likelihood bootstrap (MLbs) values ≥70% are displayed in the phylogenetic trees (Fig. 1).

3. RESULTS AND DISCUSSION

3.1 Phylogenetic Inferences

In our maximum likelihood (ML) phylogenetic analysis, the nrITS data matrix included 35 taxa and 685 nucleotide positions (gaps included), with *Phlegmacium boreicyanites* (Kytöv., Liimat., Niskanen & A.F.S. Taylor) Niskanen & Liimat. and *Phlegmacium cyanites* (Fr.) M.M. Moser serving as the outgroup (Xie et al*.,* 2023). The nrITS dataset comprised 1464/1726 conserved sites, of which 177/1726 were parsimony-informative, 51/1726 were singleton sites. The rate parameters were as follows: A-C: 0.46484, A-G: 2.79781, A-T: 1.00000, C-G: 0.46484, C-T: 2.79781, and G-T: 1.00000. The base frequencies were A: 0.245, C: 0.199, G: 0.205, and T: 0.350.

In our nrITS-based phylogenetic tree (Fig. 1), the two collections of the new species (vouchers DCM-1 and DCM-3) clustered with maximum statistical support (MLbs = 100%) and were found to be closely related to *T. pallidoriederi* (Brandrud, Dima & Bellù) Niskanen & Liimat., *T. glaucocyanopus* (Rob. Henry) Niskanen & Liimat. and *T. riederi* (Weinm.) Niskanen & Liimat., clustering in a clade with strong statistical support (MLbs = 96%), but in a distinct lineage that we recognise as a separate taxon.

3.2 Taxonomy

Thaxterogaster thindii A. Bose & D. Chakr., *sp. nov.* (Figs. 2–3).

MycoBank: MB857312

GenBank: PQ686617 (ITS, Holotype), PQ686634 (ITS, Paratype).

Holotype: Sohra, Meghalaya, India, 25°16′16″N, 91°43′55″E, 1321 m a.s.l., 24 April 2024, on the soil under *Castanopsis* sp., leg. *Dyutiparna Chakraborty*, DCM-1 (CAL 2129).

Etymology: Commemorating Dr K.S. Thind for his significant contributions to Indian mycobiota.

Diagnosis: *Thaxterogaster thindii* is distinct from its closely allied species i.e. *T. pallidoriederi*, *T. glaucocyanopus* and *T. riederi* in terms of its host preference, deep violet to greyish violet lamellae, subamygdaloid-ellipsoid basidiospores along with nrITS- based sequence data.

Description: Pileus 30–100 mm in diam., convex to planoconvex when young, then applanate at maturity; margin enrolled; surface viscid when moist, brown (7E6–5) at the center, gradually orange (5A7) to greyish orange (5B6) towards the margin. Lamellae decurrent to sinuate, crowded (12/cm at pileus margin), brownish orange (5C6); lamellulae present in 5 series, margin wavy. Stipe 55–80 × 7–18 mm, central, curved, bulbous base with white (1A1) basal mycelium; surface dry, light orange to pale

orange (5A3–4) with longitudinally striated on the surface. Pileus context solid, greyish yellow (2B3–4); unchanging when bruised. Stipe context solid, fibrous, yellowish grey to dull yellow (3B2–3). Smell and taste not recorded. Spore print rusty-brown.

Basidiospores 7.08–*9.26*–10.65 × 4.16–*5.54*–6.47 µm, Q=1.46–1.67–2.11, n=30, oval to elliptical, weakly to moderately verrucose, dextrinoid. Basidia 38.8–44.4 × 8.3–9.4 µm, clavate, 4-spored; sterigmata triangular. Sterile marginal elements 16–26 × 5–9 µm, cylindrical to clavate, thin-walled, colourless. Cheilocystidia 24–27 × 4.4–6.0 µm, emergent up to 1.5 µm beyond the basidiole tips, cylindrical to subcylindrical, occasional. Pleurocystidia 26.0–36.6 × 3.3–10.0 µm, emergent up to 0.8 µm beyond the basidiole tips, cylindrical to subcylindrical. Pileipellis duplex up to 144.4 µm; suprapellis up to 47.2 µm thick, composed of compactly arranged repent parallel hyphae, 70–80 × 3–5 µm wide; subpellis up to 97.2 µm thick consisting of inflated elements 45–50 × 16–18 µm wide, no contents. Clamp connections present.

Additional specimen examined: Sohra, Meghalaya, India, 29°18′16″N, 95°46′55″E, 1325 m a.s.l., 27 April 2024, on the soil under *Castanopsis* sp., leg. *Dyutiparna Chakraborty*, DCM-3 (Paratype: CAL 2130).

Remarks: The new species is classified in the *Thaxterogaster* subgenus *Riederorum*, section *Riederorum*. Morphologically, it aligns under the above section based on the combination of following characteristics: pileus 25 to 120 mm wide, viscid; lamellae crowded; stipe base distinctly bulbous; basidiospores elliptical; pileipellis duplex with a notable glutinous layer on the surface (Liimatainen et al., 2022).

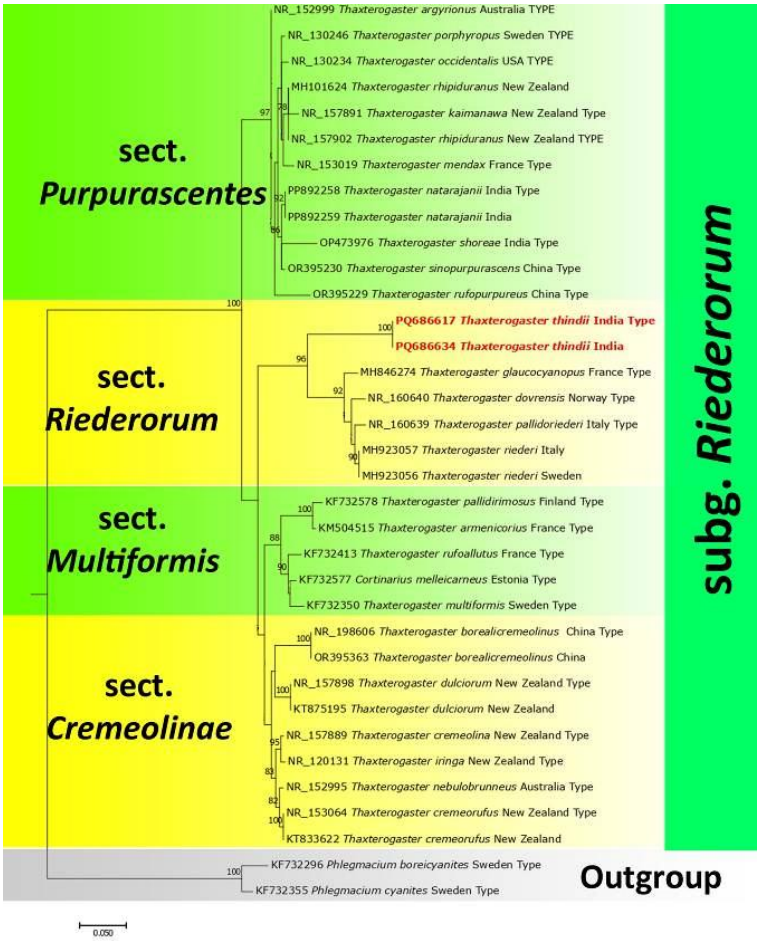

Fig. 1. Phylogram generated by maximum likelihood (ML) analysis based on ITS sequence data for *Thaxterogaster thindii* and allied species. Maximum likelihood bootstrap support values (MLbs) ≥ 70% are shown. The new species is highlighted in red to mark their phylogenetic positions in the tree

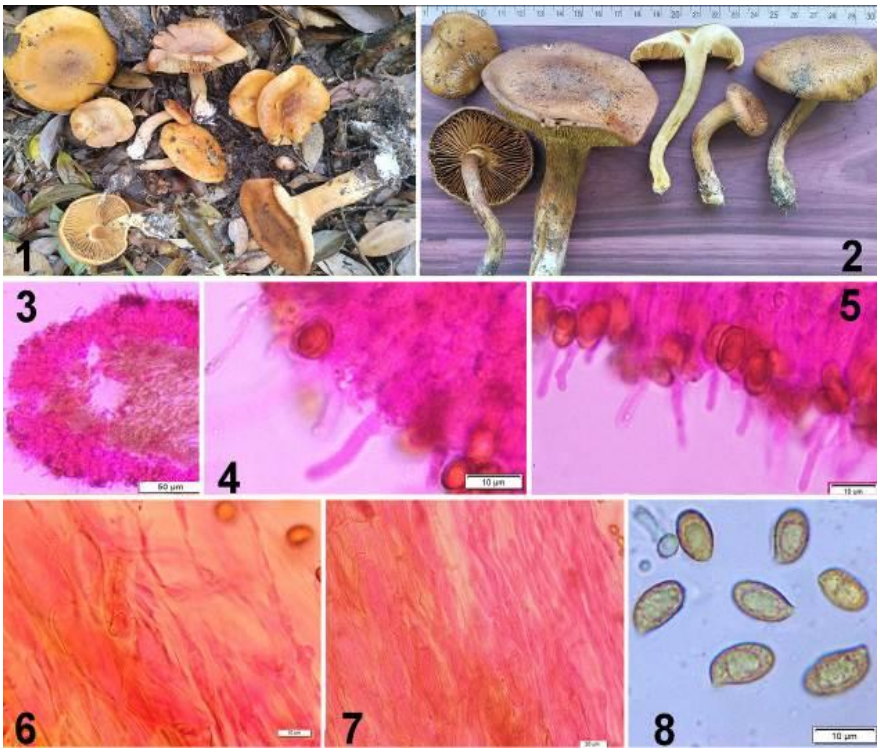

Fig. 2. *Thaxterogaster thindii* sp. nov. (CAL 2129, holotype). (1–2) Fresh basidiomata, (3–4) cheilocystidia, (5) pleurocystidia, (6–7) transverse section through pileipellis of pileus, (8) basidiospores. Scale bars: 3 = 50 µm, 4 = 10 µm, 5 = 10 µm, 6 = 10 µm, 7 = 20 µm and 8 = 10 µm

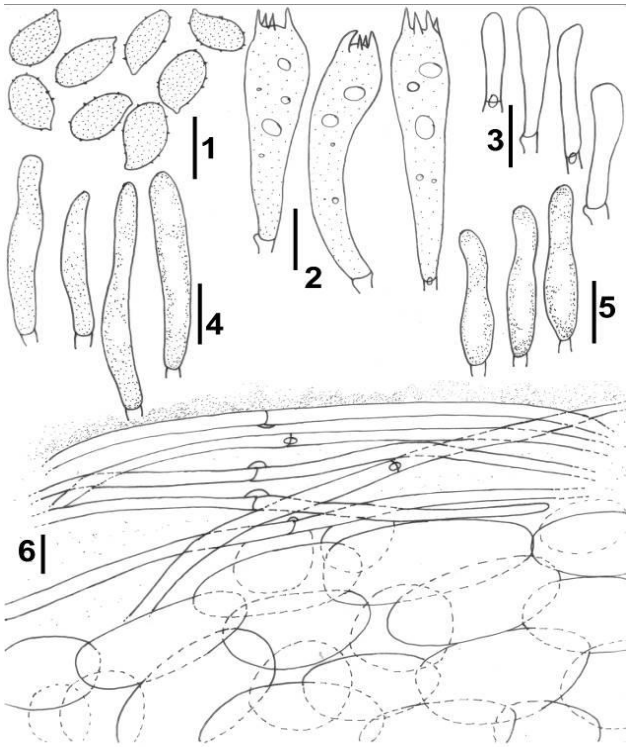

Fig. 3. *Thaxterogaster thindii* sp. nov. (CAL 2129, holotype). (1) Basidiospores, (2) basidia, (3) sterile marginal elements, (4) pleurocystidia, (5) cheilocystidia, (6) transverse section of pileipellis through pileus. Scale bars: 1–6 = 10 µm

Phylogenetically, *T. thindii* is most closely related to *T. pallidoriederi* (Brandrud, Dima & Bellù) Niskanen & Liimat., *T. glaucocyanopus* (Rob. Henry) Niskanen & Liimat., and *T. riederi* (Weinm.) Niskanen & Liimat., all of which have been reported from Europe. However, these European taxa can easily be distinguished from our Indian specimens by possessing lamellae that range from deep violet to greyish violet, subamygdaloid basidiospores, and occurrence under *Fagus* or *Pinus* to *Picea* (Brandrud et al., 2018).

4. CONCLUSION

The Cortinariaceae family remains largely unexplored in India. This family includes significant ectomycorrhizal fungi that play a crucial role in maintaining forest ecosystems. Our ongoing and extensive macrofungal surveys across various Indian states, including Uttarakhand, Himachal Pradesh, West Bengal, and Sikkim, have uncovered numerous previously overlooked species from several genera. Through a combination of morphological and molecular phylogenetic studies, our research confirms that India harbors many undiscovered or potentially new species of Cortinariaceae. We anticipate that, as we continue our macrofungal explorations across all climatic regions of India, the diversity of mushrooms in general and the Cortinariaceae in particular will be unfolded in the near future.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

ACKNOWLEDGEMENTS

We are grateful to the Director, Botanical Survey of India (BSI), Kolkata and Head of office, Central National Herbarium, BSI, Howrah for facilitating the present research. We are also thankful to the Head of Office, Eastern Regional Centre, BSI, Shillong, Meghalaya. We would like to thank and acknowledge Mr. Sherlang Khonglam and Mr. Neiphrezo Ciesotsu for assisting us to undertake the macrofungal surveys to the forested areas and the Forest Departments of Meghalaya for allowing us to undertake macrofungal surveys.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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Peer-review history:
The peer review history for this paper can be accessed here:
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