One new species of *Thaxterogaster* subgenus *Riederorum* (Agaricales) from India

ABSTRACT

The Cortinariaceae family 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.

1. INTRODUCTION

The Cortinariaceae family, R. Heim ex Pouzar em. 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 globally, 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* Singer, Niskanen & Liimatainen 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: *Thaxterogaster carneus* S.S. Ahmed, Z.A. Reshi & K.I. Andrabi, *Thaxterogaster indopurpurascens* (Dima, Semwal, Brandrud, V. Papp, & V.K. Bhatt) A. Ghosh, D. Chakr., K. Das & Vizzini, *Thaxterogaster purpurascens* (Fr.) Niskanen & Liimat., and *Thaxterogaster shoreae* A. Ghosh, D. Chakr., K. Das & Vizzini (Bose *et al.,* 2024a).

Roland Thaxter (1905-1906) 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 significant ectomycorrhizal fungi in India's forest ecosystems, spanning temperate to tropical regions. 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 antitumor 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, N.J. *et al.,* 2018). The present species is proposed herein as *Thaxterogaster thindii* sp. nov. 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. MATERIAL 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: 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 *Thaxterogaster thindii* (voucher nos. DCM-1 and DCM-3) grouped into a distinct lineage with strong statistical support (MLbs = 100%) and were found to be closely related to *T. pallidoriederi*, *T. glaucocyanopus*, and *T. riederi*. However our present species is recovered as a distinct taxon with strong statistical support (MLbs = 96%) being sister with the clade comprising four species: *T. glaucocyanopus, T. pallidoriederi* and *T. riederi*.

3.2 Taxonomy

Thaxterogaster thindii A. Bose & D. Chakr., *sp. nov.* (Fig. 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., *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., *Dyutiparna Chakraborty*, DCM-3 (Paratype: CAL 2130).

Remarks: Our Indian collection is classified under the 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 gluten layer on top (Liimatainen *et al.,* 2022).

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 specimens 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).

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 dovrensis *Type*	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 porphyropus *Type*	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**

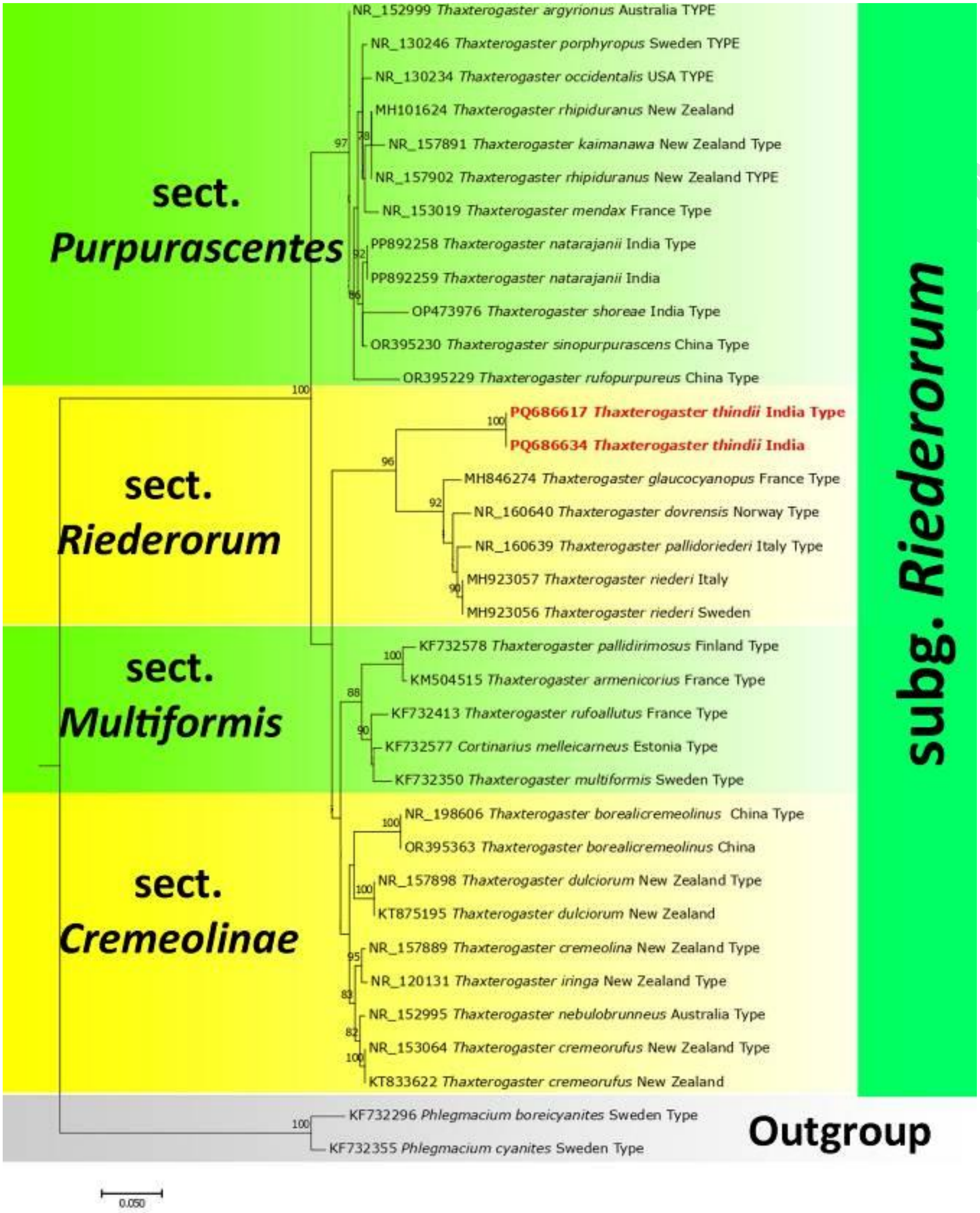
sect. Purpurascentes
NR_152999 Thaxterogaster argyrionus Australia TYPE
NR_130246 Thaxterogaster porphyropus Sweden TYPE
NR_130234 Thaxterogaster occidentalis USA TYPE
MH101624 Thaxterogaster rhipiduranus New Zealand
97
78
NR_157891 Thaxterogaster kaimanawa New Zealand Type
NR_157902 Thaxterogaster rhipiduranus New Zealand TYPE
NR_153019 Thaxterogaster mendax France Type
PP892258 Thaxterogaster natarajanii India Type
92
PP892259 Thaxterogaster natarajanii India
86
OP473976 Thaxterogaster shoreae India Type
OR395230 Thaxterogaster sinopurpurascens China Type
OR395229 Thaxterogaster rufopurpureus China Type
100
sect. Riederorum
100
PQ686617 Thaxterogaster thindii India Type
PQ686634 Thaxterogaster thindii India
96
MH846274 Thaxterogaster glaucocyanopus France Type
92
NR_160640 Thaxterogaster dovrensis Norway Type
NR_160639 Thaxterogaster pallidoriederi Italy Type
90
MH923057 Thaxterogaster riederi Italy
MH923056 Thaxterogaster riederi Sweden
sect. Multiformis
100
KF732578 Thaxterogaster pallidirimosus Finland Type
KM504515 Thaxterogaster armenicorius France Type
88
KF732413 Thaxterogaster rufoallutus France Type
90
KF732577 Cortinarius melleicarneus Estonia Type
KF732350 Thaxterogaster multiformis Sweden Type
sect. Cremeolinae
100
NR_198606 Thaxterogaster borealicremeolinus China Type
OR395363 Thaxterogaster borealicremeolinus China
100
NR_157898 Thaxterogaster dulciorum New Zealand Type
KT875195 Thaxterogaster dulciorum New Zealand
95
NR_157889 Thaxterogaster cremeolina New Zealand Type
NR_120131 Thaxterogaster iringa New Zealand Type
83
NR_152995 Thaxterogaster nebulobrunneus Australia Type
82
NR_153064 Thaxterogaster cremeorufus New Zealand Type
100
KT833622 Thaxterogaster cremeorufus New Zealand
subg. Riederorum
100
KF732296 Phlegmacium boreicyanites Sweden Type
KF732355 Phlegmacium cyanites Sweden Type
Outgroup
0.050

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.

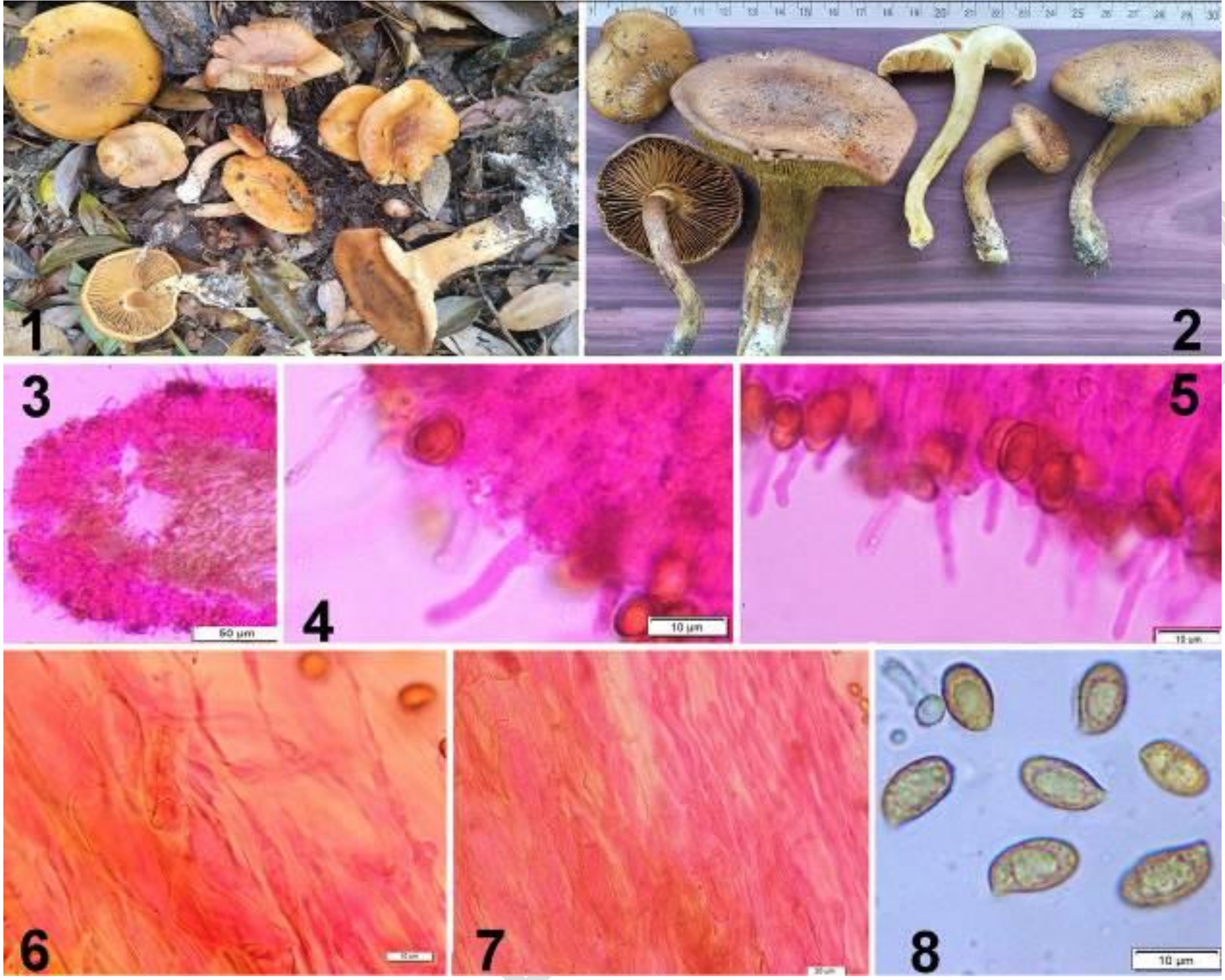

Fig. 2. *Thaxterogaster thindii* sp. nov. (DCM-1, holotype). (1–2) Fresh basidiomata, (3–4) cheilocystidia, (5) pleurocystidia, (6–7) transverse section through pileipellis of pileus, (8) basidiospores. Scale bars: 3 = 50 µm, 4 = 10 µm, 5 = 10 µm, 6 = 10 µm, 7 = 20 µm and 8 = 10 µm.

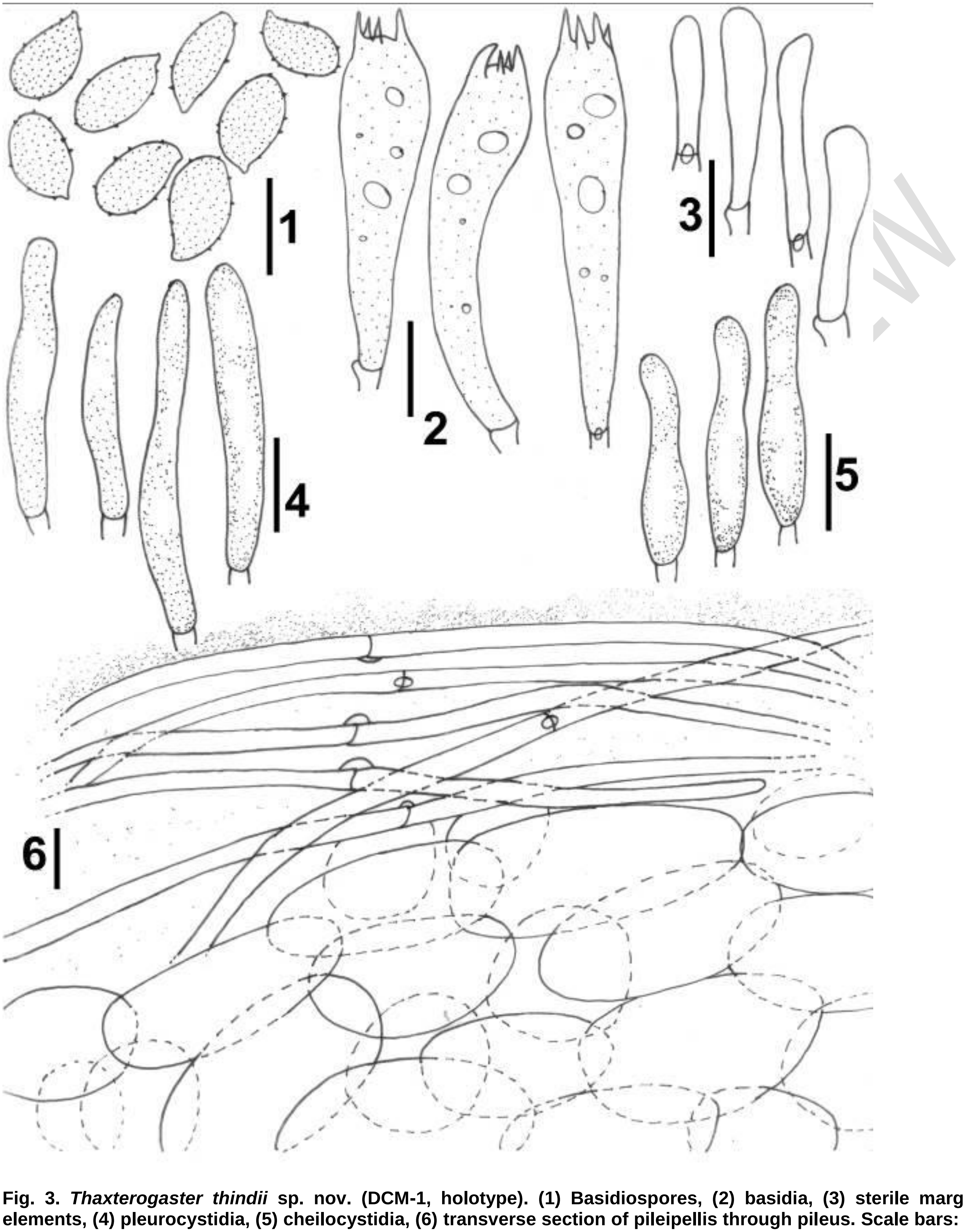

Fig. 3. ***Thaxterogaster thindii*** **sp. nov. (DCM-1, holotype). (1) Basidiospores, (2) basidia, (3) sterile marginal elements, (4) pleurocystidia, (5) cheilocystidia, (6) transverse section of pileipellis through pileus. Scale bars: 1–6 = 10 µm.**

4. CONCLUSION

The Cortinariaceae family remains largely unexplored in India. This family includes significant ectomycorrhizal fungi that play a crucial role in maintaining terrestrial 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.

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