



Thaxterogaster shoreae, a new species of *Thaxterogaster* subg. *Scauri* sect. *Purpurascentes* from Sal Forest of India based on morphology and molecular phylogeny

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ABSTRACT: Routine macrofungal explorations of different *Shorea robusta* dominated forest areas of Jharkhand and West Bengal are being undertaken since 2020. A specimen classified as "*Thaxterogaster*" was collected recently from these states and here proposed as *Thaxterogaster shoreae* sp. nov. within subg. *Scauri* sect. *Purpurascentes*. Detailed morphological description, illustrations 2-locus phylogenetic estimations and comparisons with respective allied species are provided. Moreover, in this communication one new combination in the genus *Thaxterogaster* is also proposed.

KEY WORDS: Basidiomycota, Cortinariaceae, macrofungi, , *Shorea robusta*, Taxonomy, *Thaxterogaster indopurpurascens*.

INTRODUCTION

The family Cortinariaceae R. Heim belongs to suborder Agaricinae, which contains mainly the brown and dark-spored Agaricales (Matheny *et al.*, 2015; Dentinger *et al.*, 2016). Cortinariaceae species are important ectomycorrhizal fungi associated with different trees and shrubs, belonging to the families Caesalpiniaceae, Cistaceae, Dipterocarpaceae, Fagaceae, Myrtaceae, Nothofagaceae, Pinaceae, Rhamnaceae, Rosaceae and Salicaceae as well as a few herbaceous plants in the Cyperaceae (Liimatainen *et al.*, 2020). According to some phylogenetic studies, the family Cortinariaceae includes only one genus, *Cortinarius* (Pers.) Gray, with a cosmopolitan distribution from tropical to arctic regions and over 3157 species across the world (Soop *et al.*, 2019; Kalichman *et al.*, 2020; Liimatainen *et al.*, 2020). More recently, Liimatainen *et al.*, (2022) have split the genus *Cortinarius* into 10 genera (*Cortinarius* s. str., *Phlegmacium*, *Thaxterogaster*, *Calonarius*, *Aureonarius*, *Cystinarius*, *Volvanarius*, *Hygronarius*, *Mystinarius*, and *Austrocortinarius*) based on genomic and multi-gene sequence data. The genus *Thaxterogaster* Singer, Niskanen and Liimatainen recognized as a bihemispherical genus with most species classified earlier in phlegmacioid and myxacioid taxa in genus *Cortinarius* (Pers.) Gray (Liimatainen *et al.*, 2022). This genus is characterised by the presence of small to large sized agaricoid (phlegmacioid, myxacioid) or sequestrate basidiomata with different colouration from white, ochraceous, greenish, brown to purple; a negative or, more rarely, red (in pileus, context and/or stipital veil) KOH reaction; lamellae adnate, adnexed or emarginate,

when young white, pale grey, pale brown, green, purple or with a purplish tint; stipe cylindrical, clavate, rooting or bulbous, bulb rounded to marginate white, pale brown, purple, some species with greenish colours, in some species usually turning deeper purple when bruised (Liimatainen *et al.*, 2022). *Thaxterogaster* currently includes the subgenera *Thaxterogaster* Niskanen & Liimatainen, *Cretaces* Niskanen & Liimatainen, *Multiformes* Niskanen & Liimatainen, *Riederorum* Niskanen & Liimatainen, *Scauri* Niskanen & Liimatainen, and *Variigati* Niskanen & Liimatainen and 28 sections with nearly 200 species (Liimatainen *et al.*, 2022). *Thaxterogaster* is the second largest genus of Cortinariaceae in Southern Hemisphere (*Cortinarius* s. str. still remains the largest genus in the family, with ≥ 3000 species estimated worldwide) while only few taxa have been described in Northern Hemisphere particularly from Europe and North America (Liimatainen *et al.*, 2014, 2020, 2022; Soop *et al.*, 2019).

The subgenus *Scauri*, in particular, encompasses two sections: sect. *Scauri* and sect. *Purpurascentes* (Liimatainen *et al.*, 2022). The species of sect. *Purpurascentes* are featured with hemispherical pileus, mostly stipitocarpic but few are sequestered in nature. Species of sect. *Purpurascentes* are characterised by the presence of a positive iodine-based reaction and lamellae and stipe surface turn usually turning deeper purple when bruised (Saar *et al.*, 2014; Soop *et al.*, 2019; Liimatainen *et al.*, 2020, 2022).

Shorea robusta C.F. Gaertn. (commonly known as "Sal") is an economically important common dipterocarp hardwood native to India. It is a major constituent of moist deciduous broad-leaved tropical forests in India.



The species is dominantly distributed on the plains, lower foothills, and valleys of the Himalayas (Kumar and Atri, 2019). Based on surveys of basidiomes in India, Sal trees have been reported to be putatively ectomycorrhizal and are associated with species of various fungal genera such as *Amanita* Pers., *Boletellus* Murrill, *Borofutus* Hosen & Zhu L. Yang, *Craterellus* Pers., *Indoporus* A. Parihar, K. Das, Hembrom & Vizzini, *Lactarius* Pers., *Pisolithus* Alb. & Schwein. and *Russula* Pers. etc. (Natarajan *et al.*, 2005; Kumar and Atri, 2016; Buyck *et al.*, 2017; Hembrom *et al.*, 2017; Parihar *et al.*, 2018a,b). Species of family Cortinariaceae are among the commonest obligate ectomycorrhizal mushrooms in temperate to tropical forest ecosystems in India and only 31 species were reported from India till date, which mostly occurred from eastern and western Himalaya and Kerala (Berkeley, 1852; Chona *et al.*, 1958; Sharma *et al.*, 1978; Sathe *et al.*, 1980; Sathe and Daniel, 1980; Bhavanidevi and Nair, 1983; Peintner *et al.*, 2003; Florence, 2004; Mohanan, 2011; Das *et al.*, 2013; Das and Chakraborty, 2014, 2015; Itoo *et al.*, 2015; Verma *et al.*, 2019; Crous *et al.*, 2020; Das *et al.*, 2022). The species of genus *Cortinarius* s. l. were very often identified based on overall similarity with their European and North American counterparts and without much critical comparative assessment of detailed macro- and, particularly, micromorphology. Unfortunately, in-depth taxonomic studies of Sal-associated species of family Cortinariaceae have not yet been undertaken in India so far. Till date, there is no report of members of family Cortinariaceae associated with *Shorea robusta* from India.

During extensive macrofungal surveys to different *Shorea robusta* dominated forests of two Indian states i.e., Jharkhand and West Bengal, basidiomes of an interesting species classified as *Thaxterogaster* were collected. Morphological examination and molecular phylogenetic analyses of recent collections revealed one undescribed species of *Thaxterogaster* subg. *Scauri* sect. *Purpurascetes*, here introduced as *T. shoreae* sp. nov. Detailed macro- and micromorphological descriptions of *T. shoreae* are presented here and supported by 2-locus phylogenetic analysis. This paper also proposes one new combination in the genus *Thaxterogaster*.

MATERIALS AND METHODS

Morphology

Fresh specimens were macromorphologically fully described and images of the basidiomes were taken with a Canon Power Shot SX 50 HS. Colours were noted using the Methuen Handbook of Colour (Kornerup and Wanscher, 1978) as a guide. The specimens were then dried with a field drier. All micromorphological structures were observed from free hand section of preserved dried tissues in 1% ammoniacal Congo red, after a short treatment in warm, aqueous 5% KOH

solution to dissolve the gelatinous matrix and improve tissue dissociation. Drawings of micromorphological features were made with a drawing tube attached to Olympus CX 41 at 1000× magnification. Microscopic photographs were taken with an Olympus BX 53 camera. Basidiospores were examined in Melzer's reagent and measured in side view, excluding ornamentations. Basidiospore measurements and length/width ratios (Q) are represented as: minimum–mean–maximum. Basidium length excludes the length of sterigmata. Herbarium codes follow Thiers (continuously updated).

DNA extraction, polymerase chain reaction (PCR) and sequencing

Genomic DNA was extracted from 100 mg of dried basidiome with the InstaGene™ Matrix Genomic DNA isolation kit (Biorad, USA) following the manufacturer's instructions. The primers ITS1-F and ITS4 and LR0R and LR5 were used to amplify the internal transcribed spacer region of ribosomal DNA (ITS) and a part of the ribosomal large subunit 28S region (LSU) respectively (White *et al.*, 1990; Gardes and Bruns, 1993; Liu *et al.*, 1999). PCR amplification was carried out in a PCR thermal cycler (Gene Amp PCR System 9700, Applied Biosystems) programmed for 2 min at 96 °C, followed by 30 cycles of 30 sec at 96 °C, 40 sec at 50 °C, 2 min at 72 °C, and a final 7 min extension step at 72 °C. All PCR products were checked on 1% agarose gel and purified using the QIAquick PCR Purification Kit (QIAGEN, Germany). Both strands of the PCR fragment were sequenced on the 3730xl DNA Analyzer (Applied Biosystems, USA) using the amplifying primers. The sequence quality was checked using Sequence Scanner Software ver. 1 (Applied Biosystems). Sequence alignment and required editing of the obtained sequences were carried out using Geneious ver. 5.1 (Drummond *et al.*, 2010). The newly generated sequences in this study were submitted to GenBank. Accession numbers of species used in the phylogenetic analysis are listed in the Table 1.

Phylogenetic analysis

The nrITS and nrLSU sequences of the newly generated *Thaxterogaster* species (*Thaxterogaster shoreae*) and their close relatives were retrieved from nBLAST search against GenBank (<https://www.ncbi.nlm.nih.gov/genbank>), UNITE database (<https://unite.ut.ee>) and relevant published phylogenies (Saar *et al.*, 2014; Crous *et al.*, 2020; Liimatainen *et al.*, 2020, 2022). Two datasets were created separately, one with the nrITS sequences and the other with nrLSU sequences. Both the datasets were aligned separately using the online version of the multiple sequence alignment program MAFFT v. 7 (<https://mafft.cbrc.jp/alignment/software/>) with the E-INS-i strategy (Katoh *et al.*, 2019). The two alignments were checked and trimmed manually with MEGA v. 7 (Kumar *et al.*, 2016). To eliminate ambiguously aligned

**Table 1.** *Thaxterogaster* sequences used in ML and Bayesian analyses of this study. Newly sequenced collections are in bold.

Species name	Voucher no.	GenBank accession no.	
		nrITS	nrLSU
<i>Thaxterogaster australis</i>	HO A20420A0	AY669615	—
<i>Thaxterogaster australis</i>	PDD:107712	KT875192	—
<i>Thaxterogaster caesibulga</i>	KV660	GQ890310	—
<i>Thaxterogaster campbellae</i>	Trappe 19821	AF325558	AF388747
<i>Thaxterogaster</i> cf. <i>singularis</i>	PDD:103675	KF727376	KF727326
<i>Thaxterogaster chlorophyllus</i>	PDD:103681	KF727375	KF727327
<i>Thaxterogaster cinereoseolus</i>	KV529	GQ890315	—
<i>Thaxterogaster collocandoides</i>	JAC12972	MW263688	MW263397
<i>Thaxterogaster collocandoides</i>	PC:P. Moenne-Loccoz 5087	KF732287	—
<i>Thaxterogaster genuinus</i>	PC:X. Carteret 2005-132	KF732311	—
<i>Thaxterogaster herpeticus</i>	S:F44759	KF732321	—
<i>Thaxterogaster herpeticus</i>	TUB 019814	KJ421117	—
<i>Thaxterogaster rhodophyllus</i>	TUB 020416	KJ421051	—
<i>Thaxterogaster indopurpurascens</i>	KCS 2442	MW135432	MW228124
<i>Thaxterogaster indopurpurascens</i>	KCS 2467	MW135431	—
<i>Thaxterogaster indopurpurascens</i>	KCS 2529	MW135430	—
<i>Thaxterogaster kaimanawa</i>	PDD:73133	JX000353	JX000383
<i>Thaxterogaster kaimanawa</i>	PDD:101841	KJ635213	MW263598
<i>Thaxterogaster largoides</i>	PC:P. Moenne-Loccoz 2336	KF732332	—
<i>Thaxterogaster mutabilis</i>	MICH:10379	KF732353	—
<i>Thaxterogaster occidentalis</i>	MICH:10382	KF732357	—
<i>Thaxterogaster persicanus</i>	PDD:70507	GU233345	GU233392
<i>Thaxterogaster porphyropus</i>	S:F47381	KF732387	—
<i>Thaxterogaster porphyropus</i>	TN10-004	KF732513	—
<i>Thaxterogaster porphyropus</i> var. <i>porphyrophorus</i>	PC:P. Moenne-Loccoz 5086	KF732388	—
<i>Thaxterogaster shoreae</i>	AGDC_21-04	OP473978	OP473981
<i>Thaxterogaster shoreae</i>	AGJH-017	OP473976	OP473977
<i>Thaxterogaster purpurascens</i>	IK09-1510	KF732644	—
<i>Thaxterogaster purpurascens</i>	H:I. Kytovuori 98-2121	KF732406	—
<i>Thaxterogaster purpurascens</i>	M:0275848	KT159218	—
<i>Thaxterogaster purpurascens</i>	M:0275852	KT159222	—
<i>Thaxterogaster purpurascens</i>	TUB 011401	AY174858	—
<i>Thaxterogaster purpurascens</i>	PC:A. Bidaud 07-10-175	KF732301	—
<i>Thaxterogaster purpurascens</i>	—	UDB016117	—
<i>Thaxterogaster rhipiduranus</i>	PDD:88269	JX000368	JX000399
<i>Thaxterogaster rhipiduranus</i>	PDD:103673	KF727377	KF727323
<i>Thaxterogaster scaurus</i>	UBC F17134 OC62	GQ159877	—
<i>Thaxterogaster singularis</i>	PDD:78767	JQ287672	NG_068872
<i>Thaxterogaster sphagnophilus</i>	JFA13111	FJ717592	—
<i>Thaxterogaster submagellanicus</i>	HO A20518A1	AY669614	—
<i>Thaxterogaster subpurpurascens</i>	14615	JF907905	—
<i>Thaxterogaster subpurpurascens</i>	H:K. Liimatainen & T. Niskanen 08-059	KF732449	—
<i>Thaxterogaster subpurpurascens</i>	—	UDB000736	—
<i>Thaxterogaster violaceonitens</i>	TN00-661	KF732506	—
<i>Thaxterogaster violaceonitens</i>	TN06-170	KF732505	—

positions in the alignment as objectively as possible, the online program Gblocks 0.91b (Talavera and Castresana, 2007) was used. The program was run with settings allowing for smaller blocks, gaps within these blocks and less strict flanking positions. Species delimitation was first examined using single locus phylogenies. When significant conflict was not observed among the single locus phylogenies, then we concatenated two single locus (nrITS and nrLSU) alignments into one 2-locus dataset

using BioEdit v. 7.0.9 (Hall, 1999). The 2-locus dataset was phylogenetically analyzed using both maximum likelihood (ML) and Bayesian inference (BI) approaches. ML was performed using raxmlGUI 2.0 (Edler *et al.*, 2021) with the GTRGAMMA substitution model. ML analysis was executed applying the rapid bootstrap algorithm with 1000 replicates to obtain nodal support values. For BI, 2-locus dataset was divided into four partitions: ITS1, 5.8S, ITS2 and LSU. PartitionFinder2

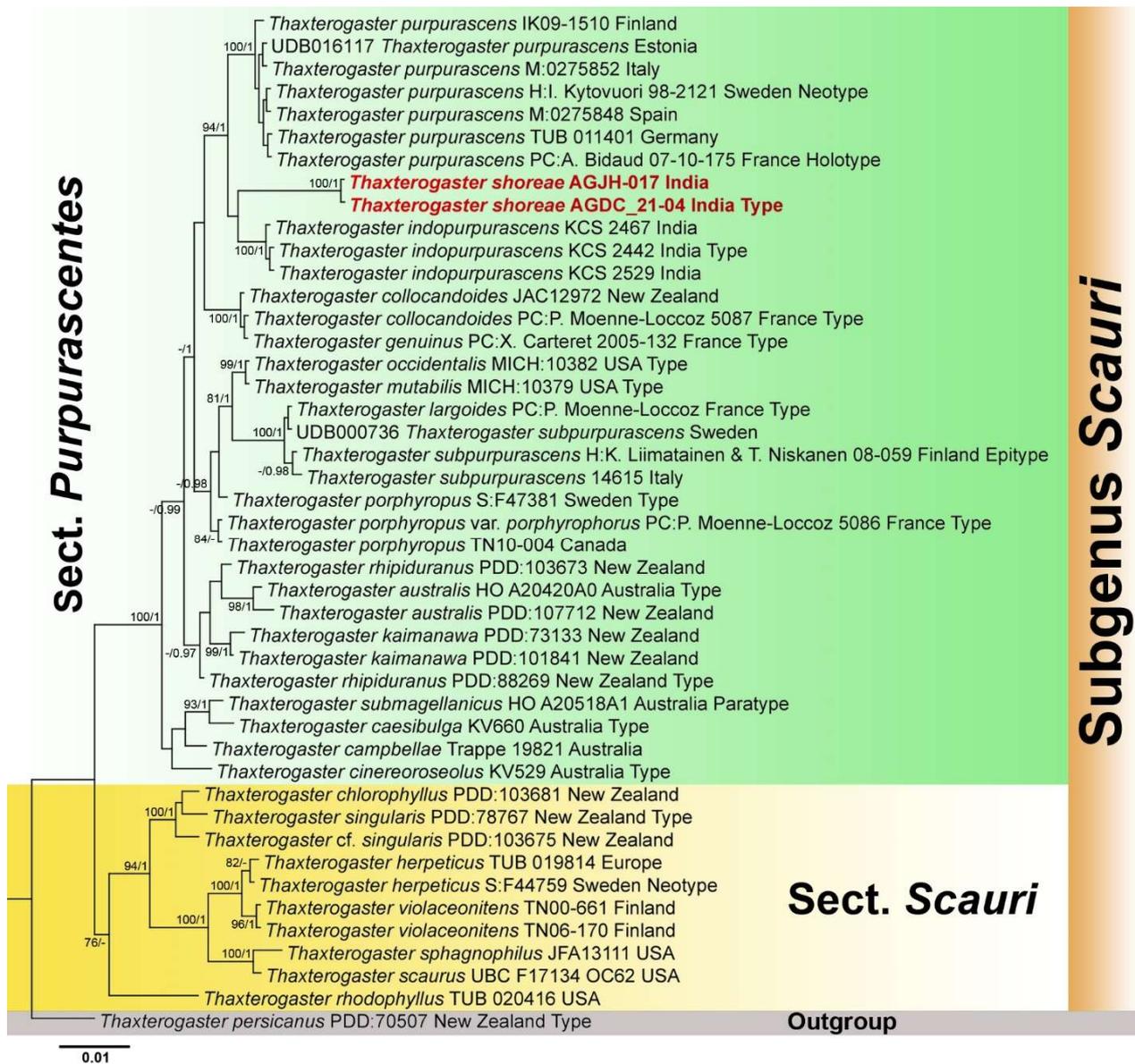


Fig. 1. Phylogram generated by Bayesian analysis based on combined sequence data of nrITS and nrLSU for *Thaxterogaster shoreae* and allied species. Maximum likelihood bootstrap support values (MLbs) $\geq 70\%$ are shown on the left of “/” and Bayesian posterior probabilities (BPP) ≥ 0.95 are shown on the right above or below the branches at nodes. *Thaxterogaster shoreae* is placed in bold red font to highlight its phylogenetic position in the tree.

was used to find the best substitution models (GTR+G for ITS1 and ITS2; JC for 5.8S and GTR+I for LSU) using the Akaike information criterion (AICc) with a greedy search over all models (Lanfear *et al.*, 2017). BI was computed in MrBayes v.3.2.6 (Ronquist *et al.*, 2012) with four Markov chain Monte Carlo (MCMC) chains for 1000000 iterations until the standard deviation of split frequencies reached below the 0.01 threshold. Trees were sampled every 100th generation. The first 25% of trees were discarded as burn-in. Chain convergence was determined using Tracer 1.5 (Rambaut *et al.*, 2014) to ensure sufficiently large effective sample size (ESS) values (>200). Gaps in the alignment were treated as

missing data in phylogenetic analyses. Maximum likelihood bootstrap (MLbs) values $\geq 70\%$ and Bayesian posterior probabilities (BPP) values ≥ 0.95 are shown in the phylogenetic tree (Fig. 1). *Thaxterogaster persicanus* (Soop) Niskanen & Liimat. was used as outgroup taxon.

RESULTS

Phylogenetic inferences

The final combined dataset (nrITS and nrLSU) consisted of 45 sequences including newly obtained sequences (GenBank accession numbers: OP473976, OP473977, OP473978 and OP473981). The final



alignment comprised 1619 characters including gaps. Both maximum likelihood (ML) and Bayesian inferences (BI) analyses resulted in essentially the same tree topologies, and only the BI phylogenetic tree (showing novel species in bold red font) is presented in Fig. 1.

Our 2-locus (nrITS and nrLSU) molecular phylogeny (Fig. 1) shows that the sequences derived from *T. shoreae* [voucher nos.: AGDC_21-04 and AGJH-017] are clustered with Indian *T. indopurpurascens* (Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt) A. Ghosh, D. Chakr., K. Das & Vizzini (see below) (voucher nos.: KCS 2442, KCS 2467 and KCS 2529) and this clade is sister to the European *T. purpurascens* (Fr.) Niskanen & Liimat. clade (IK09-1510, UDB016117, M:0275852, H:I. Kytovuori 98-2121, M:0275848, TUB 011401 and PC:A. Bidaud 07-10-175) with a strong (MLbs= 94%, BPP= 1) support.

TAXONOMIC TREATMENT

Thaxterogaster shoreae A. Ghosh, D. Chakr., K. Das & Vizzini, *sp. nov.* **Figs. 2 & 3**

Mycobank: MB 845685

Type: India, West Bengal, Jhargram district, Jhargram city, elev. 103 m, N22°25'01" E87°00'14", under *Shorea robusta* dominated forest, 12 August 2021, A. Ghosh & D. Chakraborty, AGDC_21-04 (CAL 1883, holotype!); GenBank OP473976 (nrITS) & OP473977 (nrLSU).

Diagnosis: *Thaxterogaster shoreae* sp. nov. differs from Indian *T. indopurpurascens* in its shorter stipe (25–40 mm), relatively smaller basidiospores [(7–11) × (4–6) μm], an ixo-trichodermic pileipellis, and occurrence under *Shorea robusta*.

Description: Pileus 30–55 mm broad, convex to planoconvex, umbonate or obtusely umbonate when young; surface sticky to glutinous when moist, glabrous; margin incurved with cottony velar remnants and connected to stipe by thread like cortina; split from the edge with age; surface brown or raw sienna or cinnamon brown (6E5–7) when young, gradually greyish orange to brownish orange (6B–C5–7) with age, covered with brownish radial streaks. Lamellae broadly attached, close (10–12/cm at pileus margin), thick, broad, forked near the margin; greyish magenta to deep magenta (14D–E6–8), turning darker purplish when bruised; edges entire to undulating; lamellulae present. Stipe 25–40 × 11–16 mm; cylindrical to clavate with somewhat roundish marginated bulb at the base with white mycelium; surface pastel violet, light lilac to purple (15A4–6), shiny, longitudinally fibrillose. Context greyish lilac (15B2), becoming light lilac to purple on bruising; stipe context with shallow depression; turning salmon pink (6A4) with FeSO₄ and unchanging in KOH. Odor not distinctive. Taste not checked.

Basidiospores (7.0–9.4–11.0) × (4.0–5.2–6.0) μm, Q = (1.56–1.81–2.0), ellipsoid to subamygdaloid, moderately

to strongly verrucose (mainly isolated warts), always with a distinct apiculus, light to dark ochre-yellow. Basidia 25–33 × 8–9 μm, clavate, 4-spored; sterigmata up to 4 μm long. Basidiole 11–28 × 3.5–9.0 μm, cylindrical to clavate. Pileipellis 110–315 μm thick, ixotrichoderm type; made up of cylindrical, long, tightly compact, septate hyphae; terminal elements 32–75 × 4–6 μm, cylindrical with obtuse-rounded apex. Clamp connections present in all tissues.

Etymology: ‘*shoreae*’ refers to *Shorea robusta* (Dipterocarpaceae), the host tree of the species.

Habit and habitat: Solitary to scattered, occurrence under *Shorea robusta* in tropical deciduous forests.

Additional specimens examined: India, Jharkhand, Rajmahal hills, Sahibganj district, Borio block, Pir-Baba Kairasol Forest area, under *Shorea robusta* in tropical deciduous forests, elev. 126 m, N25°09'41.7" E87°40'31.9", 23 August 2022, A. Ghosh, AGJH-017 (CAL 1901), GenBank OP473978 (nrITS) & OP473981 (nrLSU); *ibid.*, Dhogada, Paharia burial ground forest, under *Shorea robusta* in tropical deciduous forests, elev. 110 m, N25°02'23.7" E87°39'35.8", 17 September 2022, A. Ghosh, AGJH-093 (CAL 1902)

Discussion: The combination of characters such as: brown or raw sienna or cinnamon brown pileus; greyish magenta to deep magenta lamellae; pastel violet, light lilac to purple coloured stipe; surfaces and context becoming purplish-lilac on bruising, especially on the lamellae; ellipsoid to subamygdaloid, moderately to strongly verrucose basidiospores and 2-locus (ITS and LSU regions of nrDNA) phylogeny confirms the position of *T. shoreae* belong to subg. *Scauri* sect. *Purpurascentes*.

Basidiomes with lilac-purplish tinges and distinctly marginated bulb are the shared features of our newly described species with the Indian *T. indopurpurascens* and European *T. purpurascens* and *T. collocandoides* (Reumaux) Niskanen & Liimat. [= *T. geminus* (Bidaud & Carteret) Niskanen & Liimat.]. But *T. indopurpurascens* is distinguished by possessing pale bluish grey pileus when young becoming ochraceous brown at centre, larger stipe (50–70 mm long), relatively larger and broader spores (av.= 9.9 × 5.5 μm) and occurrence under the Himalayan, evergreen *Quercus leucotrichophora* (Crous *et al.*, 2020). However, comparatively larger pileus (up to 100 mm in diam.), ixocutis type pileipellis, smaller spores (7.2–8.8 × 4.5–5.3 μm) and occurrence under both coniferous and mixed broadleaf trees readily distinguish *T. purpurascens* from our newly described species (Saar *et al.*, 2014; Kibby, 2015; Kibby and Tortelli, 2022). On the other hand, *T. collocandoides* is distinct by possessing larger pileus (up to 90 mm in diam.), ixocutis type pileipellis, slightly larger spores [9–11(12) × 5–6.0 μm], and occurrence under *Quercus* spp. (Saar *et al.*, 2014; Kibby, 2015; Kibby and Tortelli, 2022). A collection molecularly attributable to *T. collocandoides* (JAC12972, PDD97071) (Fig. 1) was found on 2013 in the Eastwoodhill National Arboretum, Gisborne (New Zealand) under an allochthonous *Quercus* sp. (https://scd.landcareresearch.co.nz/Specimen/PDD_97071). Consequently, *T. collocandoides* should be considered an exotic species for New Zealand.



Fig. 2. Photoplate of *Thaxterogaster shoreae* (from CAL 1883) **A–C:** Fresh and dissected basidiomes in the field and basecamp. **D–F:** Transverse section through pileipellis. **G:** Basidiolles. **H:** Basidia. **I:** Basidiospores. Scale bars: **D–I** = 10 μ m.

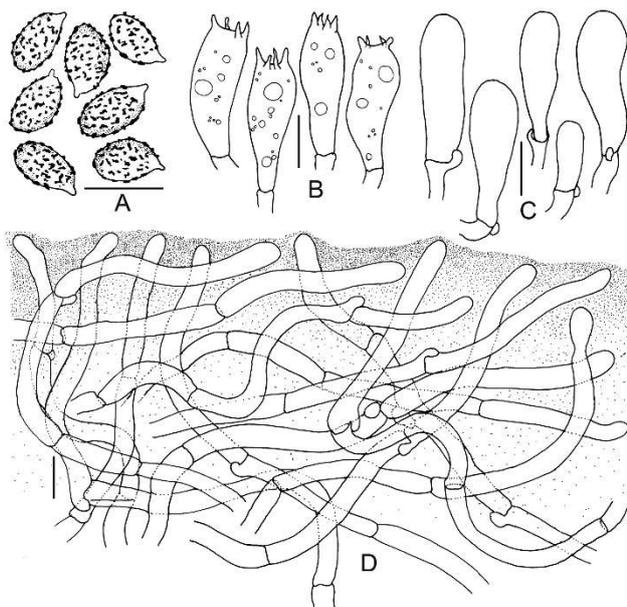


Fig. 3. Illustrations of *Thaxterogaster shoreae* (from CAL 1883) **A:** Basidiospores. **B:** Basidia. **C:** Basidioles. **D:** Transverse section through pileipellis. Scale bars: A–D = 10 μ m.

New combination in the genus *Thaxterogaster* of family Cortinariaceae

Thaxterogaster indopurpurascens (Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt) A. Ghosh, D. Chakr., K. Das & Vizzini, *comb. nov.*

Mycobank: MB 846470

Basionym: *Cortinarius indopurpurascens* Dima, Semwal, Brandrud, V. Papp & V.K. Bhatt, *Persoonia* 45: 403 (2020).

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