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Phylogeny of the genus *Volvariella* with the description of one new species and two new records from Oman

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Abstract: In the present study, a newly found species of *Volvariella* from Oman is described and named *V. darbatica*. Evidence for this decision is based on morphology and multigene phylogeny. *Volvariella darbatica* is characterized by small-sized basidiomata, pale pinkish to pale brownish pileus, and ellipsoid to ovoid basidiospores measuring 5.0–6.0 × 4.0–4.5 μm. Colour photographs of basidiomata and illustrations of anatomical characters are provided, along with the phylogenetic trees of the genus *Volvariella* and the suborder *Pluteineae* (where family *Volvariellaceae* is nested). Morphological similarities with closely related species are discussed. Furthermore, we also report the presence of *Volvariella cubensis* and *V. sathei* in Oman, extending the distribution of these species. *Volvariella sathei* was previously known only from its type locality in India.

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INTRODUCTION

The genus *Volvariella* was introduced by Spegazzini (1899). The name refers to the presence of a volva (wrapper, covering or integument) at the base of the stipe of these mushrooms. *Volvariella* is characterized by a pileostipitate basidiome, small to medium-sized (rarely large-sized), with a fibrillose to strigose pileus surface, free lamellae, brownish-rose spore print, smooth stipe with no annulus, and the presence of a volva at the base of the stipe. Microscopically, species of *Volvariella* have smooth basidiospores smaller than < 11 μm in length, which are also in-amyloid, non-dextrinoid, and lack a germ-pore, 4-spored basidia, presence of both cheilo- and pleurocystidia, inversely arranged hyphae in lamellae, absence of clamp connections, and a non-gelatinous pileipellis (Orton 1986, Boekhout 1990, Kirk *et al.* 2008, Justo *et al.* 2011, Vizzini *et al.* 2024).

There are nearly 125 described species in the genus, with *Volvariella argentina* being the type species (Malysheva *et al.* 2019, Chattopadhyay *et al.* 2022, Kumla *et al.* 2022, Haq Nawaz *et al.* 2023, Caballero *et al.* 2025, Jabeen *et al.* 2025). However, databases like Index Fungorum (<https://www.indexfungorum.org/>; accessed on 7 May 2024) and MycoBank (<https://www.mycobank.org/>; accessed on 7 February 2025), report 166 and 168 names associated with *Volvariella*, respectively. Some of the names mentioned in these databases are illegitimate or invalid, and include names widely accepted as heterotypic synonyms or

infraspecific names. Ecologically, species of the genus occur as saprotrophs on wood, woody debris, and on soil, spread over the eastern and western hemispheres in tropical, subtropical, and temperate climates, with no reports from arctic or alpine regions (Shaffer 1957, Boekhout 1990).

Species of *Volvariella* were classified into two sections, namely sect. *Macrospora* and sect. *Volvariella* by Contu (1998). This classification was based on basidiospore size, with species in *Macrospora* having spores larger than 11 μm in length, and those in sect. *Volvariella* having spores generally smaller than 11 μm. Later, species in sect. *Macrospora* were moved to the independent genus *Volvopluteus* (Justo *et al.* 2011). *Volvopluteus* differs from *Volvariella* by its smooth cap surface, basidiospores longer than 11 μm in length, and the presence of a gelatinous matrix in the pileipellis. Phylogenetically, *Volvopluteus* is more closely related to *Pluteus* in *Pluteaceae* (Vizzini *et al.* 2024). The systematic position of *Volvariella* was controversial for a long time, being placed in *Amanitaceae* (Lee *et al.* 1959), *Agariaceae* (Lee 1973), and finally transferred to *Pluteaceae* (Singer 1986). Later, *Volvariella* was thought to have a closer relationship with *Cantharocybe* and *Cuphophyllus* in the family *Hygrophoraceae* (Justo *et al.* 2011). As a result of the uncertainty, the genus was treated as incertae sedis by other authors (Niego *et al.* 2021, Kumla *et al.* 2022). In a recent study of *Agaricales* based on a 6-gene phylogeny, species of *Volvariella* formed a separate lineage inside the suborder *Pluteineae*, and a new family

Volvariellaceae was coined for it (Vizzini *et al.* 2024).

The present study is a continuation of mushroom exploration research in Oman. Oman is situated on the southeast coast of the Arabian Peninsula's. The samples were collected in Dhofar region of Oman, which experiences a yearly monsoon rain season from June to September, about 100–400 mm in these months (Bookhagen *et al.* 2005. Kwarteng *et al.* 2009). Research on mushroom diversity in the Sultanate of Oman has started only very recently, and only nine species have been reported from the entire country so far (Al-Kharousi *et al.* 2022a, b, Hussain *et al.* 2022a, b, 2024a–c). In the present work, several collections of *Volvariella* from Oman are studied. Upon morphological and phylogenetic analyses, these collections contain one new species and two new records of *Volvariella* from Oman, which are subsequently treated below.

MATERIALS AND METHODS

Sampling and morphological characterization

Basidiocarps were found in August and September, during the rainy season of the years 2022 and 2023. The specimens were found on logs, tree trunks, and soil in Wadi Darbat and Wadi Jarzeez, located in Dhofar region, southern Oman, and photographed in their natural habitat. Macromorphological characters such as size, shape, and colour of basidiocarps were recorded based on fresh materials. Basidiocarps were then dried in a fruit dehydrator set to 45 °C, sealed in zipper bags, and subjected to -80 °C for 2 wk to prepare them for long term preservation.

For microscopic studies, a thin section of the lamellae, pileus covering, and volva were mounted on glass slides, stained with 5 % aqueous KOH, and further stained with 1 % aqueous Congo red for better contrast. Different microscopic structures such as basidiospores, basidia, cystidia, pileipellis, volval structure, etc. were examined under a compound microscope (ECLIPSE Ni-U, Nikon Co., Ltd., Japan). For basidiospores, at least 50 spores were measured at 1000×, and measurements are presented as: (a–)b–c(–d) × (e–) f–g(–h), [Qm, n] where b–c and f–g include the spore length and width respectively between the 5th and the 95th percentile, (a) and (d) the extreme values of spore lengths recorded, (e) and (h) the extreme values of spores width recorded, the mean of length and width of basidiospores with ± SD (standard deviation) respectively, Qm the mean of Q coefficient (length/width ratio), n is the total number of basidiospores measured (Nawaz *et al.* 2024). All the samples are preserved at the Oman Animal and Plant Genetic Resources Center (Mawarid), Muscat, Oman.

DNA extraction, amplification, and sequencing

The X-AMP DNA extraction kit (Dubuque, Iowa, USA) was employed following the manufacturer's instructions to isolate genomic DNA from dried materials. Three DNA regions were amplified, including the nuclear ribosomal DNA internal transcribed spacer regions (ITS1-5.8S-ITS2 = ITS), the D1/D2 domain of the large subunit nrDNA (28S), and a portion of the translation elongation factor 1 alpha gene (*TEF-1α*). For amplification of these regions, the primer

combinations employed were: ITS1F/ITS4 for ITS (White *et al.* 1990, Gardes & Bruns 1993), LROR/LR5 for 28S (Vilgalys & Hester 1990, White *et al.* 1990), and EF1-983/EF1-1567R for *TEF-1α* (Rehner & Buckley 2005), respectively. The PCR optimization was according to Hussain *et al.* (2024a) and the PCR amplicons were sent to Macrogen Inc. © (Seoul, Republic of Korea) for purification and sequencing in both directions using the same amplification primers. The two reads were assembled using BioEdit v. 7.0.9 (Hall 1999) and the consensus sequences were deposited at GenBank.

Sequence alignment and phylogenetic analyses

Phylogenetic analyses were performed on two different datasets. First, a combined ITS-28S-*TEF-1α* dataset was constructed using sequences from 39 specimens of the suborder *Plutineae* (including *Lepista panaeolus* KUN-HKAS 105370 from suborder *Tricholomatineae* as the outgroup taxon) following Vizzini *et al.* (2024) – see Vizzini *et al.* (2024) for GenBank accession numbers of included sequences. This dataset mainly shows that the two species *V. darbatika* and *V. sathei* (the 3rd *V. cubensis* not included in the combined dataset) found in Oman belong to genus *Volvariella*. Second, the ITS dataset with 71 sequences of *Volvariella* plus the outgroup taxon *Cantharocybe virosa* (SDBR-CMUNK0280), was assembled to study the evolutionary relationships between species in the genus *Volvariella* (Caballero *et al.* 2025). Both datasets were constructed with sequences employed in recent phylogenetic studies of *Volvariella* and *Plutineae* (Malysheva *et al.* 2019, Chattopadhyay *et al.* 2022, Kumla *et al.* 2022, Haqnawaz *et al.* 2023, Vizzini *et al.* 2024, Caballero *et al.* 2025). The assembled datasets were aligned using MAFFT v. 7 (Kato *et al.* 2019), and manually inspected and adjusted in BioEdit v. 7.0.9 (Hall 1999), and ClustalX v. 2.1 (Larkin *et al.* 2007), respectively. Files of the ITS and the combined ITS-28S-*TEF-1α* alignments are available online at the figshare platform (doi: 10.6084/m9.figshare.25911064).

Two different phylogenetic analyses were run, maximum likelihood (ML) and Bayesian Inference (BI). The ML analysis was executed in RAxML v. 8.2.12 (Stamatakis 2014) specifying a GTRGAMMAI model for all partitions and 1000 rapid bootstrap (BS) replicates, implemented in the CIPRES Science Gateway (<https://www.phylo.org/portal2/>; Miller *et al.* 2010). The BI analysis was done using BEAST v. 1.8.2 (Drummond *et al.* 2012). A Birth-Death Incomplete Sampling model was specified (Stadler 2009). Four runs were performed, each with 10 M generations. The *log* files were loaded in Tracer v. 1.6 (Rambaut *et al.* 2014) to check the values of effective sample size (ESS) for all parameters; all of these were found to be well over 200. In LogCombiner v. 1.8.2, the tree files were merged, and TreeAnnotator v. 1.8.2 was used to create a maximum clade credibility (MCC) tree (Drummond & Rambaut 2007). Statistical support values were considered significant when the ML bootstrap (BS) percentage was ≥ 70 %, and BI posterior probabilities (PPs) were ≥ 0.95. FigTree v. 1.4.2 (Rambaut 2012) was used to visualize the phylogenetic tree, which were subsequently annotated using Adobe Illustrator CC2019.

RESULTS

Phylogenetic analyses

The combined ITS-28S-TEF-1 α dataset of 39 specimens of *Pluteineae* consisted of 1710 characters, including 996 constant sites, 601 parsimony informative sites, and 113 parsimony uninformative sites. The alignment included sequences of 38 specimens from representative species of the suborder *Pluteineae*. There were nine species of *Amanitaceae*, eight of *Pluteaceae*, nine of *Volvariellaceae*, two of *Limnoperdaceae*, and 10 of *Melanoleucaceae*. Since both ML and BI analyses produced phylogenetic trees with similar topologies, only the ML is depicted (Fig. 1) with annotated with both BS and PP values.

The final ITS dataset of *Volvariella* consisted of 71 sequences with an alignment length of 589 characters, including 181 constant sites, 346 parsimony informative sites, and 62 uninformative sites. The dataset contained 70 different specimens of the genus *Volvariella* along with the outgroup taxon *Cantharocybe virosa* (SDBR-CMUNK0280). Phylogenetic trees resulting from the ML and BI methods

were topologically similar, so only the ML tree was reproduced (Fig. 2), annotated with support values from both analyses. Species of *Volvariella* grouped into three major clades with good statistical support. The basal clade (V-I; V stands for *Volvariella*) consisted of *Volvariella bombycina*, *V. diplasia*, *V. orientalis*, and *V. volvacea*. The common morphological feature among these species is their large-sized basidiocarps. The second clade (V-II) contained *V. bilobata*, *V. niveosulcata*, *V. perciliata* and *V. pulla*. There is no common morphological feature among these species; however, brown colouration of the cap is common in *V. bilobata* and *V. pulla* (Malysheva *et al.* 2019, Chattopadhyay *et al.* 2022). Most of the species included in this study fall in the third clade (V-III). Species in V-III shared small to medium-sized basidiomata. The new species *Volvariella darbatica* formed an independent lineage in clade V-III with two conspecific sequences, deposited in GenBank as *Volvariella* sp. (KY636377 from Pakistan, MK018839 from USA). The closely related species to *Volvariella darbatica* are: *V. cubensis*, *V. morozovae*, *V. nullicystidiata*, *V. ptilotricha*, *V. taylorii*, *V. cordispora*, and *V. izmirensis*. Collection DRB2-23-001 was found to be phylogenetically similar to *V. cubensis* ARF-4948 from the

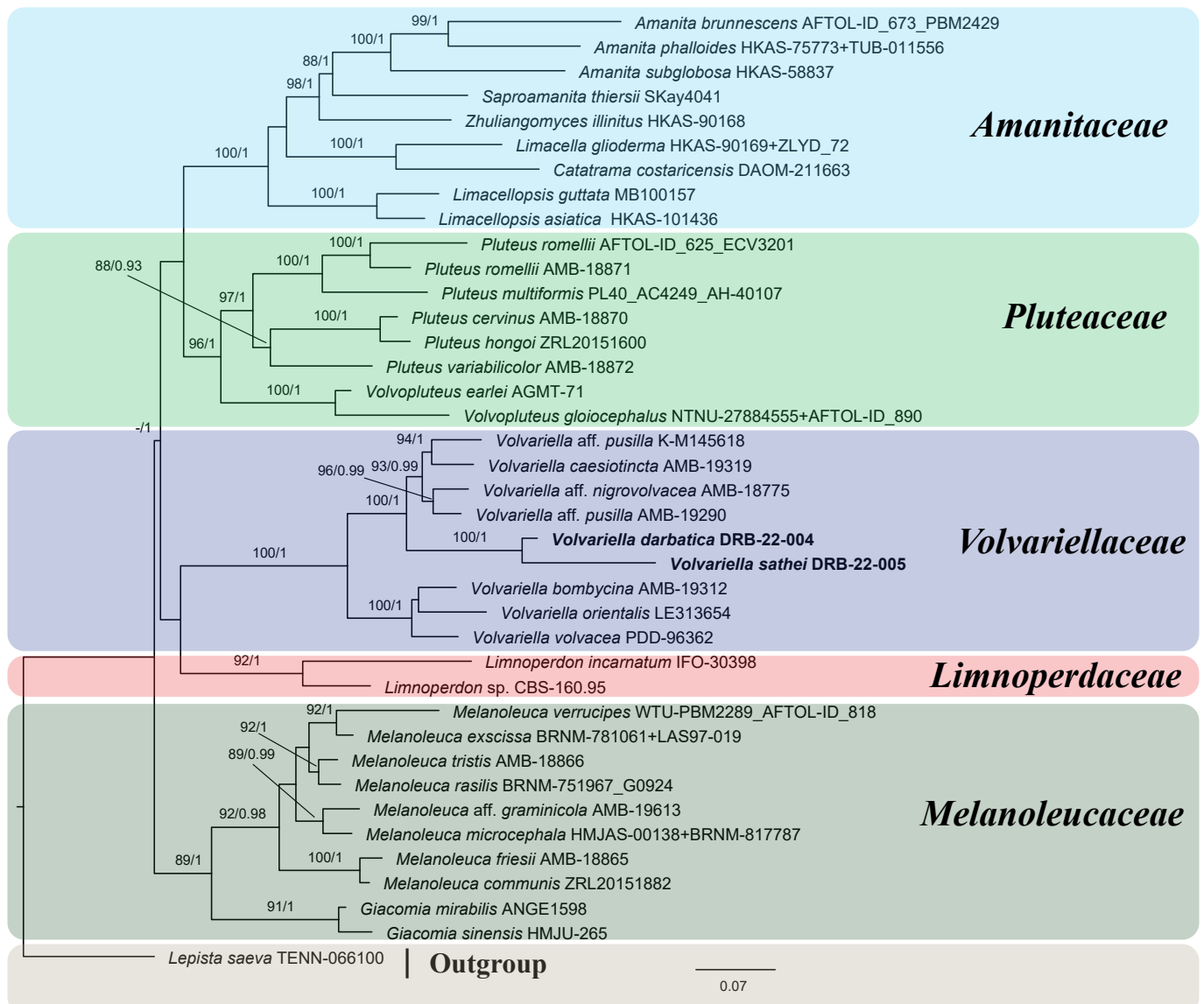


Fig. 1. Phylogeny of suborder *Pluteineae* based on multigene sequence data, individual family in the suborder recovered with excellent statistical support; values above the nodes represent maximum likelihood bootstrap and Bayesian posterior probabilities.

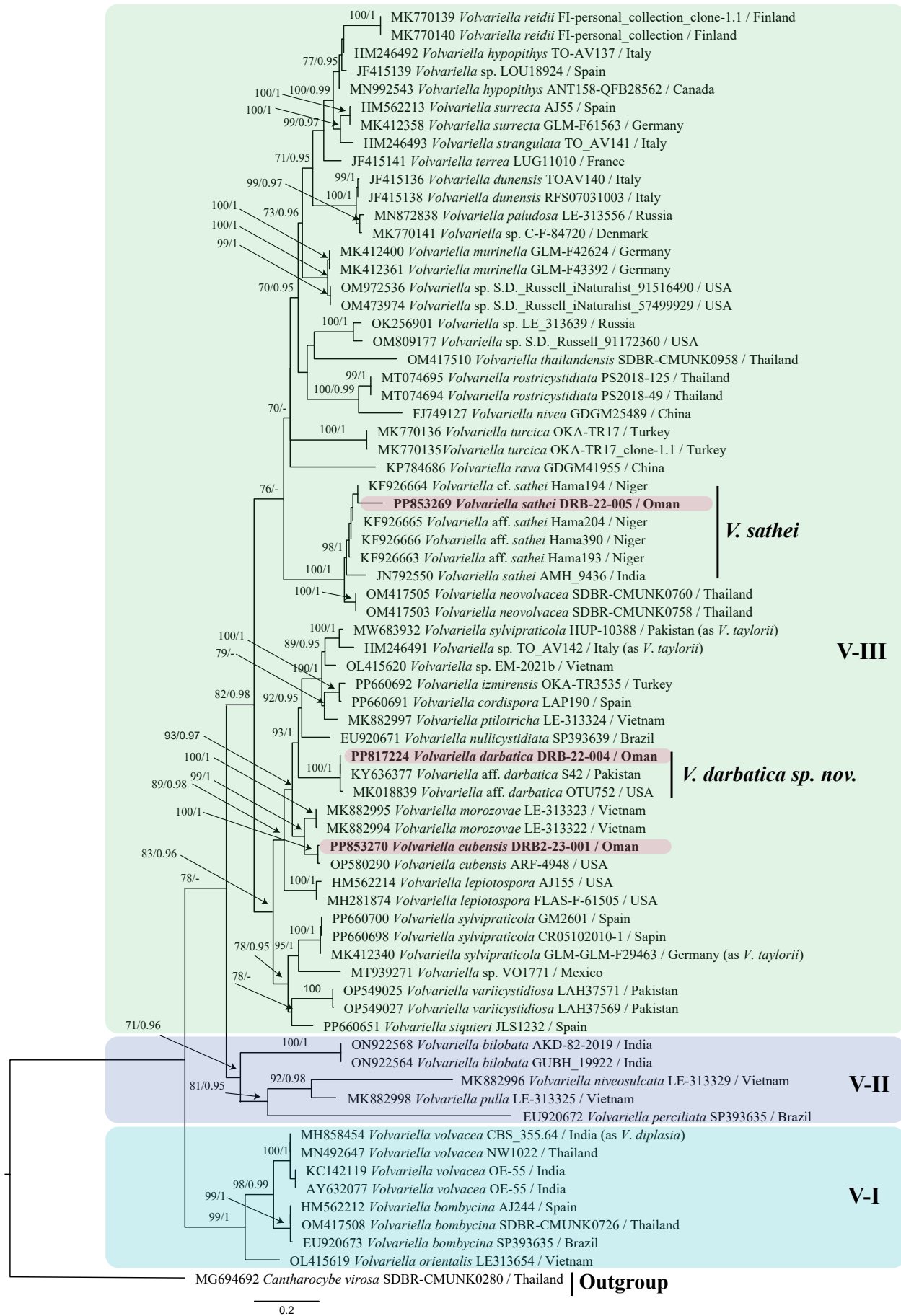


Fig. 2. The ML phylogeny of *Volvariella* based on 71 ITS sequences including the outgroup taxon *Cantharozybe virosa* (SDBR-CMUNK0280). Text on each leaf arranged in order as GenBank accession, species name, specimen's voucher, and country of origin. Above the nodes are the values of bootstrap percentages (BS) and Bayesian Posterior Probabilities (PPs). The BS values $\geq 70\%$ and PPs ≥ 0.95 are shown. Species of the genus are recovered in three major clades with excellent to moderate phylogenetic support; the pink highlighted taxa in clades V–III are the specimens studied during this study.

USA. Similarly, the specimen DRB-22-005 grouped with *Volvariella sathei*, being related also to *V. neovolvacea*. The specimen DRB-22-005 seems phylogenetically different but morphologically identical to *V. sathei*.

Taxonomy

Volvariella darbatuca S. Hussain, A. Al-Owaisi, Al-Sadi & Al-Yahya'ei, *sp. nov.* MycoBank MB 854048. Figs 3A–C, 4.

Etymology: The specific epithet “*darbatuca*” refers to the locality Darbat, a tourist spot in Dhofar region, southern Oman, where the holotype was collected.

Typus: Oman, Dhofar, Wadi Darbat, 250 m a.s.l., grassland, in soil, 9 Aug. 2022, S. Hussain & Al-Yahya'ei, DRB-22-004 (**holotype** Mawarid DRB-22-004). GenBank accessions: ITS = PP817224, 28S = PP813713, *TEF-1α* = PP826251.

Description: Basidiomata small-sized. *Pileus* 30–40 mm diam., plano-convex to convex, pale pinkish to creamy, centre pale brownish to greyish brown, slightly umbonate at the centre, surface silky fibrillose to hairy, the fibrils aggregate into squamules that arrange in radial lines when wet, with crenate margins fringed with silky fibrils; non-hygrophanous, not viscid, membranous. *Lamellae* free, subdistant, broad to slightly ventricose, pinkish to pale pink, edge entire and concolourous to lamellae, with 0–1 layer of lamellulae. *Stipe* 40–50 × 2–3 mm, central, equal, white, smooth. *Annulus* absent. *Volva* thin, membranous, saccate, greyish brown, irregularly lobed, outer surface smooth. *Odour* and *taste* not recorded. *Basidiospores* (4.7–)5.0–6.0(–6.2) × (4.2–)4.5–5.0 (–5.2) μm, (= 5.5 ± 0.23 × 4.8 ± 0.24 μm, Qm = 1.3, n = 50), in front view broadly ellipsoid to ovoid, in side view ellipsoid to broadly ellipsoid, hyaline in KOH, thick-walled, smooth, germ-pore absent. *Basidia* 22.0–26.0 × 7.5–9.5 μm, clavate to broadly cylindrical, hyaline in KOH, 4-spored. *Cheilocystidia* 50.0–62.0 × 20.0–28.0 μm, clavate to broadly fusiform, thin-walled, hyaline in KOH. *Pleurocystidia* 50.0–62.0 × 20.0–28.0 μm, ellipsoid to clavate or utriform, thin-walled, hyaline. *Lamellar trama* convergent, consisting of thin walled, hyaline hyphae, measuring 7.0–12.0 μm diam. *Pileipellis* a cutis, consisting of short, cylindrical elements, each 15.0–18.0 μm diam., terminal elements with rounded ends, each measuring 50.0–75.0 × 15.0–18.0 μm, hyaline to pale in KOH. *Volva* is arranged as an irregular trichoderm, made up of branched hyphae with terminal elements clavate to cylindrical or subglobose, greyish brown in KOH, measuring 22.0–40.0 × 11.0–22.0 μm. *Clamp connection* absent in all tissues.

Habitat and distribution: Saprobic on soil and woody debris. Solitary or dispersed in small groups among herbaceous plants. Distributed in West Asia (Oman), South Asia (Pakistan) and North America (USA).

Additional materials examined: Oman, Dhofar, Wadi Jarzeez, on woody debris under herbaceous plants, 5 Sep. 2023, S. Hussain & M. Al-Jahwari, JR22-23-021 (Mawarid JR22-23-021); *ibid.*, JR22-23-023 (Mawarid JR22-23-023).

Notes: *Volvariella darbatuca* is characterized by its small-sized and slender basidiomata with pale creamy to pale brownish and fibrillose pileus, greyish brown and membranous volva, and its small (5.0–6.0 × 4.5–5.0 μm) and broadly ellipsoid to ovoid basidiospores. On the basis of the BI and ML analyses of the ITS region, the most similar species to *Volvariella darbatuca* are: *V. cubensis*, *V. morozovae*, *V. ptilotricha*, and *V. taylorii*. *Volvariella cubensis* is a neotropical species, distributed in South America, Central America and South Asia (Shaffer 1957, Pegler 1983, Wartchow 2009, Farook *et al.* 2013, Hernández-Del Valle *et al.* 2019). In the present study the distribution of *V. cubensis* is further extended to West Asia (Oman). This species has huge basidiomata very different from that of *V. darbatuca*, with a pileus up to 116 mm diam., an olive grey colouration of fibrils, and larger basidiospores (5.5–7.5 × 4.5–6 μm; Hernández-Del Valle *et al.* 2019). *Volvariella ptilotricha* is a recently described species, only known from the type locality in Vietnam, characterized by its remarkably small basidiomata with a pileus about 5–15 mm diam., fibrillose cap surface, fibrils sandy grey to brownish, and olive grey volva (Malysheva *et al.* 2019). *Volvariella morozovae* is another small-sized species only reported from Vietnam, which differs from *V. darbatuca* by its greyish to blackish fibrillose pileus surface (Crous *et al.* 2017, Malysheva *et al.* 2019). *Volvariella izmirensis* is a recently reported species from Turkey, characterized by small to medium-sized basidiomata, with whitish pileus with cinereous centre, golden brown to ochre brown saccate volva, mainly narrow fusiform to fusiform pleurocystidia with an elongated neck, and larger basidiospores measuring 6.8–9.5 × 4.2–5.4 μm (Caballero *et al.* 2025). *Volvariella cordispora* is another small-sized species, characterized by whitish pileus with pale brown veil remnants at the centre, and a characteristic heart-shaped basidiospores (Caballero *et al.* 2025). *Volvariella taylorii* is a medium-sized, greyish coloured species, with saccate volva and large cystidia, found in coastal region, widely distributed species in Europe (Boekhout 1990). Several studies have reported this species outside Europe, such as from North and South America (Shaffer 1957), and Asia (Seok *et al.* 2002, Khan *et al.* 2021). In most of these reports the species reported as *V. taylorii* turned out to be a different species following molecular phylogenetic analysis (Caballero *et al.* 2025). For example, a collection HUP-10388 (GenBank accession MW683932) which was recently reported from Pakistan as *V. taylorii* (Khan *et al.* 2021) is actually *V. sylvipraticola* (Caballero *et al.* 2025). This could be the reason that specimens of *V. taylorii* cluster in different clades in the phylogeny of *Volvariella*.

Volvariella sathei Senthil. *et al.*, *Mycotaxon* **119**: 470. 2012. Figs 3D–E, 5.

Description: *Basidiomata* medium to large-sized. *Pileus* 60–90 mm diam., convex to hemispheric, yellowish brown to whitish, surface covered with shiny yellowish fibrils, with radial striations towards the margin, margins thin, slightly eroded. *Lamellae* free, broad to ventricose, pinkish to pinkish brown, crowded, with 0–3 layers of lamellulae. *Stipe* 70–100 × 7–10 mm, central, equal, cylindrical, solid, surface creamy to white, glabrous. *Annulus* absent. *Volva* free,



Fig. 3. Basidiomata of *Volvariella* species. **A–C.** *Volvariella darbatatica* (holotype DRB-22-004), arrows in **B** represent the radially arranged fibrils. **D–E.** *Volvariella sathei* (DRB-22-005). **F–H.** *Volvariella cubensis* (DRB2-23-001). Scale bars = 20 mm.

irregularly lobed, thick, inner surface white and glabrous, outer surface greyish and glabrous. *Odour* pleasant when fresh, pungent when dry, *taste* not recorded. *Basidiospores* $(5.5\text{--}6.0\text{--}7.0\text{--}7.5) \times (5.2\text{--}5.5\text{--}6.5\text{--}7.0) \mu\text{m}$, [= $6.5 \pm 0.26 \times 4.8 \pm 0.25 \mu\text{m}$, $Q_m = 1.1$, $n = 50$], in face view subglobose to rounded triangular or heart-shape, in side view broadly obovoid to broadly pyriform, hyaline in KOH, slightly thick-walled, germ-pore absent, apiculus visible. *Basidia* $22.0\text{--}33.0 \times 7.0\text{--}10.0 \mu\text{m}$, clavate to cylindrical, 4-spored. *Cheilocystidia* $66.0\text{--}96.0 \times 18.0\text{--}38.0 \mu\text{m}$, narrowly fusiform to fusiform, abundant, hyaline in KOH, smooth. *Pleurocystidia* $76.0\text{--}110.0 \times 25.0\text{--}54.0 \mu\text{m}$, broadly fusiform to broadly utriform, hyaline in KOH. *Lamellar trama* convergent, consisting of thin-walled hyaline, $5.0\text{--}18.0 \mu\text{m}$ diam hyphae. *Pileipellis* a cutis, consisting of thin-walled hyphae $7.5\text{--}11 \mu\text{m}$ diam., rarely branched, pale yellowish in KOH. *Volva* arranged as a cutis composed of unbranched hyaline hyphae, up to $15 \mu\text{m}$ diam., with terminal elements cylindrical to clavate, each measuring $90\text{--}160 \times 12\text{--}15 \mu\text{m}$. *Clamp connections* absent from all tissues.

Habitat and distribution: *Volvariella sathei* is a rare subtropical species, previously known only from the type locality, Pune, Maharashtra State, India (Senthilarasu *et al.* 2012). This is the second report of this species outside of India. However, *V. cf. sathei*, a similar taxon has been reported from Niger, Africa (Daniëls *et al.* 2015).

Material examined: Oman, Dhofar, Wadi Darbat, 250 m a.s.l., on soil under grasses, 9 Aug. 2022, S. Hussain & Al-Yahya'ei,

DRB-22-005 (Mawarid DRB-22-005). GenBank accessions: ITS = PP853269, 28S = PP820531.

Notes: *Volvariella sathei* is a medium to large-sized mushroom in the *Volvariellaceae*. The genus contains some important edible species, such as *Volvariella volvacea* which is called paddy straw mushroom. However, the edibility of *Volvariella sathei* has not been tested, it is therefore recommended not to consume it. It is extremely important to investigate the nutritional and biochemical properties of this mushroom to avoid poisonings.

Volvariella cubensis (Murrill) Shaffer, *Mycologia* **49**: 564. 1957. Figs 3F–H, 6.

Description: *Basidiomata* medium to large sized. *Pileus* 60 mm in diam., convex to hemispheric with umbonate centre, covered with radially arranged silky fibrils, fibrils pale greyish towards the periphery, dark greyish at centre, with entire margins. *Lamellae* free, cream to pinkish, broad, crowded with 0–2 layers of lamellulae, lamellar edge even. *Stipe* 55×5 mm, central, broader towards the base, whitish, smooth. *Annulus* absent. *Volva* fleshy, irregularly lobed, smooth, greyish brown. *Odour* and *taste* not recorded. *Basidiospores* $(5.5\text{--}6.0\text{--}7.0\text{--}7.5) \times (3.5\text{--}4.0\text{--}4.5\text{--}5.0) \mu\text{m}$, (= $6.5 \pm 0.28 \times 4.3 \pm 0.20 \mu\text{m}$, $Q_m = 1.5$, $n = 55$), in front view broadly ellipsoid to amygdaliform or ovoid, in side view ellipsoid, hyaline to light green in KOH, smooth, thick-walled, apiculus visible, germ-pore absent. *Basidia* $15.5\text{--}22.0 \times 7.5\text{--}10.0 \mu\text{m}$, cylindrical to clavate, hyaline in KOH, 2- to 4-spored.

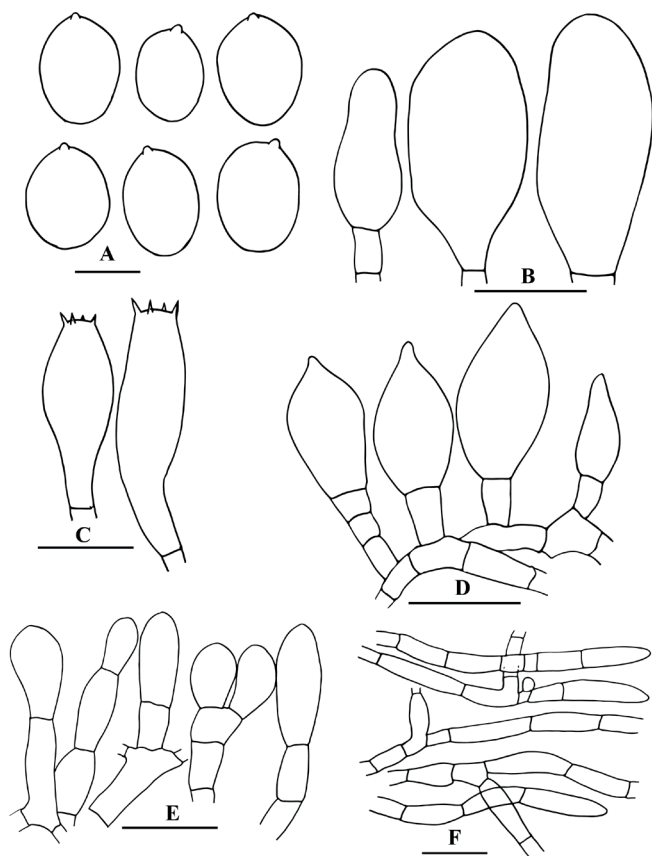


Fig. 4. Illustrations of anatomical features of *Volvariella darbatatica* (holotype DRB-22-004). A. Basidiospores. B. Basidia. C. Pleurocystidia. D. Cheilocystidia. E. Pileipellis. F. Volva elements. Scale bars: A = $5 \mu\text{m}$; B–D = $20 \mu\text{m}$; E, F = $30 \mu\text{m}$.

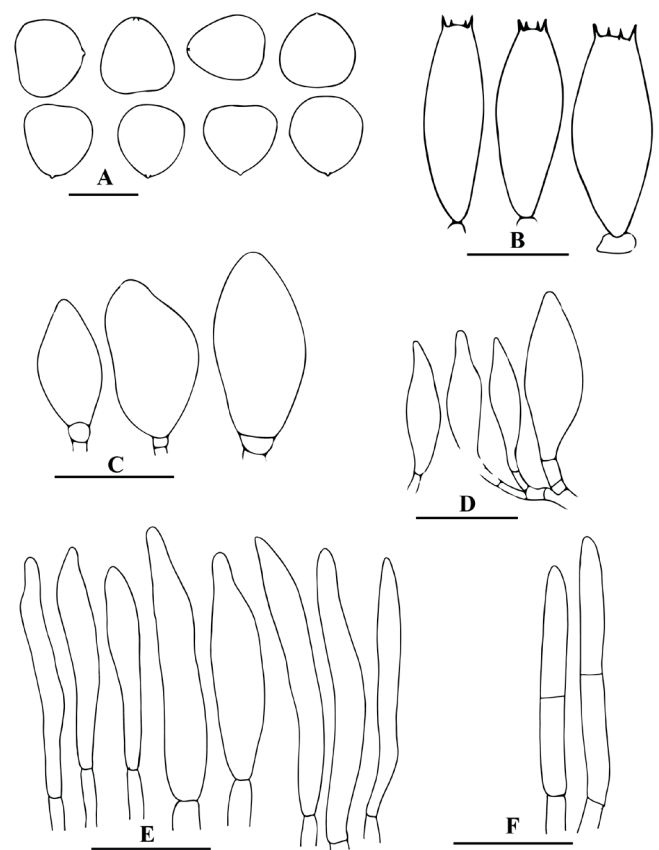


Fig. 5. Illustrations of anatomical features of *Volvariella sathei* (DRB-22-005). A. Basidiospores. B. Basidia. C. Pleurocystidia. D. Cheilocystidia. E. Pileipellis. F. Volva elements. Scale bars: A = $5 \mu\text{m}$; B–D = $20 \mu\text{m}$; E, F = $40 \mu\text{m}$.

Cheilocystidia 37.0–50.0 × 13.0–20.0 µm, utriform to broadly utriform, hyaline in KOH, thin-walled. *Pleurocystidia* 45.0–75.0 × 15–23.5 µm, utriform to clavate, hyaline in KOH, thin-walled. *Lamellar trama* convergent, consisting of thin-walled hyaline hyphae measuring 7–10 µm diam. *Pileipellis* an intricate trichoderm to irregular trichoderm, rarely branched, consisting of cylindrical elements with up to 15 µm in diam., terminal elements cylindrical to clavate, pale greyish in KOH, measuring 40.0–76.0 × 11.5–17.5 µm. *Volva* is arranged as trichoderm, consisting of branched hyphae, pale greyish to pale brownish in KOH, terminal elements clavate to fusiform with rounded end, measuring 47.5–69.0 × 14.5–18.0 µm. *Clamp connection* absent in all tissues.

Habitat and distribution: *Volvariella cubensis* is a rarely reported species, distributed in South America, Central America, and India (Shaffer 1957, Pegler 1983, Wartchow 2009, Farook et al. 2013, Hernández-Del Valle et al. 2019). In the present study, the known distribution of the species is extended to include West Asia, the Arabian Peninsula.

Material examined: Oman, Dhofar, Wadi Darbat, 250 m a.s.l., on trunk of *Ficus* tree, 2 Sep. 2023, S. Hussain & Al-Jahwari, DRB2-23-001 (Mawarid DRB2-23-001). GenBank accession: ITS = PP853270.

Notes: *Volvariella cubensis* is a medium to large-sized mushroom, characterized by greyish silky fibrillose pileus surface. The specimen we studied is morphologically similar to the published descriptions of *Volvariella cubensis* (Shaffer 1957, Pegler 1983, Wartchow 2009, Farook et al. 2013, Hernández-Del Valle et al. 2019). Using ML phylogenetic analysis of the ITS region, the sequence obtained from the Omani collection seems identical to other identified as *V. cubensis* (GenBank OP580290).

DISCUSSION

Volvariella is an important mushroom genus present in tropical, subtropical, and temperate regions (Shaffer 1957, Pegler 1977, Kirk et al. 2008, Li et al. 2009, Niego et al. 2021). Currently, the species identification of *Volvariella* is based on both morphological characters of basidiomata and molecular phylogenetic analyses of different DNA regions, including ITS, 28S, and *TEF-1α* (Justo & Castro 2010, Justo et al. 2011, He et al. 2019, Malysheva et al. 2019, Niego et al. 2021, Kumla et al. 2022). Morphologically, species of *Volvariella* are characterized by pluteoid basidiomata (free lamellae, context of the pileus discontinuous with context of the stipe, stipe usually longer than pileus), pinkish brown

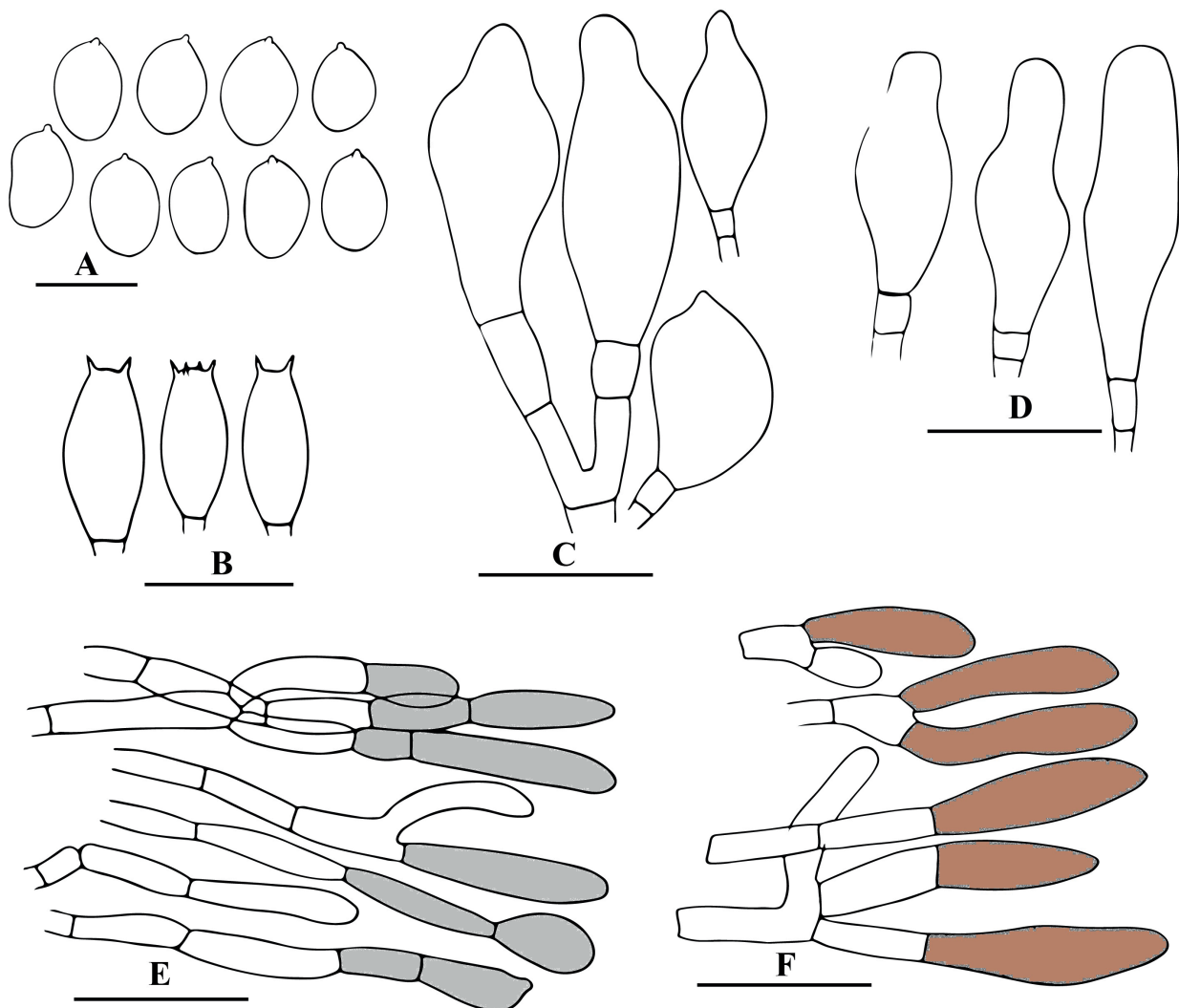


Fig. 6. Illustrations of anatomical features of *Volvariella cubensis* (DRB2-23-001). A. Basidiospores. B. Basidia. C. Cheilocystidia. D. Pleurocystidia. E. Pileipellis. F. Volva elements. Scale bars: A = 5 µm; B–D = 20 µm; E, F = 40 µm.

spore-print, and a saccate volva at the stipe base (Justo *et al.* 2011, Caballero *et al.* 2025). The taxonomic keys of the genus are mainly based on colour of basidiomata, size of pileus, lignicolous/terrestrial habitat, and basidiospore morphology (Shaffer 1957, Caballero *et al.* 2025). In the present study, we reported one new species and two first records of *Volvariella* species from Oman. *Volvariella darbatika* is a terrestrial species sporulating under grasses, characterized by a small-sized basidiomata, whitish to creamy fibrillose pileus surface, brownish membranous volva, and broadly ellipsoid to ovoid basidiospores (5.0–6.0 × 4.0–4.5 µm). There are several species in the genus with similar morphology and related habitat. For example, *V. cordispora* is a small-sized species with whitish basidiomata, sprouting under disturbed habitat, with globose to heart-shaped basidiospores measuring 5.0–8.1 × 3.8–5.2 µm (Caballero *et al.* 2025). *Volvariella alba* is a small-sized, whitish species, with volva (15 mm in length) almost half of the size of stipe (20–30 mm in length), and was recently reported from Southern Pakistan on soils with a deserted habitat (Jabeen *et al.* 2025). *Volvariella pusilla* is a European species found mostly in lawns and gardens, and occasionally in forest floor, basidiomata small-sized, whitish, with 2–3 lobed membranaceous, saccate volva (Caballero *et al.* 2025). *Volvariella reidii* is small-sized, whitish at the young stage, pale pinkish at the old stage, found on the forest floor of gymnosperms (Heinemann 1978). *Volvariella globifera*, a recently reported species from Spain, with whitish, small-sized basidiomata, with broadly ellipsoid to oblong basidiospores (4.6–7.3 × 3.3–4.6 µm), sporulates on sandy soil under *Cupressus macrocarpa* (Caballero *et al.* 2025). *Volvariella pilosipilea* might be the smallest species in the genus with a pileus diameter of 6–11 mm, both cap and volva are delicate, whitish and translucent (Caballero *et al.* 2025).

Some species of *Volvariella* are sporulating in association with other mushrooms. *Volvariella terrea* is a small to medium-sized species, characterized by having a tomentose-lanose pileus surface, growing under broad-leaved trees, with ellipsoid to cylindrical basidiospores measuring 5.9–9.9 × 3.8–5.6 µm (Caballero *et al.* 2025).

The two species *Volvariella neovolvacea* and *V. sathei* share a clade with strong phylogenetic support. Both are phylogenetically closely related, but morphologically easily distinguishable. *Volvariella sathei* is a whitish, medium to large-sized species, found on soil under trees with grasses, basidiospores globose to subglobose, measuring 6.0–6.5 × 5.0–5.5 µm (Senthilarasu *et al.* 2012, Daniëls *et al.* 2015). *Volvariella neovolvacea* is a recently reported species from Thailand, growing on soil in grasslands, with medium-sized basidiomata, brownish orange to greyish brown pileus, ellipsoid to broadly ellipsoid basidiospores, measuring 6.7–7.5 × 5.2–5.5 µm (Kumla *et al.* 2022).

The systematic position of *Volvariella* has changed multiple times. Due to the presence of a volva it was included in *Amanitaceae* (Lee *et al.* 1959), while the pinkish spore-print was the basis to transfer it to *Agariaceae* (Lee 1973), and finally, it was placed in *Pluteaceae* based on its morphology similarity to *Pluteus* (Singer 1986). Molecular phylogenetic analyses suggested that *Volvariella* is related to *Cantharocybe* and *Cuphophyllus* in the family *Hygrophoraceae* (Justo *et al.* 2011). Other studies failed to place *Volvariella* in any family and treated it as *incertae sedis* (Niego *et al.* 2021, Kumla *et*

al. 2022). Recently, an updated phylogeny of *Agaricales* was constructed with six genes, where *Volvariella* was placed in a newly erected family *Volvariellaceae* in the suborder *Pluteineae* (Vizzini *et al.* 2024). The present results confirm that *Volvariella* does not belong to the other families of *Pluteineae*, a result found in many previous studies.

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