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# Morphology and molecular phylogeny unveil a novel species of *Volvariella* (Basidiomycota) from tropical India

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ABSTRACT: The genus *Volvariella* includes edible species that are consumed as delicacies by local communities. A new species, *V. indotropica*, collected in two districts of West Bengal, is described using a polyphasic approach, combining morphology and molecular phylogeny. Closely allied Asian species of this genus are also compared.

KEY WORDS: Macrofungi, new species, *Volvariella bilobata*, *Volvariella rostricystidiata*, *Volvariella nivea*, Volvariellaceae.

## INTRODUCTION

The genus *Volvariella* Speg. was first proposed in 1898, with *Volvariella argentina* Speg. (Spegazzini, 1898; Caballero *et al.*, 2025) designated as the type species. Species of this genus are widely distributed across Africa, Asia, Australasia, Europe, and the Americas (Singer, 1951; Shaffer, 1957; Pegler, 1977; Priest and Conde, 2006; Kirk, 2008; Menolli and Capelari, 2009; Malysheva *et al.*, 2019; Niego *et al.*, 2021; Caballero *et al.*, 2025). Members of this genus are predominantly saprobic and very rarely mycoparasitic fungi. They are known to grow on decaying wood, leaf litter, and on soil in the forest floor and grasslands. Additionally, *V. surrecta* (Knapp) Singer is known to grow facultatively as a parasite on both living and decaying agarics (Singer, 1951; Celka, 2000; Kirk, 2008; Pegler, 1986; Justo and Castro, 2010; Caballero *et al.*, 2025). Morphologically, *Volvariella* is characterized by pluteoid basidiomata, the presence of a volva, an inverse hymenophoral trama, and a pink to pinkish-brown spore print. The basidiospores are ovoid to elongated with smooth walls and are inamyloid and non-dextrinoid (Kumla *et al.*, 2022; Caballero *et al.*, 2025).

The systematic position of *Volvariella* has long been controversial. Historically, the genus has been placed in several families. It was initially assigned to Amanitaceae E.-J. Gilbert (Lee *et al.*, 1959), later transferred to Agaricaceae Chevall. (Lee, 1973) and subsequently placed in Pluteaceae Kotl. & Pouzar by Singer (1986). Later phylogenetic studies suggested that *Volvariella* might share a closer relationship with *Cantharocybe* H.E. Bigelow & A.H. Sm. and *Cuphophyllus* (Donk) Bon within the family Hygrophoraceae Lotsy (Justo *et al.*, 2011). Due to these conflicting phylogenetic signals and the uncertainty surrounding its placement, the genus has also been treated as incertae sedis within Agaricales by several authors (Niego *et al.*, 2021; Kumla *et al.*, 2022). However, a molecular study by Justo *et al.* (2011) segregated species formerly placed in *Volvariella* into two genera: *Volvariella* Speg. and *Volvopluteus* Vizzini, Contu & Justo. Phylogenetic analyses based on ribosomal loci indicated that most *Volvariella* species occupy a relatively isolated position within Agaricales, with uncertain relationships to other lineages. More recently, using an updated six-gene dataset of Agaricales, Vizzini *et al.* (2024) recognized several families within the suborder Pluteineae, including Pluteaceae Kotl. & Pouzar (containing *Pluteus* Fr. and *Volvopluteus* Vizzini, Contu & Justo), Amanitaceae E.-J. Gilbert [including *Amanita* Dill. ex Boehm., *Catatrama* Franco-Mol., *Leucocortinarius* (J.E. Lange) Singer, *Limacella* Earle, *Limacellopsis* Zhu L. Yang, Q. Cai & Y.Y. Cui, *Saproamanita* Redhead, Vizzini, Drehmel & Contu, and *Zhuliangomyces* Redhead], Limnoperdaceae G.A. Escobar (*Limnoperdon* G.A. Escobar), Melanoleucaceae Locq. (*Giacomia* Vizzini & Contu and *Melanoleuca* Pat.), and Volvariellaceae Vizzini, Consiglio & P. Alvarado, which accommodates the genus *Volvariella*. Subsequently, the family Amanitaceae was elevated to the rank of suborder, as Amanitineae, by Qu *et al.* (2025).

In India, the genus has been extensively studied, as reflected in numerous taxonomic and ecological reports (Berkeley, 1850; Massee, 1899, 1912; Bose, 1920a, b; Rath, 1962; Pathak *et al.*, 1978; Lakshmanan *et al.*, 1979; Manimohan *et al.*, 1988, 2007; Pradeep *et al.*, 1998; Florence, 2004; Pradeep and Vrinda, 2007; Kumar *et al.*, 2010; Dutta *et al.*, 2011, 2013; Mohanan, 2011; Senthilarasu *et al.*, 2012; Kaur *et al.*, 2013; Chouhan and Panwar, 2021; Roy *et al.*, 2022; Chattopadhyay *et al.*, 2022), bringing the number of known species in the country to 27. The majority of these species could not be verified by molecular evidence; instead, their names were determined by comparing them to European or American lookalikes, whereas only four species, namely, *Volvariella sathei* Senthil., Rahul Sharma & S.K. Singh,

*V. minuta* M. Kumar bis, Jagad. & Kaviy., *V. bilobata* A.K. Dutta & Chattopadhyay and *V. indica* M.K. Saini, N.J. Kaur & Atri were originally established from India (Kumar *et al.,* 2010; Senthilarasu *et al.*, 2012; Kaur *et al.*, 2013; Chattopadhyay *et al.*, 2022). During repeated field surveys conducted in 2024 and 2025, a distinctive specimens were collected in the Howrah and South 24 Parganas districts of West Bengal, India. Detailed morphological and molecular analyses of the collected material revealed that it represents a previously undescribed species of the genus *Volvariella* and is presented in detail.

## MATERIALS AND METHODS

**Morphological studies**

Fresh specimens ranging from young to mature were repeatedly collected from two locations: the districts of Howrah (inside the Acharya Jagadish Chandra Bose Indian Botanic Garden formerly the Royal Botanic Garden, Calcutta) and South 24 Parganas (near Baruipur). Their macro-morphological and substrate details were recorded both in the field and at the respective base-camps. Images of the basidiomata were captured using a Canon SX 220 HS camera. Largent (1986) was followed for terminology of macro-morphological characters and Methuen Handbook of Color for color codes and their terms (Kornerup and Wanscher, 1978). After collection and macro-morphological characterization, samples were dried in a field dryer at temperature ranging from 40–50°C. Micro-morphological characters were examined from free-hand sections prepared from dried specimens. The sections were mounted in a mixture of 5% KOH and 1% ammoniacal Congo red and observed under an Olympus CX 41 compound microscope, equipped with an Olympus DP-22 camera. Illustrations of the anatomical features were drawn with the help of drawing tube at 1000× magnification. Basidiospore measurements and length/width ratios (Q) are represented as: minimum-mean-maximum. Basidium length measurements exclude the length of sterigmata. Herbarium acronym follow Index Herbariorum (https://sweetgum.nybg.org/science/ih/, continuously updated).

**DNA extraction, polymerase chain reaction (PCR) and sequencing**

Genomic DNA of collected samples was isolated from 100 mg of a dried basidiome with the HiPurA Fungal DNA Purification Kit (HIMEDIA) applying the manufacturer's instructions provided with the kit. Two nuclear loci, the ITS and LSU regions, were amplified using the primer pairs ITS1F/ITS4 and LR0R/LR5, respectively (Vilgalys and Hester, 1990; White *et al.*, 1990; Gardes and Bruns, 1993; Rehner and Samuels, 1994). The amplification of these loci was performed using ProFlex PCR system (Applied Biosystems) programmed for an initial denaturation at 94°C for 3 min, followed by 35 cycles of denaturation at 94°C for 1 min, annealing at 53°C for 40 sec, and extension at 72°C for 1 min. The final extension was performed at 72°C for 10 min. The amplified PCR products were then purified using the QIAquick PCR purification kit (QIAGEN, Germany). Both strands of the PCR fragment were sequenced on an ABI 3500 DNA Analyzer (Applied Biosystems, USA) using the amplifying primers. The sequence quality was checked and confirmed using Sequence Scanner Software ver. 1 (Applied Biosystems). Sequence alignment and required editing of the obtained sequences were carried out using BioEdit v. 7.0.9 (Hall, 1999). In this study, four sequences (two each for ITS and LSU) were generated from two separate collections (voucher nos. WBWE-24-025 and WBWE 25-036). All newly generated sequences for this study were submitted to GenBank. Accession numbers used in phylogenetic analyses (Fig. 1) are listed in Table S1.

**Phylogenetic analyses**

ITS and LSU sequences of the newly described *Volvariella* species plus close relatives were retrieved from BLASTn search against GenBank (https://www.ncbi.nlm.nih.gov/genbank) and relevant published phylogenies (Niego *et al.*, 2021; Chattopadhyay *et al.*, 2022; Kumla *et al.*, 2022; Caballero *et al.*, 2025). Two raw datasets (ITS and LSU) were prepared separately. 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 L-INS-I (Katoh *et al.*, 2019) strategy and normal alignment mode, respectively. The alignment was checked and manually trimmed based on conserved motifs with MEGA v. 7 (Kumar *et al.*, 2016). Each gene region was treated as a separate partition. The congruence of the datasets was tested using the incongruence length difference (ILD) test (Farris *et al.*, 1995a, b). The analysis was performed in PAUP version 4.0b10 (Swofford, 2003) using the partition-homogeneity test (PHT) option with 1000 heuristic search replicates. This test was used to assess the statistical congruence among datasets and to determine whether the individual data partitions could be combined for phylogenetic analysis. A p-value $\geq$ 0.05 was considered to indicate no significant incongruence among the datasets. After testing congruence, the individual gene datasets were then concatenated into a two-locus dataset using BioEdit v. 7.0.9 (Hall, 1999) and processed for the phylogenetic analyses. The partitioned alignment was analysed based on maximum likelihood (ML) method in IQ-TREE ver. 3 (Wong *et al.*, 2025) using the NEXUS file as input, employing the best models (GTR + F for ITS and LSU) determined by ModelFinder (Kalyaanamoorthy *et al.*, 2017) based on the Bayesian information criterion (BIC). Branch support was estimated using 1000 replicates

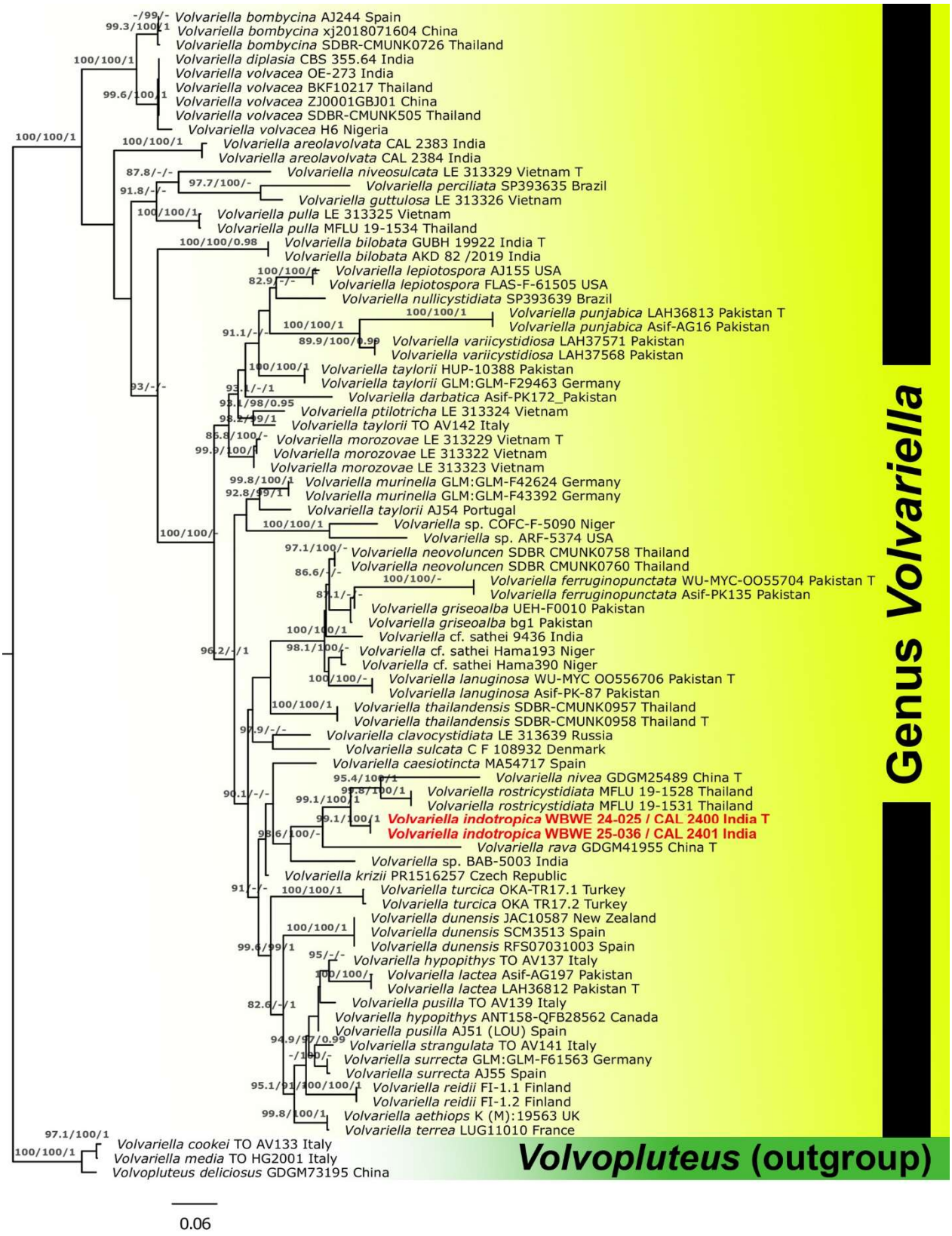


**Fig. 1.** Phylogram generated by ML analysis based on 2-locus (ITS+LSU) sequence data for ***Volvariella*** and allied species. SH-aLRT support values ≥ 80%, UFBoot values ≥ 90% for ML and BPP values ≥ 0.95 are shown as SH-aLRT/ UFBoot/BPP. Sequences generated in this study are highlighted in red.

of ultrafast bootstrap (UFBoot) and SH-like approximate likelihood ratio test (SH-aLRT), respectively (Guindon *et al.*, 2010, Hoang *et al.*, 2018). Branches in the phylogenetic tree were considered reliable when both UFBoot ≥ 90% and SH-aLRT ≥ 80% (Minh *et al.*, 2020). Bayesian inference (BI) was also computed for those aligned data sets in MrBayes v.3.2.6 (Ronquist *et al.*, 2012) with four Markov chain Monte Carlo (MCMC) chains. The optimal nucleotide substitution models for each gene partition were kept the same as obtained in IQ-TREE analysis. Two MCMC runs of four chains were executed simultaneously from a random starting tree for 100,000 generations until the standard deviation of split frequencies reached below the 0.01 threshold. Trees were sampled every 1000$^{th}$ generation. The first 25% of trees were discarded as burn-in. As both ML and BI analyses resulted in essentially the same tree topologies, the ML tree with SH-aLRT ≥ 80%, UFBoot ≥ 90%, and Bayesian posterior probabilities (BPP) values ≥ 0.95 was shown. Our novel species is presented in the phylogenetic tree in bold red font (Fig. 1).

## RESULTS

The two-locus dataset (ITS+LSU) of *Volvariella* consisted of 83 taxa and 2151 nucleotide sites, including gaps (sequence lengths were determined to be 1196 bp for ITS and 955 bp for LSU), 1241 distinct patterns, 780 parsimony-informative, 199 singleton sites, 1172 constant sites. The two-gene combined phylogenetic (ML) tree, using *Volvopluteus cookei* (henceforth '*Volvopluteus*' will be abbreviated as '*Vp.*'), *Vp. media* and *Vp. deliciosus* as outgroup, is consistent and the phylogenetic analyses (Fig. 1) including the present novel species resolved the genus *Volvariella* as monophyletic with full support. These analyses revealed that the sequences isolated from Indian specimens (voucher nos. WBWE-24-025 and WBWE 25-036) are sister to a clade bearing *V. nivea* (voucher no. GDGM25489) and *V. rostricystidiata* (voucher nos. MFLU 19 1528 and MFLU 19 1531). However, both the Indian specimens representing *V. indotropica* were recovered as distinct species within the phylogenetic tree with strong support (SH-aLRT = 99.1%, UFBoot = 100% and BPP= 1) (Fig. 1).

## TAXONOMIC TREATMENT

***Volvariella indotropica*** Su. Datta, K. Das & Vizzini**, *sp. nov.*** **Figs. 2 & 3**

**MycoBank**: **MB 863181**

***GenBank***: PZ247714 (holotype: ITS), PZ247715 (paratype: ITS); PZ234631 (holotype: LSU), PZ234632 (paratype: LSU).

***Type***: INDIA, WEST BENGAL: Howrah District, Acharya Jagadish Chandra Bose Indian Botanic Garden, on soil, 10 Jul 2024, alt. 28 m, N 22°33′36.07″ E 88°17′17.72″, *leg.* Sudeshna Datta & Kanad Das, WBWE 24-025 (CAL 2400, holotype!).

***Diagnosis***: Differs from the morphologically very similar *V. bilobata* by larger basidiomata (70–110 mm diam.), entire lamellae margin, larger basidiospores (6.3–7.2 × 4.5–6.3 µm) and larger pleurocystidia (40–77.4 × 13.5–36 µm) and from the molecularly close species *V. rostricystidiata* by cheilocystidia that are not consistently rostrate and from *V. nivea* by its greyish pileus and brown to dark-brown volva.

***Morphological description***: Basidiomata medium-sized. Pileus 70–110 mm diam., conico-convex to broadly infundibuliform with a broad umbo; surface dry, grey (5D1) at the centre, gradually brownish grey to orange-grey (5B–C2) towards margin, appressed fibrillose, with radially arranged silky fibrils, peeling easily exposing white coloured context; margin straight at maturity, rimose. Lamellae free, rather crowded, 13–15/1 cm at pileus margin, orange-white to pale orange (6A2–3); margin entire, smooth, concolourous, lamellulae in 3–4 series. Stipe 50–70 × 3–5 mm, cylindrical, subcylindrical or somewhat attenuate upward, solid; surface fibrillose, grey to orange-grey (5B1–2) on white (1A1) to dingy white or yellowish white background, gradually pinkish towards pileus, upper 2/3$^{rd}$ glabrous, lower 1/3$^{rd}$ covered with fibrils; annulus absent. Volva 20–26 mm long, 2-lobed, saccate, brittle; outer surface brown to dark brown (7E–F4–6), fibrillose; inner surface grey (5B1) or lighter. Odour insignificant and taste not recorded. Context in pileus and stipe white (1A1), unchanging. Basal mycelium white. Rhizomorphs absent. Spore print not obtained.

Basidiospores 6.3–6.75–7.2 × 4.5–5.62–6.3 µm, Q = 1.07–1.21–1.50, broadly ellipsoid to ellipsoid, slightly thick-walled (wall 0.9–1.35 µm thick), inamyloid and non-dextrinoid. Basidia 20–26 × 7.5–9 µm, broadly clavate, 4-spored. Cheilocystidia 23.4–36 × 10–13.5 µm, broadly clavate to ventricose, often with rostrate to appendiculate apex, thin-walled. Pleurocystidia 40–77.4 × 13.5–36 µm, emergent up to 50 µm, clavate to narrowly utriform, with appendiculate to rounded apex. Lamellae edge fertile. Subhymenium 10–12 µm wide, composed of isodiametric cells. Hymenophoral trama inverse, consisting of thin-walled, hyaline hyphae (4.7–5.9 µm wide). Pileipellis a cutis, up to 141 µm thick, composed of 2.7–6.75 µm wide thin-walled parallel arranged, few suberect hyphae, septate, unbranched, non-gelatinous, with faint intracellular brown pigment in KOH. Stipitipellis a cutis, 95–110 µm wide, composed of hyaline, thin-walled, cylindrical hyphae. Caulocystidia absent. Volva remnants on stipe base composed of interwoven, erect to suberect, filamentous hyphae dominant, thin-walled, septate, terminal elements cylindrical, 27–76.5 × 6.75–11.25 µm, with intracellular brown pigmentation.

***Etymology***: Referring to the tropical part of India, the type locality.

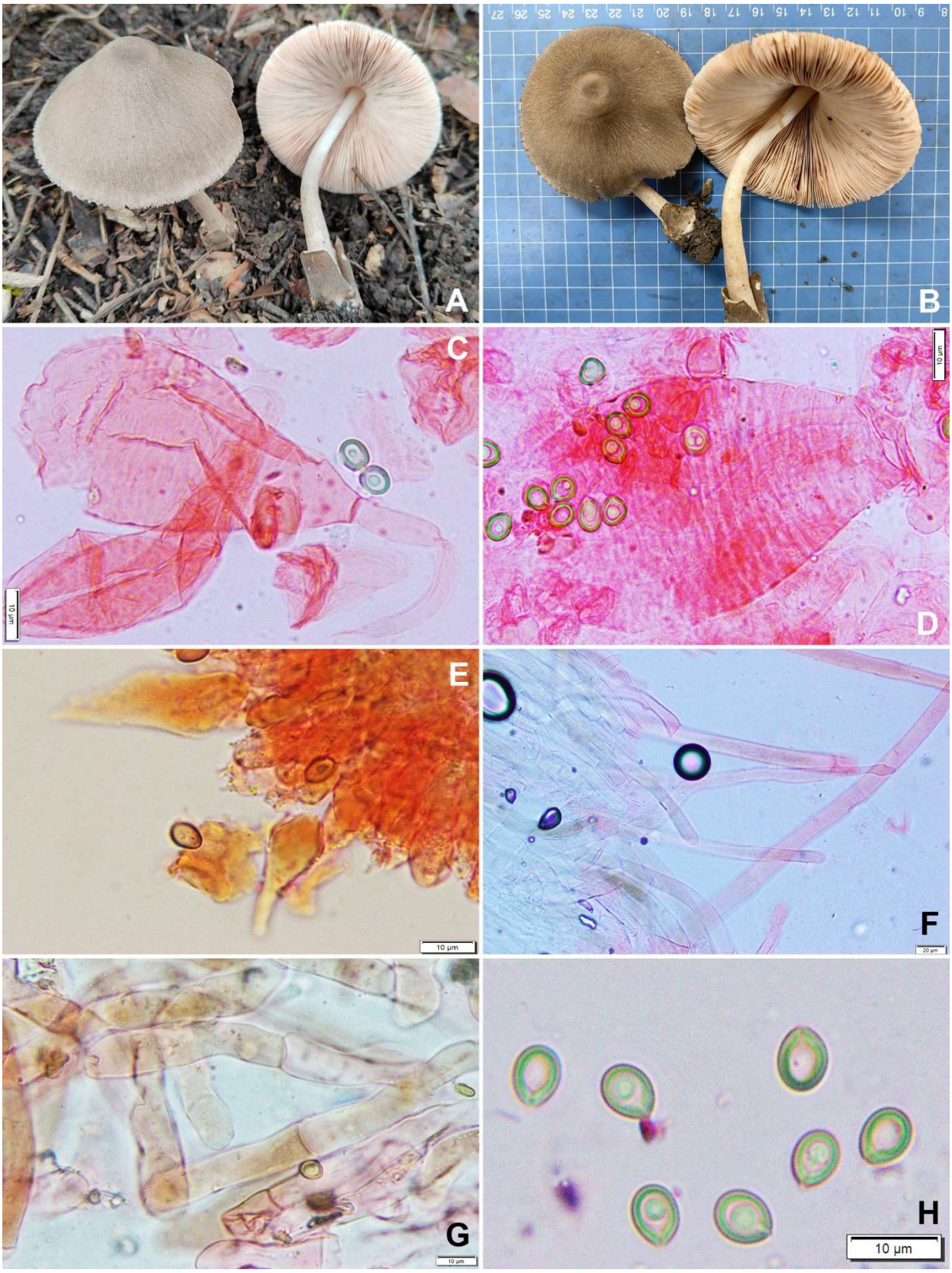


**Fig. 2.** Photoplate of ***Volvariella indotropica*** (WBWE 24-025 / CAL 2400, holotype) **A–B.** Fresh and dissected basidiomata in the field and basecamp. **C–D.** Pleurocystidia. **E.** Cheilocystidia. **F.** Transverse section through pileus showing elements/hyphae of the pileipellis. **G.** Transverse section through volva showing elements/hyphae. **H.** Basidiospores. Scale bars: C–E & G–H = 10 µm; F = 20 µm.

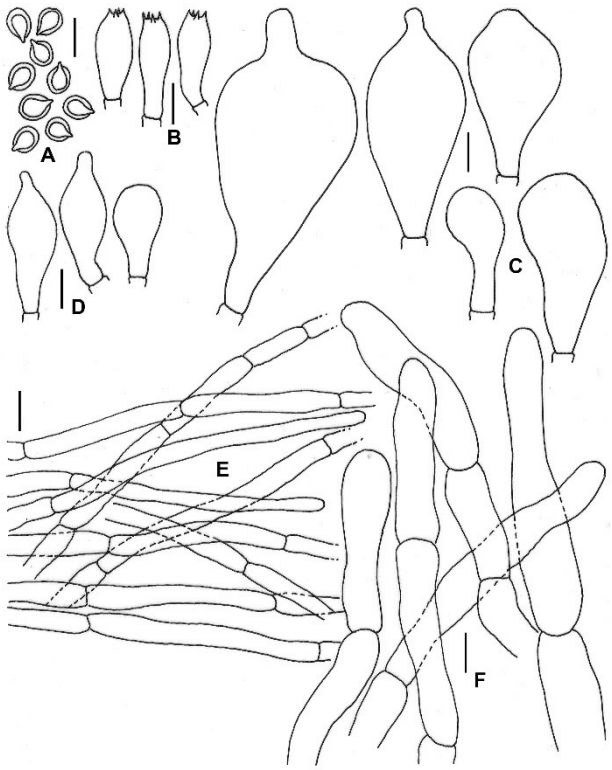


**Fig. 3.** Drawings of ***Volvariella indotropica*** (from WBWE 24-025 / CAL 2400, holotype) **A.** Basidiospores. **B.** Basidia. **C.** Pleurocystidia. **D.** Cheilocystidia. **E.** Elements of the pileipellis. **F.** Hyphal elements of volva. Scale bars: A–F = 10 µm.

***Additional specimen examined***: INDIA, WEST BENGAL: South 24 Parganas District, near Baruipur, on soil, 5 August 2025, alt. 60 m, N 22°11′20.60″ E 88°33′38.86″, *leg.* Sudeshna Datta, WBWE 25-036 (CAL 2401, paratype).

## DISCUSSION

This novel species is a choice edible mushroom, widely consumed and esteemed by local communities and morning walkers who visit Acharya Jagadish Chandra Bose Indian Botanic Garden (erstwhile Royal Botanic Garden, Calcutta).

Among the Indian species of *Volvariella*, *V. bilobata* is morphologically very similar to the present species in possessing a greyish-brown pileus with a fibrillose surface and a bilobed saccate volva with a greyish-brown outer surface and a greyish-white inner surface. However, the former differs in having a smaller convex pileus (45–70 mm diam.) lacking an umbo, lamellulae arranged in 1–2 series with serrated margins, and smaller basidiospores (4.8–5.5 × 2.7–3.5 µm) that are thin- to slightly thick-walled. Additionally, the pleurocystidia are smaller and more variable in shape (18.5–27.5 × 7–10 µm) (Chattopadhyay *et al.*, 2022). Furthermore, molecular evidence confirms distant relation between *V. bilobata* and the present new species. *Volvariella areolavolvata* E. Tarafder, Enjam & A.R. Sherpa, is morphologically quite distinct from the present species in having an externally areolate or cracked surface of volva that forms dark brown patches (Tarafder *et al.*, 2026). *Volvariella minuta* is readily distinguished by its much smaller basidiomata (7–13 mm in diameter) and white volva (Kumar *et al.*, 2010). *Volvariella sathei* can be separated by its white to yellowish-white pileus, glabrous stipe, and gelatinous volva (Senthilarasu *et al.*, 2012). *Volvariella indica* differs in possessing a scaly pileus with volval remnants and significantly larger basidiospores (10.7–14.3 × 7.1–8.9 µm) (Kaur *et al.*, 2013). Another Asian species, *V. rostricystidiata* Niego, Sysouph. & Raspé, described from Thailand, is very similar to the present species both morphologically and phylogenetically. Both species share comparable pileus coloration and an appressed fibrillose surface texture, as well as a smooth to slightly pubescent stipe. However, *V. rostricystidiata* differs in having smaller pileus (55–85 mm in diameter), a plano-convex pileus (whereas the present species possesses an infundibuliform pileus with a broad umbo), a greyish-brown stipe, relatively smaller basidiospores (5.5–6.5 × 4–5 µm), and cheilocystidia consistently exhibiting a rostrate apex (Niego *et al.,* 2021). *Volvariella nivea* T.H. Li & Xiang L. Chen (originally reported from China) is phylogenetically close to the present species but the former is characterized by pure white basidiomata, making it easily distinguishable in the field (Li *et al.*, 2009). *Volvariella neovolvacea* J. Kumla, N. Suwannarach & S. Lumyong (originally reported from Thailand), shares a similar greyish-brown pileus with a broad umbo but differs in showing a fibrillose to appressed squamulose pileus surface, a stout and pubescent stipe (85–110 × 20–25 mm), and a fimbriate lamellar edge (Kumla *et al.*, 2022). Other extralimital species reported from India, such as *V. taylorii* (Berk. & Broome) Singer, *V. caesiotincta* P.D. Orton, and *V. nigrodisca* Shaffer, also possess a fibrillose pileus surface (Shaffer, 1962; Caballero *et al*., 2025); however, the identity of these taxa is dubious and, therefore, they are here excluded from comparison as their occurrence in India has not yet been confirmed through molecular studies.

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