SYSTEMATIC STUDIES ON COPRINOID AND PSATHYRELLOID AGARICS (AGARICALES, BASIDIOMYCOTA, FUNGI) OF KERALA STATE

Thesis submitted to the
University of Calicut in partial fulfilment of
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DOCTOR OF PHILOSOPHY IN BOTANY

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CERTIFICATE

This is to certify that this thesis, titled **“Systematic studies on coprinoid and psathyrelloid agarics (Agaricales, Basidiomycota, Fungi) of Kerala State”**, submitted to the University of Calicut by **Ms. Greeshma Ganga K. G.** for the award of **Doctor of Philosophy** in Botany, is a record of bona fide research work carried out by her under our supervision and guidance and that no part of this thesis has formed the basis for the award of any degree, diploma or other similar title or recognition.

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DECLARATION

I hereby declare that this thesis, entitled **“Systematic studies on coprinoid and psathyrelloid agarics (Agaricales, Basidiomycota, Fungi) of Kerala State”**, submitted to the University of Calicut for the award of Doctor of Philosophy, is a record of bona fide research work carried out by me and that no part of this thesis has been presented earlier for the award of any degree, diploma or similar title of this or any other University.

C. U. Campus **Greeshma Ganga K. G.**
Date:

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Greeshma Ganga K. G.

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Greeshma Ganga K G. Systematic studies on coprinoid and psathyrelloid agarics (Agaricales, Basidiomycota, Fungi) of Kerala state. Thesis. Department of Botany, University of Calicut, 2023.

CHAPTER 1

INTRODUCTION

Kingdom fungi encompasses an enormous diversity of organisms with varied ecologies, life-cycle strategies and morphologies ranging from unicellular yeasts and chytrids to large mushrooms. They form the second largest group of organisms in the world after the insects (Hawksworth 1991). Fungi play a major role in decomposition, nutrient cycling and nutrient transport and hence they are essential for achieving sustainable development (Muller *et al.* 2004).

Fungi are a rich source of drugs such as antibiotics, cyclosporin and statins. Fungi are used directly as food (e.g., edible mushrooms) and are also employed in the processing of food materials such as bread, wine, cheese, and several soybean-based products. Biological control employing fungi could play a very important role in sustainable agriculture by controlling the adverse effect of pests and weeds (Jyoti & Singh 2016). Cellulases produced by some fungi are used as fabric conditioners in detergents (Prescott *et al*. 2018).

According to Hawksworth (1991), "if rock breakdown involving fungi and the establishment of mycorrhizas were crucial to the evolution of the land flora, without fungi there would have been no lichens or bryophytes, no vascular plants, no dinosaurs to feed on them, and consequently no man". Fungi play an important role in the well-being and productivity of plants as mycorrhizal partners (Hawksworth 1991). About 90% of all land plants engage in mycorrhizal association with fungi (Niskanen *et al*. 2018). In this mutualistic relationship, fungi depend on the plants for their carbohydrate requirements and plants get water and minerals from the soil through a fungal partner (Suz *et al*. 2018). Endophytes represent another plant-fungal mutualism in which the fungal partner resides inside the plant tissues and facilitates the plants to grow in harsh environments (Suz *et al*.

2018). Endophytic fungi provide several benefits to the plants such as inducing disease resistance against pathogens and protecting the plants against water deficits, saline- and heat-stress and insect pests (Boddy *et al*. 2010; Suz *et al*. 2018).

Several fungi have deleterious effects on humans causing devastating famines, eliciting allergic responses and neurotropic disorders and causing diseases. The toxins produced by them may lead to the death of both human beings and animals. Many amphibian species have reached the verge of extinction due to chytrid infections. Several fungal pathogens affect plants and cause severe agricultural loss (Evans & Boddy 2010).

Hawksworth (1991) gave a conservative estimate of 1.5 million fungi occurring on our planet. A subsequent estimate based on an updated fungus: plant ratio (9.8:1) suggests that 3.8 million fungal species exist on earth (Hawksworth & Lücking 2017). However, based on the data generated from culture-dependent and culture-independent surveys on the same sample, the number of fungal species on earth has recently been re-estimated to be between 11.7 and 13.2 million (Wu *et al.* 2019). However, only about 150,000 fungal species have been described so far (Hyde 2022). This indicates that fungi are one of the least-explored biodiversity resources of the earth. Therefore, the greatest challenge of modern fungal taxonomy is to discover and document this tremendous diversity (Hibbett & Taylor 2013).

Fungal diversity in the tropical regions is several folds higher than that in any other regions of the world because of advantageous climatic and geographic factors and unexplored habitats such as the tropical rainforests. However, the fungal wealth of the tropics remains largely unexplored or under-explored (Subramanian 1982; Hawksworth 1991; Moncalvo & Ryvarden 1997; Hawksworth 2004). Also, many of the tropical and subtropical fungi are feared to be on the verge of extinction owing to habitat destruction and/or loss.

Gilled-mushrooms (agarics) form the largest group among mushroom-forming fungi (Matheny *et al*. 2006). The order Agaricales consists of more than 13200 species in about 400 genera among 33 families (Kirk *et al*. 2008).

Coprinoid and psathyrelloid mushrooms are saprobic agarics assisting in the decomposition of wood, dung, grassy debris and forest litter. Coprinoid genera include *Coprinus, Coprinellus*, *Coprinopsis*, *Hausknechtia*, *Narcissea*, *Parasola*, *Punjabia* and *Tulosesus.* Psathyrelloid genera include *Britzelmayria, Candolleomyces, Cystoagaricus*, *Homophron*, *Kauffmania*, *Lacrymaria*, *Olotia*, *Psathyrella* and *Typhrasa*. Except for the genus *Coprinus* that presently belongs to the family Agaricaceae, all other genera belong to Psathyrellaceae (Larsson & Örstadius 2008; Wächter & Melzer 2020). Coprinoid mushrooms, commonly referred to as the inky-caps, are a very interesting group of fungi. Basidiocarps of most of them liquefy and turn into a black, ink-like fluid within a few hours after maturity. Before the advent of phylogenetic research based on the comparison of DNA sequences, most of the species that showed liquefaction or autodigestion of basidiocarps were classified under Coprinaceae, which contained all of the inky-cap mushrooms. However, in a landmark molecular phylogenetic study (Redhead *et al.* 2001), the type species of *Coprinus, Coprinus comatus*, and a few other species were found to be more closely related to Agaricaceae. The former genus *Coprinus* was split between two families, and the name “Coprinaceae” became a synonym of Agaricaceae in its 21st century phylogenetic redefinition. The rest of the genera of the old Coprinaceae are now placed in a new family, the Psathyrellaceae (Redhead *et al.* 2001). Coprinoid and psathyrelloid mushrooms were found to be one of the least described groups of gilled-mushrooms in the tropics. Only less than 100 coprinoid and psathyrelloid mushrooms are so far reported from India and only 24 species were previously recorded from Kerala State (Manjula 1983; Natarajan & Raman 1983; Farook *et al*. 2013; Amandeep *et al*. 2015a, b, c; Ganga & Manimohan 2018, 2019; Ganga *et al*. 2022; Nie *et al.* 2022; Crous *et al*. 2023).

Mushroom taxonomy has transformed drastically in the past 20 years from the conventional morphology-based systems to modern molecular-phylogeny-based systems. Modern mushroom taxonomy is characterised by the use of molecular data and associated computational tools and it requires teams of researchers with diverse skills in organismal mycology, bioinformatics and molecular biology (Hibbett & Taylor 2013). Modern molecular-phylogeny-based systems make use of several specific non-coding ribosomal regions such as the internal transcribed spacer (ITS) region, the large subunit (nLSU) and the mitochondrial small subunit (mtSSU) and protein-coding regions such as the translation elongation factor 1 α (EF1α) and the β-tubulin genes (βtub1 & βtub2) (White *et al.* 1990; Nagy 2011; Hussain *et al.* 2018a).

The Research Problem

In India, only a fraction of the total gilled-mushroom diversity has been subjected to systematic studies. India is one of the most biodiversity-rich countries of the world and yet only a few coprinoid and psathyrelloid fungi have been reported from this region. Coprinoid and psathyrelloid species remain poorly documented and studied in India. The resolution of generic limits within the family Psathyrellaceae can only be obtained by a broader sampling. A survey of the literature revealed only a few sporadic reports of coprinoid and psathyrelloid fungi from India in general and Kerala in particular. Therefore, it was assumed that an intensive, focused systematic study covering the entire State would, in all probability, reveal several species new to science and new to the region. This study envisaged to explore the diversity of this group of gilled-mushrooms in Kerala State and to unravel the evolutionary relationships of the discovered taxa using molecular phylogenetic analyses.

Objectives of the present study

- To study the diversity of the coprinoid and the psathyrelloid agarics of Kerala State.

- To prepare a systematic account of the discovered taxa with keys, detailed descriptions, photographs of microscopic structures and colour photographs of basidiocarps.
- To study the evolutionary relationships of the discovered taxa using the methods of molecular phylogenetics.

This thesis includes the following chapters: Chapter 2 provides a detailed review of the literature on the diversity and systematics of the coprinoid and psathyrelloid fungi. Chapter 3 provides information about the physiography, vegetation and climate of Kerala State A comprehensive account of the materials and methods adopted in the present study is given in Chapter 4 along with some photographs of the collection localities. Chapter 5, the major part of the thesis, is a systematic account of all the coprinoid and psathyrelloid taxa discovered during this study with detailed descriptions of the discovered taxa, their photographic illustrations and keys to the taxa. Chapter 6 discusses the results of the phylogenetic analyses. General observations and discussion along with the molecular data generated based on the present study are provided in Chapter 7. Chapter 8 includes recommendations for future studies based on the present study. Chapter 9 contains a summary of the present study. All references cited in this thesis are listed at the end, followed by tables and appendices. Table I represents a list of coprinoid and psathyrelloid species reported so far from Kerala State. Table II provides the details of the species included in the phylogenetic analyses. A list of species, their collection localities and the ITS and nLSU sequences generated in the present study are given in Table III. The appendices comprise the description sheets used to record the macro- and microscopic characters (Appendix 1), the macroscopic characters studied (Appendix 2) and the microscopic characters studied (Appendix 3). The recipes and procedures for the preparation of stains, reagents, buffers and the composition of the reaction mixtures for PCR are given in Appendix 4. Appendix 5 includes supporting publications and presentations delivered during the study. Finally, an index to all taxa discussed in this thesis is provided at the end.

Chapter 2

Review of literature

Greeshma Ganga K G. Systematic studies on coprinoid and psathyrelloid agarics (Agaricales, Basidiomycota, Fungi) of Kerala state. Thesis. Department of Botany, University of Calicut, 2023.

CHAPTER 2

REVIEW OF LITERATURE

2.1. AN OVERVIEW OF THE COPRINOID AND THE PSATHYRELLOID AGARICS

2.1.1. Introduction to the taxonomy of the coprinoid and the psathyrelloid fungi

The genus name *Coprinus* is derived from the Greek word for dung, *kopros* and this indicates the coprophilous nature of many of its species. *Coprinus* was first published as a genus name by Persoon (1797). *Coprinus* currently is a small genus of gilled-mushrooms consisting of *Coprinus comatus,* the type species, and a few of its close relatives. Until 2001, *Coprinus* was a large genus consisting of all agaric species in which the lamellae auto-digested to release their spores. The black, ink-like liquid that formed as a result of this auto-digestion gave these species their common name "inky caps". The inky cap mushrooms were traditionally classified under the family Coprinaceae. Molecular phylogenetic investigations found that *Coprinus comatus* was only a distant relative of the other species of *Coprinu*s and was closer to genera of the Agaricaceae. Since *Coprinus comatus* is the type species of *Coprinus*, only that species and its close relatives *C. sterquilinus* and *C. spadiceisporus* retained the name of the genus (Redhead *et al.* 2001). The majority of species of *Coprinus* were therefore reclassified into three genera placed in Psathyrellaceae: *Coprinellus, Coprinopsis* and *Parasola* (Redhead *et al.* 2001). Remarkably, *Coprinus,* which was the type genus of the family Coprinaceae, now belongs to the family Agaricaceae. *Coprinus* and these segregate genera are now referred to collectively as the coprinoid fungi.

Coprinoid mushrooms have a central stipe and a pileus that is usually conic or bell-shaped. In some species, the pileus becomes flat with age and maybe even upturned. These mushrooms generally have a thin, fragile flesh. The lamellae are either free or attached to the stipe and they often liquefy at maturity. If the lamellae deliquesce, it proceeds from the outside in so that the lamellae liquefy just as the spores become mature. Because of the thin flesh and the deliquescence, these mushrooms are ephemeral and they often disappear completely within a few hours. Coprinoid mushrooms produce very dark spore prints, which helps distinguish the group from most other mushrooms. The basidiospores range in colour from black to purple brown. The basidiocarps may or may not have a partial veil and/or a universal veil. Currently, inky caps are divided among four genera: *Coprinellus, Coprinopsis, Parasola* and *Coprinus* (Redhead *et al.* 2001; Nagy *et al.* 2010a; Nagy *et al.* 2013a).

Coprinellus and *Coprinopsis* together form the bulk of the inky caps and most closely match the general description given above. The two genera are very similar and it is a bit difficult to accurately differentiate between them. *Coprinellus* does not have a partial veil (and therefore has no annulus) and lacks deliquescent lamellae while *Coprinopsis* has a partial veil that leaves an annulus and has deliquescent lamellae. Additionally, *Coprinopsis* species more often produce a universal veil that leaves warts or patches on the pileus.

Parasola comprises tiny mushrooms that most closely resemble parasols, a type of small, flimsy umbrellas. These mushrooms have a very thin context and usually have deep radial grooves that extend from near the centre of the pileus to the pileal margin. *Parasola* mushrooms also have lamellae that deliquesce slowly. Additionally, these mushrooms never produce a universal veil and therefore lack any kind of warts, patches or granules on the pileal surface. Unfortunately, this last feature cannot be used to rule out other coprinoid genera as the mushrooms may have lost their velar remnants due to rain or other external factors.

Coprinus sensu stricto is characterised by large, sturdy basidiocarps. These mushrooms have a thick context compared to other coprinoid mushrooms but their lamellae do liquefy, making it impossible to confuse them with any other group. *Coprinus* species also have a partial veil that leaves an annulus, and lamellae that are initially pinkish before turning black. Many *Coprinus* species, such as the well-known *C. comatus*, feature a scaly pileus that is nearly cylindrical before they begin to open.

Psathyrella is a large genus of gilled-mushrooms consisting of about 400 species usually with a thin pileus and a white or yellowish white, hollow stem. The pileus does not auto-digest unlike those of the coprinoid fungi. Before the DNA-based phylogenetic analyses, *Psathyrella* and allied genera, along with all coprinoid fungi, were classified in the family Coprinaceae. As explained earlier, when *Coprinus sensu lato* was split between two families, the name "Coprinaceae" became a synonym of Agaricaceae. Except for *Coprinus comatus* and its close relatives, all other members of the erstwhile Coprinaceae, including *Psathyrella*, were transferred to a new family named Psathyrellaceae. *Psathyrella* and related genera belonging to the family Psathyrellaceae are collectively referred to as the psathyrelloid fungi.

The coprinoid and psathyrelloid mushrooms share developmental, morphological and ecological characters such as similar habitat preferences, basidiospore characteristics (wall structure, colour, presence of a germ-pore) and degradation of spore pigments in sulphuric acid (Singer 1986; Kües 2000; Uljé 2005; Vašutová *et al*. 2008b; Nagy *et al.* 2010a).

Members of other dark-spored gilled-mushroom families such as the Bolbitiaceae, the Agaricaceae and the Strophariaceae show morphological and ecological resemblances to Coprinaceae (Singer 1986; Hopple & Vilgalys 1999). The species of these families share characters such as a saprotrophic mode of nutrition and thick-walled, pigmented basidiospores with an apically positioned germ-pore (Hopple & Vilgalys 1999). These four families differ mainly in the colour of the basidiospores and also in the structure of the pileipellis. Species of Agaricaceae can be distinguished by their chocolate brown basidiospores. Species of Strophariaceae possess purple-brown basidiospores. While Coprinaceae is characterised by black basidiospores, species of Bolbitiaceae show yellow-brown basidiospores (Miller 1981; Hopple & Vilgalys 1999).

Psathyrellaceae is known for the deliquescent nature of some of its genera in which the lamellae and pileus of the basidiocarp turn into a black fluid and the stipe remains intact at maturity (Hopple & Vilgalys 1999; Nagy *et al.* 2010a). It is ambiguous whether auto-digestion facilitates the dispersal of basidiospores or not because active dispersal of basidiospores occurs before the lysis of tissues (Hopple & Vilgalys 1999; Nagy *et al.* 2010a). Deliquescence is also observed in other dark-spored families such as Agaricaceae and Bolbitaceae but this phenomenon is more prominent in Psathyrellaceae where almost 90% taxa show deliquescence (Keirle *et al*. 2004; Nagy *et al.* 2010a). Section *Pseudocoprinus*, a non-deliquescent group of coprinoid fungi, was previously treated under the genus *Coprinus* (Orton & Watling 1979). These taxa were later transferred to either of the genera *Parasola* and *Coprinellus* (Uljé 2005). According to an earlier evolutionary concept regarding auto-digestion, deliquescent forms were ancestral and psathyrelloid (non-deliquescent) forms arose from within the coprinoid taxa (Singer 1986; Nagy *et al.* 2010a). Contemporary mycologists found that non-deliquescence is the ancestral character and deliquescence of basidiocarps evolved independently several times during evolution in each of the large clades and genera such as *Parasola*, *Coprinopsis*, *Coprinellus*, /Psathyrella candolleana clade and /Coprinus patouillardii clade (Nagy *et al.* 2010a; Watling & Richardson 2010).

Henderson *et al*. (1969) classified the erstwhile Coprinaceae into two subfamilies and four genera (Panaeoloideae comprising *Panaeolus* and Coprinoideae comprising *Lacrymaria*, *Psathyrella* and *Coprinus*). Singer (1969, 1986) rearranged the family Coprinaceae into three subfamilies Coprinoideae, Psathyrelloideae, and Panaeoloideae and introduced four more genera

(*Macrometrula*, *Panaeolina*, *Copelandia*, *Anellaria*). These classifications are now outdated and have historical value only.

2.1.2. Modern concepts regarding coprinoid and psathyrelloid agarics

The introduction of tools of molecular phylogenetics was an important milestone in the history of the taxonomy of agarics and one of the outcomes was the revelation of the phylogenetic relationships of the coprinoid and psathyrelloid fungi. Drastic changes have happened in the nomenclature and classification of these taxa both at the genus and family levels.

Molecular phylogenetic analysis of the group was started by Hopple & Vilgalys (1994) with DNA sequences of some coprinoid species. The results indicated that *Coprinus comatus* (the type species of the genus *Coprinus* and the family Coprinaceae) showed more affinity towards Agaricaceae than to other coprinoid members. Studies of Johnson & Vilgalys (1998) on *Coprinus* and some related genera inferred that not only *Coprinus comatus* but also most of the species in the section *Comati* were clustered in the family Agaricaceae. Characters such as the general absence of pleurocystidia, the reddening of tissues, the melanisation of spores, the deliquescence of basidia, the large paraphyses and the inaequihymeniferous hymenia of *C. comatus* and related taxa are shared by members of Agaricaceae and hence the nesting of *Coprinus comatus* within the Agaricaceae clade was not surprising (Redhead *et al*. 2001).

Hopple & Vilgalys (1999) identified three clades in coprinoid mushrooms amongst which clade 1 included the genus *Lacrymaria* in addition to most of the coprinoid taxa. Clade 2 represented the entire genus *Psathyrella* and some coprinoid mushrooms that are seen derived within the same clade. Due to this reason, the delimitation between coprinoid and psathyrelloid taxa was not clear. The third clade comprised rest of the *Coprinus* members that formed part of a bigger clade comprising members of the family Agaricaceae. Also, they concluded that clade 1 and clade 2 together formed a monophyletic group that was sister to Strophariaceae members (Hopple & Vilgalys 1999).

The studies of Moncalvo *et al.* (2000, 2002) supported the findings of Hopple & Vilgalys (1999) and they also recognised three distinct clades (represented as R, T, U) where the members of Coprinaceae were distributed. The core elements in Coprinaceae such as *Psathyrella* and a major part of the genus *Coprinus* were nested in clade T. Interestingly, the taxa belonging to the subfamily Panaeoloideae was found to be clustered (clade R) near the family Bolbitaceae. A few coprinoid taxa including *Coprinus comatus* (clade U) showed more affinity towards Agaricaceae (Moncalvo *et al.* 2000, 2002).

Redhead *et al.* (2001) reviewed the nomenclatural history and typifications of names previously treated as synonyms of *Coprinus* and they demonstrated that taxonomic characters previously considered as not significant become important in the light of molecular evidence. Based on the results obtained from the molecular studies, Redhead *et al.* (2001) split the old family Coprinaceae between two families. A few species (previously considered as sect. *Comati*) representing *Coprinus sensu stricto* was placed under Agaricaceae. The remaining family was renamed as Psathyrellaceae as the previous name Coprinaceae became a synonym of Agaricaceae. The remaining coprinoid taxa of Psathyrellaceae were split between three new genera, namely *Coprinopsis*, *Coprinellus* and *Parasola.* The subgenus *Panaeoloidae* was removed from Psathyrellaceae but the exact position of this group was still uncertain (Redhead *et al*. 2001).

This progress in the classification of coprinoid fungi was not accepted by a few mycologists. Horak (2005), for example, used the invalid family name Coprinaceae and followed the traditional classifications. He recorded seven genera including *Montagnea*, *Lacrymaria*, *Psathyrella*, *Coprinus*, *Copelandia*, *Anellaria* and *Panaeolus* under Coprinaceae (Horak 2005). Uljé (2005) did not follow the concept of Redhead *et al*. (2001) that split *Coprinus sensu lato* into segregate genera. In his classification, *Coprinus sensu lato* was divided into three sections (*Coprinus*, *Veliformis* and *Pseudocoprinus*) and these sections were further subdivided into subsections. Section *Coprinus* included four subsections (subsect. *Coprinus*, subsect. *Atramentarii*, subsect. *Lantuli* and subsect. *Alachuani*). Section *Veliformes* contained four subsections (subsect. *Micacei*, subsect. *Domestici*, subsect. *Nivei* and subsect. *Narcotici*). Section *Psuedocoprinus* included three subsections (subsect. *Glabri*, subsect. *Auricomi* and subsect. *Setulosi*) (Uljé 2005).

Padamsee *et al*. (2008) evaluated 132 ribosomal sequences from approximately one-tenth of the known *Psathyrella* species worldwide, including representatives of most subgeneric subdivisions, and three closely related coprinoid genera (*Parasola, Coprinopsis* and *Coprinellus*) using multiple phylogenetic methods. Their results indicated that *Psathyrella* was polyphyletic and they suggested that the genus can be separated into 11 clades of which five can be raised as genera.

Nagy *et al.* (2013a) presented a well-resolved phylogeny and morphological circumscriptions for fourteen clades of Psathyrellaceae based on sequence data from a matrix of four nuclear genes. Their results reinforced the para/polyphyly of *Psathyrella* and suggested an extensive rearrangement of the taxa including the creation of new genera (Nagy *et al*. 2013a).

Based on a four-gene dataset on Psathyrellaceae, Örstadius *et al*. (2015) recognised nine clades such as “Coprinellus”, “cordisporus,” “Kauffmania,” “Cystoagaricus,” “Typhrasa” “Parasola,” “Coprinopsis”, “Homophron” and “Lacrymaria” within Psathyrellaceae but outside the “Psathyrella” clade. From their molecular phylogenetic analysis, they introduced three new genera (*Homophron*, *Kauffmania* and *Typhrasa*) under Psathyrellceae (Örstadius *et al*. 2015).

The genus-level placement of *Coprinus cordisporus* was an unresolved issue among the coprinoid and psathyrelloid taxa. Watling & Richardson (2010) included

Coprinus cordisporus in the genus *Coprinopsis*. In the phylogenetic analysis of Hopple & Vilgalys (1999), *C. cordisporus* was placed next to *C. curtus* (Redhead *et al*. 2001). According to the analysis of Nagy *et al*. (2013a), the exact generic placement of *Coprinus patouillardii* clade (equivalent to *C. cordisporus*) is still uncertain and this clade clustered as a sister clade to /Coprinellus. The development of the veil in the early stages of ontogeny shows the relationship of this clade with *Coprinellus* (Nagy *et al*. 2013a). The velar elements of *C. patouillardii* are not clearly delimited from the pileipellis but they can be easily demarcated from the hymeniderm of *Coprinellus* (Keirle *et al*. 2004; Nagy *et al*. 2013a; Örstadius *et al*. 2015).

A recent molecular phylogenetic study proposed a new system of classification for family Psathyrellaceae (Wächter & Melzer 2020). This new classification included the known genera *Coprinellus*, *Coprinopsis*, *Cystoagaricus*, *Homophron*, *Hormographiella*, *Kauffmania*, *Lacrymaria*, *Parasola*, *Psathyrella* and *Typhrasa*. In addition to these existing genera, six new, monophyletic genera (*Britzelmayria*, *Candolleomyces*, *Narcissea*, *Olotia*, *Punjabia* and *Tulosesus*) were recognised. *Galerella floriformis* was found to be clustered within Psathyrellaceae and a new genus *Hausknechtia* was proposed for this species. Seven new sections (*Noli-tangere*, *Saponaceae*, *Stridvalliorum*, *Arenosae*, *Confusae*, *Sublatisporae* and *Sinefibularum*) were added to genus *Psathyrella*. The genus *Coprinellus* was found clustered in two separate clades (/Coprinellus A and /Coprinellus B) and five new sections (*Disseminati*, *Aureogranulati*, *Curti*, *Hepthemeri* and *Deminuti*) were introduced. /Patouillardii was seen clustered between /Coprinellus A and /Coprinellus B. *Coprinopsis* was divided into 20 sections, in which 13 are new (*Cinereae*, *Filamentiferae*, *Melanthinae*, *Alopeciae*, *Xenobiae*, *Phlyctidosporae*, *Krieglsteinerorum*, *Erythrocephalae*, *Geesteranorum*, *Mitraesporae*, *Radiatae*, *Subniveae* and *Canocipes*). The genus *Parasola* was subdivided into section *Parasola* and section *Conopileae*.

2.1.3. Geographical distribution of coprinoid mushrooms

2.1.3.1. World distribution

Coprinoid mushrooms are cosmopolitan in distribution. There are several reports from different parts of the world. A survey of the literature showed that most of the species were recorded from Europe. These records include regions such as Ukraine (Batyrova 1990; Prydiuk 2010, 2011), Italy (Uljé *et al*. 1998; Doveri *et al*. 2011), Poland (Gierczyk *et al*. 2011, 2017), Croatia (Tibpromma *et al*. 2017), Switzerland (Breitenbach & Kränzlin 1994), France (Lange & Smith 1953; Courtecuisse 1984; Enderle & Moreno 1985), Denmark (Lange & Smith 1953; Petersen 1970), Sweden (Lange & Smith 1953; Házi *et al*. 2011; Nagy *et al*. 2012; Szarkándi *et al*. 2017), Finland (Lange & Smith 1953; Larsson & Örstadius 2008), Iceland (Lange & Smith 1953), Norway (Lange & Smith 1953; Nagy *et al*. 2012; Szarkándi *et al*. 2017), Austria (Lange & Smith 1953), Germany (Enderle & Moreno 1985; Bender & Enderle 1986; Ludwig & Roux 1995; Nagy *et al*. 2013b; Szarkándi *et al*. 2017), the Iberian Peninsula (González *et al*. 1995), Slovakia (Nagy *et al*. 2012; Szarkándi *et al*. 2017), Estonia (Saar *et al*. 2015), Latvia (Saar *et al*. 2015), the Netherlands (Kits van Waveren 1968; Uljé 1988; Uljé & Bas 1988; Uljé & Bas 1991; Uljé & Bas 1993; Uljé & Noordeloos 1997; Uljé *et al*. 1998; Uljé 2005), the United Kingdom (Kits van Waveren 1968; Orton 1969; Orton 1976; Schafer 2014), Hungary (Ludwig & Roux 1995; Nagy 2007; Nagy *et al*. 2012; Nagy *et al*. 2013b; Szarkándi *et al*. 2017) and Spain (Enderle & Moreno 1985; Ortega & Esteve-Raventos 2003; Crous *et al*. 2017).

In addition to the records from Europe, there are some reports from other geographical regions. These include records from Mexico (Pérez-Silva & Aguirre-Acosta 1986), USA (Lange 1948; Lange & Smith 1953; Thiers 1959), Canada (Lange & Smith 1953), Greenland (Lange & Smith 1953), the Hawaiian Islands (Keirle *et al*. 2004), the Lesser Antilles (Pegler 1983), the Galápagos Islands (Lange 1948), the

Falkland Islands (Watling & Richardson 2010), Brazil (Gomes & Wartchow 2018), South Africa (Reid & Eicker 1999), Uganda (Pegler 1977), Tunisia (Pegler 1977), Algeria (Pegler 1977); Australia (Grgurinovic 1997), Sri Lanka (Pegler 1986), China (Huang & Bau 2018), Pakistan (Shah *et al*. 2018a, 2018b), Iran (Asef *et al*. 2015), Armenia (Badalyan *et al*. 2011) and Vietnam (Nguyen *et al.* 2019).

2.1.3.2. Records from India

Coprinoid mushrooms are a poorly documented group of fungi in India. Only about 50 species have been reported so far from India (Lange & Smith 1953; Sathe & Kulkarni 1980; Manjula 1983; Natarajan & Raman 1983; Natarajan *et al*. 2005; Pradhan *et al*. 2012; Amandeep *et al.* 2015a; Ganga & Manimohan 2018; Ganga *et al*. 2022).

2.1.3.3. Records from Kerala State

Only 13 species of coprinoid mushrooms have been reported from Kerala State so far (Natarajan & Raman 1983; Vrinda *et al.* 1999; Florence 2004; Varghese *et al*. 2010; Mohanan 2011; Vrinda *et al*. 2012; Farook *et al*. 2013; Vrinda & Pradeep 2014; Ganga & Manimohan 2018; Ganga *et al*. 2022; see Table 1).

2.1.4. Geographical Distribution of psathyrelloid fungi

2.1.4.1. World distribution

Psathyrelloid mushrooms form a very large group with more than 1000 members distributed worldwide (www.indexfungorum.org). Among the entire world records of psathyrelloid mushrooms, most are from different regions of Europe such as Norway (Weholt *et al*. 2016), Denmark (Örstadius *et al*. 2015), Finland (Örstadius *et al*. 2015), Poland (Ronikier *et al*. 2007), Ukraine (Prydyuk 2014), Czech Republic (Vašutová 2008a), Slovakia (Vašutová 2008a), Italy (Contu 1991; Enderle & Zuccherelli 1993; Örstadius *et al*. 2015; Sicoli *et al*. 2019), Switzerland (Clémencon

1985), Spain (Esteve-Raventós & Barrasa 1989; Heykoop & Esteve-Raventós 1994; Heykoop & Moreno 1998; Esteve-Raventós & Villarreal 2002; Heykoop & Moreno 2002; Arenal *et al*. 2003; Heykoop *et al*. 2017; Broussal *et al*. 2018) Austria (Hausknecht & Krisai 1987; Örstadius 1992; Friebes & Melzer 2009; Örstadius *et al*. 2015; Friebes & Melzer 2018), France (Courtecuisse 1984; Kits van Waveren 1985; Esteve-Raventós & Villarreal 2002; Broussal *et al*. 2018), Great Britain (Kits van Waveren 1985, 1987), the Netherlands (Kits van Waveren 1985, 1987), Germany (Örstadius 1992; Hausknecht 1995; Enderle 1996; Örstadius *et al*. 2015), Sweden (Örstadius 1992; Larsson & Örstadius 2008; Örstadius *et al*. 2015), Scotland (Watling & Jurand 1971) and Slovenia (Melzer & Ferisin 2018).

Reports of Psathyrelloid fungi from regions outside of Europe include those from the USA (Smith 1941; Thiers 1959; Alessio 1984), Mexico (Moreno *et al*. 2015), Cuba (Nieves-Rivera 2001); Brazil (Cortez & Coelho 2005), the Lesser Antilles (Pegler 1983); Nigeria (Pegler & Young 1992), Kenya (Pegler 1977), Tanzania (Pegler 1977), Uganda (Pegler 1977), Sri Lanka (Pegler & Young 1992), Turkey (İleri *et al*. 2019), China (Yan & Bau 2017; Yan & Bau 2018a; Yan & Bau 2018b), Japan (Takahashi 2000) and Korea (Seok *et al*. 2010).

2.1.4.2. Records from India

So far, about 39 psathyrelloid taxa have been reported from India (Sathe & Deshpande 1980; Manjula 1983; Natarajan & Raman 1983; Natarajan *et al*. 2005; Kaur *et al*. 2011; Farook *et al*. 2013; Kaur *et al.* 2013; Amandeep & Munruchi 2014; Amandeep *et al*. 2015b; Ganga & Manimohan 2019; Crous *et al*. 2023).

2.1.4.3. Distribution from Kerala State

Only 11 species of psathyrelloid fungi have, so far, been reported from Kerala State (Pradeep *et al*. 1996; Vrinda *et al*. 2001; Vrinda *et al*. 2003; Farook *et al*. 2013; Vrinda & Pradeep 2014; Ganga & Manimohan 2019; Crous *et al*. 2023; see Table 1).

2.2. GENERA OF COPRINOID AND PSATHYRELLOID AGARICS

2.2.1 Genera split off from *Coprinus sensu lato* by Redhead *et al.* (2001)

2.2.1.1. *Coprinus sensu stricto*

2.2.1.1.1. Genus concept

After the transfer of a majority of the species of the original, big genus *Coprinus* (*Coprinus sensu lato*) to three new genera (*Coprinellus*, *Parasola* and *Coprinopsis*) of Psathyrellacae, what is remaining is a very small genus (*Coprinus sensu stricto*) belonging to the family Agaricaeae. The genus *Coprinus,* like other coprinoid mushrooms, is primarily distinguished by deliquescent lamellae and a dull-coloured, ovoid, paraboloid, conical or campanulate pileus expanding to become applanate with an upturned or revolute margin. The presence of pseudoparaphyses around the basidia is a distinctive microscopic character. These sterile structures, 3–9 in number, surround the basidia and are larger than basidia and often double the diameter of basidia (Orton & Watling 1979; Pegler 1986; Singer 1986; Uljé 2005). The characters shared by species of the genus *Coprinus* but not by other coprinoid mushrooms include the presence of an annulus on the stipe, the pinkish young lamellae and the presence of a string-like strand of fibres inside the hollow stipe. The di- or trimorphic basidia found on the same lamella are useful to differentiate *Coprinus* species from psathyrelloid species (Orton & Watling 1979; Singer 1986; Uljé 2005). Keirle *et al*. (2004) used a few key characters such as a veil composed of tenacious, floccose remnants that do not easily wash away from the pileus surface, the presence of an annulus, absence of pleurocystidia and sterigmata plugged with a gold-coloured material to separate *Coprinus* from species of *Podaxis*.

2.2.1.1.2. Characters used in taxonomy

Coprinus species have coprinoid or mycenoid basidiocarps that may be small, medium-sized or large. The pileus is globose, cylindrical or paraboloid in most cases expanding to become applanate often with an upturned margin at maturity. The pileus surface may be plicate, striate, folded or furrowed, silvery-white, grey, ochre-brown, yellow-brown or rarely a shade of green in colour, tomentose, floury-floccose, pruinose or glabrous. The stipe may be with or without an annulus. A veil may be present or absent and if present it may be granular, felty or as hairy flocks. The lamellae may be parallel to subparallel, initially white later becoming dark grey to black and then autolysed to form an ink. The spores are dark brown to black, smooth or warty, commonly large, variable in size and shape and with a central or eccentric germ-pore. The basidia are 1-, 2-, 3- or 4-spored and trimorphic. About 3–8 pseudoparaphyses are observed around the basidia. Cheilo- and pleurocystidia are normally present but are rarely absent (Moser 1978; Orton & Watling 1979; Uljé 2005).

2.2.1.1.3. Infrageneric classification

The arrival of molecular phylogenetic studies almost completely remoulded the classifications of not only the genus *Coprinus* but also the entire family Coprinaceae. Modern phylogenetic analysis inferred that residual coprinoid taxa (*Coprinus sensu stricto*) except *Parasola*, *Coprinellus* and *Coprinopsis* form the genus *Coprinus* (Hopple & Vilgallis 1999; Redhead 2001; Larsson & Örstadius *et al*. 2008). Therefore, the old infrageneric classifications proposed for *Coprinus sensu lato* have become obsolete. No infrageneric classifications have been proposed for *Coprinus sensu stricto*, which currently has only a very limited number of species.

2.2.1.1.4. Ecology

Basidiocarps of *Coprinus* commonly appear as gregarious, clustered or sometimes solitary on dung of herbivores, straw, lawn, coastal sand, wood chips and hard-packed soil (Keirle *et al*. 2004; Uljé 2005; Gierczyk *et al.* 2011).

2.2.1.1.5. Economic importance

Some species of *Coprinus* are best known for their edibility. Species such as *C. comatus* are considered as excellent edible mushrooms (Singer 1986; Reyes *et al.* 2009; Thatoi & Singdevsachan 2014; Tiimub *et al*. 2015)*. Coprinus comatus* is reported to have anti-cancer properties (Zaidman *et al*. 2008; Asatiani *et al*. 2011). Comatin, a compound isolated from *C. comatus,* is an inhibitor of non-enzymatic glycosylation reaction (NEG) thereby reducing blood glucose level and is a potential anti-diabetic drug (Ding *et al*. 2010).

2.2.1.2. *Coprinellus*

2.2.1.2.1. Genus concept

The genus *Coprinellus* is represented by approximately 80 species worldwide (Redhead *et al*. 2001; Walther *et al*. 2005; Padamsee *et al*. 2008; Nagy *et al*. 2011, 2012, 2013a; Örstadius *et al*. 2015; Hussain *et al*. 2018b). Initially, Lange (1915) recognised the genus *Coprinellus* for accommodating non-deliquescent coprinoid taxa such as *C. disseminatus* and *C. impatiens* (Lange & Buchwald 1936; Smith & Hesler 1946; Lange & Smith 1953; Redhead *et al*. 2001). A segregate genus from *Coprinus*, namely *Pseudocoprinus* was erected by Kühner (1928) for the insertion of non-deliquescent members of the genus, later Kühner (1980) synonymised *Pseudocoprinus* with *Coprinus* (Keirle *et al.* 2004). In the literature, there exists confusion whether the taxa now belonging to *Parasola* are deliquescent or not. Some authors treated them as non-deliquescent and retained the genus *Pseudocoprinus* for these taxa (Kühner 1928; McKnight & Allison 1969). But all authors did not follow this concept (Uljé 2005; Nagy *et al.* 2009; Redhead *et al*. 2001). Based on molecular phylogenetic studies, Redhead *et al*. (2001) recognised again *Coprinellus* as a distinct genus separated from *Coprinu*s *sensu lato* and included in it the type species of *Pseudocoprinus* (*P. disseminatus*) based on anatomical similarities such as a cystoderm-type pileipellis and frequent or abundant pileocystidia (Redhead *et al*. 2001).

A species of *Coprinopsis* (*C. cordispora*) shows some morphological similarity to *Coprinellus* in having setule-like cells among cheilocystidia but molecular phylogenetic analyses did not support relationship and some species of *Psathyrella* are seen clustered between *Coprinellus* and *C. cordisporus* (Redhead *et al*. 2001; Keirle *et al*. 2004; Padamsee *et al*. 2008). Some species of *Psathyrella,* including the type species *P. gracilis,* are seen clustered with *Coprinellus* and these appeared to be derived from *Psathyrella*. Therefore, it is very difficult to sort out coprinoid taxa from psathyrelloid taxa. *Coprinellus* was seen clustered with psathyrelloid species in a clade denoted as clade A in the molecular phylogenetic tree of Padamsee *et al*. (2008) and *Coprinellus* could not be considered as monophyletic but two major clades arise within clade A.

According to Keirle *et al.* (2004), the distinguishing characters of *Coprinellus* are a hymeniderm- or cystoderm-type pileipellis with pileocystidia and often round-tipped secretory cells, veil tissues usually composed of globular cells forming granules, non-deliquescent or partially deliquescent or fully deliquescent basidiocarps, basidia that are dimorphic, trimorphic or even tetramorphic and the occasional presence of pleurocystidia and ozonium (mycelial mats of branching filamentous structures that are seen around the base of basidiocarps and outside the substrate).

In the molecular phylogenetic analysis of Örstadius *et al.* (2015), the /Coprinellus clade was part of a major clade labelled /Psathyrella sensu lato and was sister to /cordisporus clade. They observed that the morphologically variable *Coprinopsis cordispora* can be distinguished by a cutis-type of pileipellis (Keirle *et al*. 2004) while the species of *Coprinellus* have a hymeniderm-type pileipellis (Örstadius *et al*. 2015).

According to a recent molecular phylogenetic analysis of the family Psathyrellaceae (Wächter & Melzer 2020), the species of *Coprinellus sensu lato* are distributed in two monophyletic groups, namely /Coprinellus A and /Coprinellus B. Another clade named /patouillardii, was found nested between these two clades. The clade /patouillardii was previously treated as a species (*C. patouillardii*) under the genus *Coprinus* (Patouillard 1884), but now it has been elevated as a new genus, *Narcissea* in the family Psathyrellaceae (Wächter & Melzer 2020). The clade /Coprinellus A represents the genus *Coprinellus sensu stricto*, with 15 taxa, including the type species, *Coprinellus deliquescens,* scattered over 9 sections (*Aureogranulati*, *Coprinellus*, *Curti*, *Deminuti, Disseminati*, *Domestici*, *Flocculosi*, *Hepthemeri* and *Micacei*) within the genus *Coprinellus.* The clade /Coprinellus B contains 39 taxa that were previously part of *Coprinellus sensu lato* and this clade has now been elevated as a new genus, *Tulosesus* (Wächter & Melzer 2020).

2.2.1.2.2. Characters used in taxonomy

Species of *Coprinellus* are characterised by a veil usually made of globular cells sometimes bearing superficial lageniform to bulbous-based filament-bearing cells (setulae) converted into secretory round-tipped pileocystidia. Lamellae may be non-deliquescent or often fully or partially deliquescent during sporulation. If lamellae are non-deliquescent, sometimes they are geotropic, otherwise lamellae are ageotropic. Pleurocystidia may be present or absent and when present sometimes they are concentrated towards the margins; Pileus may be membranous or fleshy or very fragile; Basidia are di-, tri- or tetramorphic. Species may be lignicolous, terrestrial, or coprophilous. Ozonium is present or absent (Redhead *et al*. 2001).

Keirle *et al*. (2004) distinguished *Coprinellus* from the other coprinoid genera based on the following combination of features: an agaricoid habit; a pileipellis that is either a hymeniderm or a cystoderm; pileocystidia often with round, secretory tips; a veil composed of globular cells forming granules; fully-, partially-, or non-deliquescent lamellae and pileus; dimorphic, trimorphic or tetramorphic basidia and the occasional presence of both pleurocystidia and ozonium.

According to Örstadius *et al*. (2015) *Coprinellus* has the following features: a veil is present or rarely absent and if present the velar tissue is composed subglobose cells or hyphae; lamellae may be fully-, partially- or non-deliquescent; basidiospores are typically smooth but rarely warty; basidia may be mono-, di-, tri- or tetramorphic; pseudoparaphyses are present; pileocystidia are often present; sclerocystidia are sometimes present; pileipellis is either a hymeniderm or a paraderm; clamp connections are sometimes present and cheilocystidia are often present.

2.2.1.2.3. Infrageneric classification

Schafer (2010) considered three sections under the genus *Coprinellus* (sect. *Setulosi*, sect. *Micacei* and sect. *Domestici*). Section *Setulosi* is characterised by the presence of thin-walled pileocystidia and caulocystidia, with or without a veil and thick-walled sclerocystidia. Species of sect. *Micacei* possess characters such as a pileus with brown, ochre or orange colours, sometimes very pale but never pure white and conical or campanulate in shape, remaining not fully expanded for most of the time of basidiospore discharge; absence of setules; and velar elements as scattered, granulose flocks consisting of globose cells arising from a matrix of narrow branched hyphae and turning pink or lilaceous in alkali. Sect *Domestici* is differentiated by a veil seen as floccose scales on pileus and consisting of chains of cells expanded to fusiform or subglobose form between narrower septa, not colouring in alkali and lacking clamp connections (Schafer 2010).

Three large clades are recognised under the genus *Coprinellus*. The first one is characterised by a continuous sheath of a veil (Domestici/Micacei clade) and the other two clades consist of setulose (haired) species (eurysporoid and Core Setulosi clades) (Nagy *et al.* 2012).

2.2.1.2.4. Ecology

The basidiocarps of *Coprinellus* are found clustered, gregarious or solitary on wood chips, cow or horse dung, soil, rotten wood or bark, leaves of *Musa* (banana) or rarely on mud associated with deer dung (Keirle *et al*. 2004; Örstadius *et al*. 2015).

2.2.1.2.5. Economic importance

Coprinellus micaceus and *C. disseminatus* are well known edible species (Singer 1986; Vrinda & Pradeep 2014).

2.2.1.3. *Coprinopsis*

2.2.1.3.1. Genus concept

The genus *Coprinopsis* is the largest among the coprinoid genera with more than 150 species described from all around the world (www.indexfungorum.org). A combination of morphological characters such as a cutis-type pileipellis, the presence of a veil leaving shaggy scales, deliquescent lamellae and pileus, dimorphic basidia, the presence of pleurocystidia and the absence of both pileocystidia and ozonium differentiates genus *Coprinopsis* from other coprinoid genera such as *Coprinellus*, *Parasola* and *Coprinus* (Keirle *et al*. 2004).

2.2.1.3.2. Characters used in taxonomy

Coprinopsis is distinguished by a set of unique characters. The pileipellis is a cutis composed of a layer of radially arranged hyphae the cells of which may be short and swollen but are not organised in a palisade and not a sheet of primarily subglobose cells (i.e., neither a hymeniderm nor a cystoderm). Pileocystidia (both setulae and setae) are absent. A veil is present and the velar tissues are usually floccose and consist of filamentous or swollen, sometimes globose cells or a mixture of both, often leaving shaggy scales or broad membranous patches on the pileus. The lamellae become deliquescent while sporulating. Pileus become lacerate (form deliquescent margins) with margin often uplifted, especially in smaller species, or pendant in larger species. Basidia are dimorphic. Ozonium is absent but pseudorrhizae are present in some coprophilous species such as *C. atramentaria*, *C. lagopus*, *C. narcotica*, *C. friesii* and *C. insignis* (Redhead *et al*. 2001).

Based on molecular phylogenetic studies, Örstadius *et al*. (2015) characterised the genus *Coprinopsis* by the presence of a veil formed of hyphae or subglobose cells or a mixture of both, mostly deliquescent lamellae, smooth basidiospores that are rarely warty or with a myxosporium, dimorphic basidia, presence of pseudoparaphyses around the basidia, a cutis-type pileipellis and the occasional presence of cheilocystidia.

2.2.1.3.3. Infrageneric classification

According to Schafer (2010), the genus *Coprinopsis* can be further classified into sect. *Atramentarii,* sect. *Lanatuli,* sect. *Alachuani,* sect. *Narcotici* and sect. *Nivei*. The members of the sect. *Atramentarii* are characterised by ochre-brown, grey-brown or grey, often pale, medium-sized to large pileus with thin, appressed scales or fine and silky veil remnants and the pileus surface is sometimes laterally wrinkled but not plicate and a stipe with a ring-like line at its original point of contact with the pileus. The sect. *Lanatuli* is differentiated from the other sections by characters such as a pileus lacking setules, a hairy-floccose veil, often in tufts with pointed tips on the pileus surface, consisting of chains of largely unbranched elongate hyphae wider at one end of the chain, narrower at the other with distinct terminal elements and hyphae constricted at the septa and with clamp connections. The sect. *Alachuani* is distinguished by features such as a pileus devoid of setules and a hairy-floccose or felty veil consisting of branched and/or diverticulate hyphae, lacking globose or subglobose elements. Distinctive characters of species of the sect. *Narcotici* are a small, thin-fleshed pileus expanding to become applanate, usually radially grooved and splitting, a white to grey, mealy-powdery veil entirely covering the pileus surface and at the centre of pileus often becoming woolly-floccose or forming clumps, velar tissue composed of globose or subglobose cells with nipple-shaped warts that form part of the cell wall and are not dissolved by aqueous acid and basidiospores often with a myxosporium. The sect. *Nivei* is characterised by a small, thin-fleshed pileus and a white to grey, mealy-powdery veil composed of globose, subglobose or irregularly rounded cells that are smooth or with a crystalline encrustation that dissolves in aqueous acid, sometimes with broad diverticulae but lacking more regularly distributed and smaller nipple-like warts, and basidiospores lacking a myxosporium (Schafer 2010).

Molecular phylogenetic study recovered three important clades (/crown Lanatuli, /Atramentarii and /Cinerea) within the genus *Coprinopsis.* /Crown Lanatuli is a large clade with multiple lineages of *Coprinopsis lagopus* complex and /radiata clade, characterised by a rich, fibrillose to hairy veil and ellipsoid spores. The young basidiocarps are whitish to pale grey and the veil is white in all but one species. The /Atramentarii clade is circumscribed by pale, greyish or silver-coloured, robust, stout basidiocarps with, silvery, well-developed or scarce, radially splitting veils. Characteristic morphological features of the /Cinerea clade are ellipsoid basidiospores, often radicate stipes and a white veil (Nagy *et al*. 2013b).

Recently, Wächter & Melzer (2020) proposed 20 sections within the genus *Coprinopsis* based on 20 subclades identified in their molecular phylogenetic study of the family Psathyrellaceae, namely *Alopeciae, Atramentariae, Canocipes. Cinereae, Coprinopsis, Erythrocephalae, Filamentiferae, Geesteranorum, Krieglsteinerorum, Lanatulae, Melanthinae, Mitraesporae, Narcoticae*, *Niveae, Phlyctidosporae, Picaceae, Quartoconatae Radiatae, Subniveae* and *Xenobiae*.

2.2.1.3.4. Ecology

Species of *Coprinopsis* are often found in groups on dung, vegetable refuses, wood chips and soil (Uljé 2005).

2.2.1.3.5. Economic importance

Coprinopsis cinerea is extensively used as a classic experimental model for multicellular development in fungi. This species grows on defined media and completes its life cycle within two weeks (Stajich *et al*. 2010).

2.2.1.4. *Parasola*

2.2.1.4.1. Genus concept

Redhead *et al*. (2001) recognised the genus *Parasola* for species that were formerly treated under the large genus *Coprinus sensu lato*. They designated *Parasola plicatilis* as the type species and proposed the genus name *Parasola* owing to the parasol-like basidiocarps of the species. *Parasola* species can be distinguished by the absence of a veil, a deeply plicate pileus and non-deliquescent lamellae (Redhead *et al*. 2001). However, *P. conopilea* and *P. psathyrelloides* lack plicate-striate pileus (Ganga & Manimohan 2019).

Keirle *et al*. (2004) delimited *Parasola* from other coprinoid genera by the following morphological features: smooth, hymeniform or palisade-type pileipellis, absence of pileocystidia but occasional presence of non-secretory setae, absence of veil tissues, partially deliquescent or non-deliquescent basidiocarps, irregularly dimorphic to trimorphic basidia, presence of pleurocystidia and absence of ozonium.

In the molecular phylogenetic analysis by Padamsee *et al*. (2008), species belonging to the genus *Parasola* were clustered in a large clade named clade F (/Parasola). The authors observed that the members of the /Parasola clade have shared morphological features such as the presence of setae (i.e., thick-walled bristles on pileipellis). Both *Parasola auricoma* and *Psathyrella conopilus* (now belonging to *Parasola*) show this character. *Parasola conopilus* has strongly striate pileus that resembles the plicate-striate pileus of *Parasola* species. In the light of two characters, i.e., the presence of thick-walled pileocystidia and the absence pleurocystidia, they suggested placing *P. conopilus* in a separate genus (Padamsee *et al*. 2008). According to Nagy *et al*. (2009), spore characteristics such as the size and shape of the basidiospores and the position of the germ-pore are most useful for the delimitation of species in *Parasola*.

Larsson & Örstadius (2008) renamed *Psathyrella conopilus* as *Parasola conopilus* based on both morphological features and molecular phylogenetic evidence. The argument of Padamsee *et al.* (2008) to place *Parasola conopilus* in a separate genus was rejected by rechecking and verifying the absence of pileocystidia in the previous descriptions (Smith 1972; Kits van Waveren 1985; Larsson & Örstadius 2008; Nagy *et al*. 2009). The authors considered a set of characters such as large dark spores with an eccentric germ-pore, utriform cystidia, absence of veil, presence of setae and weakly deliquescent lamellae for placing this species in *Parasola* (Larsson & Örstadius 2008; Nagy *et al*. 2009). These uncertainties regarding the position of *Parasola conopilus* point towards a basic unresolved taxonomic problem: how *Psathyrella* and its allies can be taxonomically separated from the phylogenetically related coprinoid genera (Nagy *et al*. 2009; Ganga & Manimohan 2019).

Most of the members previously treated under subsect. *Glabri* and subsect. *Auricomi* of genus *Coprinus* are now considered as belonging to the genus *Parasola* although there is a controversy in the position of *P. auricoma* (Uljé & Bass 1988; Uljé & Bender 1997; Nagy *et al*. 2009, 2010b). Molecular phylogenetic studies showed that *P. auricoma* is a member of /Parasola clade, but its position within that group is still obscure due to poor taxon sampling (Hopple & Vilgalys 1999;

Moncalvo *et al*. 2002; Walther *et al*. 2005; Padamsee *et al*. 2008; Nagy *et al*. 2009). Recent molecular phylogenetic studies support the placement of *P. auricoma* in *Parasola* (Szarkándi *et al*. 2017; Hussain *et al*. 2017, 2018a; Ganga & Manimohan 2019).

2.2.1.4.2. Characters used in taxonomy

The genus *Parasola* is distinguished by features such as a thin or membranous, always strongly plicate, diaphanous pileus, post mortem collapse of the entire basidiocarp, complete absence of a veil, lamellae that remain non-deliquescent during sporulation, a smooth, hymeniform palisade-type pileipellis forming a membranous layer lacking superficial lageniform to bulbous-based filament-bearing cells (setulae) converted into secretory round-tipped pileocystidia (but some with non-secretory, conspicuously projecting, brown setae on pileus), presence of pleurocystidia, irregularly dimorphic or trimorphic basidia and the absence of ozonium (Redhead *et al*. 2001).

Nagy *et al*. (2009) gave an idea about the group of characters that could be considered diagnostic not only for *Parasola* taxa but also for other coprinoid lineages as well. The characters associated with the emergence of the parasoloid lineage are the loss of a veil, the appearance of plicate pilei, pleurocystidia and brachybasidia and the ability of basidiocarps to collapse at maturity. It was found that the loss of veil and thick-walled hairs evolved on the same branch and these two structures may stand for the same function of protecting the pileus from water droplets or insects (Nagy *et al*. 2009, 2010b).

Örstadius *et al*. (2015) also recognised a distinct /Parasola clade in their molecular phylogenetic studies. They described the genus based on key features such as the absence of a veil, non-deliquescent or collapsing pileus and lamellae, smooth basidiospore surface, di- or trimorphic basidia, presence of pseudoparaphyses, absence of pileocystidia, presence of setae in some species, a hymeniderm-type pileipellis, hyphae showing clamp connections and the absence of lageniform cheilocystidia (Örstadius *et al*. 2015).

2.2.1.4.3. Infrageneric classification

According to Schafer (2010), *Parasola* consists of two sections, sect. *Glabri* and sect. *Auricomi*. The sect. *Glabri* is characterised by a complete absence of veil, pileocystidia and setae. The species of sect *Auricomi* are also devoid of velar elements and pileocystidia but their pileus surface shows long, narrow, thick-walled setae (Schafer 2010).

Modern molecular studies recovered two important clades, namely /Crown Parasola clade and /Parasola clade respectively (Nagy *et al*. 2009). /Crown Parasola clade is larger and the majority of *Parasola* taxa are clustered here. /Parasola clade is a small clade containing two small subclades (/conopilus and /auricoma) (Nagy *et al*. 2009). Recent phylogenetic studies recognised two sections in genus *Parasola,* namely sect. *Parasola* and sect. *Auricomi* (Szarkándi *et al*. 2017; Hussain *et al*. 2017, 2018a; Ganga & Manimohan 2018, 2019).

2.2.1.4.4. Ecology

Species of *Parasola* are frequently found in terrestrial habitats such as lawns, gardens, meadows, pastures and forest trails where the basidiocarps occur on soil, wood chips or rarely on dung (Redhead *et al*. 2001; Gierczyk *et al*. 2011).

2.2.1.4.5. Economic importance

Parasola plicatilis has been reported as an edible species in Kerala State, India (Vrinda & Pradeep 2014).

2.2.2 Genera included in the family Psathyrellaceae after Redhead *et al.* (2001)

2.2.2.1. *Cystoagaricus*

2.2.2.1.1. Genus Concept

The genus *Cystoagaricus* is a small genus of the family Psathyrellaceae. The Index Fungorum database currently lists eleven species under this genus. *Cystoagaricus* species can be distinguished by fibrillose, squamulose, spiny or squarrose pileus and stipe, irregular, subtriangular, subrectangular, or mitriform basidiospores and utriform or clavate cheilo- and pleurocystidia (Örstadius *et al*. 2015). According to Nagy *et al*. (2013a), most species of *Cystoagaricus* show a firm stipe and pileus. The pileus surface is rarely smooth but mostly covered with appressed scales that are darker than the background and sometimes only remaining at the centre of the pileus and the basidiospores are small and either smooth or subangular.

Initially, Murril (1945) described the type species of *Cystoagaricus* (*C. strobilomyces*) in the genus *Nolanea* (presently belonging to Entolomataceae) as *Nolanea strobilomyces*. Singer (1947) found that this species was not entolomataceous and described the new genus *Cystoagaricus* to accommodate this species. The possible relationship of *Cystoagaricus* with *Psathyrella* was rejected and he treated the genus in Leucocoprinaceae (Singer 1947). Later, however, Singer (1986) placed *Cystoagaricus* in Agaricaceae after describing a new species.

According to Singer (1947, 1986), the external appearance and the less angular dark brown basidiospores of *Cystoagaricus* highly resemble genus *Agaricus*. But the presence of clamp connections on hyphae, the slightly irregular outline of the basidiospores and the absence of a distinct annulus differentiate *Cystoagaricus* from *Agaricus*. *Cystoagaricus* shows a close similarity to *Lepiota* but these genera differ in the colour of the basidiospores. *Lepiota* species have pale (whitish) basidiospores (Singer 1947, 1986).

Recent molecular phylogenetic analyses proved the relationship of *Cystoagaricus* with *Psathyrella* and placed this genus in Psathyrellaceae. Because of the genetic relatedness, *Cystoagaricus* was found to be nested within Psathyrellaceae (Vellinga *et al*. 2004; Padamsee *et al*. 2008; Nagy *et al*. 2013a; Örstadius *et al*. 2015).

Padamsee *et al*. (2008) distinguished clade /Cystoagaricus from other Psathyrellaceae members by the globose or wedge-shaped basidiospores. A single species from genus *Cystoagaricus* and three species of *Pathyrella* (*P*. *ogemawensis*, *P*. *subtruncatispora* and *P*. *subamaria*) were found to be clustered in clade /Cystoagaricus. According to Nagy *et al*. (2013a) clade /Cystoagaricus is not monophyletic and contains three species of *Psathyrella* and one species of *Cystoagaricus*. The species were distinguished by the size of the basidiocarps and the darkening of the veil on ageing (Padamsee *et al*. 2008).

Örstadius *et al*. (2015) examined and renamed four selected species (*C*. *hirtosquamulosus*, *C. silvestris*, *C. olivaceogriseus*, *C. squarrosiceps*) described by Smith as *Psathyrella*. Most of the *Cystoagaricus* species can be identified by a brown squamulose cap surface, rather small, subrectangular, mitriform, or phaseoliform basidiospores and utriform cystidia (Örstadius *et al*. 2015).

2.2.2.1.2. Characters used in taxonomy

Singer (1947) described *Cystoagaricus* based on the following characters: small to medium-sized, non-deliquescent, lignicolous basidiocarps; grey, brown, dark brown, sometimes olivaceous, fibrillose, squamulose, spiny, or squarrose pileus; the presence of a veil; often crowded, adnate to adnexed, pale lamellae that finally become dark brown; a fibrillose, scaly stipe with an annulus; a blackening context; small to medium-sized, often irregular, subtriangular, subrectangular, or mitriform basidiospores and utriform or clavate cheilo- and pleurocystidia.

Singer (1986) later expanded the circumscription of *Cystoagaricus.* According to this revised circumscription, the genus is characterised by pluteoid to scaly or shaggy, *Agaricus*-like or else collibioid basidiocarps; a convex or applanate pileus with a squamulose, scaley, squarrose-spinose, subglabrous, slightly verruculose-flocculose, subfibrillose or granular surface; a pileipellis formed of chains of subisodiametric, ellipsoid, short-fusoid, or short-cylindric cells, with a few multiseptate filamentous hyphae intermixed, and these chains often subparallel to slightly interwoven and densely aggregated to form the ornamentation; free to very narrowly adnexed lamellae; elongate to sub-isodiametric basidiospores lacking a germ-pore and with a hilar appendage that do not project but strongly eccentric; normal, small, four-spored basidia; a hymenium showing both cheilocystidia and pleurocystidia; inamyloid hyphae with pigment incrusting the hyphal wall and with clamp connections (Singer 1986).

According to the modern phylogenetic studies, the *Cystoagaricus* clade is characterised by scales, flocci or bundles of fibrils on pileus and stipe, rather small, subrectangular, mitriform, or phaseoliform basidiospores and utriform cystidia (Örstadius *et al*. 2015).

2.2.2.1.3. Infrageneric classification

Singer (1986) described three species of *Cystoagaricus* and arranged them in two sections (sect. *Cystoagaricus* and sect. *Jujuyenses*) based on the difference in basidiospore shape and features of the pileus and stipe.

2.2.2.1.4. Ecology

Species of *Cystoagaricus* are found on sandy soil or decaying wood (Singer 1947, 1986).

2.2.2.1.5. Economic importance

Species of *Cystoagaricus* currently have no known economic value.

2.2.2.2. *Homophron*

2.2.2.2.1. Genus Concept

Örstadius *et al*. (2015) elevated *Homophron* to the genus level before which it had been treated as a subgenus or a section under the genus *Psathyrella*. *Homophron* *spadiceum* is the type species. The genus *Homophron* is morphologically characterised by the absence of a veil and the presence of cystidia with crystals or incrustations (Larsson & Örstadius 2008; Padamsee *et al.* 2008; Örstadius *et al.* 2015). *Homophron* is considered as a sister group of *Lacrymaria* (Vašutová 2008b; Larsson & Örstadius 2008; Padamsee *et al*. 2008). Species of *Lacrymaria* also show incrustations on pleurocystidia but they can be distinguished by a strongly developed cortina, ornamented spores with very dark verrucae or rarely reduced to insignificant verruculae and the less abundant crystalline incrustations on cystidia (Watling 1979; Larsson & Örstadius 2008).

2.2.2.2.2. Characters used in taxonomy

Smith (1972) considered *Homophron* as a subgenus under the genus *Psathyrella* distinguished by thick-walled pleurocystidia where the wall thickness is more towards the neck and sometimes with crystalline incrustations over the apex of the cystidia (Smith 1972). Singer (1986) used some key characters to separate *Homophron* from other subgenera and these include ventricose-ampullaceous or ventricose-conical, metuloidal pleurocystidia that are rarely thick-walled near the apex, strongly or rarely muricate with incrusting crystals and often somewhat coloured; an often fleshy and rather thick pileus, a fasciculate stipe; a white and pallid veil and a dull red or vinaceous spore print.

Örstadius *et al*. (2015) characterised *Homophron* based on features such as small to large, fragile or rigid, non-deliquescent, lignicolous basidiocarps; a brown, striate and hygrophanous pileus; absence of a veil; small to medium-sized, moderately pigmented to hyaline basidiospores with or without an indistinct germ-pore; 4-spored basidia; muricate pleurocystidia i.e., often thick-walled and with crystals or incrustations at the apex; a hymeniform pileipellis that may transit to a paraderm and absence of clamp connections.

2.2.2.2.3. Infrageneric classification

Infrageneric classifications have not been proposed for *Homophron* after it was elevated as a distinct genus but earlier, several mycologists further divided subgenus *Homophron* into sections. Smith (1972) classified the subgenus *Homophron* based on spore colour in KOH and the presence of the veil. He divided the subgenus *Homophron* as sect. *Homophron* and sect. *Cystidiosae*. Later, Singer (1986) included two sections under the same subgenus, based on the difference in cystidial wall thickness and basidiocarp consistency (i.e., fleshy or rigid), in which one section was named *Cystidiosae* and other was kept unnamed.

2.2.2.2.4. Ecology

Basidiocarps of *Homophron* species are commonly seen as caespitose clusters around deciduous trees and conifers, both on dead stumps and at the base of living trees (Örstadius *et al*. (2015).

2.2.2.2.5. Economic importance

Homophron spadiceum has been reported as an edible wild mushroom in Kerala State (Vrinda & Pradeep 2014).

2.2.2.3. *Kauffmania*

2.2.2.3.1. Genus Concept

Kauffmania is a monotypic genus described in the family Psathyrellaceae by Örstadius *et al*. (2015). The only known species, *Kauffmania larga,* was previously considered as *Psathyrella larga* under subgenus *Pannucia* and sect. *Appendiculatae* (Smith 1972). The genus is differentiated from other related genera mainly by the large-sized basidiocarps with a scanty veil and pale-coloured basidiospores.

2.2.2.3.2. Characters used in taxonomy

The basidiocarps are often connected to decaying wood. The pileus is dark reddish brown, moist-striate, hygrophanous and pallescent on drying. The lamellae are crowded, adnate to adnexed, pale, becoming reddish brown and with white fimbriate edges. The stipe is rather firm. The basidiospores are medium-sized, pale, without or with an indistinct germ-pore. The basidia sometimes show brown intracellular pigment. Pleuro- and cheilocystidia are present and are mostly pigmented. The pileipellis is either a hymeniderm or a paraderm. Clamp connections are present on the hyphae (Örstadius *et al*. 2015).

2.2.2.3.3. Infrageneric classification

Only a single species (*K. larga*) is currently known in this genus.

2.2.2.3.4. Ecology

The only known species of *Kauffmania* is usually found on rotten wood, wood chips, sticks or twigs, or directly on the soil, in deciduous or coniferous forests during summer and autumn seasons (Smith 1972; Örstadius *et al*. 2015).

2.2.2.3.5. Economic importance

This monotypic genus has no known economic importance.

2.2.2.4. *Lacrymaria*

2.2.2.4.1. Genus Concept

Lacrymaria is a psathyrelloid genus and the name was first used by Patouillard (1887). Initially, many mycologists such as Smith (1972), Singer (1986), Guzmán *et al*. (1990) and Fouchier (1995) treated *Lacrymaria* as a subgenus of the large genus *Psathyrella* but some others (Pegler & Young 1971; Largent & Watling 1977; Watling 1979; Pegler 1983; Kits van Waveren 1985; Watling & Gregory 1987) treated *Lacrymaria* as a distinct genus under Coprinaceae (Cortez & Coelho 2005). The genus is distinguished by ornamented basidiospores, often fasciculated pleurocystidia and yellow-brown fibrils on the superficial layer of the pileus (Smith 1972; Largent & Watling 1977; Singer 1986).

In the studies of Hopple & Vilgalys (1999), Redhead *et al*. (2001) and Moncalvo *et al*. (2002), *Lacrymaria* formed a distinct clade within Psathyrellaceae (Cortez & Coelho 2005). The genus was found to be clustered with a large coprinoid clade in Hopple & Vilgalys's (1999) phylogenetic tree (clade I) containing the sect. *Hemerobii* of genus *Coprinus*, now treated as genus *Coprinopsis*.

In Larsson & Örstadius's (2008) study, *Lacrymaria* was found closely related to /spadiceae clade containing three *Psathyrella* species, *P. cernua*, *P. spadicea* and *P. comptopoda* (now belonging to the genus *Homophron*). Most of the morphological features of these taxa are dissimilar to those of *Lacrymaria* except the presence of crystalline incrustations on cystidia. The genus *Lacrymaria* is characterised by a strongly developed cortina, ornamented basidiospores with very dark verrucae or rarely with reduced to insignificant verrucae (Watling 1979; Larsson & Örstadius 2008) and cystidia lacking crystalline incrustations (Larssson & Örstadius 2008).

Lacrymaria formed a distinct clade in the molecular phylogenetic tree of Örstadius *et al*. (2015) sister to /Homophron and according to these authors, the species belonging to this clade can be identified by a tomentose, brown to reddish brown pileus, mottled lamellae, verrucose spores and often capitate pleurocystidia occurring in small fascicles.

2.2.2.4.2. Characters used in taxonomy

The morphological features that Örstadius *et al*. (2015) observed in genus *Lacrymaria* are the presence of a veil with tissue composed of hyphae, non-deliquescent lamellae, often warty basidiospores, mono- to dimorphic basidia, a hymeniderm-type pileipellis and the presence of clamp connections.

2.2.2.4.3. Infrageneric classification

No infrageneric classification has been proposed after the molecular phylogenetic analysis of genus *Lacrymaria*. In the classification of Singer (1986), *Lacrymaria* is split between two sections namely sect. *Lacrymaria* and sect. *Psathyroides*. Smith (1972) recognised three strips under subgenus *Lacrymaria,* namely *Velutina*, *Rigidipes* and *Echiniceps*.

2.2.2.4.4. Ecology

Basidiocarps of *Lacrymaria* species occur as solitary, scattered or as clusters on grassy areas, gravel, soil or on rotten wood (Smith1972).

2.2.2.4.5. Economic importance

Information regarding the economic importance of species of *Lacrymaria* is not available.

2.2.2.5. *Psathyrella*

2.2.2.5.1. Genus Concept

Psathyrlla is a large genus with around 600 species described so far worldwide. *Psathyrella* is distinguished from other genera of Agaricales by a dark brown to brownish black or reddish brown or pinkish grey spore-print, basidiospores that become paler in concentrated sulfuric acid and a fragile pileus. The genus name is based on the fragile nature of its pileus (*Psathyros*, Greek = fragile), which is composed of ellipsoid or more or less round cells. The generic limits, however, are still uncertain due to the under-sampling of psathyrelloid taxa (Nieves-Rivera 2001; Padamsee *et al*. 2008). Fries (1838) recognised *Psathyrella* as a wide assemblage of some dark-spored agarics, including *Psathyra* and *Psilocybe,* without mentioning its taxonomic status. Quélet (1886) suggested a new genus name *Drosophila* and assembled the core elements of *Psathyrella* in this genus but this invalid name was never used by any mycologist after 1953 (Smith 1972). Saccardo (1887) followed the Friesian tradition but accommodated species of some other genera such as

Stropharia and *Hypholoma* (currently belonging to Strophariaceae) in the genus *Psathyrella*.

Psilocybe (now belonging to the family Hymenogastraceae) is a genus of dark-spored, hallucinogenic mushrooms showing some resemblance to *Psathyrella*. Fayod (1889) considered *Psathyrella* as a synonym of *Psilocybe*. Morgan (1907a, 1907b) included an unranked group Spadiceae consisting of sixteen species under the genus *Psilocybe* (Smith 1972). Later, Kits van Waveren (1985) modified and treated this group in *Psathyrella* based on muricate and thick-walled pleurocystidia. According to the Index Fungorum database (www.indexfungorum.org), several species have been transferred from *Psilocybe* to *Psathyrella*.

Some species of the genus *Panaeolus* show similarity to *Psathyrella* as their dark brown basidiospores fade to grey when treated with concentrated sulphuric acid but molecular phylogenetic analysis excluded this group from *Psathyrella* and their family status is still uncertain (Manimohan *et al*. 2007; Örstadius *et al*. 2015).

The phylogenetic studies by Örstadius *et al*. (2015) found that species of *Psathyrella* clustered within a large, well-supported clade /Psathyrella sensu lato. The statistical support was low for /Psathyrella sensu stricto but this formed the major part of /Psathyrella sensu lato. and included the majority of the species described in *Psathyrella* (Örstadius *et al*. 2015). The rest of the species of *Psathyrella* were clustered in clades such as /Cystoagaricus, /Kauffmania, /Typhrasa and /Homophron. The genus *Coprinellus* and the clade /cordisporus also fell within the large clade and all the psathyrelloid species and the two coprinoid clades are collectively named as /Psathyrella sensu lato (Örstadius *et al*. 2015). A clear demarcation was difficult due to the clustering of coprinoid taxa amongst psathyrelloid species (Padamsee *et al*. 2008).

In their recent phylogenetic study of the family Psathyrellaceae, Wächter & Melzer (2020) elevated some distinct clades that were previously treated under the polyphyletic genus *Psathyrella sensu lato* into nine discrete genera (/supernula: *Britzelmayria*; /candolleana: *Candolleomyces*; /floriformis: *Hausknechtia*; /codinae: Olotia; /pakistanicus: *Punjabia*; /patouillardii: *Narcissea*; /Coprinellus A: *Coprinellus*; /Coprinellus B: *Tulosesus*; /Psathyrella sensu stricto*:* *Psathyrella*) within the family Psathyrellaceae. The genus *Psathyrella* now comprises 18 sections or clades, namely *Arenosae*, *Atomatae*, *Confusae*, *Cystopsathyra*, *Hydrophilae*, *Jacobssoniorum*, *Lutenses*, *Microrhizae*, *Noli-tangere*, *Obtusatae*, *Pennatae*, *Psathyrella*, *Pseudostropharia*, *Pygmaeae, Saponaceae*, *Sinefibularum*, *Spadiceogriseae* and *Stridvalliorum*.

2.2.2.5.2. Characters used in taxonomy

According to Padamsee *et al*. (2008), the genus *Psathyrella* is differentiated from the other genera of Agaricales by its spore deposit colour in mass (dark brown to brownish black or reddish brown or pinkish grey), spores that discolour in concentrated sulfuric acid, and typically, a fragile pileus with a cellular pileipellis composed of ellipsoid or more or less round cells. Owing to the lack of a striking character such as deliquescent lamellae, the generic concept for *Psathyrella* was rather cloudy until Singer (1949, 1962) recognised it as a major genus within the Agaricales (Padamsee *et al*. 2008).

Other morphological characters used to distinguish species of *Psathyrella* include a veil tissue formed of hyphae or rarely subglobose cells; non-deliquescent lamellae; basidiospore with a smooth or granulose surface or with myxosporium; monomorphic basidia; a pileipellis that is either a hymeniderm, a paraderm or rarely a cutis; lamella edges often with cheilocystidia; rare occurrence of pseudoparaphyses and pileocystidia and hyphae mostly with clamp connections (Örstadius *et al.* 2015).

2.2.2.5.3. Infrageneric classification

Two major monographic treatments had proposed infrageneric classifications for *Psathyrella sensu lato*. Smith (1972) treated over 400, mostly North American species and Kits van Waveren (1985) recognised 123 European taxa. Several additional *Psathyrella* species described from other parts of the world are not or are poorly integrated into either of these classification systems (Dennis 1955; Singer 1986). Kits van Waveren (1985) employed a broad morphological species concept and synonymised many species treated in Smith (1972), who, on the other hand, used a narrow species concept. Kits van Waveren (1985) divided the genus into two subgenera while Smith's system (1972) comprised 11 subgenera. These subgenera are further subdivided into sections. *Lacrymaria,* one of the subgenera recognised by Smith (1972), is treated as a genus by Kits van Waveren (1985) and others (Watling 1979; Watling and Gregory 1987).

Padamsee *et al*. (2008) found that *Psathyrella* was polyphyletic with species distributed within several clades/subclades. Majority of the species of *Psathyrella* along with its type species (*P. gracilis*) were clustered in clade A (Psathyrella-Coprinellus clade) and this large clade was an aggregate of five smaller clades (I- /coprinellus, II- /candolleana, III- /ammophila, IV- /cystidiosa and V- /psathyrella sensu stricto). Clade B (/delineata), Clade C (/cystoagricus) and Clade D (/larga) represented smaller lineages of *Psathyrella* while Clade E consisted of genus *Coprinopsis* and three species of *Psathyrella*. Clade F (/Parasola) consisted of members of *Parasola* and psathyrelloid species (*Parasola conopilea*). Clade G, in turn, had two subclades (I, II), /Lacrymaria with genus *Lacrymaria* and one *Psathyrella* species and the other (/spadicea) with six species of *Psathyrella*.

The phylogenetic analysis of Örstadius *et al*. (2015) recognises six major clades within the family Psathyrellaceae, of which /Psathyrella sensu lato represents the entire psathyrelloid lineage and consists of 19 major and minor clades including /Psathyrella sensu stricto. Voto *et al*. (2019) made an intensive focused phylogenetic study of the section *Spadiceogriseae* of genus *Psathyrella* that revealed nine distinct subclades under the /Spadiceogriseae group. The most recent phylogenetic analysis of the family Psathyrellaceae by Wächter & Melzer (2020) proposed 18 sections (*Arenosae, Atomatae, Confusae, Cystopsathyra, Hydrophilae, Jacobssoniorum, Lutenses, Microrhizae, Noli-tangere, Obtusatae, Pennatae, Psathyrella, Pseudostropharia, Pygmaeae, Saponaceae, Sinefibularum, Spadiceogriseae* and *Stridvalliorum*) within the genus *Psathyrella*.

2.2.2.5.4. Ecology

The species of *Psathyrella* are mostly saprotrophic and are primary or secondary decomposers (Padamsee *et al.* 2008; Örstadius *et al.* 2015). They commonly grow on wood, soil, dung, plant residues, humus, swamps, bogs and lawns and have either broad or specific substrate relationships (Smith 1972; Padamsee *et al*. 2008). Other nutritional modes have also been reported such as the association with mycoheterotrophic orchids (Selosse *et al*. 2010; Örstadius *et al*. 2015). Mycoparasitism is prominent in *P. epimyces* on host mycelium of *Coprinus comatus*. *Psathyrella arneluna* and *P. ammophila* were found to be growing on dead roots of dune grass and this seems to be a mycorrhizal association (Smith 1972).

2.2.2.5.5. Economic importance

Psathyrella coprinoceps was found to be edible and widely used in Haiti (Nieves-Rivera 2001). *Psathyrella hymenocephala* is used as a spice in Haiti (Paul & Akrers 2000). The natives of Nigeria extensively collect the basidiocarps of *Psathyrella delineata* from the wild for food (Adejumo *et al*. 2015). *Psathyrella atroumbonata* is also used as an important foodstuff and they cultivate this mushroom in large scale in Nigeria (Gbolagade 2004). *Psathyrella candolleana* was found to be a farmer-friendly mushroom for their ability to decompose coarse lignicolous debris such as herbaceous stem and piles of leaves (Smith 1972).

2.2.2.6. *Typhrasa*

2.2.2.6.1. Genus Concept

Typhrasa is a new genus recognised by Örstadius *et al*. (2015). The unique morphological features of the genus *Typhrasa* are the presence of large, rostrate pleuro- and cheilocystidia with oil globules (Örstadius *et al*. 2015).

2.2.2.6.2. Characters used in taxonomy

Species of *Typhrasa* are characterised by medium-sized basidiocarps; a distinct veil; a brown, striate or sometimes smooth, hygrophanous pileus; crowded, adnate to adnexed, pale lamellae becoming brown with white-edges; small to medium-sized basidiospores with colours from red to reddish yellow; large, rostrate hymenial cystidia with intracellular oil-globules; a hymeniform- or paraderm-type pileipellis and clamped hyphae (Örstadius *et al*. 2015).

2.2.2.6.3. Infrageneric classification

There are no infrageneric classifications proposed as only four species (*Typhrasa polycystis, T. rugocephala, T. gossypina and T. nanispora)* are reported so far under the genus.

2.2.2.6.4. Ecology

The species of this genus are found growing on wood or soil. *Typhrasa gossypina* basidiocarps may be solitary, gregarious or in caespitose clusters and are seen in deciduous or coniferous forests on logs, twigs and wood chips. *Typhrasa nanispora* grows on bare soil, maybe attached to buried wood, in forests dominated by deciduous trees (Örstadius *et al*. 2015).

2.2.2.6.5. Economic importance

Information regarding the economic importance of this genus is not available.

2.2.3. Recently included genera in the family Psathyrellaceae based on Wächter & Melzer (2020)

2.2.3.1. *Britzelmayria*

2.2.3.1.1. Genus Concept

Britzelmayria, is a new genus established recently in the family Psathyrellaceae (Wächter & Melzer 2020). The genus is proposed to include the species previously assigned to the clade /multipedata (equivalent to /supernula) of the genus *Psathyrella sensu stricto* (Örstadius *et al*. 2015). In their molecular studies of the family Pasthyrellaceae, Wächter & Melzer (2020) elevated the clade /supernula to the genus *Britzelmayria.* This genus now includes only two species, *B. supernula* and *B. multipedata*.

2.2.3.1.2. Characters used in taxonomy

Species of *Britzelmayria* are distinguished from other genera of the family Psathyrellaceae mainly by the presence of pileocystidia or cystidium-like elements on the pileipellis. The genus is characterised by medium-sized basidiocarps with a faintly developed veil; a distinctly rooting stipe; medium- to large-sized, phaseoliform basidiospores with an inconspicuously, dark, central germ-pore; a lamella-edge with lageniform cheilocystidia interspersed with clavate elements with deposits turning green in ammonia solution; a pileipellis with pileocystidia and subcylindrical velar hyphae and clamped hyphae (Wächter & Melzer 2020).

2.2.3.1.3. Infrageneric classification

Infrageneric classification is not yet constituted for the present genus as it includes only two species.

2.2.3.1.4. Ecology

The members of the genus *Britzelmayria* are found to be caespitose or tightly gregarious in terrestrial habitat (Wächter & Melzer 2020).

2.2.3.1.5. Economic importance

Economic importance of this genus is not known.

2.2.3.2. *Candolleomyces*

2.2.3.2.1. Genus Concept

Candolleomyces is a newly proposed genus in the family Psathyrellaceae (Wächter & Melzer 2020) to accommodate the taxa in the clade /candolleana, which was previously treated as a section (*Candolleana*) under the genus *Psathyrella sensu stricto* (Örstadius *et al*. 2015). The genus is a complex group of psathyrelloid taxa that are morphologically very similar but genetically distinct. The absence of pleurocystidia distinguishes *Candolleomyces* species from the rest of the clades of *Psathyrella sensu stricto* (Wächter & Melzer 2020).

2.2.3.2.2. Characters used in taxonomy

Species of *Candolleomyces* are characterised by small to large-sized basidiocarps; a pileus with fugacious, fibrillose, scaly or granulose velar remnants; occasional presence of annulus on the stipe; pale to medium dark, phaseoliform basidiospores with a central, often invisible germ-pore; a lamella-edge with versiform cheilocystidia; a hymenium devoid of pleurocystidia, a pileipellis composed of chains of slightly thick-walled, brown subcylindrical velar elements with sphaerocysts and the presence of clamp connections (Wächter & Melzer 2020).

2.2.3.2.3. Infrageneric classification

Recent molecular phylogenetic studies (Wächter & Melzer 2020) identified 13 distinct subclades within the clade /candolleana, which could be recognised as sections based on phylogenetic studies in the near future (Wächter & Melzer 2020). The major subclades are /candolleana sensu stricto, /efflorescens, /cacao, /subsingeri, /leucotephra, /tuberculata, /sulcatotuberculosa, /luteopallida and /typhae (Wächter & Melzer 2020).

Species of *Candolleomyces* grow on soil, decaying wood and rarely on animal dung (Wächter & Melzer 2020).

2.2.3.2.4. Economic importance

The species of *Candolleomyces* are known for their medicinal value. *Candolleomyces candolleanus* shows antibacterial, antifungal and antitumor activities in animals (Al-Habib *et al*. 2014). Studies have proven that the extract of *C. efflorescens* inhibits the proliferation of breast cancer cell lines by acting as an antagonist of estrogen in estrogen receptors (Benie *et al*. 2007; Al-Habib *et al*. 2014).

2.2.3.3. *Hausknechtia*

2.2.3.3.1. Genus Concept

The genus *Hausknechtia* was originally proposed as a monotypic genus with a single species, *H. floriformis,* in the family Psathyrellaceae (Wächter & Melzer 2020). The species was previously treated under the genus *Galerella* as *G. floriformis* (Hausknecht & Contu 2003). However, owing to its deliquescent lamellae, a hymenium devoid of cheilocystidia and its distinct phylogenetic position within the family Psathyrellaceae, *G. floriformis* could not sensibly be placed under the genus *Galerella.* Hence, a new genus, *Hausknechtia,* was introduced to accommodate *G. floriformis* (Wächter & Melzer 2020). Recently, Nie *et al.* (2022) discovered a species

(‘*Coprinus leucostictus*’) from India and China and recognised its generic position within the genus *Hausknechtia* based on a multigene phylogenetic analysis (Nie *et al.* 2022). As a result, ‘*Coprinus leucostictus*’ was merged with *Hausknechtia* as *H. leucosticta* and thus emending the so far monotypic genus *Hausknechtia.* Currently, the genus is represented by two species, *H. floriformis* and *H. leucosticta*. The characters such as the terrestrial habitat and a sulcate-striate pileus make it quite distinct from other genera of the family Psathyrellaceae. The genus *Hausknechtia* is phylogenetically found to be sister to the species of the genus *Candolleomyces* (Wächter & Melzer 2020; Nie *et al*. 2022).

2.2.3.3.2. Characters used in taxonomy

The genus *Hausknechtia* is characterised by small basidiocarps; a sulcate pileus with a radially splitting margin especially when young; a fugacious veil; deliquescent or non-deliquescent lamellae; medium-sized, pale, subcylindrical, ellipsoid or narrowly ellipsoid basidiospores with an indistinct or distinct germ-pore; a hymenium devoid of pleurocystidia; a lamellae edge with or without cheilocystidia; a hymeniderm-type pileipellis with branched and subcylindrical velar elements and the presence of clamp connections (Wächter & Melzer 2020; Nie *et al*. 2022).

2.2.3.3.3. Infrageneric classification

Currently, only two species are described under this genus.

2.2.3.3.4. Ecology

Species of *Hausknechtia* are found to grow on sandy soil (Wächter & Melzer 2020; Nie *et al.* 2022).

2.2.3.3.5. Economic importance

There is no known economic importance for this genus.

2.2.3.4. *Narcissea*

2.2.3.4.1. Genus Concept

Narcissea, a new genus introduced recently in the family Psathyrellaceae with three species, namely *N. cordispora*, *N. patouillardii* and *N. lahorensis* (Wächter & Melzer 2020; Usman *et al*. 2022). Earlier, the genus was considered as /patouillardii, an uncertain lineage/clade (nested within the large clade *Psathyrella sensu lato*), which was previously represented by *Coprinus patouillardii* (equivalent to *C. cordisporus*) (Örstadius *et al*. 2015; Nagy *et al.* 2013a). Later, this lineage was transferred to the genus *Coprinopsis* because of the comparable pileipellis structure (Moreno & Manjón 2010). The pileipellis structure of *C. patouillardii* was always in dispute, as different authors have given different interpretations. Keirle *et al*. (2004) found that the pileipellis of *C. cordisporus* is a cutis with somewhat inflated to cylindrical and radially arranged hyphae. In their description of *C. cordisporus,* Uljé & Noordeloos (1993) stated that pileipellis is made up of (sub)globose to ellipsoid and smooth to granular elements. However, in the recent molecular studies of the family Psathyrellaceae, Wächter & Melzer (2020) revealed that the pileipellis description of Uljé & Noordeloos (1993) is an editorial error and the structures they mentioned are clearly veil features. This point was also evident in Rejinders (1979), who observed that immediately above the pileus, the hyphae are divided into short cells in turn, with no clear demarcation between the veil and pileus trama in the pileipellis structure.

The phylogenetic results of Wächter & Melzer (2020) also showed that /patouillardii (equivalent to /cordisporus) can neither be placed in *Coprinopsis* nor *Coprinellus.* Consequently, a new genus, *Narcissea* is established based on the distinct pileipellis structure and flattened and polygonal basidiospores. The species delimitation in the genus is found to be difficult due to the overlapping of morphological characters (Keirle *et al*. 2004). The genus *Narcissea* is distinguished from the other genera of the family by a pileus with mealy granular velar remnants and a pileipellis composed of encrusted, globose elements and chains of subcylindrical velar elements.

2.2.3.4.2. Characters used in taxonomy

The members of *Narcissea* are characterised by small-sized basidiocarps with granular velar remnants on the pileus; triangular to polygonal basidiospores with a well-developed, laterally flattened and central germ-pore; four-spored basidia; a lamella-edge with lageniform to utriform cheilocystidia interspersed with spearopedunculate and clavate cells; a hymenium with utriform pleurocystidia; a pileipellis with velar elements composed of encrusted, globose elements mixed with chains of subcylindrical cells and the absence of pileocystidia and clamp connections.

2.2.3.4.3. Infrageneric classification

According to recent molecular phylogenetic studies, three clades (/cordispora A, /cordispora B and /patouillardii) are recognised in the genus *Narcissea* (Wächter & Melzer 2020).

2.2.3.4.4. Ecology

The members of the genus *Narcissea* are often fimicolous or growing on fertilised soil, rarely on plant remnants (Wächter & Melzer 2020).

2.2.3.4.5. Economic importance

Species of *Narcissea* have no known economic value.

2.2.3.5. *Olotia*

2.2.3.5.1. Genus Concept

Olotia, a recently described monotypic genus in the family Psathyrellaceae (Wächter & Melzer 2020). The genus is represented by a single species, *O. codinae,* which was earlier identified as a species of *Psathyrella*, *P. codinae* (Deschuyteneer *et* *al*. 2018). However, based on the recent phylogenetic studies of the family Psathyrellaceae, Wächter & Melzer (2020) elevated *P. codinae* as a new genus, *Olotia,* as it clearly appeared as a distinct lineage within the family Psathyrellaceae. The presence of spatula-shaped and thick-walled pleurocystidia distinguishes *Olotia* from *Psathyrella.*

2.2.3.5.2. Characters used in taxonomy

The genus is characterised by small basidiocarps with a sparse veil; ellipsoid to slightly ovoid, dark basidiospores with a central germ-pore; a lamella-edge with lageniform to clavate cheilocystidia; a hymenium with spatula-shaped, brown, thick-walled pleurocystidia and the presence of clamp connections.

2.2.3.5.3. Infrageneric classification

No infrageneric classification is proposed for the genus as it comprises only a single species.

2.2.3.5.4. Ecology

The genus is usually found in lignicolous habitat (Wächter & Melzer 2020).

2.2.3.5.5. Economic importance

The genus *Olotia* has no known economic importance.

2.2.3.6. *Punjabia*

2.2.3.6.1. Genus Concept

It was Wächter & Melzer (2020), who proposed the monotypic genus, *Punjabia,* in the family Psathyrellaceae. *Punjabia pakistanica* is the only representative of the genus *Punjabia,* which was earlier treated as a species of *Coprinellus, C. pakistanicus* (Hussain *et al*. 2018b). In their recent phylogenetic study of the family Psathyrellaceae, Wächter & Melzer (2020) shifted the species from *Coprinellus* and identified a new genus, *Punjabia,* to accommodate it. The genus *Punjabia* is differentiated from other genera of the family by the presence of a greenish-tinted pileus and a pileipellis with pileocystidia.

2.2.3.6.2. Characters used in taxonomy

The genus is characterised by the following features: medium-sized basidiocarps; a greenish-tinted, plicate pileus with sparse veil; broadly ellipsoid to slightly ovoid and dark basidiospores with a central germ-pore; a lamella-edge with subcylindrical to utriform cheilocystidia with crystals at the apex; the absence of pleurocystidia; a pileipellis composed of pileocystidia intermixed with slightly thick-walled, subglobose and globose velar elements and clamped hyphae (Wächter & Melzer 2020).

2.2.3.6.3. Infrageneric classification

There is no infrageneric classification proposed for the genus *Punjabia*.

2.2.3.6.4. Ecology

The genus is usually found scattered in moist soil (Hussain *et al.* 2018b; Wächter & Melzer 2020).

2.2.3.6.5. Economic importance

The economic value of the genus is not known so far.

2.2.3.7. *Tulosesus*

2.2.3.7.1. Genus Concept

The genus *Tulosesus* is established for the species that were previously nested under the clade /Coprinellus B of the genus *Coprinellus sensu lato* (Wächter & Melzer 2020). The genus *Tulosesus* presently comprises about 40 species (www.indexfungorum). The members of *Tulosesus* are phylogenetically distinct from the species of *Coprinellus,* but they are hard to separate morphologically. Although the genus *Tulosesus* differs by often lacking a veil on the pileus, if one is present, it usually consists of chains of slightly diverticulate cells in the pileipellis.

2.2.3.7.2. Characters used in taxonomy

The general features of *Tulosesus* are the following; tiny- to medium-sized basidiocarps; presence or absence of a veil on the pileus that if present consisting of chains of diverticulate elements sometimes mixed with subglobose, occasionally encrusted elements; deliquescent or withering lamellae; mostly larger basidiospores, rarely with a polygonal outline and often with an eccentric or central germ-pore; a lamella-edge with clavate to sphaeropeduculate or lageniform cheilocystidia; the presence or absence of pleurocystidia; capitate to subcapitate pileocystidia or sclerocystidia on the pileipellis and the presence or absence of clamp connections (Wächter & Melzer 2020).

2.2.3.7.3. Infrageneric classification

Currently, there are no infrageneric classifications proposed for *Tulosesus*.

2.2.3.7.4. Ecology

Species of *Tulosesus* are usually lignicolous, subfimicolous or fimicolous (Wächter & Melzer 2020).

2.2.3.7.5. Economic importance

There is no information on the economic value of *Tulosesus* species.

Chapter 3

Physiography, vegetation and climate of Kerala State

Greeshma Ganga K G. Systematic studies on coprinoid and psathyrelloid agarics (Agaricales, Basidiomycota, Fungi) of Kerala state. Thesis. Department of Botany, University of Calicut, 2023.

CHAPTER 3

PHYSIOGRAPHY, VEGETATION AND CLIMATE OF KERALA STATE

3.1. PHYSIOGRAPHY

Kerala State is a land mass of 38,863 km^2 located along the windward side of the Western Ghats in the south-west region of peninsular India. It lies between 8° 18' and 12° 48' N latitude and 74° 52' and 77° 22' E longitude. The State is bordered by the Arabian Sea at the west, Karnataka State at the north and Tamil Nadu at the southern and eastern sides. The topography of Kerala includes mountains, valleys, ridges and slopes (Sasidharan 2004).

The altitude of Kerala ranges from sea level to 2695 m above sea level. Based on the altitude, the terrain of Kerala has three natural regions, namely the highlands, the midlands and the lowlands. The highlands have a complex geography at 600-1800 m height and mainly constitute the mountain ranges of the Western Ghats. Except for a 30 km wide gap in the Palakkad District, these mountain ranges are continuous from north to south. The Western Ghats have a great influence on the climate of the State. These mountain ranges have an average height of 900 m, but there are several peaks above 1800 m, with Anamudi being the highest peak at 2694 m. The midlands are situated at an altitude range of 300-600 m, found in between the mountains and the coastal belt. The midland region is composed of undulating hills and valleys. The lowlands range between 1-300 m and include estuaries, river deltas, backwaters and the coast of the Arabian Sea (Sasidharan 2004).

3.2. VEGETATION

Kerala has some of the most diverse tropical vegetations in the country. The forest area in the State is 11,125.59 km^2, accounting for 28.88% of the total land area. The major forest areas of Kerala are primarily restricted to the Western Ghats. The enormous biodiversity in the Western Ghats is largely maintained by a moist environment with luxuriant rainfall. The Western Ghats have recently been added to the list of UNESCO World Heritage Sites as they represent one of the world's eight "hottest hotspots" of biodiversity. More than 30% of India's plant and animal species are found in the Western Ghats (Myers *et al.* 2000).

According to Champion & Seth (1968), twenty-six forest types have been identified in Kerala. West Coast tropical evergreen, West Coast tropical semi-evergreen, Southern moist mixed deciduous, Southern dry mixed deciduous, Southern montane wet temperate forests, Southern subtropical hill forests, Southern montane wet temperate grasslands and littoral forests (mangroves) are the major forest types found in Kerala. In addition to these, certain bamboo brakes, cane brakes, reed brakes, euphorbiaceous scrub jungles, laterite thorn forests and myristica swamp forests are also present (Sasidharan 2004). The main tree species found in the evergreen forests of Kerala are *Artocarpus heterophyllus, A. hirsutus, Bombax ceiba, Cinnamomum zeylanicum, Dipterocarpus indicus, Elaeocarpus tuberculatus, Ficus nervosa, Flacourtia montana, Hopea parviflora, Hydnocarpus macrocarpus, Litsea bourdillonii, Mallotus tetracoccus, Mangifera indica, Mimusops elengi, Myristica beddomei, Persea macrantha, Pterospermum reticulatum, Syzygium gardneri, Terminalia bellirica, T. travancorensis* and *Vateria indica.*

As part of conserving the tremendous biodiversity, the forested zones in Kerala have been protected as national parks, wildlife sanctuaries and biosphere reserves. There are five national parks in Kerala: Anamudi Shola National Park, Eravikulam National Park, Silent Valley National Park, Mathikettan Shola National

Park and Pampadum Shola National Park. Kerala has thirteen wildlife sanctuaries: Aaralam Wildlife Sanctuary, Chimmini Wildlife Sanctuary, Chinnar Wildlife Sanctuary, Idukki Wildlife Sanctuary, Mangalvanam Bird Sanctuary, Neyyar Wildlife Sanctuary, Parambikulam Wildlife Sanctuary, Peechi-Vaazhaani Wildlife Sanctuary, Peppara Wildlife Sanctuary, Periyar Wildlife Sanctuary, Shendurney Wildlife Sanctuary, Thattekkad Bird Sanctuary and Wayanad Wildlife Sanctuary. The two biosphere reserves in Kerala are the Nilagiri Biosphere Reserve and the Agasthyamalai Biosphere Reserve (Latha & Manimohan 2017).

In addition to the above-mentioned biodiversity conservation zones, there are about 2000 small and large sacred groves encompassing roughly 500 hectares of land area in Kerala State. Sacred groves are small patches of forest traditionally conserved as religious or cultural heritage and also considered repositories of rare and endemic wild plants and animals. *Adenanthera pavonina*, *Antiaris toxicaria*, *Artocarpus hirsutus*, *Caryota urens*, *Celtis timorensis*, *Cinnamomum malabathrum*, *Ficus mysorensis*, *Ficus virens*, *Flocourtia Montana*, *Garcinia gummi-gutta*, *Hopea parviflora*, *H. ponga*, *Ixora brachiata* and *Macaranga peltata* are some of the common tree species found in the sacred groves of Kerala (Chandrashekara & Sankar 1998).

3.3. CLIMATE

Kerala State has a humid, maritime, tropical and monsoonal climate. Due to its location along the windward side of the Western Ghats, the State receives about 3000 mm of rain per year on average. The highest precipitation often reaches about 5000 mm during the South-West and North-East Monsoon seasons, particularly in the higher altitudes of the Wayanad and Idukki plateaus. The South-West monsoon commences in early June and lasts until September and the North-East Monsoon starts from October and ends in December. The mean annual temperature ranges from 25.4°C to 31°C in most parts of the State. The maximum day temperature can be as high as 40°C in some places in the summer and the minimum night temperature in the winter may be as low as 0°C in some parts of the highlands in the winter (Aravindakshan & Manimohan 2015).

Chapter 4

Materials and methods

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CHAPTER 4

MATERIALS AND METHODS

4.1. FLORISTIC STUDY

4.1.1. Study Area

For the present study, mushrooms were collected from various forested areas within the political boundary of Kerala State. The major collection localities are indicated in Map 1 and representative photographs of some collection localities are also provided.

4.1.2. Field study and research material

All the coprinoid and the psathyrelloid agarics described in this thesis were collected by the author from various localities of Kerala State including natural forests and other woodlands. The majority of the collections were obtained from decaying dung and a few from decayed wood, leaf-litter and soil. Field studies were conducted during the two monsoon seasons, i.e., south-west monsoon (June to September) and north-east monsoon (October to December), for four consecutive years (2016-2019). The coprinoid and the psathyrelloid fungi are very fragile and short-living. The deliquescent nature of the basidiocarps of the coprinoid mushrooms makes their collection quite challenging. Some of these mushrooms mature during midnight and the pileus and lamellae turn into a black, ink-like liquid within a few hours. In such cases, the entire substratum was collected from the field and incubated in the laboratory for observing the development of basidiocarps and the basidiocarps emerged were collected and dried before collapsing. Macroscopic characters of the specimens were noted at the time of collection and colour photographs of the agarics in their natural habitat were taken with a digital camera. In the laboratory, each collection was carefully examined with the aid of a stereomicroscope and the macroscopic characters were recorded systematically. The collected specimens were dried and are currently preserved in the mycology laboratory of the Department of Botany, University of Calicut.

4.1.3. Recording of macroscopic characters

Basidiocarps of all stages were collected from the field as far as possible. A digital camera was used to take colour photographs of the basidiocarps in their natural habitats. Unique collection numbers were provided for each collection. Ecological characters such as the habitat and substratum of the specimens and macromorphological characters such as the surface features and size of the pileus and stipe were noted at the time of collection. The colours of the various parts of the basidiocarps were also noted at the time of collection using the colour chart of Kornerup & Wanscher (1978). The collected specimens were carefully wrapped in tissue paper to reduce damage while transporting. The fresh basidiocarps were brought to the laboratory or the base camp as soon as possible to avoid decay. The specimens were kept in a hot-air oven at 60ºC in the lab and under a 60-watt incandescent bulb suspended in a closed cardboard box in the base camps (in the field) until they were properly dried. Dried collections were packed in labelled paper bags and kept in a plastic box with the base filled with silica gel. The plastic boxes containing the dried specimens were stored in a refrigerator to avoid the attack of moulds and mites.

4.1.4. Recording of microscopic characters

The microscopical analysis was conducted on dried specimens. Thin, free-hand sections were made from different parts of the basidiocarps with the aid of a stereomicroscope using a razor blade. The sections were stained with 1% Congo red and mounted in 3% KOH. All the sections were also mounted in distilled water to find the presence of pigments in the fungal tissues. The microscopic preparations were observed under a trinocular compound microscope (Olympus CX21). The morphological features of basidiospores, basidia, cystidia, and hyphae of hymenophoral trama, pileus trama, pileipellis, and stipitipellis were recorded using the oil-immersion objective of the microscope. The measurements of all microscopic structures were noted using a calibrated ocular micrometer. The length of the sterigmata was separately measured while measuring the length of the basidia. Photomicrographs of all the microscopic structures were captured using a digital camera attached to the microscope. For evaluation of the range of size of basidiospores, 40, 20, and 20 basidiospores were considered for measurement of length, breadth, and width respectively. Basidiospore measurements are represented as the length range × the breadth range × the width range. Q_1 and Q_2 values were calculated as Q_1 = length divided by the breadth and Q_2 = length divided by width (Hussain *et al*. 2017; Szarkándi *et al.* 2017).

4.1.5. Taxonomic concepts and phylogenetic classification system followed

The coprinoid and psathyrelloid agarics belong to two families, Agaricaceae and Psathyrellaceae. A total of nine genera, namely *Candolleomyces*, *Coprinellus, Coprinus, Coprinopsis, Hausknechtia, Narcissea, Parasola, Psathyrella* and *Tulosesus* were studied during this work. Several phylogenetic studies have been conducted worldwide to elucidate the classification of coprinoid and psathyrelloid agarics (Hopple & Vilgalys 1994, 1999; Redhead *et al*. 2001; Keirle *et al*. 2004; Larsson & Örstadius 2008; Padamsee *et al.* 2008; Nagy *et al*. 2013a; Nagy *et al*. 2013b; Örstadius *et al*. 2015; Szarkándi *et al*. 2017; Nagy *et al.* 2019; Wächter & Melzer 2020). However, the most recent and widely accepted phylogenetic classification proposed by Wächter & Melzer (2020) is largely followed in this study for all the genera (*Candolleomyces*, *Coprinellus, Coprinopsis, Hausknechtia, Narcissea, Psathyrella* and *Tulosesus*) except *Coprinus* and *Parasola.* The concepts elucidated by Hopple &

Vilgalys (1994, 1999) and Redhead *et al*. (2001) were adopted for the genus *Coprinus.* The phylogenetic classification of Szarkándi *et al*. (2017) was followed for the genus *Parasola*.

4.1.6. Major monographs and floras consulted

The major monographs and floras consulted for the identification of coprinoid and psathyrelloid agarics in the present study were: British Fungus Flora, Part 2: Coprinaceae: *Coprinus* (Orton & Watling 1979); Flora Agaricina Neerlandica, Volume 6 (Uljé 2005); A Preliminary Agaric Flora of East Africa (Pegler 1977); Agaric Flora of the Lesser Antilles (Pegler 1983); Agaric Flora of Sri Lanka (Pegler 1986); The North American Species of *Psathyrella* (Smith 1972); The Dutch, French and British Species of *Psathyrella* (Kits van Waveren 1985) and Fungi of Switzerland, Volume 4: Agarics (Part 2). Apart from these major works, several hundreds of research articles on coprinoid and psathyrelloid species worldwide were also consulted.

4.2. MOLECULAR PHYLOGENETIC ANALYSIS

The molecular phylogenetic analysis consisted of seven steps: 1) isolation of genomic DNA from the collected specimens; 2) PCR amplification of the selected markers using specific primers; 3) separation and visualisation of the amplified DNA using agarose gel electrophoresis; 4) purification and sequencing of the amplified DNA; 5) determination of the quality of generated sequences; 6) BLASTn search and 7) sequence alignment, data matrix assembly and phylogenetic analysis using suitable software.

4.2.1. Isolation of Genomic DNA

Genomic DNA isolation was conducted using a modified protocol of Izumitsu *et al*. (2012). A small piece (0.1-1.0 μg) of dry lamella from the specimen was homogenised using a micro pestle in a 1.5 ml microcentrifuge tube containing 100 μl TE buffer (tris ethylenediaminetetraacetic acid). The tube was then placed in a microwave oven at 600 W for 1 minute followed by cooling for 30 seconds at room temperature and the tube was again microwaved for 1 minute. This tube was then rapidly transferred to -20ºC and kept at that temperature for at least 10 minutes. The sample was then centrifuged at 10000 rpm for about 5 minutes and the supernatant containing genomic DNA was used for PCR amplification.

4.2.2. PCR amplification

Two non-coding ribosomal DNA regions, the internal transcribed spacers (ITS1, 5.8 rRNA gene, ITS2) and the large subunit (nLSU), were used in this study. The PCR reactions were carried out using the primers ITS1 (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') for the ITS (White *et al*. 1990) and LROR (5'-ACCCGCTGAACTTAAGC-3') and LR7 (5'-TACTACCACCAAGATCT-3') for the nLSU regions (Vilgalys & Hester 1990). The PCR amplification mixture (final volume 30 µl) included 15 µl of EmeradAmp GT PCR Master Mix, 6 µl of ddH_2O, 3 µl of 10 µM primers (ITS1 and ITS4 for ITS or LROR and LR7 for nLSU) and 3 µl of template DNA. The DNA amplification reactions were carried out in an Applied Biosystems Veriti^{TM} Thermal Cycler (U.S.A). Temperature setting for PCR was 2 min at 95ºC, 1 min at 50ºC, 1 min at 72ºC; 34 times a cycle of 30 sec at 94ºC, 1min at 50ºC, 1min at 72ºC and a final extension step of 10 min at 72ºC.

4.2.3. Agarose gel electrophoresis

The amplified DNA samples were subjected to agarose gel electrophoresis. 1% agarose solution (1g agarose powder in 100 ml 1xTBE (tris-Borate-EDTA) buffer) was used for making the gel and the mixture was melted in a hot water bath. The melted agarose solution was stained with ethidium bromide (EtBr) before transferring to the gel casting tray with a suitably placed comb. The poured agarose solution was allowed to cool until the solution completely solidified into a gel and then the combs were carefully removed. The gel was slowly transferred to the electrophoretic apparatus containing 0.5 x TBE buffer just covering the gel surface. The PCR products were loaded in each well with a micropipette. A voltage (100V) was applied across the gel to separate the DNA according to their size. The DNA bands on the gel were observed using a UV-transilluminator and the samples showing perfect bands were selected for further sequencing.

4.2.4. Purification and sequencing

Purification and sequencing of the PCR-amplified DNA samples were performed at a commercial facility (AgriGenome, Cochin). Gel extraction or column purification techniques were adopted for purifying the PCR products. The DNA sequencing was done with an ABI3730xl DNA analyser (Applied Biosystems, Foster City, California, USA) using the same primers used for PCR amplification.

4.2.5. Determination of the sequence quality

The generated sequences were manually edited by BioEdit sequence alignment editor v.7.2.5 (Tom Hall, lbis Biosciences, Carlsbad, CA, USA) to avoid errors in the identification of bases while sequencing and remove unreadable sequences at the 3′ and 5′ ends. Standard practices and guidelines provided by Nilsson *et al*. (2012) and Hyde *et al.* (2013) were followed for ensuring the reliability and authenticity of the newly generated sequences.

4.2.6. BLAST search

The quality-checked DNA sequences were used for similarity searches using the BLAST (Basic Local Alignment Search Tool) online tool available at the NCBI GenBank DNA database (www.ncbi.nlm.nih.gov). BLASTn results with a zero e-value was considered for phylogenetic analysis.

4.2.7. Sequence alignment, data matrix assembly and Phylogenetic analyses

The ITS sequences were used for phylogenetic analyses to reveal the evolutionary relatedness of the 35 species identified in this study. Although the present study generated nLSU sequences, they were not used in the phylogenetic analyses due to the lack of adequate, reliable nLSU sequences available in the GenBank database. In addition to the ITS sequences, however, the nLSU sequences were used in BLASTn searches. BLASTn searches were carried out (last searched on 25th March 2023) to find the sequences of the closely related species available in the GenBank database. A total of nine data matrices, designated I to IX, were prepared for performing the phylogenetic analyses. The first data matrix (I) was generated for an overview of all the coprinoid and psathyrelloid agarics belonging to the two families, Agaricaceae and Psathyrellaceae, encountered during the investigation. The remaining eight data matrices (II–IX) were constructed to represent the nine genera, namely *Coprinus*, *Candolleomyces*, *Coprinellus*, *Coprinopsis*, *Hausknechtia, Narcissea*, *Parasola*, *Psathyrella* and *Tulosesus*. It was meaningless to construct an individual data matrix for the genus *Hausknechtia* as it is represented only by two species so far and therefore lacks sufficient ITS sequences in the GenBank database. This forced the inclusion of the available sequences of *Hausknechtia* (8 sequences) in the data matrix prepared for the genus *Candolleomyces*, which has proven to be a sister genus to *Hausknechtia.*

Each data matrix included the newly generated ITS sequences, the sequences retrieved from the GenBank database based on the sequence similarity in BLASTn searches and the sequences of morphologically similar species that are available in the GenBank. In addition, representative sequences used in the previous phylogenetic analyses (Nagy *et al*. 2013a; Örstadius *et al*. 2015; Szarkándi *et al*. 2017; Wächter & Melzer 2020; Nie *et al*. 2022; Usman *et al.* 2022) were also incorporated into the data matrices (Table II).

The data matrix I, comprising a total of 164 ITS sequences, was prepared to depict the overall phylogenetic placement of all the coprinoid and psathyrelloid agarics (35 species) discovered during the study. Of these 164 sequences, 52 were generated from 35 species of the present study. *Amanita muscaria* (Amanitaceae) was selected as the outgroup for this data matrix following Varga *et al*. (2019). The data matrix II of 23 ITS sequences was prepared for the genus *Coprinus*, including a single sequence from the present study. *Montagnea arenaria* (Agaricaceae) was the outgroup taxon for this analysis based on the study of Johnson & Vilgalys (1998).

The data matrix III encompassing 53 ITS sequences was prepared for the genera *Candolleomyces* and *Hausknechtia*. Of these, 14 ITS sequences were from the present study. *Psathyrella multipedata* (Psathyrellaceae) was selected as an outgroup taxon for rooting purposes. The data matrix IV was constructed for the genus *Coprinellus*, which includes 36 ITS sequences. Among these, three ITS sequences were obtained from a single species of *Coprinellus* described in the present study. *Candolleomyces candolleanus* and *C. typhae* (Psathyrellaceae) were chosen as the outgroups for this data matrix.

The data matrix V comprising 82 ITS sequences was constructed for the genus *Coprinopsis*. Among these, 10 sequences were yielded from nine species discovered during the present study. *Lacrymaria glareosa* (Psathyrellaceae) was taken as the outgroup taxon for rooting the tree. A total of 34 ITS sequences were included in the data matrix VI for the genus *Narcissea*. Of these, 7 ITS sequences were generated from two species of the present study. *Narcissea* species 1, a species described in this study, showed an unpublished collection of *Tulosesus*, *T. bisporus* KACC49409 as the closest hit in the BLASTn search and this sequence was added to the data matrix. In addition, four sequences of *Tulosesus bisporus* (SZMC-NL-0158, OT3-179b, WU6011 and SZMC-NL-2512) used in previous phylogenetic analysis (Wächter and Melzer 2020) were included in this data matrix to confirm whether *T. bisporus* KACC49409 belongs to the genus *Tuloseus* or is a misidentified species that should be under the genus *Narcissea. Coprinellus campanulatus* (Psathyrellaceae) was chosen as the outgroup for this data matrix based on the study of Usman *et al.* (2022).

The data matrix VII with 41 ITS sequences, including the outgroup *Coprinopsis lagopus* (Psathyrellaceae), was assembled for the genus *Parasola*, following Szarkándi *et al*. (2017). Among these, 8 sequences were obtained from the 5 species of *Parasola* discovered during the present study. A total of 49 ITS sequences were used to prepare the data matrix VIII for the genus *Psathyrella*. Of these, 3 ITS sequences were from the present study. *Coprinellus disseminatus* (Psathyrellaceae) was taken as an outgroup taxon following Örstadius *et al*. (2015).

The data matrix IX was constructed for the genus *Tulosesus*. It comprised 44 ITS sequences, of which 6 were from the present study. *Psathyrella pseudogracilis* and *P*. *prona* (Psathyrellaceae) were chosen as outgroups for this data matrix. The outgroups for the data matrices III, IV, V and IX were selected following Wächter & Melzer (2020).

All the data matrices were aligned separately using the MAFFT web tool (http://align.bmr.kyushu-u.ac.jp/mafft/online/server/) with default settings. The aligned data matrices were then imported individually into AliView v.1.15 (Larsson 2014) for manual alignment. The Maximum likelihood (ML) analyses were performed using RAxML-HPC2 (v.8.2.10) (Stamatakis 2014) on the XSEDE platform as implemented in the CIPRES Science Gateway web server (Miller *et al.* 2010). GTRGAMMA was selected as the evolutionary model with 1000 rapid ML bootstrap replicates and default settings for other options. FigTree v.1.4.3 (Rambaut 2014) was used to display the phylograms inferred from the ML analyses.

Map 1

Map of Kerala showing collection localities

Muthanga forest, Wayanad District

Aralam forest, Kannur District

Thattekkad forest, Ernakulam District

Chimmini forest, Thrissur District

Kakkayam forest, Kozhikode District

Shendurney forest, Kollam District

Chapter 5

Systematic account

Greeshma Ganga K G. Systematic studies on coprinoid and psathyrelloid agarics (Agaricales, Basidiomycota, Fungi) of Kerala state. Thesis. Department of Botany, University of Calicut, 2023.

CHAPTER 5

SYSTEMATIC ACCOUNT

5.1. Key to the families of the coprinoid and psathyrelloid genera treated in this study

1. Stipe with a central cord; pseudoclamps present.. ....Genus *Coprinus sensu stricto* (**Agaricaceae)**

1. Stipe without a central cord; pseudoclamps absent ....Other coprinoid and psathyrelloid genera (**Psathyrellaceae)**

5.1.1. AGARICACEAE Chevall., Fl. gén. env. Paris (Paris) 1: 121 (1826)

Basidiocarps pluteoid, lepiotoid or tricholomatoid, small and delicate to large and robust. Pileus convex expanding, often umbonate, mostly fleshy; surface silky, glabrous, velutinous or characteristically squamulose. Lamellae mostly free, more rarely adnexed, thin, often very crowded with numerous lamellulae, occasionally deliquescent. Stipe central, occasionally with a central cottony extractable loose cord, fibrous, often with a bulbous base, veil forming a membranous to cortinoid annulus, often as characteristic squamules on the pileus and stipe surfaces. Context usually fleshy, often showing colour changes on bruising or exposure to air. Spore print extremely variable, pure white, ochraceous, green, purplish or dark sepia. Basidiospores small to very large, ovoid, ellipsoid, subcylindric or amygdaliform, with or without a germ-pore; hyaline to sepia; wall structure simple to complex, smooth or more rarely with fine or coarse ornamentation. Basidia clavate, mostly tetrasporic. Pleurocystidia absent, occasionally present. Lamella-edge sterile, heterogeneous or rarely fertile. Cheilocystidia often abundant and crowded, versiform, thin-walled, hyaline or coloured. Lamellar trama either regular or subregular, never bilateral. Pileipellis highly variable ranging from undifferentiated repent hyphae to a trichodermal palisade, an epithelium, or chains of detersile sphaerocytes. Pileocystidia occasionally present. Stipitipellis mostly a cutis, sometimes overlaid with velar elements. Caulocystidia present or absent. Clamp connections present or absent, at times pseudoclamps present. Habitat mostly terrestrial or humicolous, sometimes lignicolous.

Type genus: *Agaricus* Linn.: Fr

5.1.1.1. ***COPRINUS*** Pers., Tent. disp. meth. fung. (Lipsiae): 62 (1797)

Coprinusella Peck ex Zerov, in Zerov & Peresipkin, Viznachnik Ukraïnĭ Basidiomycetes 5: 405 (1979)
Onchopus P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 28 (1879)

Basidiocarps small and ephemeral to large and fleshy, deliquescent. Pileus subglobose, conical or campanulate, frequently expanding; surface often plicate-striate particularly towards the margin; margin sometimes revolute. Lamellae free to sinuate or adnate, at first pale then darkening and deliquescing from the edge upwards. Stipe central, well-developed, with a central cottony extractable loose cord, usually elongating only in the later stages. Veil present or absent, sometimes forming a persistent annulus and usually present as floccose squamules on the pileus. Context whitish, membranous to fleshy. Spore print fuscous to black. Basidiospores medium to large, subglobose to ellipsoid, limoniform, mitriform or hexagonal often lenticular, always deeply pigmented although pigment easily removed by concentrated sulphuric acid, opaque or translucent, smooth or with an exosporial ornament, always with an apical germ-pore. Basidia bisporic or tetrasporic. Lamella-edge mostly heterogeneous, often remaining remnants of partial veil. Cheilocystidia present or absent. Pleurocystidia generally present, large, trabecular. Lamellar trama regular, with inflating hyphae. Pileipellis variable, typically forming an epithelium, stratified or not, but sometimes formed by loose sphaerocytes or a filamentous epicutis, frequently covered by the remnants of the universal veil. Clamp connections present or absent. Habitat terrestrial, lignicolous or coprophious. Cosmopolitan.

Type species: *Coprinus comatus* (O. F. Mueller: Fr) S. F. Gray.

Only one genus, *Coprinus* with a single species belonging to this family, was discovered during the present study.

***Coprinus* species 1** **Plate 1.**

Description:—Basidiocarps large, fragile. Pileus 54–64 × 20–31 mm when mature, initially cylindrical, expanding to broadly conical with age; surface white all over when young, becoming brown (6F7) to greyish orange (5B4) at the apex of the squamules, white to grey (6E1) elsewhere at maturity, initially appressed-fibrillose all over, becoming squamulose on and around the centre; margin straight when young, revolute at maturity, soon collapsed to black ink, strongly deliquescent. Lamellae free, crowded, initially white, becoming black at maturity; edge not observed due to deliquescence. Stipe 111–130 × 8.0–13 mm, central, terete, slightly tapering towards the apex, hollow with a central mycelial cord connecting the apex and the base; surface white, slightly floccose towards the base, smooth elsewhere, often with a white, movable inferior annulus; base subbulbous with long rhizoids. Odour and taste not distinctive.

Basidiospores (9)10–12 × 6–7 × 5–7 μm, on an average 10.8 × 6.8 × 6 μm, Q_1 = 1.42–1.84, Q_{1avg} = 1.6, Q_2 = 1.61–2.0, Q_{2avg} = 1.77, lenticular, ellipsoid or oblong in face view, oblong in side view, with a rounded apex and base, dark brown, thick-walled, with an eccentric germ-pore up to 2.5 μm wide. Basidia 26–46 × 9–12 μm, clavate or pedicellate-clavate, hyaline, thin-walled, 4-spored; sterigmata up to 4 μm long. Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 17–42 × 13–23 μm, abundant, subglobose, clavate, sphaeropedunculate or subcylindrical, hyaline, thin-walled. Pileipellis a cutis overlaid with chains of short, unbranched, segmented velar hyphae; hyphae 5–8 μm wide, hyaline, thin-walled; velar hyphae 33–85 × 12–

20 µm, with a yellowish brown wall pigment and brown encrustations towards the apex of the velar hyphae, hyaline elsewhere, slightly thick-walled. Stipitipellis a cutis with chains of short, unbranched, segmented velar hyphae; hyphae 20–30 µm wide, hyaline, thin-walled; velar hyphae 50–200 × 4–25 µm, hyaline, thin-walled. Clamp connections and pseudoclamps observed only on the hyphae of stipitipellis.

Habit and Habitat:—Solitary or in small groups, on soil mixed with dung.

Collection examined:—INDIA. Kerala State, Wayanad District, Muthanga forest: 04 July 2017, *K. G. Greeshma Ganga G164*.

Observations:—The present species is characterised by larger basidiocarps; a cylindrical to broadly conical pileus with fibrillose to squamulose velar remnants; free lamellae; a stipe with a movable, inferior annulus; ellipsoid to oblong basidiospores with an eccentric germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; a cutis-type pileipellis with brown encrusted velar hyphae; a cutis-type stipitipellis with chains of hyaline velar hyphae and a terrestrial habitat.

Coprinus comatus (O.F. Müll.) Pers, a species widespread in Europe (Orton & Watling 1979; Uljé 2005), seems to be very close to the present species in having a similar morphology of pileus, crowded lamellae, a stipe with an annulus, a hymenium devoid of pleurocystidia, a pileipellis with chains of velar elements, the hyphae of stipitipellis with pseudoclamps and a terrestrial habitat. However, *C. comatus* differs from the present species in having basidiocarps with a larger pileus (50–200 × 25–70 mm), a stipe with a brownish colour when bruising, basidiospores with a conical base and truncate apex, a lamella-edge with larger cheilocystidia (40–110 × 15–40 µm) and a gregarious habit. *Coprinus sterquilinus* (Fr.) Fr., a species reported from the Netherlands, Asia, America and East Africa (Pegler 1977; Uljé 2005), shows some similarity with the present species in having basidiocarps with an almost similar shape, a stipe with a movable annulus and a narrow mycelial

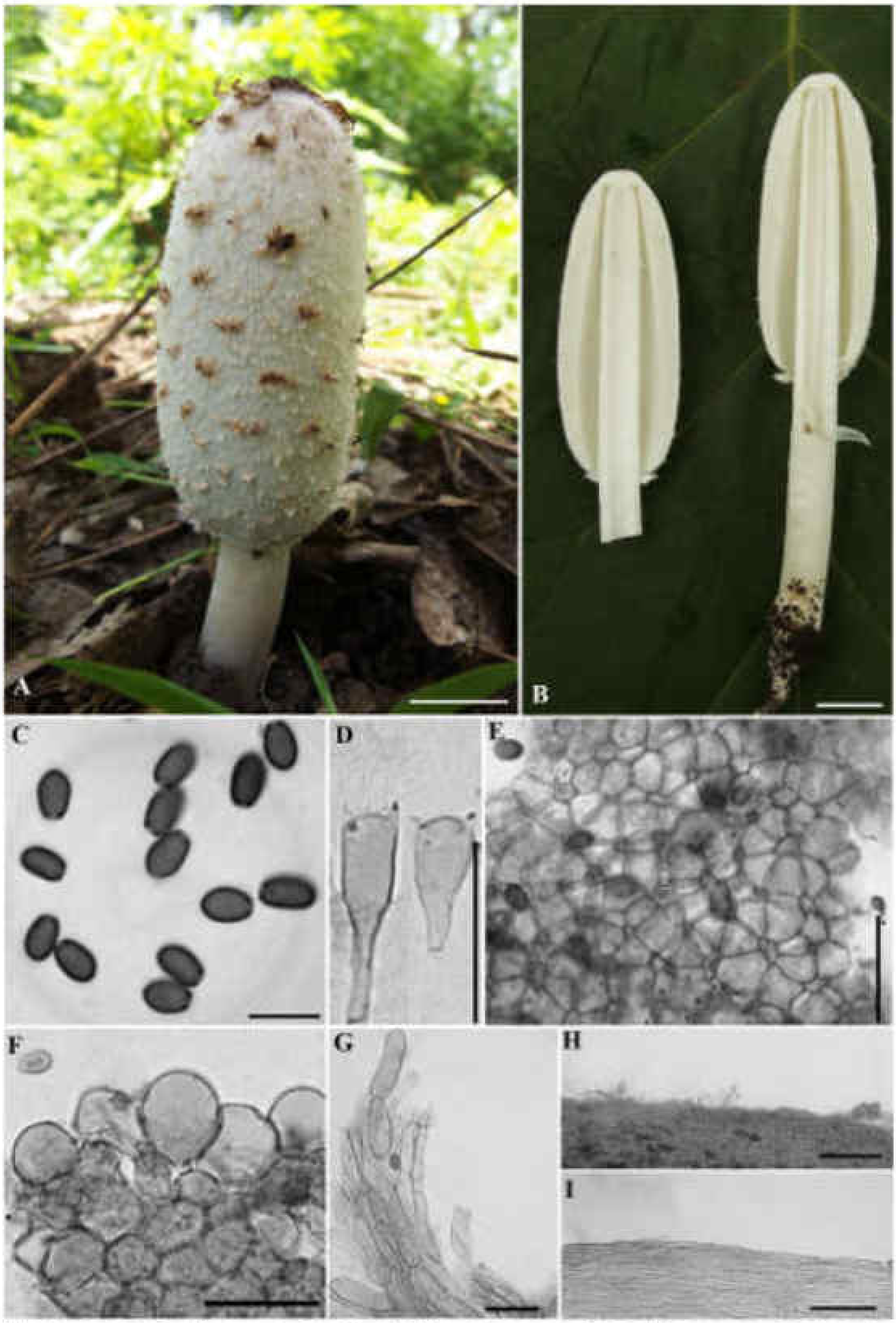

Plate 1. A-I: *Coprinus* species 1. A-B. Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Pseudoparaphyses. **F.** Cheilocystidia. **G.** Velar elements on the pileipellis. **H.** Pileipellis. **I.** Stipitipellis. Scale Bars: **A-B** = 10 mm; **C, D & H** = 20 µm; **E-H** = 50 µm; **I** = 200 µm.

cord inside, a lamella-edge with similar-sized cheilocystidia and a hymenium devoid of pleurocystidia. *Coprinus sterquilinus,* however, differs from the present species in having larger basidiospores (17–26 × 10–15 μm), a pileipellis with smooth, hyaline to pale yellow velar elements, absence of clamp connections and a coprophilous habitat.

Coprinus littoralis G. Moreno, Carlavilla, Heykoop, Manjón & A. Sánchez, a species recently reported from Spain (Crous *et al*. 2016), resembles the present species in having an almost similar shape and size of basidiocarp, a stipe with a narrow mycelial cord inside, basidiospores with an eccentric germ-pore and a solitary habit. However, *C. littoralis* has larger basidiospores (13–20 × 8–12 μm) and a habitat on sand.

Comparison of the ITS (627 bp) and the nLSU (870 bp) sequences derived from the present *Coprinus* species with the nucleotide sequences available in GenBank revealed that the present species has distinct ITS and nLSU sequences. *Coprinus comatus* (MW989737, AY207179) resulted as the closest hit in BLASTn searches using both the ITS and nLSU sequences with 96.50% and 99.77% identities respectively.

5.1.2. **PSATHYRELLACEAE** Vilgalys, Moncalvo & Redhead, in Redhead, Vilgalys, Moncalvo, Johnson & Hopple, Taxon 50 (1): 226 (2001)

Psathyrellaceae Locq., Mycol. gén. struct. (Paris): 153 (1984)
Psathyrellaceae Locq., Syn. gen. fung. (Paris): 1 (1972)

Basidiocarps psathyrelloid or coprinoid, small to large, often fragile. Pileus ovoid to ellipsoid, becoming uplifted, lacerate, convex, campanulate to plano-convex; surface glabrous, minutely pubescent, covered with loose granules or micaceous flecks or scales, mostly plicate- to sulcate-striate, sometimes translucent-striate. Lamellae andnate to adnexed, sometimes free or with a psuedocollarium, white then blackish or dusky, rarely with pinkish intermediate tints, close to crowded with lamellulae in 1–3 tiers, occasionally deliquescent. Stipe central, devoid of a central cord, often with a slightly enlarged base; veil absent or fugacious or sometimes leaving an annulus, basal flange or scales. Context mostly reduced sometimes fleshy. Spore print black, brown or pale brown. Basidiospores small to large, ovoid, ellipsoid, subglobose or angular, sometimes with an apical papilla, with or without a germ-pore; black to pale brown, often smooth, rarely warty, at times with a myxosporium. Basidia di-, tri- or tetramorphic. Pleurocystidia mostly present or sometimes absent, if present appears as large, projecting, conspicuous or sparse, subglobose, cylindrical, utriform or lageniform, mostly hyaline, thin- or thick-walled. Lamella-edge fertile, heterogeneous or rarely sterile. Cheilocystidia often abundant, subglobose, cylindrical, utriform or lageniform, mostly hyaline, thin- or thick-walled. Lamellar trama mostly very narrow, rarely wide, regular to subregular. Pileipellis an epithelium, epithelioid hymeniderm, hymeniderm or a cutis; velar elements mostly present, filamentous or swollen cells or mixtures of both, hyaline or with a brown wall pigment, smooth or encrusted. Pileocystidia occasionally present, versiform, mostly hyaline, thin- or thick-walled. Stipitipellis always a cutis, sometimes overlaid with velar elements. Caulocystidia present or absent. Clamp connections present or absent, pseudoclamps absent. Habitat coprophilous, lignicolous or terrestrial.

Type genus: *Psathyrella* (Fr.) Quél.

Key to the genera of the family Psathyrellaceae described in this study

1. Basidiocarps without a veil; pileipellis elements with pigments…………… ***Parasola***
1. Basidiocarps with a veil; pileipellis elements without pigments………………………… **2**
2. Pileipellis never a cutis or an undifferentiated cutis; caulocystidia present…….. **3**
2. Pileipellis mostly a cutis or an undifferentiated cutis, occasionally epithelioid hymeniderm in such case pileus with radial splitting; caulocystidia absent……. **6**
3. Pileus with plicate-striations; basidiospores black; pileocystidia present………… **4**

3. Pileus without plicate-striations; basidiospores brown; pileocystidia absent..... **5**
4. Habit gregarious; habitat always lignicolous, never coprophilous or terrestrial... .... ***Coprinellus***
4. Habit not gregarious; habitat lignicolous, coprophilous or terrestrial.. ***Tulosesus***
5. Basidiospores dark brown; pleurocystidia present .... ***Psathyrella***
5. Basidiospores pale brown; pleurocystidia absent......................... ***Candolleomyces***
6. Pileus completely covered with fibrillose, floccose, mealy or squamulose velar remnants; pileipellis a cutis... ***Coprinopsis***
6. Pileus not completely covered with fibrillose, floccose, mealy or squamulose velar remnants; pileipellis not a cutis **7**
7. Pileus without granular velar remnants; clamp connections present. .... ***Hauskntnechtia***
7. Pileus with granular velar remnants; clamp connections absent.......... ***Narcissea***

5.1.2.1. *CANDOLLEOMYCES* D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1228 (2020)

Basidiocarps small to large-sized. Pileus surface fibrillose, scaly or granulose. Veil present, often fugacious. Stipe occasionally with an annulus. Basidiospores mostly medium-sized, laterally often phaseoliform, somewhat hyaline to medium dark, germ-pore central, often invisible. Basidia 4-spored. Pleurocystidia absent. Cheilocystidia utriform, subutriform or subcylindrical. Pileipellis with velar elements, consisting of sphaerocysts and chains of subcylindrical, slightly thick-walled and brownish-pigmented cells. Clamp connections often present. Habitat terrestrial or lignicolous rarely fimicolous.

Type species: *Candolleomyces candolleanus* Wächter & A. Melzer

A total of nine species of the genus *Candolleomyces* were observed during the present study.

Key to the species

1. Stipe with a connate base; basidiospores ≥10 µm long ....***Candolleomyces typhae***

1. Stipe without a connate base; basidiospores ≤10 µm long **2**

2. Basidiocarps medium-sized; pileus with an appendiculate margin **3**

2. Basidiocarps small-sized; pileus without an appendiculate margin **4**

3. Pileus with white velar remnants; cheilocystidia thin-walled .... ***Candolleomyces candolleanus***

3. Pileus with brown velar remnants; cheilocystidia thick-walled................................. ....***Candolleomyces* species 1**

4. Pileus with an upturned margin; habitat terrestrial ....***Candolleomyces* species 2**

4. Pileus without an upturned margin; habitat lignicolous **5**

5. Basidiocarps turning black when dried; basidiospores with a distinct germ-pore .... ***Candolleomyces efflorescens***

5. Basidiocarps not turning black when dried; basidiospores without a distinct germ-pore **6**

6. Cheilocystidia with amorphous materials ....***Candolleomyces* species 3**

6. Cheilocystidia without amorphous materials **7**

7. Pileus with invisible velar remnants; pileipellis with encrusted velar elements ....***Candolleomyces* species 4**

7. Pileus with visible velar remnants; pileipellis without encrusted velar elements. **8**

8. Pileus dark brown; pileipellis with hyaline velar elements.. ....***Candolleomyces sulcatotuberculosus***

8. Pileus orange white; pileipellis with brown velar elements....................................... ....***Candolleomyces* species 5**

Candolleomyces candolleanus (Fr.) D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1233 (2020). **Plate 2.**

Agaricus appendiculatus Bull., Herb. Fr. (Paris) 9: 392 (1789)
Agaricus appendiculatus var. *lanatus* Berk. & Broome, Ann. Mag. nat. Hist., Ser. 57: 127 (1881)
Agaricus candolleanus Fr., Observ. mycol. (Havniae) 2: 182 (1818)
Agaricus candolleanus var. *nigrescens* Lasch, Linnaea 3: 424 (1828)
Agaricus catarius Fr., Hymenomyc. eur. (Upsaliae): 296 (1874)
Agaricus corrugis var. *vinosus* Cooke, Ill. Brit. Fung. (London) 4: 612 (1886)
Agaricus egenulus Berk. & Broome, Ann. Mag. nat. Hist., Ser. 3 7: 375 (1861)
Agaricus felinus Pass., Nuovo G. bot. ital. 4: 82 (1872)
Agaricus stipatus var. *appendiculatus* (Bull.) Pers., Syn. meth. fung. (Göttingen) 2: 423 (1801)
Agaricus stipatus var. *candolleanus* (Fr.) Pollini, Flora veronensis quam in prodomum florae italiae septentrionalis 3: 646 (1824)
Agaricus vinosus Corda, in Sturm, Deutschl. Fl., 3 Abt. (Pilze Deutschl.) (19-20): 13 (1841)
Drosophila appendiculata (Bull.) Quél., Enchir. fung. (Paris): 116 (1886)
Drosophila candolleana (Fr.) Quél., Enchir. fung. (Paris): 115 (1886)
Drosophila cataria (Fr.) Romagn., Revue Mycol., Paris 2 (6): 245 (1937)
Hypholoma appendiculatum (Bull.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 25: 146 (1872)
Hypholoma appendiculatum var. *candolleanum* (Fr.) R. Heim, Treb. Mus. Ciènc. nat. Barcelona, sér. bot. 15 (3): 132 (1934)
Hypholoma appendiculatum var. *flocculosum* Boud., Icon. Mycol. (Paris) 1: 137 (1906)
Hypholoma candolleanum (Fr.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 25: 146 (1872)
Hypholoma candolleanum var. *annulatum* Quél., Bull. Soc. bot. Fr. 23: 328 (1877)
Hypholoma candolleanum var. *platincola* Speg., Boln Soc. Cienc. Córdoba 28: 335 (1926)
Hypholoma candolleanum var. *squarrosum* Naveau, Natuurw. Tijdschr. 5: 84 (1923)
Hypholoma catarium (Fr.) Massee, Brit. Fung.Fl. (London) 1: 393 (1892)
Hypholoma egenulum (Berk. & Broome) Sacc., Syll. fung. (Abellini) 5: 1040 (1887)
Hypholoma felinum Pass., in Saccardo, Syll. fung. (Abellini) 5: 1040 (1887)
Hypholomopsis appendiculata (Bull.) Earle, Bull. New York Bot. Gard. 5: 436 (1909)
Psathyra appendiculata (Bull.) G. Bertrand, Bull. Soc. mycol. Fr. 17: 278 (1901)
Psathyra candolleana (Fr.) G. Bertrand, Bull. Soc. mycol. Fr. 17: 278 (1901)
Psathyra corrugis var. vinosa (Berk. & Broome) Rea, Brit. basidiomyc. (Cambridge): 414 (1922)
Psathyrella appendiculata (Bull.) Maire & Werner, Mém. Soc. Sci. Nat. Maroc. 45: 112 (1938)
Psathyrella candolleana (Fr.) Maire, in Maire & Werner, Mém. Soc. Sci. Nat. Maroc. 45: 112 (1937)
Psathyrella candolleana (Fr.) Maire, Bull. Soc. mycol. Fr. 29: (1913)
Psathyrella candolleana f. *pallida* Raithelh., Hong. Arg. (Buenos Aires) 2: 128 (1978)
Psathyrella candolleana var. *solitaria* A.H. Sm., Mem. N. Y. bot. Gdn 24: 91 (1972)
Psathyrella candolleana var. *sterilis* J.Aug. Schmitt, Abhandlungen der Delattinia 45: 276 (2020)
Psathyrella corrugis var. *vinosa* Berk. & Broome, Ill. Brit. Fung. (London) 4: 612 (1886)
Psathyrella egenula (Berk. & Broome) M.M. Moser, in Gams, Kl. Krypt. -Fl. Mitteleuropa - Die Blätter- und Bauchpilze (Agaricales und Gastromycetes) (Stuttgart) 2: 206 (1953)
Psathyrella microlepidota P.D. Orton, Trans. Br. mycol. Soc. 43(2): 375 (1960)

Description:—Basidiocarps medium-sized, fragile. Pileus 8–58 × 8–20 mm at maturity, initially paraboloid, expanding to broadly convex; surface brownish orange (6C3) at the centre, white on the velar remnants and orange white (6A2) towards the margin when young, becoming orange grey (6B2) to orange white (6A2) at the centre, paler towards the margin when mature, hygrophanous and becoming paler, fibrillose velar patches scattered on and around the centre, smooth elsewhere; margin straight, somewhat appendiculate, rarely fissile. Lamellae adnate, crowded, initially white, becoming brownish orange (6C3), with lamellulae in 2–3 tiers; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 35–105 × 3–5 mm, central, terete, slightly tapering towards the apex, hollow, often with a white cortina; surface white, finely floccose all over, pruinose at the apex; base slightly enlarged, inserted. Odour and taste not distinctive.

Basidiospores 6–7 × 4–5 × 3–4 µm, on an average 6.33 × 4.05 × 3.85 µm, Q_1 = 1.3–1.75, Q_{1avg} = 1.57, Q_2 = 1.5–2.0, Q_{2avg} = 1.65, lenticular, ellipsoid, oblong, oblong-ellipsoid in face view, phaseoliform in side view, not opaque, hilar appendix indistinct, pale brown to greyish brown, slightly thick-walled, with a central germ-pore up to 1.5 µm wide. Basidia 15–18 × 7–8 µm, pedicellate-clavate, hyaline, thin-walled, 4-spored; sterigmata up to 3 µm long. Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 21–35 × 12–18 µm, abundant, versiform: globose, subglobose, utriform or lageniform, often with a short pedicel, hyaline, thin-walled. Pileipellis an irregular epithelium composed of globose to subglobose elements in 2–3 layers, overlaid with scattered velar elements; epithelial elements 32–36 × 30–40 µm, hyaline, thin-walled; velar elements 5–9 µm wide, short, branched, cylindrical hyphae, hyaline, slightly thick-walled. Stipitipellis a cutis disrupted with scattered caulocystidia often in clusters, more so towards the apex of the stipe; hyphae 4–7 µm, hyaline, slightly thick-walled. Caulocystidia 18–80 × 9–12 µm, mostly lageniform to subcylindrical or rarely utriform, hyaline, slightly thick-walled.

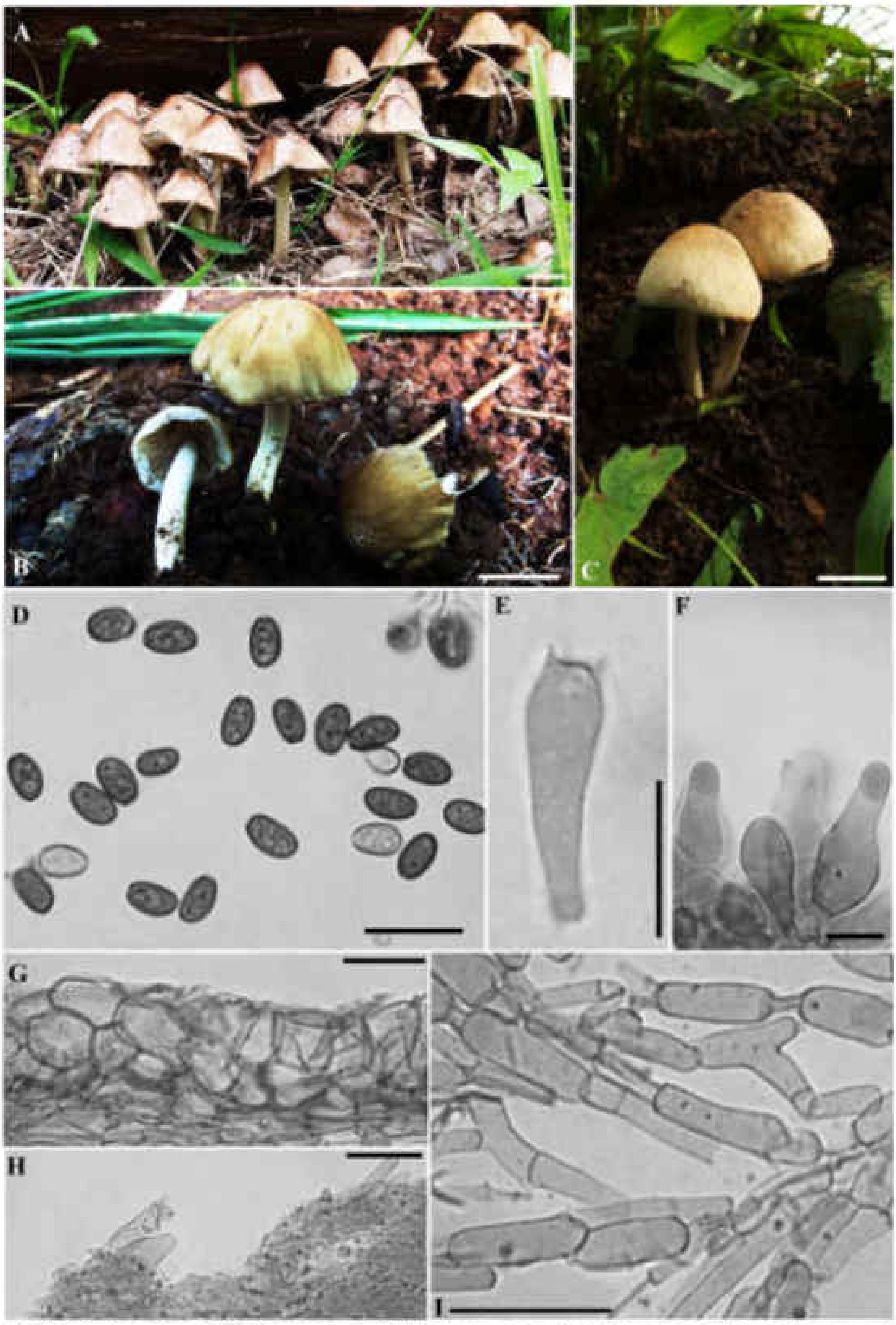

Plate 2. A-I: *Candolleomyces candolleanus*. A-C. Basidiocarps. **D.** Basidiospores. **E.** Basidium. **F.** Cheilocystidia. **G.** Pileipellis. **H.** Stipitipellis. **I.** Velar elements on the pileipellis. Scale Bars: **A-C** = 10 mm; **D-F** = 20 µm; **G-I** = 50 µm.

Clamp connections observed only on velar elements of the pileipellis and the hyphae of the stipitipellis.

Habit and Habitat:—Gregarious or sometimes in small groups, on humus rich soil.

Collections examined:—INDIA. Kerala State, Malappuram District, Mylanjivalavu: 28 June, *K. G. Greeshma Ganga G159*; Wayanad District, Muthanga forest: 05 July 2017, *K. G. Greeshma Ganga G171*; *K. G. Greeshma Ganga G173*.

Observations:—*Candolleomyces candolleanus*, a species with cosmopolitan distributions, reported from Europe, Asia, North and South Americas, East Africa and West Africa (Kits van Waveren 1985; Pegler 1977, 1983, 1986) and also recorded from India (Natarajan & Raman 1983), is characterised by medium-sized basidiocarps; a broadly convex pileus with an appendiculate margin; crowded lamellae; a stipe with a white cortina; oblong-ellipsoid basidiospores with a central germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; an irregular epithelium-type pileipellis with scattered velar elements and a cutis-type stipitipellis disrupted with clusters of caulocystidia.

Comparison of the ITS and the nLSU sequences of the present collections with those available in the GenBank database suggests that the present species is *C. candolleanus*. A total of three ITS (G159: 671 bp; G171: 677 bp; G173: 683 bp) and two nLSU (G171: 914 bp; G173: 873 bp) sequences were generated from *C. candolleanus.* A BLASTn search using the ITS sequence (G173: 683 bp) showed *Psathyrella candolleana* (presently as *Candolleomyces candolleanus*) as the closest hit (KX611650) with 99.56% identity. While using the nLSU sequence (G171: 914 bp), an unnamed species of *Psathyrella* from USA, *Psathyrella* species SH4 (DQ986242) was the closest hit with 99.77% identity.

Candolleomyces efflorescens (Sacc.) D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1233 (2020) **Plate 3.**

Agaricus efflorescens Berk. & Broome, J. Linn. Soc., Bot. 11 (56): 555 (1871)
Pilosace efflorescens (Sacc.) Kuntze, Revis. gen. pl. (Leipzig) 3 (3): 504 (1898)
Psathyra efflorescens Sacc., Syll. fung. (Abellini) 5: 1067 (1887)
Psathyrella efflorescens (Sacc.) Pegler, Kew Bull., Addit. Ser. 6: 432 (1977)

Description:—Basidiocarps small, fragile. Pileus initially 9–15 mm diam., up to 28 mm diam. at maturity, convex when young, becoming convex to broadly convex with age; surface initially brownish orange (6C3) all over, becoming orange grey (6B2) at the centre and middle, paler towards the margin, hygrophanous and becoming paler, smooth all over when young, becoming fibrillose more so towards the centre, smooth elsewhere at maturity, translucent-striate; margin straight, entire. Lamellae adnexed, moderately crowded, initially white, becoming greyish brown (6D3), with lamellulae in 2 tiers; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 12–20 mm, central, laterally compressed, slightly tapering towards the apex, hollow; surface white, smooth, finely pruinose towards the apex; base not enlarged, inserted. Odour and taste not distinctive. All parts of the basidiocarps turn black on drying.

Basidiospores 7–9 × 4–5 × 4–5 µm, on an average 7.52 × 4.85 × 4.45 µm, Q_1 = 1.4–1.8, Q_{1avg} = 1.56, Q_2 = 1.4–2.25, Q_{2avg} = 1.7, lenticular, broadly ovoid to oblong, ellipsoid in face view, phaseoliform in side view, hilar appendix indistinct, often truncate apex, not opaque, pale brown to brown, thick-walled, with a central germ-pore <1 µm wide. Basidia 14–20 × 8–9 µm, clavate, hyaline, slightly thick-walled, 4-spored; sterigmata up to 3 µm long. Pleurocystidia absent. Lamella-edge heterogeneous. Cheilocystidia 16–22 × 10–12 µm, abundant, subglobose, ellipsoid to clavate, hyaline, slightly thick-walled. Pileipellis a hymeniderm composed of clavate elements along with scattered, elongated velar hyphae; hymeniderm elements 21–31 × 20–25 µm, clavate, hyaline, thin-walled; velar hyphae 5–8 µm wide, branched, hyaline, slightly thick-walled. Stipitipellis a cutis with scattered

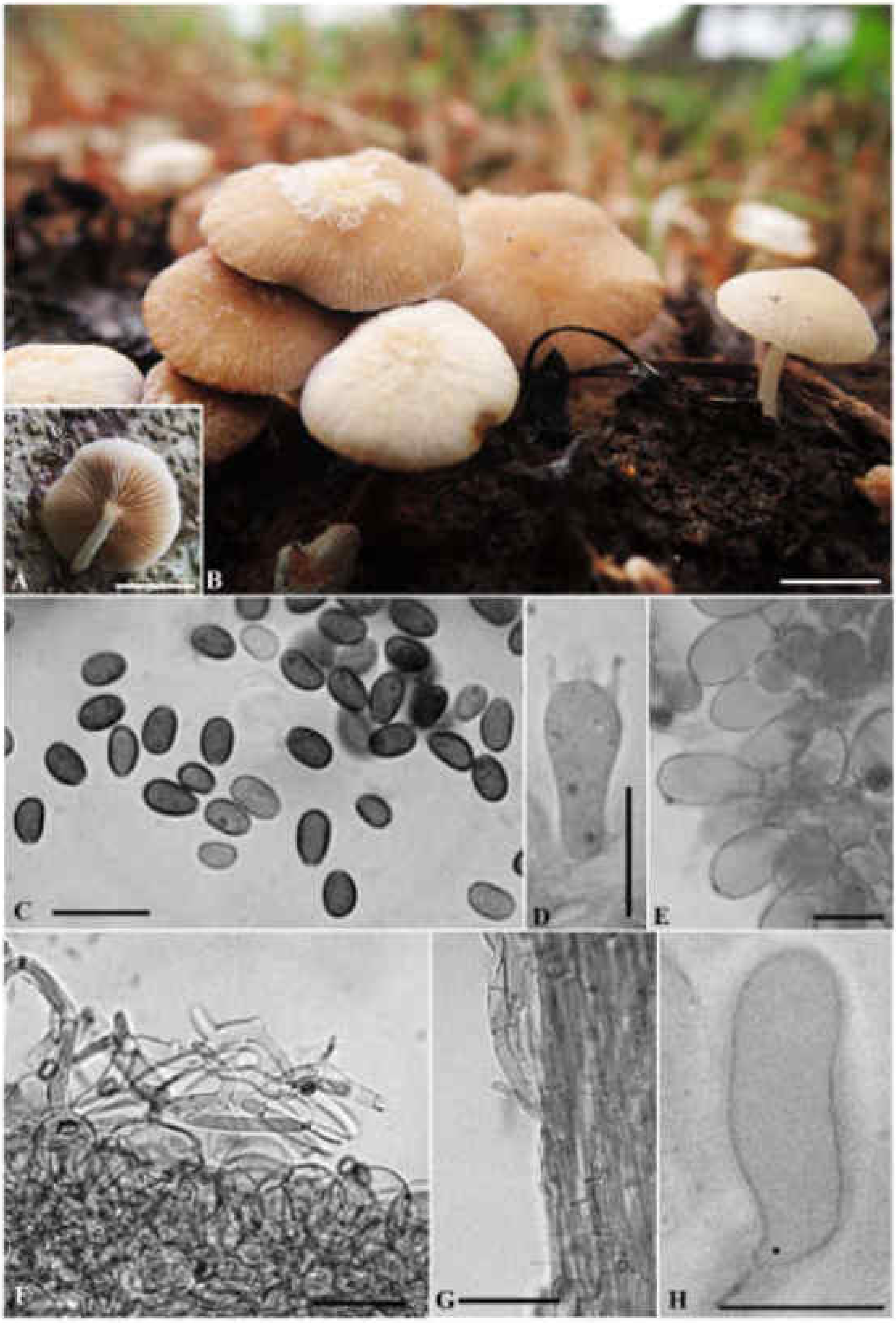

Plate 3. A-H: *Candolleomyces efflorescens*. A-B. Basidiocarps. **C.** Basidiospores. **D.** Basidium. **E.** Cheilocystidia. **F.** Pileipellis with velar hyphae. **G.** Stipitipellis. **H.** Caulocystidium. Scale Bars: **A-B** = 10 mm; **C-E & H** = 20 µm; **F & G** = 50 µm.

patches of velar hyphae and caulocystidia, more so towards the apex of the stipe; hyphae 4–6 µm, hyaline, slightly thick-walled; velar hyphae 4–7 µm wide, branched, hyaline, slightly thick-walled. Caulocystidia 25–43 × 10–15 µm, abundant, ellipsoid to subcylindrical, hyaline, thin-walled. Clamp connections observed only at the base of cheilocystidia and on velar hyphae on the pileipellis, the hyphae of the stipitipellis and the pileus trama.

Habit and Habitat:—Gregarious or rarely in small groups, on rotten bark of a tree or trunk of a coconut tree .

Collections examined:—INDIA. Kerala State, Kozhikode District, Mukkam: 6 December 2016, *K. G. Greeshma Ganga G130*; Malappuram District, Calicut University Campus: 11 July 2018, *K. G. Greeshma Ganga G270*.

Observations:—*Candolleomyces efflorescens*, a species previously reported from Sri Lanka (Pegler 1986) and East Africa (Pegler 1977), is characterised by smaller basidiocarps that turn black when dried; a hygrophanous pileus with a translucent-striate surface; adnexed lamellae; a stipe with a pruinose apex; oblong to ellipsoid basidiospores with a truncate apex and central germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; a hymeniderm-type pileipellis with scattered velar hyphae; a cutis-type stipitipellis disrupted with velar hyphae and caulocystidia and a lignicolous habitat.

A BLASTn search using the ITS (G130: 676 bp; G270: 666 bp) sequences with those of the sequences present in the GenBank nucleotide database revealed *Psathyrella efflorescens* (presently as *Candolleomyces efflorescens*) (G130: KC992941) as the closest hit with 99.11% identity. A BLASTn search with the nLSU sequence of the present species (G130: 841 bp) showed *Psathyrella trinitatensis* (presently as *Candolleomyces trinitatensis*) as the closest hit (KC992882) with 99.64% identity.

***Candolleomyces* species 1** **Plate 4.**

Description:—Basidiocarps medium-sized, fragile. Pileus 9–16 × 10–12 mm when young, 20–45 mm diam. at maturity, initially convex to paraboloid, becoming broadly conical to applanate with age; surface white on the velar remnants, yellowish brown (5C8) elsewhere when young, becoming golden brown (5D7) at the centre and on the velar remnants, paler at the middle and greyish brown (5F3) towards the margin at maturity, hygrophanous and becoming paler, with fibrillose patches of velar remnants scattered over the surface; margin straight, appendiculate with white, dentate scales. Lamellae adnate, crowded, initially white, becoming dark brown (6F7), with lamellulae in 2 tiers; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 31–60 × 2–3 mm, central, terete, slightly tapering towards the apex, hollow; surface white, finely floccose all over, pruinose towards the apex; base not enlarged, inserted. Odour and taste not distinctive.

Basidiospores (6)7–9 × 4–6 × 4–5 µm, on an average 7.56 × 4.85 × 4.3 µm, Q_1 = 1.33–2.0, Q_{1avg} = 1.54, Q_2 = 1.66–2.0, Q_{2avg} = 1.80, lenticular, ellipsoid to oblong in face view, phaseoliform in side view, hilar appendix indistinct, not opaque, brown, thick-walled, with a distinct germ-pore up to 1.5 µm wide. Basidia 12–15 × 7–11 µm, broadly clavate or sphaeropedunculate, hyaline, thin-walled, 4-spored; sterigmata up to 3 µm long. Pleurocystidia absent. Lamella-edge heterogeneous. Cheilocystidia 22–38 × 11–20 µm, abundant, subglobose, ellipsoid, utriform to subutriform, hyaline, slightly thick-walled or thick-walled at the constrictions. Pileipellis an irregular epithelium composed of globose to subglobose elements and scattered short chains of velar hyphae; elements 18–30 × 11–26 µm, hyaline, thin-walled; velar hyphae 40–60 × 7–15 µm, branched, with a yellowish brown wall pigment at the centre and hyaline towards the margin. Pileus trama loosely interwoven; hyphae 4–10 µm wide, with a yellowish brown wall pigment, thin-walled. Stipitipellis a cutis overlaid with clumps of long, chains of velar hyphae and

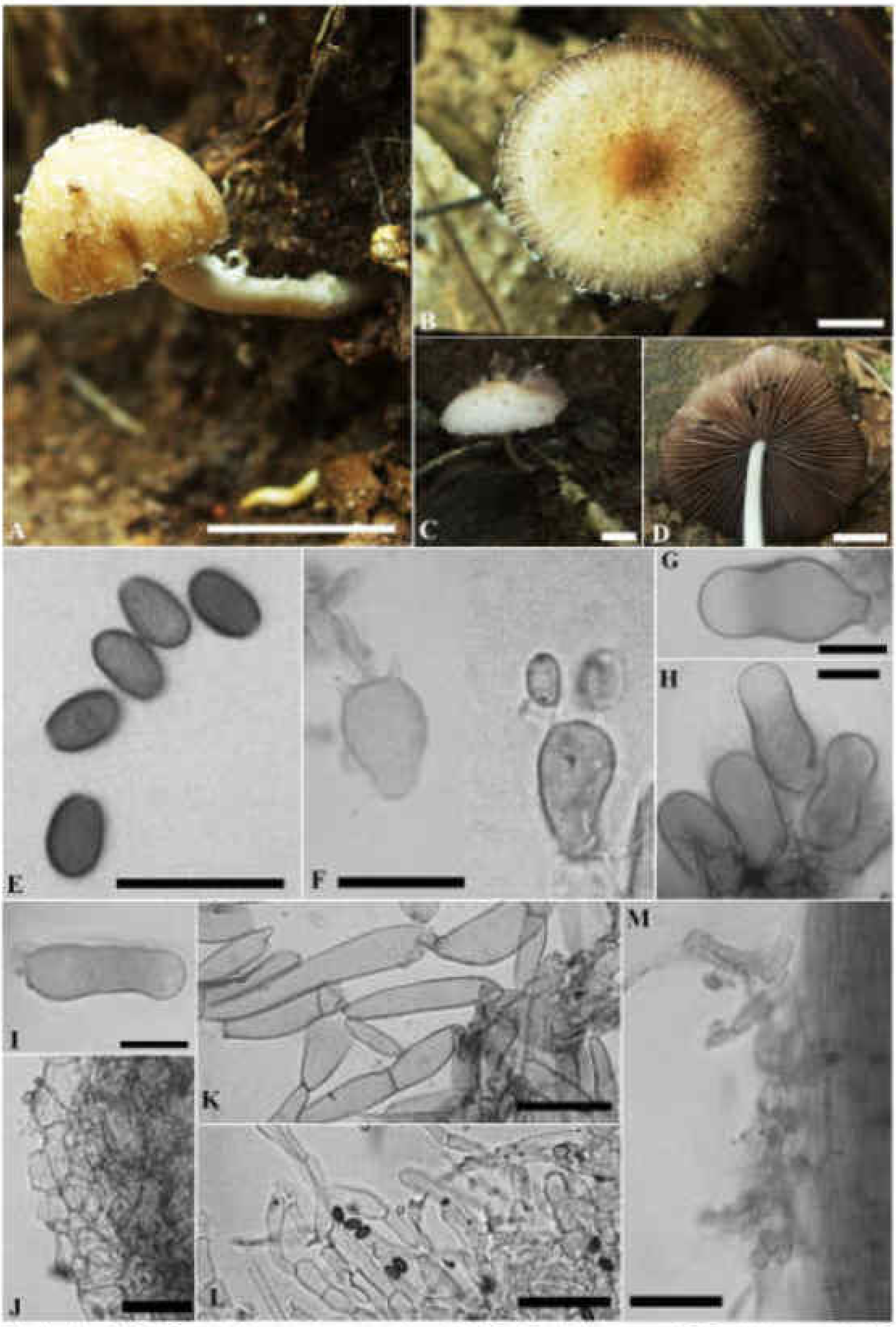

Plate 4. A-M: *Candolleomyces* species 1. A-D. Basidiocarps. **E.** Basidiospores. **F.** Basidia. **G & H.** Cheilocystidia. **I.** Caulocystidium. **J.** Pileipellis. **K.** Velar elements on the pileipellis at the center of pileus. **L.** Velar elements on the pileipellis at the margin of pileus. Scale Bars: **A-D** = 10 mm; **E-I & K** = 20 µm; **J, L & M** = 50 µm.

caulocystidia, densely so towards the apex of the stipe; hyphae 3–6 µm wide, hyaline, slightly thick-walled; velar hyphae 3–7 µm wide, branched, hyaline, thin-walled. Caulocystidia 30–43 × 10–23 µm, abundant, utriform to clavate with a broad apex, hyaline, thick-walled. Clamp connections observed only on velar elements on the pileipellis and at the base of cheilocystidia.

Habit and Habitat:—Solitary or scattered, mostly on decaying roots of an unknown tree, rarely on humus rich soil.

Collection examined:—INDIA. Kerala State, Ernakulam District, Thattekkad forest: 24 October 2018, *K. G. Greeshma Ganga G291*.

Observations:—Medium-sized basidiocarps; an applanate pileus with an appendiculate margin; adnate lamellae; a stipe with a finely floccose surface; ellipsoid to oblong basidiospores with a distinct germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with subglobose to utriform, slightly thick-walled cheilocystidia; an irregular epithelium-type pileipellis with velar elements; a cutis-type stipitipellis disrupted with velar hyphae and caulocystidia and a lignicolous habitat are the characteristic features of the present species.

Candolleomyces candolleanus is strikingly similar to the present species in having a paraboloid to broadly conical pileus with an appendiculate margin, similar-sized basidiospores with a distinct germ-pore and a hymenium devoid of pleurocystidia. However, *C. candolleanus* differs from the present species in having a stipe with a cortina, basidiospores with a short hilar appendix, a lamella-edge with thin-walled and larger cheilocystidia (30–70 × 9–20 µm) and a gregarious habit (Pegler 1977).

Psathyrella pseudogordonii Kits van Wav., a species described from England (Kits van Waveren 1985), shares some characters with the present species in having a paraboloid to broadly conical pileus with an appendiculate margin, smaller and utriform cheilocystidia with a thick-walled neck and the absence of pleurocystidia. *Psathyrella pseudogordonii,* however, has a pileus with white velar remnants, a white stipe that changes to dirty brown towards the base, larger basidiospores (8–11 × 5–6.5 μm) with a distinct hilar appendix and a caespitose habit. *Psathyrella spintrigera* (Fr.) Konrad & Maubl., a species from France (Kits van Waveren 1985), resembles the present species in having almost similar-sized basidiospores, utriform cheilocystidia and a hymenium devoid of pleurocystidia. However, *P. spintrigera* differs from the present species in having basidiocarps with a larger pileus (60–95 mm diam.) lacking velar remnants at maturity, a stipe with an incomplete annulus, a pileipellis devoid of brown velar hyphae and a lamella-edge with thin-walled cheilocystidia.

Comparison of the ITS (601 bp) and the nLSU (873 bp) sequences obtained from the present species with those nucleotide sequences of species available in GenBank suggests that the present *Candolleomyces* species has distinct ITS and nLSU sequences. A BLASTn search with the ITS sequence, the closest hit was an unnamed species of *Psathyrella* from China*, Psathyrella* species 110117MFBPC126 (MW554230) with 95.18% identity. *Psathyrella atricastanea* (Murrill) A. H. Sm. (MW301083: 99.54% identity) resulted as the closest hit in a BLASTn search using the nLSU sequence. *Psathyrella atricastanea*, a species originally reported from Cuba (Smith 1972), has medium-sized basidiocarps, a stipe with a floccose surface, similar size and shape of basidiospores with a distinct germ-pore, a hymenium devoid of pleurocystidia and a lignicolous habitat. However, the characters such as a glabrous pileus, a lamella-edge with ellipsoid and thin-walled cheilocystidia and a pileipellis lacking velar hyphae make it different from the present species.

***Candolleomyces* species 2** **Plate 5.**

Description:—Basidiocarps small, fragile. Pileus up to 25 mm diam. when mature, initially convex, becoming applanate to concave at maturity; surface brown (6E8) to dark brown (6F8) at the centre, brownish orange (6C4) to light brown (6D4) on velar remnants and towards the margin, hygrophanous and becoming paler, with

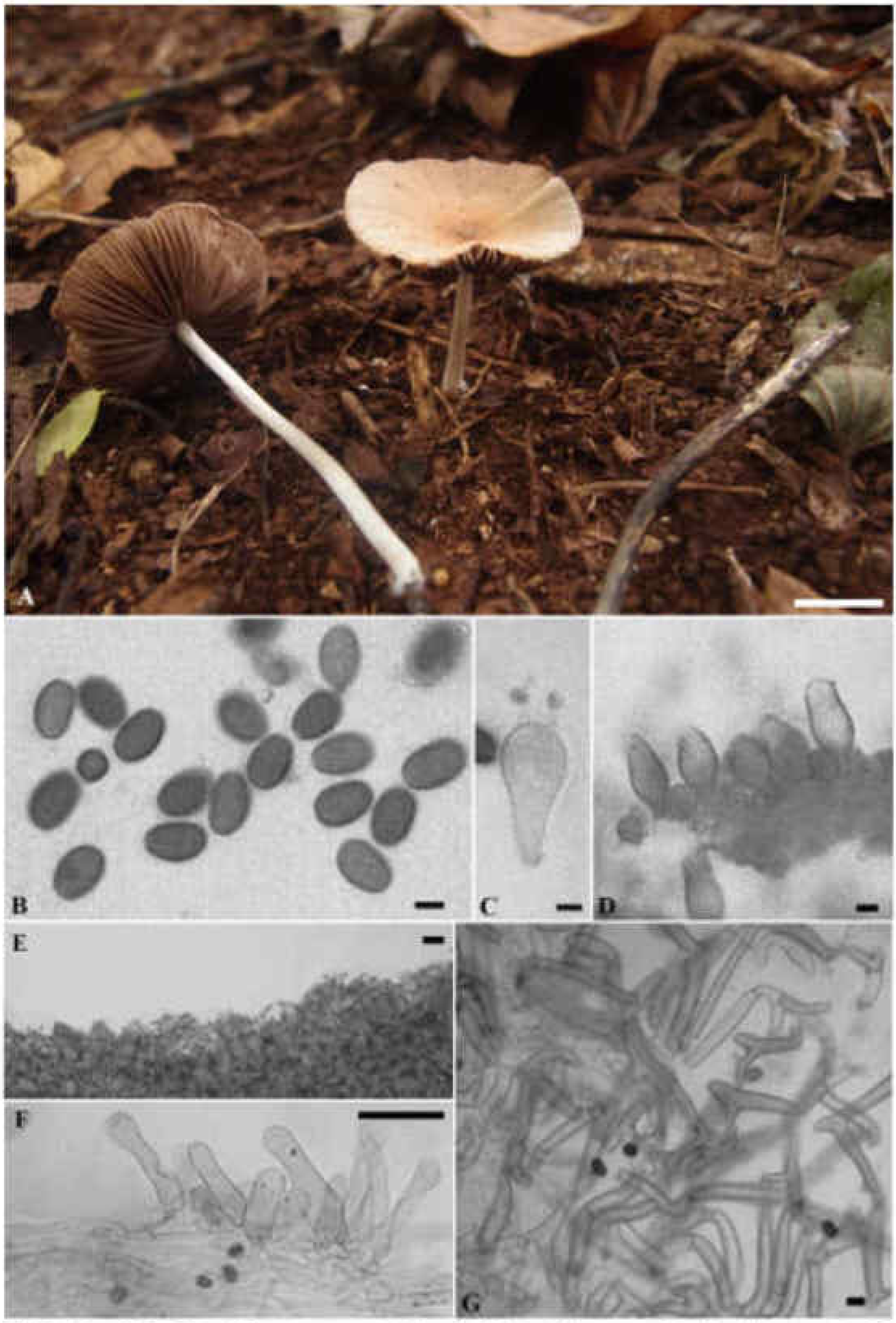

Plate 5. A-G: *Candolleomyces* species 2. A. Basidiocarps. **B.** Basidiospores. **C.** Basidium. **D.** Cheilocystidia. **E.** Pileipellis. **F.** Stipitipellis with caulocystidia. **G.** Velar elements on the pileipellis. Scale Bars: **A** = 10 mm; **B-C** = 5 µm; **D&G** = 10 µm; **F&E** = 50 µm.

patches of fibrillose velar remnants scattered over the surface, finely sulcate-striate towards the margin; margin upturned, sometimes slightly fissile, wavy. Lamellae adnate to adnexed, moderately crowded, initially white, becoming brown (6E6) to dark brown (6F6) when mature, with lamellulae in 2 tiers; edge finely pruinose, concolourous with the sides. Stipe 30–45 × 2 mm, central, terete, slightly tapering towards the apex, hollow; surface white, smooth all over, slightly pruinose towards the apex and the base; base slightly enlarged with a sparse basal mycelium. Odour and taste not distinctive.

Basidiospores 7–9(10) × 5–6 × 4–5 µm, on an average 7.8 × 4.95 × 4.45 µm, Q_1 = 1.4–2.0, Q_{1avg} = 1.62, Q_2 = 1.4–2.0, Q_{2avg} = 1.72, lenticular, ovoid to ellipsoid in face view, phaseoliform in side view, hilar appendix indistinct, not opaque, brown, thick-walled, with a distinct germ-pore up to 1 µm wide. Basidia 12–17 × 8–9 µm, clavate, hyaline, slightly thick-walled, 4-spored; sterigmata up to 5 µm long. Pleurocystidia absent. Lamella-edge heterogeneous. Cheilocystidia 30–45 × 11–19 µm, abundant, subglobose, subcylindrical utriform or rarely lageniform, hyaline, slightly thick-walled. Lamellar trama subregular with inflated elements; elements 48–102 × 31–40 µm, hyaline, thin-walled. Pileipellis an irregular epithelium composed of globose elements and scattered velar hyphae; epithelial elements 37–60 × 30–56 µm, hyaline, thin-walled; velar elements 5–10 µm wide, short, branched, brown or hyaline, thick-walled. Pileus trama subregular composed of both narrow and inflated hyphae; hyphae 2.5–6 µm, inflated up to 20 µm wide, hyaline or with a brown wall pigment and brown encrustations, thin-walled. Stipitipellis a cutis disrupted with scattered caulocystidia, more so towards the apex of the stipe; hyphae 6–15 µm wide, with a pale yellow wall pigment, thin-walled. Caulocystidia 30–50 × 10–13 µm, abundant, clavate or utriform to lageniform, hyaline, slightly thick-walled. Clamp connections observed only on the hyphae of pileus- and lamellar trama and on velar elements on the pileipellis.

Habit and Habitat:—Scattered, among litter rich soil.

Collection examined:—INDIA. Kerala State, Malappuram District, Calicut University Campus: 28 September 2016, *K. G. Greeshma Ganga G102.*

Observations:—The present species is characterised by smaller basidiocarps; a concave pileus with brown velar flocks; adnate to adnexed lamellae; a stipe with a sparse basal mycelium; ovoid to ellipsoid basidiospores with a distinct germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with thin-walled cheilocystidia; an irregular epithelium-type pileipellis with branched and thick-walled velar elements; a cutis-type stipitipellis with caulocystidia and a habitat on soil.

Candolleomyces candolleanus, a widely distributed species, seems to be close to the present species in having almost similar-sized basidiospores, the absence of pleurocystidia and a lamella-edge with utriform cheilocystidia. However, *C. candolleanus* differs from the present species in having larger basidiocarps (Pileus up to 80 mm diam. and stipe 30–90 × 2–8 mm) and a paraboloid to broadly conical pileus with white velar flocks and appendiculate margin (Kits van Waveren 1985). *Candolleomyces pseudocandolleanus* (A.H. Sm.) D. Wächt. & A. Melzer, a species originally reported from Michigan (Smith 1972), shows some similarity with the present species in having basidiospores with a distinct germ-pore, a hymenium devoid of pleurocystidia and a lamella-edge with cheilocystidia of similar size and shape. However, *C. pseudocandolleanus* has a convex and larger pileus (2.4–4 cm) with an appendiculate margin, a stipe with greyish, pallid fibrils at the base, slightly compressed and smaller basidiospores (7–8 × 3.5–4 µm) and a gregarious habitat.

A BLASTn search using the ITS (681 bp) sequence of the present species revealed *Psathyrella candolleana* 3-F7 (presently as *Candolleomyces candolleanus*) as the closest hit (MW081329) with 98.82% identity followed by *P. thiersii* (MT429166) with 99.54% identity. *Psathyrella thiersii* A.H. Sm. is presently considered a synonym of *Candolleomyces candolleanus*. While using the nLSU (878 bp) sequence, *Psathyrella trinitatensis* (presently as *Candolleomyces trinitatensis*) was the closest hit (KC992882) with 99.9% identity. *Candolleomyces trinitatensis* (R.E.D. Baker & W.T. Dale) D. Wächt. & A. Melzer, a species from Trinidad (Pegler 1983), shares some characters with the present species in having similar-sized basidiocarps with a finely floccose pileus, ellipsoid basidiospores with a distinct and central germ-pore, a hymenium devoid of pleurocystidia and a terrestrial habitat. However, *C. trinitatensis* has a pileus with white, denticulate velar squamules at the margin and smaller basidiospores (6–7 × 3.5–4 µm).

***Candolleomyces* species 3 Plate 6.**

Description:—Basidiocarps small, fragile. Pileus 11–38 mm diam. at maturity, initially convex, expanding to applanate with age; surface reddish brown (9E6) all over when young, becoming reddish brown (9E5) at the centre and dull red (9C3) towards the margin with age, hygrophanous and becoming paler, with fibrillose patches of velar remnants scattered over the surface, translucent-striate towards the margin; margin straight, sometimes upturned, even to finely crenulate. Lamellae adnate, crowded, initially white, becoming orange grey (6B2), with lamellulae in 2 tiers; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 31–51 × 2–3 mm, central, terete, slightly tapering towards the apex, hollow; surface orange white (5A2) all over, smooth or scarcely floccose towards the base, pruinose at the apex; base slightly enlarged or subbulbous. Odour and taste not distinctive.

Basidiospores 7–9 × 5–6 × 5 µm, on an average 8.42 × 5.22 × 5 µm, Q_1 = 1.45–1.8, Q_{1avg} = 1.63, Q_2 = 1.4–1.67, Q_{2avg} = 1.67, lenticular, ovoid in face view, somewhat phaseoliform in side view, hilar appendix indistinct, not opaque, pale brown, slightly thick-walled, with an indistinct germ-pore. Basidia 13–19 × 8–12 µm, clavate, pedicellate-clavate or sphaeropedunculate, hyaline, thin-walled, 4-spored; sterigmata up to 4 µm long. Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 18–28 × 10–15 µm, abundant, versiform: subglobose, utriform, oblong, subcylindrical or rarely sphaeropedunculate, hyaline, slightly thick-walled, sometimes with amorphous materials at the apex, pale green in 3% aqueous KOH. Pileipellis an epithelium composed of subglobose elements and scattered short velar hyphae; epithelial elements 33–50 × 30–40 µm, mostly hyaline, thin-walled; velar hyphae 18–40 × 5–13 µm, branched, diverticulate, with a yellow-brown wall pigment and hyaline spiral encrustations, slightly thick-walled. Stipitipellis a disrupted cutis with caulocystidia, more so towards the apex of the stipe; hyphae 4–10 µm wide, hyaline or with a pale yellow wall pigment, slightly thick-walled. Caulocystidia 15–43 × 7–11µm, abundant, mostly utriform, sphaeropedunculate or clavate, hyaline, slightly thick-walled. Clamp connections observed only on velar elements on the pileipellis and hyphae of the stipitipellis.

Habit and Habitat:—In small groups, on the decayed rachis of coconut leaves or on rotten wood.

Collections examined:—INDIA. Kerala State, Kollam District, Shendurney forest: 30 July 2017, *K. G. Greeshma Ganga G192*; Thrissur District, Punnayoorkulam: 13 August 2017, *K. G. Greeshma Ganga G203*.

Observations:—The present species is characterised by small basidiocarps; an applanate pileus with brown velar flocks; adnate lamellae; a stipe with a slightly enlarged base; ovoid basidiospores with an indistinct germ-pore; a hymenium devoid of pleurocystidia; abundant cheilocystidia with amorphous contents; an epithelium-type pileipellis with velar hyphae and a disrupted cutis-type stipitipellis with caulocystidia and velar hyphae.

Candolleomyces subsingeri (T. Bau & J.Q. Yan) D. Wächt. & A. Melzer, a species originally described from China (Yan & Bau 2018a) and also reported from Slovenia (Melzer & Ferisin 2018), shows some similarity with the present species in having almost similar size and shape of the basidiocarps, basidiospores with an indistinct germ-pore, a hymenium devoid of pleurocystidia and a lamella-edge with utriform to sphaeropedunculate cheilocystidia. However, *C. subsingeri* differs from

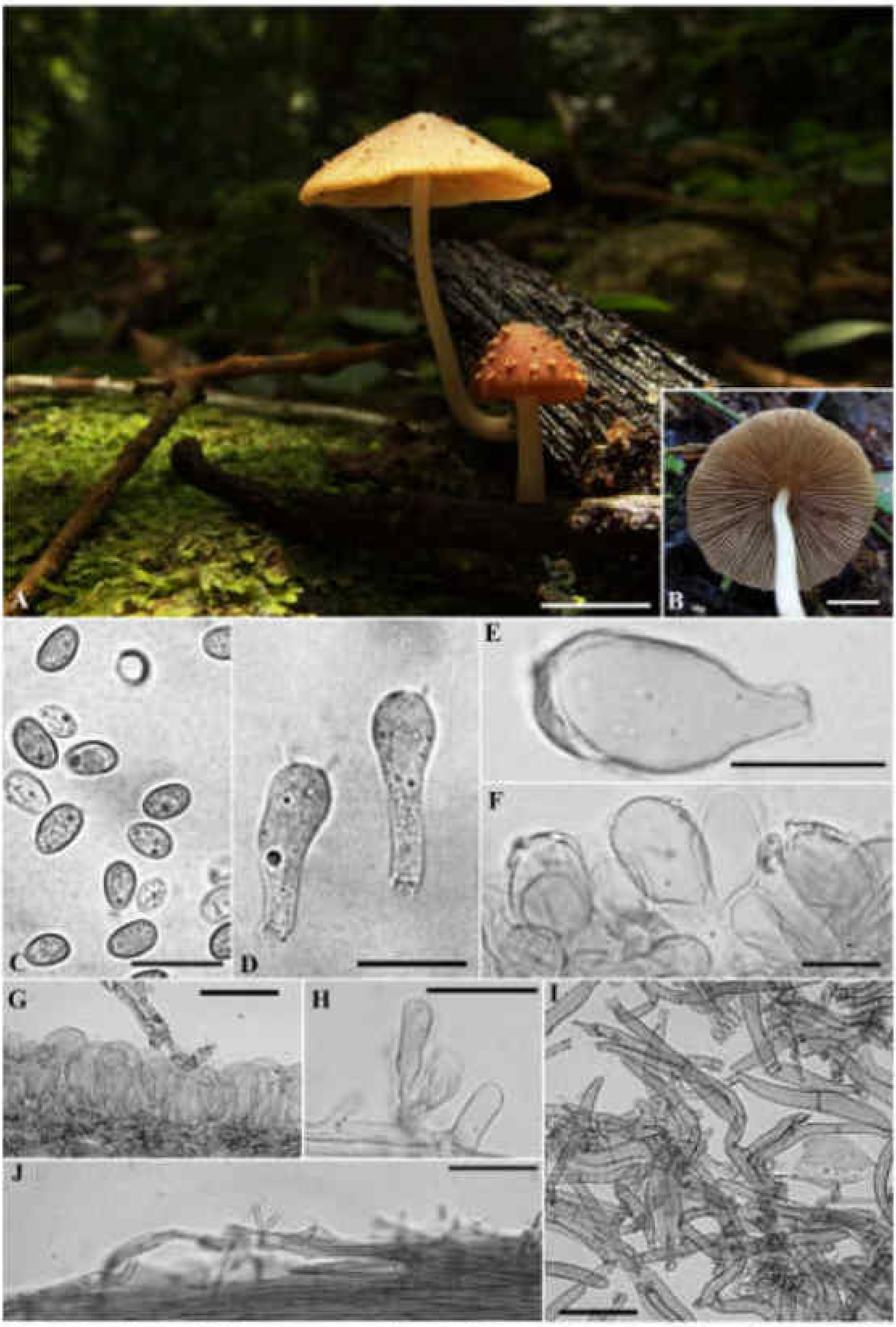

Plate 6. **A-J: *Candolleomyces* species 3. A-B.** Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E, F.** Cheilocystidia. **G.** Pileipellis. **H.** Caulocystidia. **I.** Velar elements on the pileipellis. **J.** Stipitipellis. Scale Bars: **A-B** = 10 mm; **C-F** = 20 µm; **G-J** = 50 µm.

the present species in having an umbonate pileus with white velar remnants, ellipsoid to oblong and smaller basidiospores (5.8–8.8 × 3.8–4.4(5) µm), cheilocystidia lacking amorphous deposits at the apex and a habitat on humus rich soil.

Candolleomyces singeri (A.H. Sm.) D. Wächt. & A. Melzer, a species recorded from Florida (Smith 1972) and also from India (Harwinder *et al*. 2020), resembles the present species in having a reddish brown pileus, hyaline or pale yellow basidiospores with an indistinct germ-pore and a habitat on rotten wood. *Candolleomyces singeri,* however, has a glabrous pileus, smaller basidiospores (7–7.8 × 4.0–4.6 µm) and cheilocystidia devoid of amorphous materials at the apex. *Candolleomyces subcacao* T. Bau & J. Q. Yan, a Chinese species, seems to be close to the present species in having basidiocarps with almost similar size and shape, hyaline or pale yellow basidiospores, a hymenium devoid of pleurocystidia and a habitat on rotten wood. However, *C. subcacao* differs from the present species in having a stipe with a white basal mycelium, ovoid and smaller basidiospores (6.8–8.8 × 3.9–4.9 µm) with a distinct germ-pore and cheilocystidia without amorphous materials at the apex (Bau & Yan 2021).

Two ITS (G203: 669 bp; G192: 672 bp) and two nLSU (G203: 868 bp; G192: 828 bp) sequences were derived from the present *Candolleomyces* species collected from two different localities. The closest hit in a BLASTn search using the ITS (G192) sequence was *Psathyrella subsingeri* (presently as *Candolleomyces subsingeri*) with 96.44% identity (MG734742). An unnamed species of *Psathyrella, Psathyrella* species HCL2021-8-32 (OL336481; 99.65% identity) resulted as the closest hit in a BLASTn search with the nLSU (G203) sequence.

***Candolleomyces* species 4** **Plate 7.**

Description:—Basidiocarps small, fragile. Pileus 8–17 × 7–13 mm when young, becoming up to 15 mm diam. when mature, initially ellipsoid to convex, becoming broadly campanulate with age; surface reddish brown (8E7) to dark brown (8F7) all over when young, becoming dark brown (7F8) at the centre, brown (7E7) in the middle, paler towards the margin at maturity, hygrophanous and becoming paler, smooth all over, translucent-striate towards the margin; margin straight, eroded. Lamellae adnate, moderately crowded, initially white, becoming greyish orange (6B3) at maturity, with lamellulae in 2 tiers; edge even to the naked eye, pruinose under a lens, concolourous with the sides. Stipe 25–40 × 2–3 mm, central, terete, slightly tapering towards the apex, hollow; surface white, smooth towards the base, finely pruinose towards the apex; base slightly enlarged with a sparse, cottony basal mycelium. Odour and taste not distinctive.

Basidiospores 7–8 × 5 × 4–5 µm, on an average 7.22 × 5 × 4.35 µm, Q_1 = 1.4–1.6, Q_{1avg} = 1.46, Q_2 = 1.4–2.0, Q_{2avg} = 1.66, lenticular, ellipsoid in face view, phaseoliform in side view, hilar appendix indistinct, not opaque, pale brown, slightly thick-walled, with an indistinct germ-pore. Basidia 18–23 × 8–9 µm, clavate, hyaline, slightly thick-walled, 4-spored; sterigmata up to 3 µm long. Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 31–35 × 11–13 µm, abundant, utriform to lageniform, hyaline, slightly thick-walled. Lamellar trama subregular with inflated elements; elements 37–50 × 10–34 µm, hyaline, thin-walled. Pileipellis a hymeniderm composed of clavate elements and scattered velar hyphae; clavate elements 30–50 × 21-31 µm, with a pale yellow wall pigment, thin-walled; velar hyphae 19–50 × 6–13 µm, short, branched, diverticulate, with a pale brown wall pigment and hyaline encrustations, slightly thick-walled. Pileus trama subregular composed of narrow and inflated hyphae; narrow hyphae 4–11 µm wide, with a pale yellow wall pigment, thin-walled; inflated elements 36–70 × 22–37 µm wide, hyaline, thin-walled. Stipitipellis a cutis with scattered caulocystidia and clumps of velar hyphae, densely so towards the apex of the stipe; hyphae 2–6 µm, hyaline, slightly thick-walled; velar hyphae 2–4 µm wide, rarely branched, hyaline, thin-walled. Caulocystidia 32–55 × 8–18 µm, mostly lageniform to cylindrical, hyaline, slightly thick-walled. Clamp connections observed only on velar elements on the pileipellis, the hyphae of the stipitipellis and the lamellar trama and at the base of cheilocystidia.

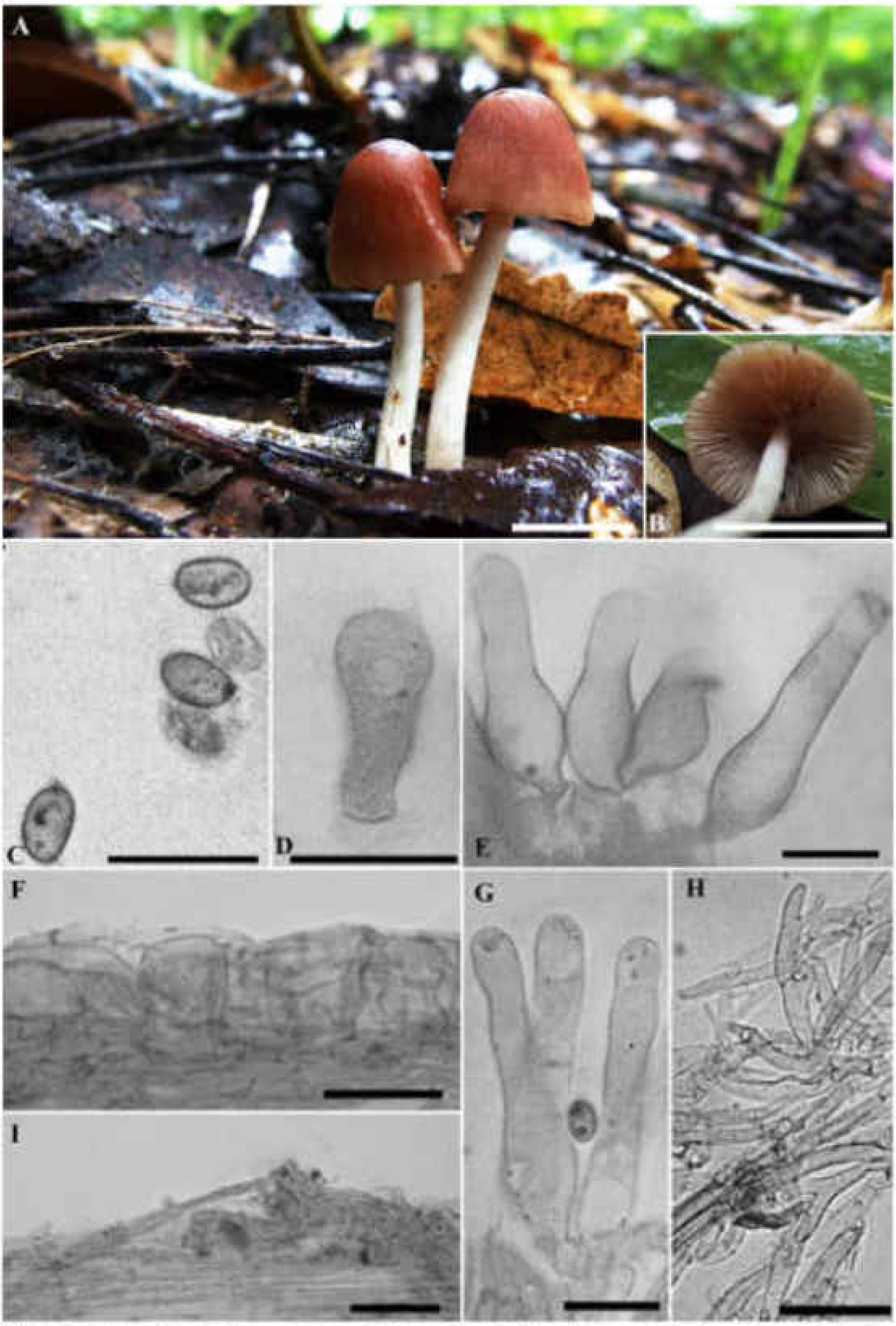

Plate 7. A-I: *Candolleomyces* species 4. A-B. Basidiocarps. **C.** Basidiospores. **D.** Basidium. **E.** Cheilocystidia. **F.** Pileipellis. **G.** Caulocystidia. **H.** Velar elements on the pileipellis. **I.** Stipitipellis. Scale Bars: **A-B** = 10 mm; **C-E, G & H** = 20 µm; **F & I** = 50 µm.

Habit and Habitat:—Scattered or in small groups, on rotten twigs and leaf litter.

Collection examined:—INDIA. Kerala State, Palakkad District, Olavakkode: 18 August 2017, *K. G. Greeshma Ganga G206*.

Observations:—Smaller basidiocarps; a broadly campanulate, dark brown pileus; adnate lamellae; a stipe with a sparse, cottony basal mycelium; ellipsoid basidiospores with an indistinct germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with cheilocystidia; a hymeniderm-type pileipellis with velar hyphae and a cutis-type stipitipellis with caulocystidia and clumps of velar hyphae are the salient features of the present species.

Candolleomyces cacao (Desjardin & B.A. Perry) D. Wächt. & A. Melzer, an African species (Desjardin & Perry 2016), shows close resemblance to the present species in having a basidiocarp with almost similar size and shape, a glabrous pileus, a stipe with a basal mycelium, basidiospores with an indistinct germ-pore, a hymenium devoid of pleurocystidia and a stipitipellis with almost similar size and shape of caulocystidia. However, *C. cacao* differs from the present species in having smaller basidiospores (5.7–6.8 × 3.5–4.8 µm), a lamella-edge with broadly lageniform and smaller cheilocystidia (16–29 × 8–12 µm) and a gregarious habit.

Candolleomyces subcacao, an uncommon species originally described from China (Bau & Yan 2021), seems to be somewhat similar to the present species in having a stipe with a white basal mycelium, basidiospores of similar size, a hymenium devoid of pleurocystidia and a lignicolous habitat. *Candolleomyces subcacao,* however, differs in having a larger, hemispherical to applanate pileus (11–35 mm) with a finely fibrillose surface, basidiospores with a distinct germ-pore and utriform cheilocystidia with a broad, obtuse apex. *Candolleomyces candolleanus*, a widely distributed species (Kits van Waveren 1985), resembles the present species in having a convex to broadly conical pileus, basidiospores with almost similar size and a hymenium devoid of pleurocystidia. However, *C. candolleanus* has larger basidiocarps (pileus 15–70 (80) mm diam. and stipe 30–90 × 2–8 mm) with a cortinoid veil, reddish brown basidiospores with a distinct germ-pore, a lamella-edge with utriform to cylindrical cheilocystidia and a caespitose habitat.

The distinct status of the ITS (675 bp) sequence of the present *Candolleomyces* species was confirmed in the megablast searches. An unnamed species of *Psathyrella* from India*, Psathyrella* species BAB-4747 (KR154976), followed by *Candolleomyces candolleanus* (MZ735401) resulted as the closest hits with 99.56% and 97.64% identities respectively. No nLSU sequence was obtained from the present collection.

***Candolleomyces* species 5** **Plate 8.**

Description:—Basidiocarps small, fragile. Pileus 9–17 × 6–7 mm when mature, initially convex, expanding to broadly convex or conical with age; surface brown (6E8) on velar remnants, orange white (5A2) to orange grey (5B3) elsewhere, hygrophanous and becoming paler, with fibrillose patches of velar remnants scattered over the surface; margin straight, entire. Lamellae adnate, crowded, initially white, becoming greyish orange (5B3), with lamellulae in 3 tiers; edge finely pruinose, concolourous with the sides. Stipe 26–34 × 1–2 mm, central, terete, slightly tapering towards the apex, hollow; surface orange white (5A2), smooth towards the base, pruinose at the apex; base not enlarged, with abundant, short, white strigose hairs. Odour and taste not distinctive.

Basidiospores 6–9 × 5 × 4–5 µm, on an average 7.65 × 5 × 4.62 µm, Q_1 = 1.4–1.8, Q_{1avg} = 1.61, Q_2 = 1.4–2.0, Q_{2avg} = 1.57, lenticular, ellipsoid to ovo-ellipsoid in face view, phaseoliform in side view, hilar appendix indistinct, pale brown to almost hyaline, not opaque, slightly thick-walled, with an indistinct germ-pore. Basidia 12–15 × 8–9 µm, clavate, hyaline, thin-walled, 4-spored; sterigmata up to 3 µm long.

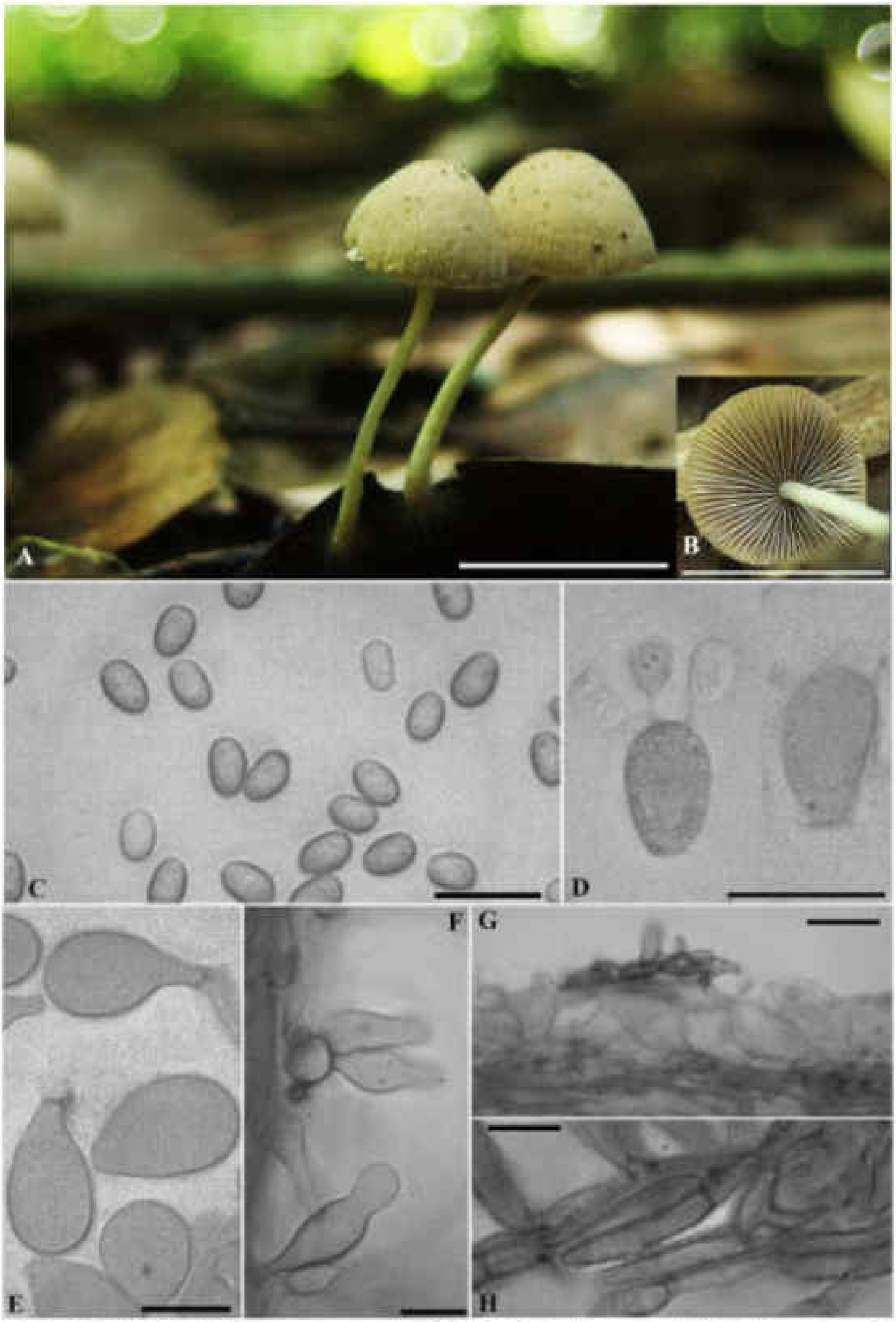

Plate 8. A-H: ***Candolleomyces*** **species 5. A-B.** Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Cheilocystidia. **F.** Stipitipellis showing caulocystidia. **G.** Pileipellis. **H.** Velar elements on the pileipellis. Scale Bars: **A & B** = 10 mm; **C-F & H** = 20 µm; **G** = 50 µm.

Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 14–25 × 9–15 µm, abundant, mostly ellipsoid to subglobose or rarely utriform, hyaline, slightly thick-walled. Pileipellis an epithelium composed of globose to subgobose elements with loosely bound, chains of velar hyphae; epithelial elements 30–40 × 28–43 µm, mostly hyaline, thin-walled; velar hyphae 14–52 × 5–11 µm, short, branched, diverticulate, dark brown, thick-walled (up to 1 µm thick). Pileus trama loosely interwoven; hyphae 11–28 µm wide, hyaline or with a brown encrusting pigment, thick-walled (up to 1 µm thick). Stipitipellis a disrupted cutis with scattered caulocystidia and velar hyphae, more so towards the apex of the stipe; hyphae 4–6 µm, hyaline, slightly thick-walled; velar hyphae 2–4 µm wide, narrowly cylindrical, hyaline, slightly thick-walled. Caulocystidia 32–50 × 12–16 µm, mostly lageniform, hyaline, slightly thick-walled. Clamp connections observed only on velar elements on the pileipellis, the hyphae of the stipitipellis and at the base of cheilocystidia.

Habit and Habitat:—Scattered or in small groups, on decaying leaves.

Collection examined:—INDIA. Kerala State, Ernakulam District, Thattekkad forest: 24 October 2018, *K. G. Greeshma Ganga G289.*

Observations:—The present species is characterised by smaller basidiocarps; a convex pileus with scattered velar flocks; adnate lamellae; a stipe with abundant, short, white strigose hairs at the base; ellipsoid to ovo-ellipsoid basidiospores with an indistinct germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; an epithelium-type pileipellis with thick-walled velar hyphae; a disrupted cutis-type stipitipellis with caulocystidia and velar hyphae and a habitat on decaying leaf litter.

Candolleomyces aberdarensis (A. Melzer, Kimani & R. Ullrich) D. Wächt. & A. Melzer, a species recently described from Kenya (Melzer *et al*. 2018; Wächter & Melzer 2020), is strikingly similar to the present species in having smaller basidiocarps, a stipe with strigose hairs at the base, a hymenium devoid of pleurocystidia, basidiospores with an indistinct germ-pore, thick-walled and encrusted velar elements and a stipitipellis with utriform to lageniform caulocystidia. However, *C. aberdarensis* has a reddish brown to brown pileus with a revolute margin, a stipe with a brownish base, a pileipellis with globose velar elements, a lamella-edge with mostly utriform to rarely lageniform cheilocystidia and a gregarious habit.

Candolleomyces candolleanus, a common species (Pegler 1983), shares a few characters with the present species in having a convex to broadly conical pileus, similar-sized basidiospores and a hymenium devoid of pleurocystidia. However, *C. candolleanus* differs from the present species in having larger basidiocarps (pileus 15–80 mm and stipe 30–90 × 2–8 mm) with a cortinoid veil, a pileus with an appendiculate margin, a stipe devoid of strigose hairs at the base, brown basidiospores with an indistinct germ-pore, a lamella-edge with utriform cheilocystidia and a gregarious habitat. *Candolleomyces sulcatotuberculosus* (J. Favre) D. Wächt. & A. Melzer, an uncommon species originally reported from Switzerland (Battistin *et al*. 2014), seems to be close to the present species in having smaller basidiocarps, pale brown basidiospores with an indistinct germ-pore, a hymenium devoid of pleurocystidia, a lamella-edge with utriform to lageniform cheilocystidia and a habitat on leaf litter. However, *C. sulcatotuberculosus* has an ochre-orange to orange brown pileus with white velar remnants, a lamella-edge with utriform to lageniform or cylindrical cheilocystidia and a pileipellis with pale brown velar hyphae.

Comparison of the ITS (683 bp) and the nLSU (986 bp) sequences derived from the present *Candolleomyces* species with those available in the GenBank revealed that the present *Candolleomyces* species has distinct ITS and nLSU sequences. A megablast search using the ITS sequence showed *Candolleomyces candolleanus* (MT658050) as the closest hit with 98.54% identity. *Candolleomyces* *aberdarensis* (MK421517: 99.80% identity) was the closest hit in a BLASTn search with the nLSU sequence.

Candolleomyces sulcatotuberculosus (J. Favre) D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1234 (2020) **Plate 9.**

Drosophila typhae var. *sulcatotuberculosa* (J. Favre) Kühner & Romagn., Fl. Analyt. Champ. Supér. Paris: 366 (1953)
Psathyrella sulcatotuberculosa (J. Favre) Einhell., Ber. dt. bot. Ges. 47: 123 (1976)
Psathyrella typhae var. *sulcatotuberculosa* J. Favre, Beitr. Kryptfl. Schweiz 10 (3): 215 (1948)

Description:—Basidiocarps small, fragile. Pileus 7–15 × 6–10 mm when young, 20–23 × 15–17 mm at maturity, initially convex, becoming broadly conical to convex with age; surface white on the velar remnants, dark brown (7F8) to brown (7E6) elsewhere when young, becoming light orange (5A4) to brown (6E6) all over with age, hygrophanous and becoming paler, with patches of velar remnants scattered over the surface, striate towards the margin; margin initially straight, becoming wavy when mature. Lamellae adnate to adnexed, close to moderately crowded, initially white, greyish orange (5B3) at maturity, with lamellulae in 3 tiers; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 21–34 × 1–2 mm, central, terete, slightly tapering towards the apex, hollow; surface white, finely floccose all over, pruinose at the apex; base slightly enlarged with a white strigose mycelium. Odour and taste not distinctive.

Basidiospores 7–10 × 5 × 4–5 µm, on an average 8.13 × 5 × 4.8 µm, Q_1 = 1.4–1.8, Q_{1avg} = 1.61, Q_2 = 1.4–2.25, Q_{2avg} = 1.72, lenticular, oblong to ellipsoid in face view, phaseoliform in side view, hilar appendix indistinct, not opaque, pale brown to almost hyaline, slightly thick-walled, with an indistinct germ-pore. Basidia 17–23 × 9–10 µm, clavate, hyaline, slightly thick-walled, 4-spored; sterigmata up to 4 µm long. Pleurocystidia absent. Lamella-edge heterogeneous. Cheilocystidia 17–30 × 9–17 µm, abundant, subcylindrical, utriform or lageniform, hyaline, slightly thick-walled. Lamellar trama subregular with inflated elements; elements 20–40 ×

13–35 µm, hyaline, thin-walled. Pileipellis a hymeniderm composed of clavate elements overlaid with scattered, short velar hyphae; clavate elements 30–37 × 28–30 µm, hyaline, thin-walled; velar hyphae 2–8 µm wide, branched, hyaline, thick-walled. Stipitipellis a cutis with loosely interwoven velar elements and scattered caulocystidia; hyphae 3–5 µm wide, hyaline, thin-walled; velar elements 3–6 µm wide, hyaline, thin-walled. Caulocystidia 16–33(55) × 7–17 µm, utriform, lageniform or clavate, hyaline, slightly thick-walled. Clamp connections observed only on the velar elements on the pileipellis.

Habit and Habitat:—In small groups, on rotten twigs.

Collection examined:—INDIA. Kerala State, Wayanad District, Muthanga Forest: 04 July 2017, *K. G. Greeshma Ganga G166.*

Observations:—*Candolleomyces sulcatotuberculosus*, an uncommon species originally described from Switzerland and also reported from Spain, Germany and Italy (Kits van Waveren 1985; Battistin *et al*. 2014), has smaller basidiocarps; conico-convex pileus with white velar remnants; adnate to adnexed lamellae; a stipe base with a white strigose mycelium; pale brown basidiospores with an indistinct germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; a hymeniderm-type pileipellis with velar hyphae and a cutis-type stipitipellis with caulocystidia and velar hyphae.

Psathyrella sulcatotuberculosus (presently as *Candolleomyces sulcatotuberculosus*) resulted as the closest hit in BLASTn searches using both the ITS (673 bp; MN523296 (99.54% identity)) and the nLSU (870 bp; KJ138422 (99.77% identity)) sequences.

Candolleomyces typhae (Kalchbr.) D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1234 (2020) **Plate 10.**

Agaricus typhae Kalchbr., Mathem. Természettud. Közlem. 2: 160 (1863)
Drosophila typhae (Kalchbr.) Romagn., Bull. mens. Soc. linn. Soc. Bot. Lyon 13: 51 (1944)

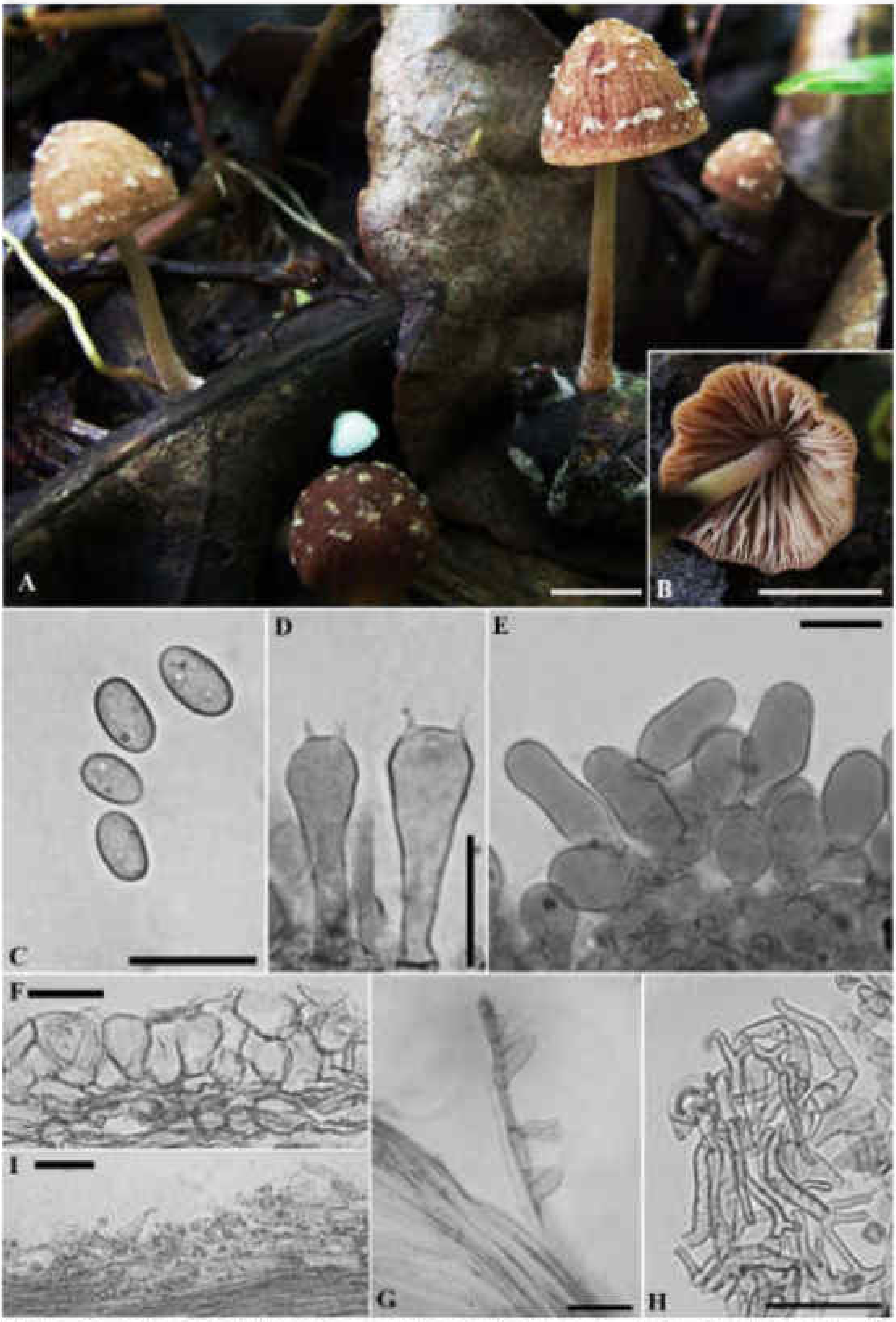

Plate 9. A-I: ***Candolleomyces sulcatotuberculosus.*** **A-B.** Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Cheilocystidia. **F.** Pileipellis. **G.** Stipitipellis with caulocystidia. **H.** Velar elements on the pileipellis. I. Stipitipellis. Scale Bars: **A & B** = 10 mm; **C-E & H** = 20 µm; **F, G & I** = 50 µm.

Pilosace typhae (Kalchbr.) Kuntze, Revis. gen. pl. (Leipzig) 3 (3): 504 (1898)
Pratella typhae (Kalchbr.) Henn., in Engler & Prantl, Nat. Pflanzenfam. (Leipzig) 1: 235 (1898)
Psathyra typhae (Kalchbr.) Sacc., Syll. fung. (Abellini) 5: 1067 (1887)
Psathyra typhae var. *iridis* Boud., Bull. Soc. mycol. Fr. 13 (1): 13 (1897)
Psathyrella typhae (Kalchbr.) A. Pearson & Dennis, Trans. Br. mycol. Soc. 31 (3-4): 185 (1948)
Psathyrella typhae f. *acori* J. Veselský, Čas. slezsk. Mus. Opavě, Ser. A 14: 56 (1965)
Psathyrella typhae var. *bispora* Kits van Wav., Persoonia, Suppl. 2: 282 (1985)

Description:—Basidiocarps small, fragile. Pileus initially 5–10 × 4–8 mm, finally up to 14 mm diam. at maturity, convex to broadly campanulate when young, becoming applanate or somewhat concave with age; surface orange brown (6C6) to light orange (6D6) all over when young, becoming orange brown (6C5) at the centre and orange white (6A2) towards the margin with age, hygrophanous and becoming paler, finely floccose velar patches all over when young, becoming somewhat fibrillose at maturity; margin initially somewhat straight to upturned, becoming revolute with age, wavy. Lamellae adnexed, crowded, initially white, becoming light brown (6D4), with lamellulae in 2 tiers; edge white, pruinose, concolourous with the sides. Stipe 31–51 × 2–3 mm, central, terete, slightly tapering towards the apex, hollow; surface orange grey (6B2), finely pruinose at the apex, floccose towards the base, longitudinally-striated; base connate, slightly enlarged, inserted, often with a white strigose mycelium. Odour and taste not distinctive.

Basidiospores 15–19(20) × 9–12 × 7–9 µm, on an average 17.32 × 10.3 × 8.05 µm, Q_1 = 1.41–2.0, Q_{1avg} = 1.67, Q_2 = 1.66–2.57, Q_{2avg} = 2.18, lenticular, ovo-ellipsoid to subtriangular, rarely triangular in face view, phaseoliform in side view, hilar appendix indistinct, not opaque, pale brown, slightly thick-walled, with an indistinct germ-pore. Basidia 36–48 × 10–12 µm, elongate-clavate or pedicellate-clavate to narrowly clavate, hyaline, thin-walled, 2-spored; sterigmata up to 4.5 µm long. Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 32–45 × 12–15 µm, abundant, versiform: subglobose, subutriform, subcylindrical or fusiform, hyaline, thin-walled. Pileipellis a hymeniderm composed of clavate elements along with scattered, short velar hyphae; hymeniderm elements 27–63 × 12–30 µm, mostly hyaline, thin-walled; velar hyphae 14–52 × 5–11 µm, branched, diverticulate, pale yellow, slightly thick-walled. Stipitipellis a cutis with loosely tangled, elongated velar hyphae and scattered caulocystidia, densely so towards the apex of the stipe; hyphae 3–6 µm wide, with a pale yellow wall pigment, slightly thick-walled; velar hyphae 3–7 µm wide, branched, hyaline, slightly thick-walled. Caulocystidia 30–56 × 6–10 µm, scarce, utriform, lageniform or cylindrical, hyaline, slightly thick-walled. Clamp connections observed only on velar hyphae on the pileipellis and at the base of cheilocystidia.

Habit and Habitat:—In small groups, on rotten pseudostem of *Musa* sp.

Collection examined:—INDIA. Kerala State, Thrissur District, Punnayoorkulam: 13 August 2017, *K. G. Greeshma Ganga G202*.

Observations:—*Candolleomyces typhae*, a species originally described from the Netherlands (Kits van Waveren 1985), is characterised by smaller basidiocarps; a concave pileus with a fibrillose surface; adnexed lamellae; a stipe with a connate base; ovo-ellipsoid to subtriangular basidiospores with an indistinct germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; a hymeniderm-type pileipellis with velar hyphae and a cutis-type stipitipellis with caulocystidia and velar hyphae.

Comparison of the ITS (680 bp) and the nLSU (863 bp) sequences of the present species with those available in GenBank revealed that the present species is *C. typhae*. BLASTn searches using both the ITS and the nLSU sequences showed *Psathyrella typhae* (presently as *Candolleomyces typhae*) as the closest hit (DQ389721) with 99.27% and 99.7% identities.

5.1.2.2. ***COPRINELLUS*** P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 28 (1879)

Annularius Roussel, Fl. Calvados, Edn 2: 61 (1806)
Ephemerocybe Fayod, Annls Sci. Nat., Bot., sér. 7 9: 380 (1889)
Pseudocoprinus Kühner, Botaniste 20: 155 (1928)

Plate10. A-I: ***Candolleomyces typhae.*** **A-B.** Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Cheilocystidia. **F.** Pileipellis. **G.** Velar elements on the pileipellis. **H.** Caulocystidia. **I.** Stipitipellis Scale Bars: **A & B** = 10 mm; **C & D** = 20 µm; **E-I** = 50 µm.

Pileus membranous or fleshy or very fragile. Veil present. Lamellae fully, partially, or non-deliquescent. basidia di-, tri-, tetramorphic. Pleurocystidia present or absent, sometimes concentrated towards margin. Pileipellis comprises velar elements and pileocystidia; velar elements usually of globular cells. Pileocystidia lageniform to bulbous-based filament-bearing cells (setulae). Habitat lignicolous, terrestrial or coprophilous.

Type species: *Coprinellus deliquescens* (Bull.) P. Karst.

Only one section of the genus *Coprinellus* was observed during the present study.

Coprinellus **section** ***Disseminati*** D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1092 (2020)

Basidiocarps small. Veil sparse. Lamellae non-deliquescent. Basidiospores fusiform to ovoid with a central germ-pore. Basidia 4-spored. Cheilocystidia clavate, utriform, subcylindrical. Pleurocystidia absent. Pileipellis with velar elements consisting of chains of often somewhat thick-walled and pigmented subcylindrical and globose cells. Pileocystidia very large, utriform. Clamp connections absent. Habit in groups or gregarious. Habitat lignicolous or terrestrial.

Type species: *Coprinellus disseminatus* (Pers.) J.E. Lange

Only one species belonging to the section *Disseminati* was observed during the present study.

Coprinellus disseminatus (Pers.) J.E. Lange [as '*disseminata*'], Dansk bot. Ark. 9 (6): 93 (1938) **Plate 11.**

Agaricus digitaliformis Bull., Herb. Fr. (Paris) 1: 22 (1781)
Agaricus disseminatus Pers., Syn. meth. fung. (Göttingen) 2: 403 (1801)
Agaricus disseminatus f. *digitaliformis* (Bull.) Fr., Syst. mycol. (Lundae) 1: 305 (1821)
Agaricus disseminatus var. *digitaliformis* (Bull.) Pers., Syn. meth. fung. (Göttingen) 2: 403 (1801)
Agaricus disseminatus var. minor Alb. & Schwein., Consp. fung. (Leipzig): 199 (1805)

Agaricus minutulus Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 4: 72 (1774)
Agaricus striatus Bull., Herb. Fr. (Paris) 12: tab. 552, fig. 2 (1792)
Coprinarius disseminatus (Pers.) P. Kumm., Führ. Pilzk. (Zerbst): 68 (1871)
Coprinarius disseminatus (Pers.) Trog, Flora, Regensburg 15: 550 (1832)
Coprinus digitaliformis (Bull.) Fr., Epicr. syst. mycol. (Upsaliae): 249 (1838)
Coprinus disseminatus (Pers.) Gray, Nat. Arr. Brit. Pl. (London) 1: 634 (1821)
Coprinus disseminatus var. *striatus* (Bull.) Gray, Nat. Arr. Brit. Pl. (London) 1: 634 (1821)
Coprinus floridanus Murrill, Proc. Fla Acad. Sci. 7 (2/3): 125 (1945)
Drosophila disseminata (Pers.) Romagn., Bull. Soc. mycol. Fr. 83(1): 67 (1967)
Psathyrella disseminata (Pers.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 25: 123 (1872)
Psathyrella minutula (Schaeff.) Murrill, Mycologia 10 (1): 26 (1918)
Pseudocoprinus disseminatus (Pers.) Kühner, Botaniste 20: 156 (1928)

Description:—Basidiocarps small, fragile. Pileus 3–4 × 3–5 mm when young, finally up to 10 mm diam. at maturity, initially paraboloid, becoming broadly paraboloid or rarely campanulate often with an umbo at maturity; surface yellowish white (4A2) all over when young, becoming white (4A1) to grey (4B1) when mature, with fine glimmering hairs all over, plicate-striate, deliquescent; margin initially straight, crenate. Lamellae adnate, L = 19–20, close, initially white, becoming black with age, with lamellulae in 1 tier; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 13–30 × 1–1.5 mm, central, terete, slightly tapering towards the apex, hollow; surface white to off-white, finely pubescent all over; base slightly enlarged to subbulbous, often with a white, dense strigose mycelium. Odour and taste not distinctive.

Basidiospores 7–9 × 4.5–5 × 4–5 µm, on an average 7.9 × 4.9 × 4.22 µm, Q_1 = 1.5–1.8, Q_{1avg} = 1.61, Q_2 = 1.55–2.0, Q_{2avg} = 1.85, lenticular, ovo-ellipsoid with a slightly pointed base and truncate apex in face view, ellipsoid in side view, dark brown, thick-walled, with a central germ-pore up to 2.5 µm wide. Basidia 12–39 × 7–9 µm, clavate to pedicellate-clavate, hyaline, thin-walled, surrounded by 3–5 pseudoparaphyses, 4-spored; sterigmata up to 4 µm long. Pleurocystidia absent. Lamella-edge heterogeneous. Cheilocystidia 25–72 × 15–21 µm, abundant, mostly lageniform, rarely cylindrical or subglobose, hyaline, thin-walled. Pileipellis an epithelioid hymeniderm disrupted by pileocystidia; epithelioid hymeniderm elements 32–35 × 26–35 µm, broadly clavate, hyaline, thin-walled. Pileocystidia 52–147 × 18–23 µm, abundant, mostly lageniform or rarely with a short pedicel,

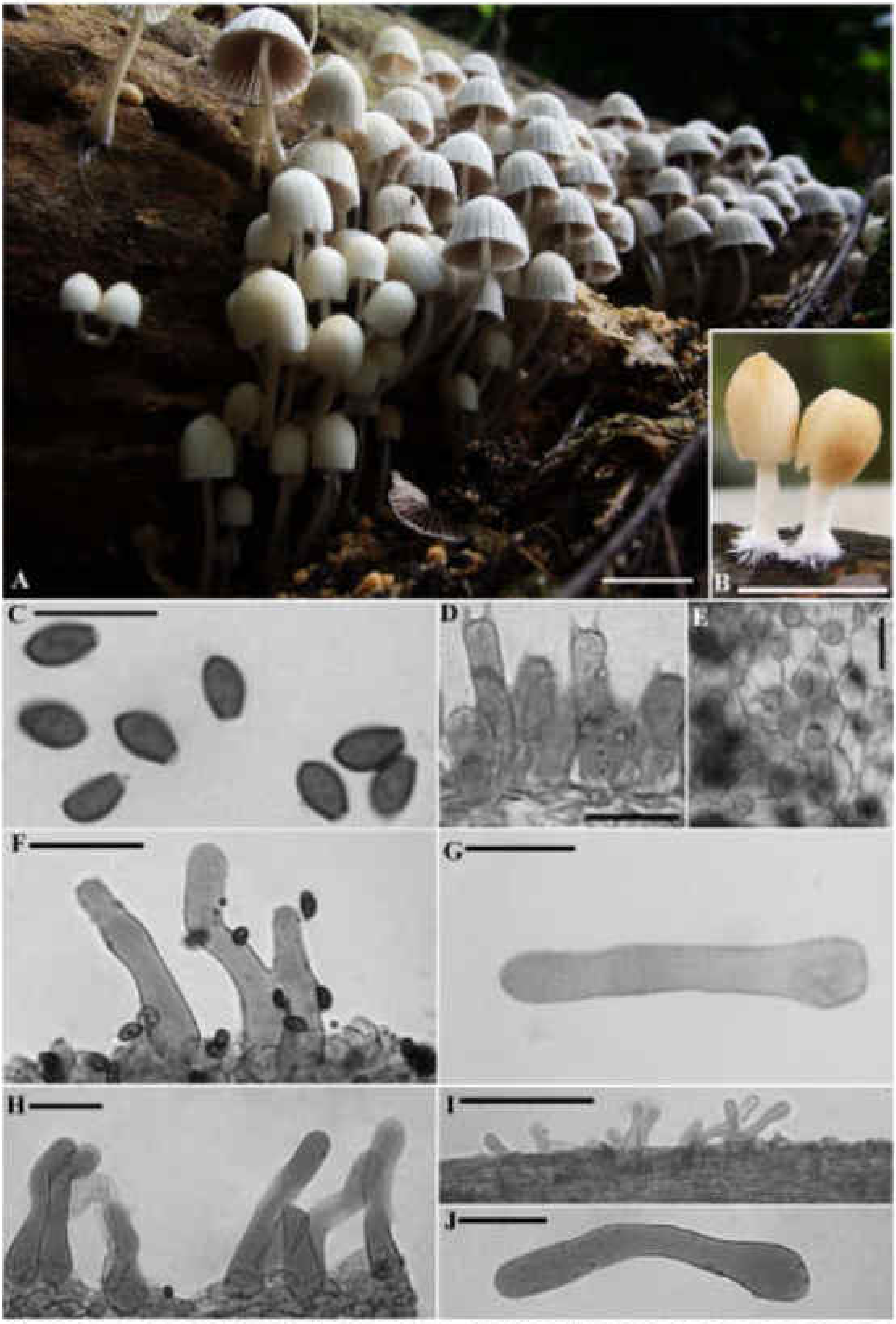

Plate 11. A-J: *Coprinellus disseminatus*. **A-B.** Basidiocarps. **C.** Basidiospores **D.** Basidia. **E.** Pseudoparaphyses. **F.** Cheilocystidia. **G.** Pileocystidium. **H.** Pileipellis. **I.** Stipitipellis. **J.** Caulocystidium. Scale Bars: **A-B** = 10 mm; **C-D** = 20 µm; **E-H & J** = 50 µm; **I** = 200 µm.

hyaline, slightly thick-walled. Stipitipellis a cutis disrupted by clusters of caulocystidia; hyphae 3–7 µm wide, hyaline, slightly thick-walled. Caulocystidia 31–130 × 16–23 µm, abundant, lageniform, hyaline, thin-walled. Clamp connections not observed on any hyphae.

Habit and Habitat:—In small groups, on rotten twigs and barks of logs.

Collections examined:—INDIA. Kerala State, Kozhikode District, Peruvannamuzhi forest: 02 June 2017, *K. G. Greeshma Ganga, G134*; Wayanad District, Edakkal Caves: 18 October 2017, *K. G. Greeshma Ganga, G228*; Ernakulam District, Thattekkad forest, 25 October 2018, *K. G. Greeshma Ganga G292*.

Observations:—*Coprinellus disseminatus*, a widely distributed species (Pegler 1977, 1986*;* Manjula 1983; Uljé 2005), is characterised by small basidiocarps; a broadly paraboloid to campanulate pileus with fine glimmering hairs and plicate-striations; adnate lamellae; a stipe with a slightly enlarged base and strigose mycelium; ovo-ellipsoid basidiospores with a slightly pointed base and truncate apex; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; an epithelioid hymeniderm-type pileipellis with pileocystidia and a cutis-type stipitipellis with caulocystidia. Because of the smaller basidiocarps, the absence of pleurocystidia and clamp connections and a caespitose habit, the present collection belongs to the section *Disseminati* (Wächter & Melzer 2020).

Three ITS (G134: 661 bp; G228: 619 bp; G292: 486 bp) and two nLSU (G134: 894 bp; G228: 874 bp) sequences were generated from the present species. *Coprinellus disseminatus* (MN209934: 99.85% identity) and an unnamed species of *Coprinellus* from Ecuador*, Coprinellus* species DIS 360d (DQ674802: 100% identity) were the closest hits in BLASTn searches using the ITS and nLSU (G134) sequences respectively.

5.1.2.3. *COPRINOPSIS* P. Karst., Acta Soc. Fauna Flora fenn. 2 (1): 27 (1881)

Lentispora Fayod, Annls Sci. Nat., Bot., sér. 79: 379 (1889)
Pselliophora P. Karst., Bidr. Känn. Finl. Nat. Folk 32: 28 (1879)
Rhacophyllus Berk. & Broome, J. Linn. Soc., Bot. 11: 559 (1871)
Zerovaemyces Gorovij, Dokl. Akad. Nauk Ukrainskoĭ SSR, Ser. B: 745 (1977)

Pileus surface usually floccose, often leaving shaggy scales or broad membranous patches, becoming lacerate; margin often uplifted or pendant during deliquescence. Veil present. Lamellae always deliquescent. Basidia dimorphic. Pileipellis a cutis of radially arranged elongated hyphae, often with velar elements; elements consisting of filamentous or swollen, sometimes globose cells or mixtures short or swollen filamentous cells.

Type species: *Coprinopsis friesii* (Quél.) P. Karst.

Key to the sections of the genus *Coprinopsis* described in this study

1. Basidiocarps psathyrelloid; lamellae not deliquescent .... **Section *Quartoconatae***
1. Basidiocarps coprinoid; lamellae deliquescent.. **2**
2. Basidiospores with a myxosporium; pileipellis with globose and warty velar elements.. **Section *Narcoticae***
2. Basidiospores without a myxosporium; pileipellis without globose and warty velar elements.. **3**
3. Pileipellis with thick-walled velar elements **4**
3. Pileipellis with thin-walled velar elements.. **5**
4. Pleurocystidia with lobes or apical projections; velar elements on the pileipellis coralloid.. **Section *Coprinopsis***
4. Pleurocystidia without lobes or apical projections; velar elements on the pileipellis not coralloid ....**Section *Lanatulae***
5. Basidiocarps smaller; pileipellis with gelatinisation .... **Section *Xenobiae***
5. Basidiocarps larger; pileipellis without gelatinisation.. **6**
6. Stipe base with a pseudorrhiza; velar elements on the pileipellis not diverticulate .... **Section *Cinereae***
6. Stipe base without a pseudorrhiza; velar elements on the pileipellis diverticulate .... **Section *Picaceae***

Coprinopsis **section** ***Cinereae*** D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1238 (2020)

Basidiocarps medium- to large-sized. Veil distinct. Stipe often with a pseudorrhiza. Lamellae deliquescent. Basidiospores large, ellipsoid to slightly ovoid in frontal view, smooth or warty, with a truncate, central germ-pore often surrounded by a ridge. Basidia 4-spored. Cheilocystidia globose, ellipsoid or utriform. Pleurocystidia subglobose, ellipsoid, subcylindrical, utriform or lageniform. Pileipellis with velar elements, consisting of chains of more or less hyaline, subcylindrical, not diverticulate cells. Clamp connections present. Habit gregarious to caespitose. Habitat on fimicolous or lignicolous.

Type species: *Coprinopsis cinerea* (Schaeff.) Redhead, Vilgalys & Moncalvo

Only one species belonging to the section *Cinereae* was observed during the present study.

Coprinopsis cinerea (Schaeff.) Redhead, Vilgalys & Moncalvo, in Redhead, Vilgalys, Moncalvo, Johnson & Hopple, Taxon 50 (1): 227 (2001)

Plate 12.

Agaricus cinereus Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 4: 100 (1774)
Agaricus cinereus var. *macrorhizus* (Pers.) Fr., Syst. mycol. (Lundae) 1: 311 (1821)
Agaricus cinereus var. *pullatus* (Bolton) Pers., Syn. meth. fung. (Göttingen) 2: 399 (1801)
Agaricus cinereus var. *tomentosus* Pers., Syn. meth. fung. (Göttingen) 2: 399 (1801)
Agaricus cinereus macrorhizus (Pers.) Fr., Syst. mycol. (Lundae) 1: 311 (1821)
Agaricus cinereus tomentosus (Bull.) Fr., Syst. mycol. (Lundae) 1: 311 (1821)
Agaricus fimetarius var. *cinereus* (Schaeff.) Rabenh., Deutschl. Krypt. -Fl. (Leipzig) 1: 457 (1844)
Agaricus macrorhizus Pers., Observ. mycol. (Lipsiae) 1: 47 (1796)
Agaricus pullatus Bolton, Hist. fung. Halifax (Huddersfield) 1: 20 (1788)
Agaricus radians Batsch, Elench. fung. (Halle): 61 (1783)
Agaricus tomentosus Bull., Herb. Fr. (Paris) 6: 138 (1786)
Coprinopsis cinerea var. *foersterorum* A. Melzer, Der Tintling 61: 5 (2009)
Coprinus cinereus (Schaeff.) Gray, Nat. Arr. Brit. Pl. (London) 1: 634 (1821)
Coprinus cinereus f. *microsporus* (Hongo) Hongo, Trans. Mycol. Soc. Japan 16 (4): 379 (1975)

Coprinus cinereus var. *depressus* Bogart, The Genus *Coprinus* in Washington and Adjacent Western States (Seattle): 84 (1975)
Coprinus cinereus var. *depressus* Bogart, Mycotaxon 8 (1): 290 (1979)
Coprinus cinereus var. *pullatus* (Bolton) Gray, Nat. Arr. Brit. Pl. (London) 1: 634 (1821)
Coprinus cinereus var. *tomentosus* Gray, Nat. Arr. Brit. Pl. (London) 1: 634 (1821)
Coprinus delicatulus Apinis, Trans. Br. mycol. Soc. 48 (4): 653 (1965)
Coprinus fimetarius subsp. *pullatus* (Bolton) Sacc., Syll. fung. (Abellini) 5: 1087 (1887)
Coprinus fimetarius var. *cinereus* (Schaeff.) Fr., Epicr. syst. mycol. (Upsaliae): 246 (1838)
Coprinus fimetarius var. *macrorhizus* (Pers.) Fr., Hymenomyc. eur. (Upsaliae): 324 (1874)
Coprinus fimetarius var. *pullatus* (Bolton) Fr., Epicr. syst. mycol. (Upsaliae): 247 (1838)
Coprinus macrorhizus (Pers.) Rea, Brit. basidiomyc. (Cambridge): 503 (1922)
Coprinus macrorhizus f. *microsporus* Hongo, J. Jap. Bot. 27 (5): 161 (1952)
Coprinus macrorhizus var. *microsporus* (Hongo) Bogart, The Genus *Coprinus* in Washington and Adjacent Western States [Ph.D. dissertation] (Seattle): 81 (1975)
Coprinus macrorhizus var. *microsporus* (Hongo) Bogart, Mycotaxon 8 (1): 287 (1979)
Coprinus pullatus (Bolton) Fr., Epicr. syst. mycol. (Upsaliae): 246 (1838)
Coprinus tomentosus (Bull.) Fr., Epicr. syst. mycol. (Upsaliae): 246 (1838)
Lentispora tomentosa (Bull.) Fayod, Annls Sci. Nat., Bot., sér. 79: 410 (1889)

Description:—Basidiocarps large, fragile. Pileus 12–18 × 9–12 mm when young, finally up to 40 mm diam., initially paraboloid to conical, expanding to applanate; surface white all over when young, becoming white at the centre and on the velar remnants, grey (4E1) elsewhere at maturity, initially covered with a dense, matted-fibrillose veil all over, later the veil radially spitting into appressed- to recurved hairy or fibrillose flocks all over, densely so at the centre, smooth elsewhere at maturity, strongly deliquescent; margin initially straight, later collapses at maturity. Lamellae adnexed, crowded, initially white, becoming black with age; edge not observed due to deliquescence. Stipe 105–170 × 5–11 mm, central, tapering towards the apex, hollow; surface white, smooth, slightly floccose towards the base; base subbulbous often with a psuedorrhiza. Odour and taste not distinctive.

Basidiospores 8–11 × 5–6 × 5–6 µm, on an average 9.42 × 5.95 × 5.85 µm, Q_1 = 1.42–1.83, Q_{1avg} = 1.65, Q_2 = 1.33–1.8, Q_{2avg} = 1.54, lenticular, oblong-ellipsoid to ovo-ellipsoid in face view, oblong in side view with an apical cap or ridge, dark brown, thick-walled, with a central germ-pore up to 2 µm wide. Basidia 12–20 × 8–10 µm, clavate to pedicellate-clavate, hyaline, slightly thick-walled, surrounded by 4–7 pseudoparaphyses, 4-spored; sterigmata up to 4 µm long. Pleurocystidia 60–80 × 27–40 µm, abundant, clavate to subcylindrical, hyaline, thin-walled. Lamella-

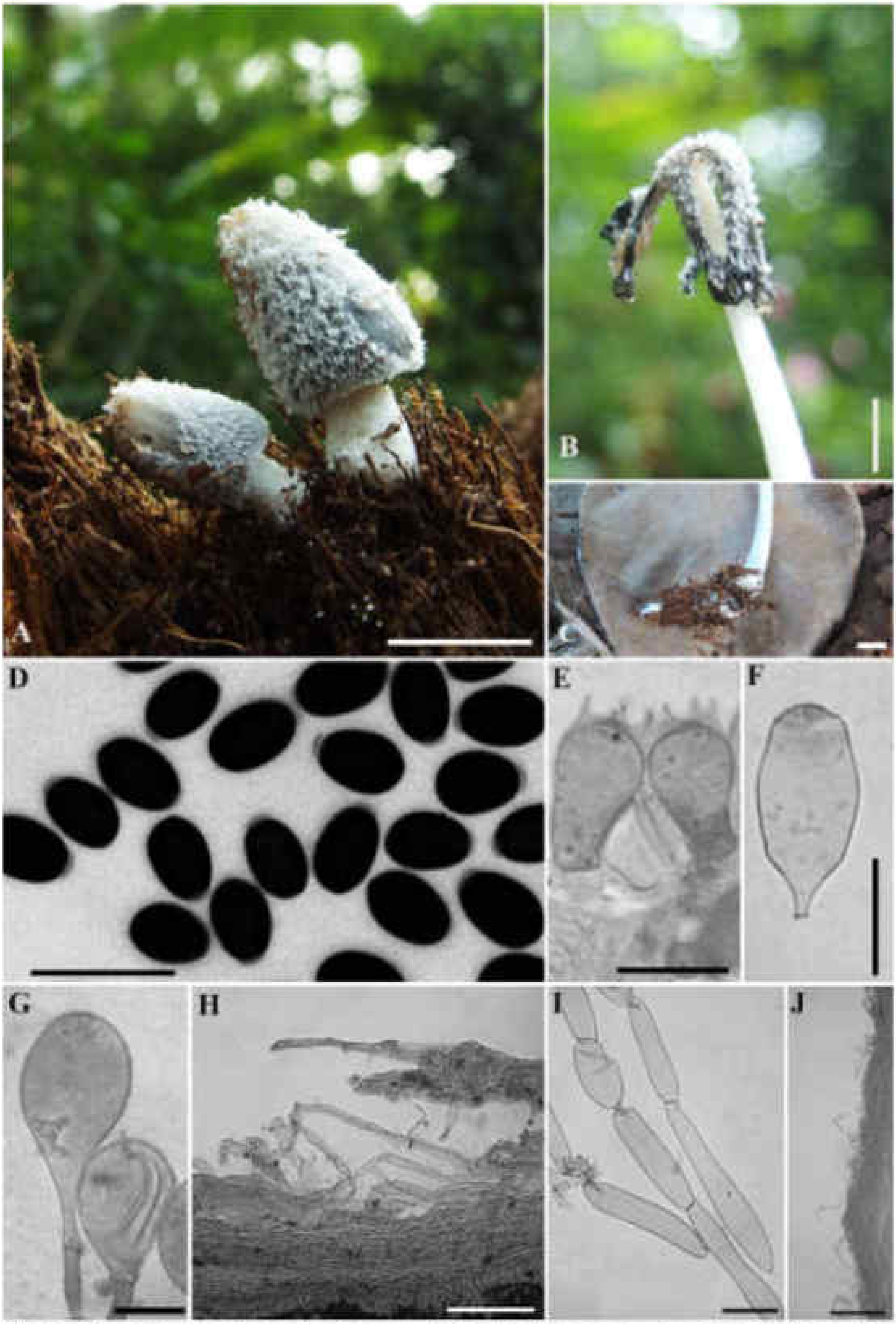

Plate 12. A-J: *Coprinopsis cinerea*. A-B. Basidiocarps. **C.** psuedorrhiza. **D.** Basidiospores. **E.** Basidia. **F.** Pleurocystidium. **G.** Cheilocystidia. **H.** Pileipellis. **I.** Velar elements on the pileipellis. **J.** Stipitipellis. Scale Bars: **A-B** = 10 mm; **D, E & G** = 20 µm; **F, I** = 50 µm; **H, J** = 200 µm.

edge sterile. Cheilocystidia 23–45 × 20–30 µm, abundant, often pedicellate-clavate, sometimes subglobose to clavate, hyaline, thin-walled. Pileipellis a cutis overlaid with chains of velar elements; hyphae 10–15 µm wide, hyaline, thin-walled; velar elements 34–140 × 13–30 µm, cylindrical to sausage-shaped, often constricted at the septa, hyaline, thin-walled. Stipitipellis a cutis with scattered patches of velar hyphae; hyphae 7–10 µm wide, hyaline, thin-walled; velar hyphae 2–11 µm wide, hyaline, thin-walled. Clamp connections observed only on velar elements on the pileipellis and at the base of cheilocystidia.

Habit and Habitat:—In small groups, on decaying coconut tree trunk or on decaying cow dung.

Collections examined:—INDIA. Kerala State, Thrissur District, Punnayoorkulam: 05 October 2017, *K. G. Greeshma Ganga G222*; 09 October 2017, *K. G. Greeshma Ganga G113*; Malappuram District, Calicut University Campus: 17 October 2018, *K. G. Greeshma Ganga G285*.

Observations:—*Coprinopsis cinerea*, a species reported from several geographic regions, including India (Manjula 1983; Uljé 2005), is characterised by larger basidiocarps; a pileus with white, hairy to fibrillose velar remnants; deliquescent lamellae; a stipe with a subbulbous base and psuedorrhiza; larger basidiospores with an apical cap or ridge; 4–7 pseudoparaphyses surrounding each basidium; a lamella-edge with cheilocystidia; a hymenium with clavate to subcylindrical pleurocystidia; a cutis-type pilei- and stipitipellis with velar elements. The presence of larger basidiocarps, ellipsoid to ovoid basidiospores with an apical cap surrounding the germ-pore, the absence of diverticulate velar elements on the pileipellis and a caespitose habit and lignicolous habitat placed the present species to the section *Cinereae* (Wächter & Melzer 2020).

Coprinopsis cinerea was the closest hit in megablast searches with both the ITS (476 bp; MN173118 (99.79% identity)) and the nLSU sequences (916 bp; MH87582 (99.56% identity)).

Coprinopsis **section** ***Coprinopsis*** P. Karst., Acta Soc. Fauna Flora fenn. 2 (1): 27 (1881)

Basidiocarps small to medium-sized. Pileus with strongly developed veil. Lamellae deliquescent. Basidiospores medium to large-sized, ellipsoid, ovoid, subtriangular or subglobose in frontal view, laterally sometimes distinctly flattened. Basidia 4-spored. Cheilocystidia utriform, clavate or fusiform. Pleurocystidia utriform, subcylindrical, clavate, fusiform or sometimes mucronate. Pileipellis with velar elements consisting of chains of diverticulate, thin- or thick-walled, hyaline to brownish pigmented, more or less coralloid cells. Clamp connections present in most cases. Habitat fimicolous, terrestrial, herbicolous or lignicolous.

Type species: *Coprinopsis friesii* (Quél.) P. Karst.

Two species belonging to the section *Coprinopsis* were encountered during the present study.

Key to the species

1. Pileus with white and floccose velar remnants; pileipellis with hyaline velar elements.. ***Coprinopsis minuta***

1. Pileus with brown and squamulose velar remnants; pileipellis with brown velar elements...***Coprinopsis squamulosa***

Coprinopsis minuta K.G.G. Ganga, Manim. & K.P.D. Latha, Phytotaxa 575 (2): 151 (2022) **Plate 13.**

Description:—Basidiocarps very small, fragile. Pileus 3–6 mm diam. when mature, initially ovoid, paraboloid or cylindrical, then expanding to broadly paraboloid to convex; surface pure white when young, becoming orange grey (5B2) with white velar remnants, initially completely covered with a thick floccose veil that later splitting into superficial, velar patches all over; margin initially incurved to straight,

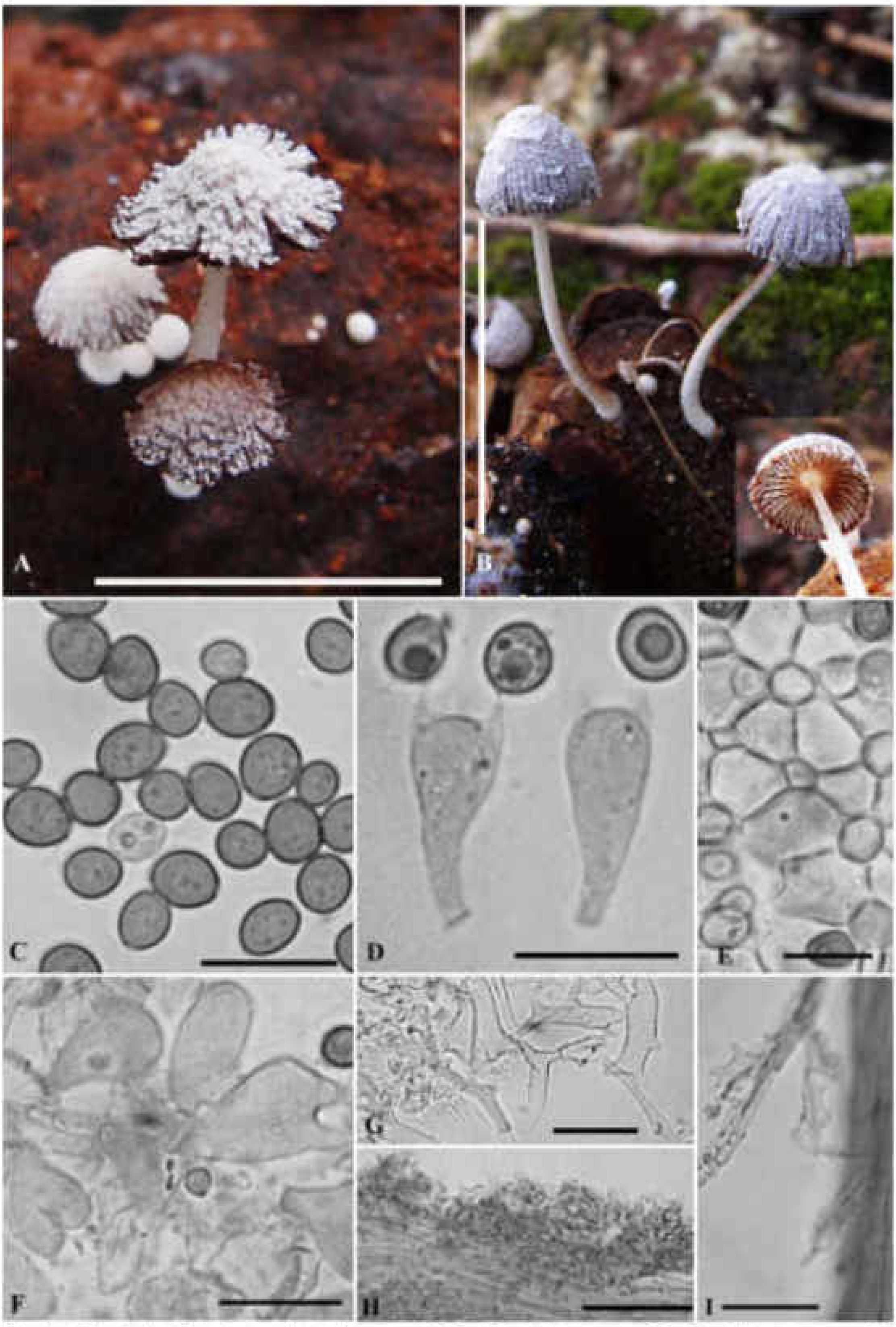

Plate 13. A-I: ***Coprinopsis minuta***. **A-B.** Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Psuedoparaphyses. **F.** Pleurocystidia. **G.** Velar elements on the pileipellis. **H.** Pileipellis. **I.** Stipitipellis. Scale Bars: **A-B** = 10 mm; **C-F** = 20 µm; **G-I** = 50 µm.

becoming decurved or slightly revolute, often fissile, deliquescent at maturity. Lamellae free, crowded, initially white, becoming dark brown (7F7) with age; edge not observed due to deliquescence. Stipe 11–15 × 0.5–1 mm, central, tapering towards the apex, hollow; surface white, finely squamulose all over, slightly floccose towards the base; base somewhat marginate-bulbous with a profuse basal mycelium. odour and taste not distinctive.

Basidiospores 6–8(9) × 5–7.5 × 5–6 µm, on an average 7.22 × 6.2 × 5.47 µm, Q1 = 1–1.4, Q1avg = 1.17, Q2 = 1–1.4, Q 2avg = 1.23, lenticular, subglobose to ovoid with a rounded base and apex, ellipsoid in side view, brown, thick-walled, with a central germ-pore up to 2 µm wide. Basidia 15–20 × 6–9 µm, clavate to pedicellate-clavate, hyaline, slightly thick-walled, surrounded by 5–6 pseudoparaphyses, 4-spored; sterigmata up to 3 µm long. Pleurocystidia 13–22 × 7–15 µm, broadly clavate with 2–3 lobed apex, hyaline, thin-walled. Lamella-edge not observed due to deliquescence. Cheilocystidia not observed. Pileipellis a cutis frequently disrupted by clumps of velar elements; hyphae 3–5 µm wide, subcylindrical, hyaline, thin-walled; velar elements 17–50 × 5–15 µm, branched, coralloid, hyaline, slightly thick-walled. Stipitipellis a cutis disrupted with velar elements; hyphae 3–8 µm wide, hyaline, slightly thick-walled; velar elements 5–14 × 2–8 µm, almost similar to the velar elements on the pileipellis, hyaline, slightly thick-walled. Clamp connections not observed on any hyphae.

Habit and Habitat:—In small groups or scattered, on decaying twigs or rotten fruit pods of rubber tree (*Hevea brasiliensis*).

Collections examined:—INDIA. Kerala State: Malappuram District, Calicut University Campus, 23 July 2016, *K. G. Greeshma Ganga G23*; 12 August 2016. *K. G. Greeshma Ganga G63* (CALI).

Observations:—Very small basidiocarps with floccose velar remnants on the pileus; free lamellae; a stipe with a profuse basal mycelium; subglobose to ovoid basidiospores with a rounded base, 5–6 pseudoparaphyses surrounding each basidium; a hymenium with pleurocystidia; a lamellae-edge devoid of cheilocystidia and a cutis-type pilei- and stipitipellis with velar hyphae are the characteristic features of *C. minuta*. The characters such as smaller basidiocarps, deliquescent lamellae, subglobose basidiospores and a cutis-type pileipellis with hyaline and coralloid velar elements lead the present species into the section *Coprinopsis* (Wächter & Melzer 2020). A detailed description including the taxonomy and phylogeny of this species has been provided by Ganga *et al*. (2022).

Coprinopsis squamulosa K.G.G. Ganga, Manim. & K.P.D. Latha, Phytotaxa 575 (2): 155 (2022) **Plate 14.**

Description:—Basidiocarps small, fragile. Pileus 7–15 × 4–12 mm when young, finally 10–24 mm diam., initially paraboloid to cylindrical, expanding to plano-convex with age; surface brown (6E6) all over when young, at maturity the squamules becoming dark brown (6F6) at the centre and whitish elsewhere, initially completely covered with appressed-squamules, at maturity with recurved squamules scattered on and around the centre and floccose elsewhere, strongly deliquescent; margin initially straight, becoming upturned with age. Lamellae not observed due to deliquescence, initially white, becoming black at maturity. Stipe 20–55 × 2–3 mm, central, tapering towards the apex, hollow; surface white, smooth, slightly fibrillose towards the base; base slightly enlarged, often with a distinct basal disc. Odour and taste not distinctive.

Basidiospores (7)8–9 × 5–7 × 5–6 µm, on an average 8.6 × 5.2 × 5.0 µm, Q1 = 1.1 1.6, Q1avg = 1.3, Q2 = 1.3–1.8, Q 2avg = 1.4, lenticular, ovoid to ovo-ellipsoid with a rounded base and somewhat truncate apex in face view, amygdaliform to subamygdaliform in side view, dark brown, thick-walled, with a central germ-pore up to 2.5 µm wide. Basidia 12–25 × 9–10 µm, clavate, hyaline, slightly thick-walled, surrounded by 4–5 pseudoparaphyses, 4-spored; sterigmata up to 5 µm long.

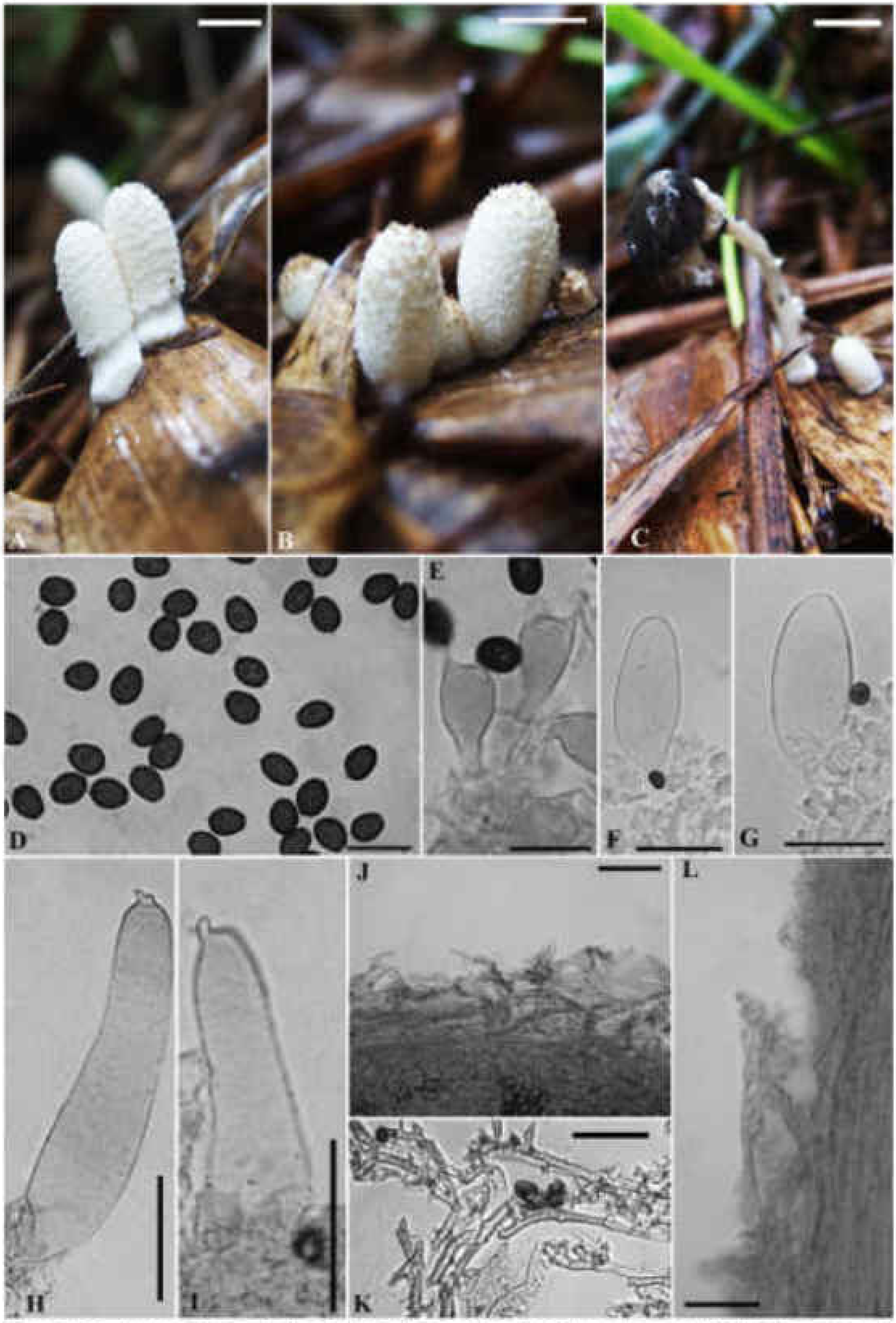

Plate 14. A-L: ***Coprinopsis squamulosa*****. A-C.** Basidiocarps. **D.** Basidiospores. **E.** Basidia. **F-G.** Cheilocystidia. **H-I.** Pleurocystidia. **J.** Pileipellis. **K.** Velar elements on the pileipellis. **L.** Stipitipellis. Scale Bars: **A-C** = 10 mm; **D, E** = 20 µm; **F-L** = 50 µm.

Pleurocystidia 78–95 × 20–38 µm, abundant, cylindrical to sublageniform with short finger-like projections at the apex, finely encrusted, hyaline, thick-walled. Lamella-edge heterogeneous. Cheilocystidia 46–65 × 22–27 µm, ellipsoid to cylindrical often with finger-like projections at the apex, hyaline, thin-walled. Pileipellis a cutis composed of elongate, parallelly arranged hyphae with loosely bound, narrow and inflated velar elements; hyphae 3–12 µm wide, hyaline, thick-walled; narrow velar elements 4–14 µm wide, cylindrical to subcylindrical or coralloid, regularly branched, diverticulate, hyaline, thin-walled; inflated velar elements 5–10 µm wide, frequently coralloid, pale brown to brown, thick-walled (up to 3 µm thick). Stipitipellis a cutis finely overlaid with velar elements; hyphae 10–32 µm wide, hyaline, thin-walled; velar elements similar to those on the pileipellis, 2–6 µm wide, hyaline, slightly thick-walled. Clamp connections observed only on velar elements on both the pilei- and stipitipellis.

Habit and Habitat:—Scattered or in small groups, on decaying bamboo litter.

Collection examined:—INDIA. Kerala State: Malappuram District, Calicut University Botanical Garden, 12 June 2019, *K. G. Greeshma Ganga G297* (CALI).

Observations:—*Coprinopsis squamulosa* is characterised by small basidiocarps; a floccose pileus with dark brown squamules at the centre; strongly deliquescent lamellae; a stipe with a distinct basal disc; ovoid to ovo-ellipsoid basidiospores with a wide and central germ-pore, 4–5 pseudoparaphyses surrounding each basidium; a hymenium with finely encrusted pleurocystidia; a lamella-edge with cheilocystidia and a cutis-type pilei- and stipitipellis with thick-walled and coralloid velar elements. Smaller basidiocarps, cylindrical to sublageniform pleurocystidia and a cutis-type pileipellis with coralloid, brown velar elements assigned *C. squamulosa* to the section *Coprinopsis* (Wächter & Melzer 2020). The taxonomy and phylogeny of this species have been discussed in Ganga *et al*. (2022).

Coprinopsis **section** ***Lanatulae*** (J.E. Lange) D.J. Schaf. [as 'Lanatuli'], Field Mycology 11 (2): 51 (2010)

Basidiocarps small to large-sized. Veil strongly developed. Lamellae deliquescent. Basidiospores medium to large-sized, ellipsoid in frontal view, regularly without a myxosporium, germ-pore central. Basidia mostly 4-spored. Pleurocystidia often present. Cheilocystidia globose, ellipsoid, clavate or sometimes mixed utriform. Pileipellis with velar elements consisting of chains of subcylindrical to subglobose, hyaline or brownish-pigmented cells. Clamp connections present. Habitat terrestrial or fimicolous.

Type species: *Coprinopsis lagopus* (Fr.) Redhead, Vilgalys & Moncalvo.

Only one species of this section, *Lanatulae,* was observed during the present study.

Coprinopsis pachyderma (Bogart) Redhead, Vilgalys & Moncalvo, in Redhead, Vilgalys, Moncalvo, Johnson & Hopple, Taxon 50 (1): 230 (2001)

Plate 15.

Coprinus pachydermus Bogart, Mycotaxon 8 (1): 274 (1979)
Coprinus pachydermus Bogart, The Genus *Coprinus* in Washington and Adjacent Western States [Ph.D. dissertation] (Seattle): 71 (1975)

Description:—Basidiocarps small, fragile. Pileus 17–20 mm diam. at maturity, initially ellipsoid to cylindrical, expanding to broadly conico-convex; surface white when young, becoming dark brown (6F6) to yellowish brown (5F7) on the velar squamules at the centre and paler towards the margin, white elsewhere, initially appressed-fibrillose all over, becoming hairy to squamulose all over at maturity, plicate-striate, partially deliquescent at maturity; margin straight when young, incurved at maturity. Lamellae free, subclose to close, initially white, becoming black with age; edge even, concolourous with the sides. Stipe 45–57 × 3–4 mm, central, tapering towards the apex, hollow; surface white, finely fibrillose all over,

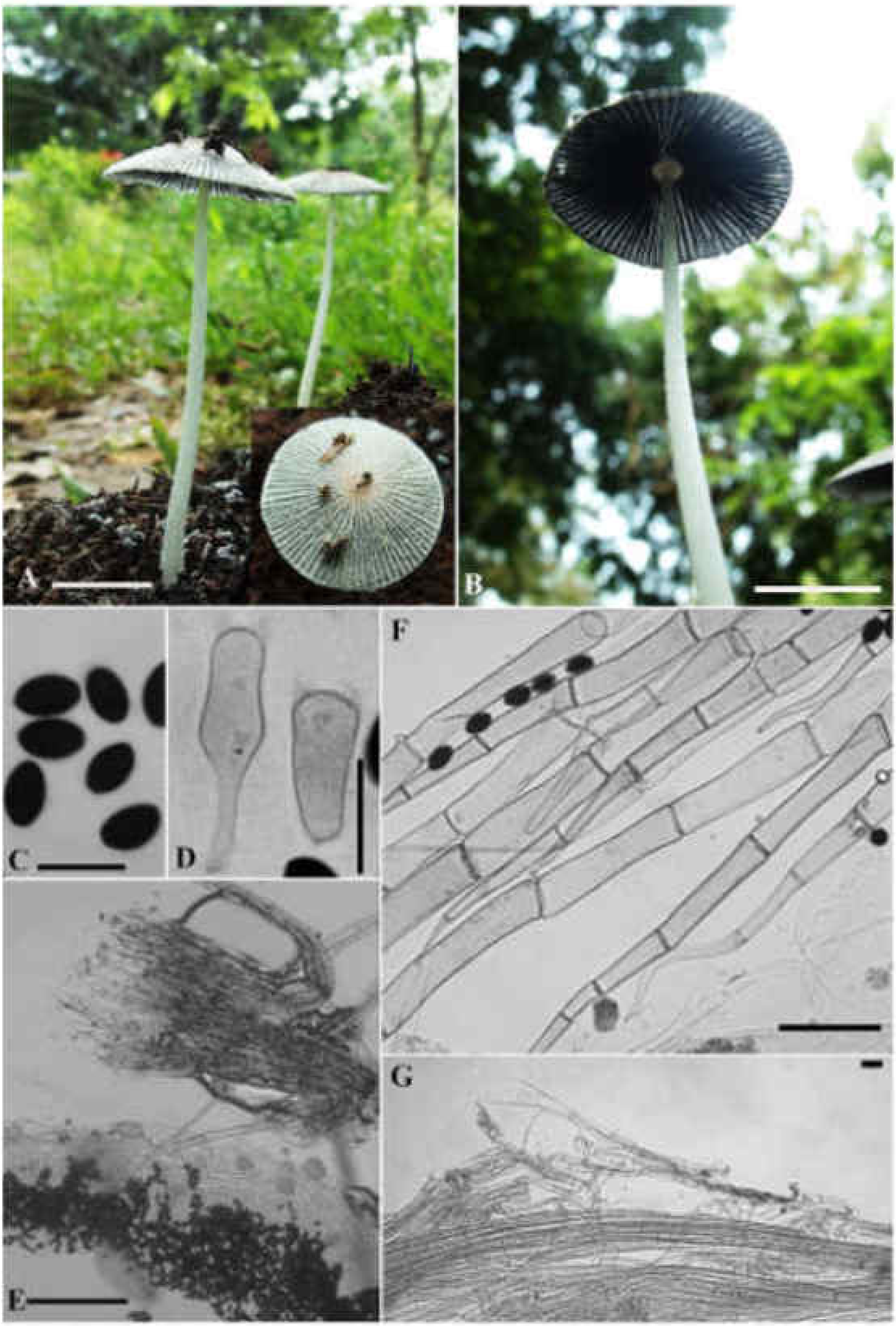

Plate 15. A-G: ***Coprinopsis pachyderma*****. A-B.** Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Pileipellis. **F.** Velar elements on the pileipellis. **G.** Stipitipellis. Scale Bars: **A-B** = 10 mm; **C & D** = 20 µm; **E** = 200 µm; **F & G** = 50 µm.

more so towards the base; base not enlarged, inserted. Odour and taste not distinctive.

Basidiospores 10–11 × 6 × 6–7 µm, on an average 10.3 × 6 × 6.1 µm, Q_1 = 1.66–1.83, Q_{1avg} = 1.72, Q_2 = 1.57–1.83, Q_{2avg} = 1.68, lenticular, ellipsoid to oblong-ellipsoid with a pointed base in face view, ellipsoid in side view, black to dark brown, thick-walled, with a central germ-pore up to 2 µm wide. Basidia 16–30 × 7–9 µm, clavate or elongate-clavate with a median constriction, hyaline, slightly thick-walled, surrounded by 4–5 pseudoparaphyses, 4-spored; sterigmata up to 3 µm long. Pleurocystidia not observed. Lamella-edge fertile. Cheilocystidia not observed. Pileipellis a cutis disrupted with clusters of chains of velar hyphae; hyphae inflated, 25–55 × 12–39 µm, hyaline, thin-walled; velar hyphae >300 µm long, septate, subcylindrical, gradually tapering to an acute apex, brown, thick-walled, terminal cells 20–125 µm long. Stipitipellis a cutis overlaid with elongated velar hyphae; hyphae 9–14 µm wide, hyaline, thin-walled; velar hyphae somewhat similar to those on the pileipellis, hyaline, thin-walled. Clamp connections observed only on velar elements on the pileipellis.

Habit and Habitat:—Solitary or in small groups, on decaying elephant dung.

Collection examined:—INDIA. Kerala State, Kannur District, Dung samples collected from Aralam Forest and incubated in the lab: 15 September 2017, *K. G. Greeshma Ganga G213.*

Observations:—*Coprinopsis pachyderma*, a species originally described from Washington (Bogart 1979), is characterised by smaller basidiocarps; a broadly conico-convex pileus with squamules; free lamellae; a white stipe with a finely fibrillose surface; ellipsoid to oblong-ellipsoid basidiospores; a hymenium devoid of pleuro- and cheilocystidia; a cutis-type pileipellis with clusters of thick-walled velar hyphae and a cutis-type stipitipellis with thin-walled velar hyphae. As this collection includes only mature specimens, the cystidia might collapse due to deliquescence. Because of ellipsoid basidiospores, strongly developed velar remnants on the pileus, a cutis-type pileipellis with chains of subcylindrical, brown velar hyphae and the habitat on dung, the present collection could be placed in the section *Lanatulae* (Wächter & Melzer 2020).

Comparison of the ITS (670 bp) and the nLSU (888 bp) sequences with those available in GenBank showed that the present species is *C. pachyderma*. *Coprinopsis pachyderma* was the closest hit in megablast searches for both the ITS (MK169350; 99.55% identity) and the nLSU (OL376337; 99.56% identity) sequences.

Coprinopsis **section** ***Narcoticae*** (Uljé & Noordel.) D.J. Schaf., Field Mycology 11(2): 51, (2010)

Basidiocarps tiny to medium-sized. Pileus with a strongly developed veil. Lamellae deliquescent. Odour sometimes unpleasant. Basidiospores small to large-sized, ellipsoid in frontal view, always with a more or less distinct myxosporium and a central germ-pore. Basidia 4-, 2-, rarely 3-spored. Pleurocystidia subglobose cells and utriform, fusiform or lageniform cheilocystidia. Cheilocystidia similar to pleurocystidia usually slightly larger. Pileipellis with velar elements predominantly consisting of globose, densely warty cells, connected by thin, often also warty and diverticulate hyphae, mostly hyaline, thin-walled or slightly thick-walled. Clamps present or absent. Terrestrial, lignicolous or fimicolous.

Type species: *Coprinopsis narcotica* (Batsch) Redhead, Vilgalys & Moncalvo

Only one species belonging to the section *Narcoticae* was observed during the present study.

Coprinopsis sclerotiger (Watling) Redhead, Vilgalys & Moncalvo, in Redhead, Vilgalys, Moncalvo, Johnson & Hopple, Taxon 50 (1): 231 (2001)

Plate 16.

Coprinus sclerotiger Watling, Notes R. bot. Gdn Edinb. 32 (1): 130 (1972)

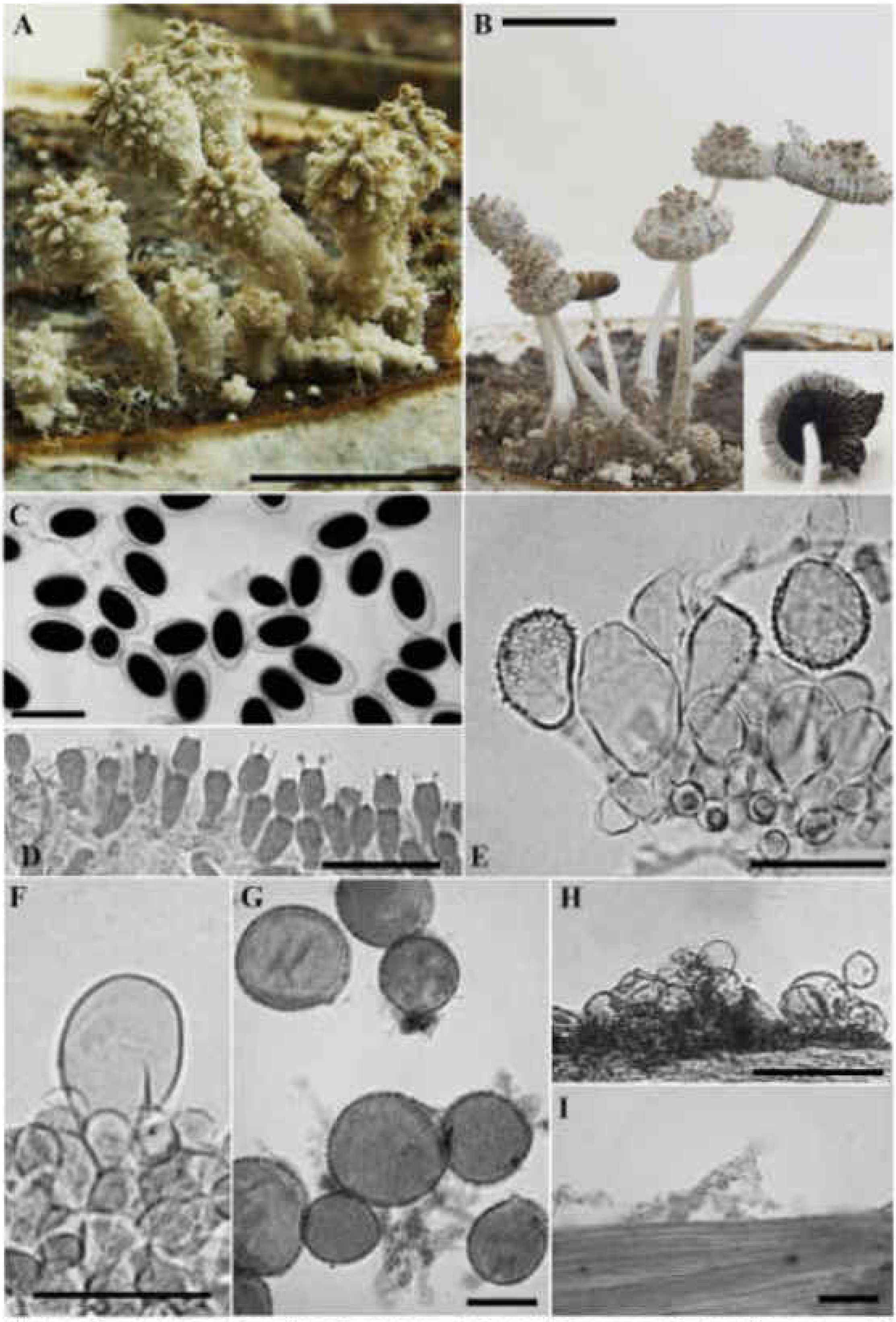

Plate 16. A-I: ***Coprinopsis sclerotiger***. **A-B.** Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Cheilocystidia. **F.** Pleurocystidium. **G.** Velar elements on the pileipellis. **H.** Pileipellis. **I.** Stipitipellis. Scale Bars: **A** = 5 mm; **B** = 10 mm; **C,E** = 20 µm; **D, F, G & I** = 50 µm; **H** = 200µm.

Description:—Basidiocarps small, fragile. Pileus 2 × 4 mm when young, finally up to 7 mm diam., initially oblong to ellipsoid, expanding to convex; surface white when young, becoming light brown (5D4) or yellowish brown (5F8) on the velar remnants, white elsewhere with age, initially completely covered with a mealy or granulose veil that later splitting into conical flocks of velar remnants all over, densely so towards the centre, matted-fibrillose elsewhere at maturity, partially deliquescent; margin initially straight or incurved, becoming inrolled or sometimes revolute at maturity. Lamellae free, crowded, initially white, becoming black with age; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 20–37 × 1.5–2 mm, central, tapering towards the apex, hollow; surface off-white, floccose towards the base, often with an inferior annulus; base subbulbous, often with a dark and cylindrical sclerotium. Odour and taste not distinctive.

Basidiospores 7–10 × 5–6 × 5 µm, on an average 9.22 × 5.05 × 5 µm, Q_1 = 1.4–2.0, Q_{1avg} = 1.86, Q_2 = 1.4–2.0, Q_{2avg} = 1.81, lenticular, oblong in face view, ellipsoid in side view, with a rounded base and apex, black to dark brown, thick-walled, with a well-developed myxosporium, extended up to 4 µm wide, with a central germ-pore up to 2 µm wide. Basidia 16–24 × 9–11 µm, clavate to pedicellate-clavate, hyaline, thin-walled, surrounded by 4–5 pseudoparaphyses, 4-spored; sterigmata 4 µm long. Pleurocystidia 37–78 × 24–36 µm, abundant, subglobose, cylindrical to clavate, hyaline, thin-walled. Lamella-edge sterile. Cheilocystidia 23–45 × 20–30 µm, abundant, subglobose, cylindrical to clavate often with a short pedicel, smooth or warty, hyaline, thin-walled. Pileipellis a cutis overlaid with velar elements; hyphae 5–8 µm wide, hyaline or with a pale brown wall pigment and brown encrustations, thin-walled; velar elements 23–73 µm wide, globose, often with warty or nipple-like projections, connected with a network of narrow, diverticulate hyphae, 5–10 µm wide, hyaline, thin-walled. Stipitipellis a cutis overlaid with velar hyphae; hyphae 5–14 µm, hyaline, thin-walled; velar hyphae 3–6 µm wide, branched, diverticulate, hyaline, thin-walled. Clamp connections not observed on any hyphae.

Habit and Habitat:—In small groups, on decaying cow dung that incubated in the lab.

Collection examined:—INDIA. Kerala State, Malappuram District, Mongam: 22 November 2017, *K. G. Greeshma Ganga G247*.

Observations:—*Coprinopsis sclerotiger,* a species originally described from Britain (Watling 1972), has smaller basidiocarps; a pileus covered with conical flocks of velar remnants; partially deliquescent lamellae; a stipe with an inferior annulus and a sclerotium at the base; oblong to ellipsoid basidiospores with a rounded base and myxosporium; a hymenium with abundant pleurocystidia; a lamella-edge with cheilocystidia; a cutis-type pileipellis with warty velar elements and a cutis-type stipitipellis with diverticulate velar hyphae. The present collection agrees with almost all characters of *C. sclerotiger* except for warty cheilocystidia and a coprophilous habitat. The present collection shows warty globose velar elements connected with a network of narrow and diverticulate hyphae on the pileipellis and a myxosporium enveloping each basidiospore; hence, it belongs to the section *Narcoticae* (Wächter & Melzer 2020).

Comparison of the ITS (674 bp) and nLSU (902 bp) sequences with those available in GenBank showed that the present species is *C. sclerotiger*. The closest hits in a BLASTn search using the ITS sequence were an unnamed species of *Coprinopsis* from Vietnam*, Coprinopsis* species PTN2018-1 (LC425103; 99.85% identity), followed by *C. sclerotiger* (KR869759; 99.41% identity). The nLSU sequence also revealed *C. sclerotiger* (GQ249286; 99.56% identity) as the closest hit.

Coprinopsis* section *Picaceae (Penn.) D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1254 (2020)

Basidiocarps large-sized. Pileus initially completely covered with velar remnants, later tearing into patches. Lamellae deliquescent. Basidiospores medium- to large-sized, ellipsoid to slightly ovoid in frontal view, germ-pore central. Basidia 4-spored. Pleurocystidia utriform, lageniform, subcylindrical, fusiform, ellipsoid, globose. Cheilocystidia versiform, often mixed with clavate cells. Pileipellis with velar elements consisting of chains of somewhat diverticulate, thin-walled, hyaline cells. Clamp connections present. Habitat terrestrial or lignicolous.

Type species: *Coprinopsis picacea* (Bull.) Redhead, Vilgalys & Moncalvo

Only one species belonging to the section *Picaceae* was encountered during this study.

***Coprinopsis* species 1** **Plate 17.**

Description:—Basidiocarps large, delicate. Pileus 23–35 × 18–30 mm, initially ellipsoid to paraboloid, becoming campanulate, never fully expanding to applanate; surface off-white all over when young, becoming light brown (6D5) to brown (6E6) or dark brown (6F5) all over with age, strongly deliquescent, initially completely covered with an off-white veil that later splitting into small felty patches all over, translucent-striate or striate towards the margin; margin straight when young, revolute at maturity, initially even, splits during deliquescence. Lamellae adnate, strongly crowded, initially grey (5C1), becoming black at maturity, hard to separate individual lamellae from adjacent ones; edge even, initially white, becoming black with age. Stipe 60–160 × 5–10 mm, central, terete, equal, hollow; surface white, finely pruinose, more so towards the base; base slightly enlarged. Odour and taste not distinctive.

Basidiospores 6–7(8) × 4–5 × 4–5 µm, on an average 6.4× 4.9 × 4.9 µm, Q_1 =1.2–1.5, Q_{1avg} = 1.25, Q_2 = 1.2–1.75, Q_{2avg} = 1.38, ellipsoid with a rounded base and apex in face view, oblong ellipsoid in side view, brown, thick-walled, with a central germ-pore up to 2 µm wide. Basidia 19–27 × 6–8 µm, clavate, hyaline, thin- to slightly thick-walled, surrounded by 4–6 pseudoparaphyses, 4-spored; sterigmata up to 3 µm long. Pleurocystidia 150–195 × 30–45 µm, abundant, sublageniform or subcylindrical to utriform, often with a short pedicel, hyaline with encrustations, slightly thick-walled. Lamella-edge fertile. Cheilocystidia not observed. Pileipellis a differentiated cutis with parallelly arranged narrow hyphae and a distinct hypodermium composed of inflated elements and velar elements; narrow hyphae 2–4 µm wide, hyaline, thin-walled; inflated elements 38–96 × 15–30 µm, hyaline, thin-walled; velar elements 8–17 µm wide, branched or diverticulate, hyaline, thin-walled. Stipitipellis a cutis rarely overlaid with clumps of nodulose-diverticulate velar hyphae; hyphae 3–11 µm wide, hyaline, thin-walled; velar hyphae 4–9 µm wide, hyaline, thin-walled. Clamp connections observed only on the hyphae of pileipellis and velar elements.

Habit and Habitat:—Solitary or in small groups, scattered on humus rich soil.

Collections examined:—INDIA. Kerala State, Kollam District, Thenmala: 22 June 2018, *K. G. Greeshma Ganga G265*; 23 June 2018, *K. G. Greeshma Ganga G268.*

Observations:—The present species is characterised by larger basidiocarps; a campanulate pileus that never becomes applanate at maturity; strongly deliquescent lamellae; a white stipe with a pruinose surface; small, ellipsoid basidiospores with a truncated apex; 4–6 pseudoparaphyses surrounding each basidium; a fertile lamella-edge devoid of cheilocystidia; a hymenium with abundant and encrusted pleurocystidia; a differentiated cutis-type pileipellis with diverticulate velar elements; a cutis-type stipitipellis with nodulose diverticulate velar elements and a habitat on soil. The characters such as the larger

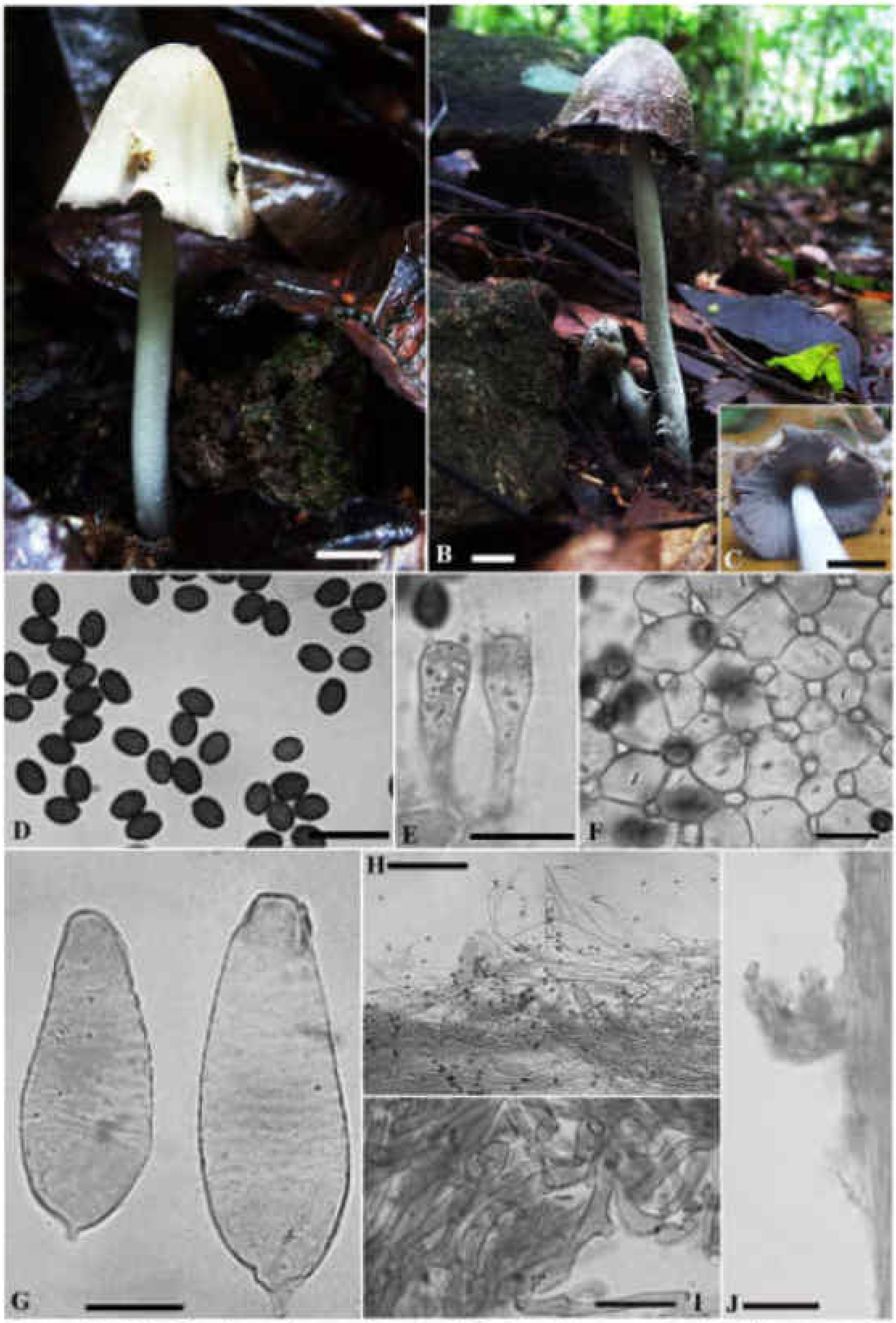

Plate 17. A-J: ***Coprinopsis* species 1**. **A-C.** Basidiocarps. **D.** Basidiospores. **E.** Basidia. **F.** *Pseudoparaphyses*. **G.** Pleurocystidia. **H.** Pileipellis. **I.** Velar elements on the pileipellis. **J.** Stipitipellis. Scale Bars: **A-C** = 10 mm; **D, E, G & I** = 20 µm; **F, H & J** = 50 µm.

basidiocarps, a pileus with patches of velar remnants, ellipsoid basidiospores with a central germ-pore, a hymenium with sublageniform, subcylindrical or utriform pleurocystidia, a pileipellis composed of diverticulate, thin-walled and hyaline velar elements, clamped hyphae and a terrestrial habitat are indicatives of the section *Picaceae* (Wächter & Melzer 2020).

Coprinopsis strossmayeri (Schulzer) Redhead, Vilgalys & Moncalvo, a species previously reported from the Netherlands and Japan (Uljé 2005), resembles the present species in having similar size and shape of the basidiocarps, light brown to brown pileus and the presence of small, felty velar patches on the pileus surface. However, *C. strossmayeri* differs from the present species in having an umbonate pileus, dark brown hairs at the base of the stipe with dense rhizomorphs, a strong odour of mould, larger basidiospores (7.0–9.0 µm), 3–5 pseudoparaphyses surrounding each basidium, a hymenium with smooth pleurocystidia, a lamella-edge with cheilocystidia, encrusted velar elements on the pileipellis and a fasciculate and lignicolous habitat. *Coprinopsis atramentaria* (Bull.) Redhead, Vilgalys & Moncalvo, a cosmopolitan species (Uljé 2005), shows some similarity to the present species in having almost similar-sized basidiocarps, crowded lamellae and ellipsoid basidiospores with a rounded base and apex. However, *C. atramentaria* differs from the present species by the following features; a pileus which is applanate when mature, larger basidiospores (8–12 × 6–8 µm), a lamella-edge with cheilocystidia, non-encrusted pleurocystidia, elongate and unbranched velar elements on the pileipellis and a habitat on dung mixed with rotten straws and vegetable refuse.

Coprinopsis goudensis (Uljé) Redhead, Vilgalys & Moncalvo, a species originally described from the Netherlands (Uljé & Bas 1993), is similar to the present species in having white velar remnants on the pileus, thin-walled and ellipsoid basidiospores and branched and diverticulate velar elements on the pileipellis. However, *C. goudensis* has smaller basidiocarps (pileus up to 20 mm diam. and stipe 40 × 1–1.5 mm) with an applanate pileus, larger basidiospores (7.0–9.8 × 4.6–6.0 µm), a lamella-edge with cheilocystidia and a lignicolous habitat. *Coprinopsis lagopus* (Fr.) Redhead, Vilgalys & Moncalvo, a widespread species (Uljé 2005), shares a few characters with the present species in having almost similar-sized basidiocarps, a pileus with whitish velar remnants and ellipsoid basidiospores with a rounded apex and base. However, *C. lagopus* differs from the present species in having an applanate pileus with hairy to fibrillose and often pointed velar remnants, larger basidiospores (10–14 × 6–8.5 µm), the presence of cheilocystidia, a pileipellis with elongate and unbranched velar hyphae and a lignicolous habitat.

A total of three nucleotide sequences were generated from two different collections of the present species, including one ITS (G268: 483 bp) and two nLSU (G265: 873 bp; G268: 764 bp) sequences. *Coprinopsis strossmayeri* was the closest hit in BLASTn searches with 97.08% identity for the ITS (FJ403471) and 99.31% identity for one of the nLSU (G265: MN096847) sequences. While using the other nLSU sequence of the present collection (G268), *Coprinopsis variegata* (MH867473) resulted as the closest hit with 99.48% identity. The morphological characters of *Coprinopsis variegata* (Peck) Redhead, Vilgalys & Moncalvo, a species from the USA, are in no way comparable to those of the present species.

Coprinopsis **section** ***Quartoconatae*** D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1255 (2020)

Basidiocarps medium- to large-sized. Pileus not radially sulcate. Veil present at the margin. Lamella not deliquescent. Basidiospores small to large-sized, ellipsoid to slightly ovoid. Basidia 4-spored, clavate or sphaeropedunculate. Pleurocystidia absent. Cheilocystidia predominantly utriform, occasionally subcapitate, mixed with only a few globose, subglobose or ellipsoidal cells. Pileipellis with velar elements consisting of chains of subcylindrical, occasionally branched, hyaline, sometimes slightly encrusted cells. Clamp connections present.

Type species: *Coprinopsis marcescibilis* Örstadius & E. Larss.

Only one species belonging to the section *Quartoconatae* was discovered during the present study.

Coprinopsis fragilis K.G.G. Ganga, Manim. & K.P.D. Latha, in Crous *et al*., Persoonia 50: 225 (2023) **Plate 18.**

Description:—Basidiocarps small, fragile, psathyrelloid. Pileus 3–10 × 2–4 mm at maturity, initially convex, becoming broadly conical with age; surface white all over when young, becoming white on velar remnants and brownish grey (6C3) elsewhere with age, hygrophanous and becoming paler, initially completely covered with a fibrillose veil that later splitting into finely fibrillose patches, more so on and around the centre, translucent-striate towards the margin; margin straight, crenate. Lamellae adnexed, crowded, initially white, becoming brownish orange (6C4) to light brown (6D4) at maturity, with lamellulae of 2 tiers; edge finely torn under a lens, concolourous with the sides. Stipe 9–25 × 1 mm, central, terete, equal, hollow; surface white all over, smooth to finely floccose; base slightly enlarged to subbulbous with short strigose hairs, often connate, inserted. Odour and taste not distinctive.

Basidiospores 8–10(11) × 5–6 × 5–6 µm, on an average 9.32 × 5.75 × 5.4 µm, Q_1 = 1.5–2.0, Q_{1avg} = 1.63, Q_2 = 1.5–2.0, Q_{2avg} = 1.73, lenticular, ovoid in face view, somewhat phaseoliform to subamygdaliform in side view, pale brown, almost hyaline, slightly thick-walled, with an indistinct germ-pore. Basidia 19–23 × 10–11 µm, pedicellate-clavate, hyaline, thin-walled, 4-spored; sterigmata up to 5 µm long. Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 20–28 × 9–12 µm, abundant, utriform to subutriform, rarely clavate, often with amorphous contents that dissolve partially in 3% aqueous KOH, hyaline, slightly thick-walled. Lamellar trama subregular with inflated elements; hyphae 5–12 µm wide, hyaline, thin-walled. Pileipellis a cutis overlaid with a suprapellis composed of globose to subglobose elements intermixed with scattered velar hyphae; hyphae 5–10 µm wide, with a pale brown wall pigment, thin-walled; elements 30–47 × 20–33 µm, hyaline to pale brown, thin-walled; velar hyphae 3–9 µm wide, short, cylindrical, branched, often with a clavate terminal cell, hyaline, thin-walled. Stipitipellis a cutis overlaid by velar hyphae; hyphae 3–8 µm, hyaline, slightly thick-walled; velar hyphae 5–10 µm wide, velar hyphae similar to those on the pileipellis. Clamp connections observed only at the base of the cheilocystidia and on velar elements on the pileipellis.

Habit and Habitat:—In large groups, on decaying bark of logs.

Collections examined:—INDIA. Kerala State, Malappuram District, Calicut University: 26 July 2016, *K. G. Greeshma Ganga G45*; 28 July 2016, *K. G. Greeshma Ganga G46*; Ernakulam District, Thattekad forest: 23 October 2018, *K. G. Greeshma Ganga G286* (CALI).

Observations:—A brownish grey pileus with scattered patches of velar remnants; adnexed and crowded lamellae; a stipe with short strigose hairs at the connate base; ovoid and almost hyaline basidiospores with an indistinct germ-pore, utriform to lageniform or clavate cheilocystidia with amorphous contents; a hymenium devoid of pleurocystidia; a cutis-type pileipellis overlaid with suprapellis composed of globose to subglobose elements intermixed with scattered velar hyphae and a cutis-type stipitipellis with slightly thick-walled velar hyphae are the diagnostic features of *C. fragilis*. The following characters such as a pileus that lacks radial sulcations, non-deliquescent lamellae, ovoid basidiospores and the absence of pleurocystidia suggest *C. fragilis* in the section *Quartoconatae* (Wächter & Melzer 2020). Crous *et al.* (2023) discussed the taxonomy and phylogeny of this species in detail.

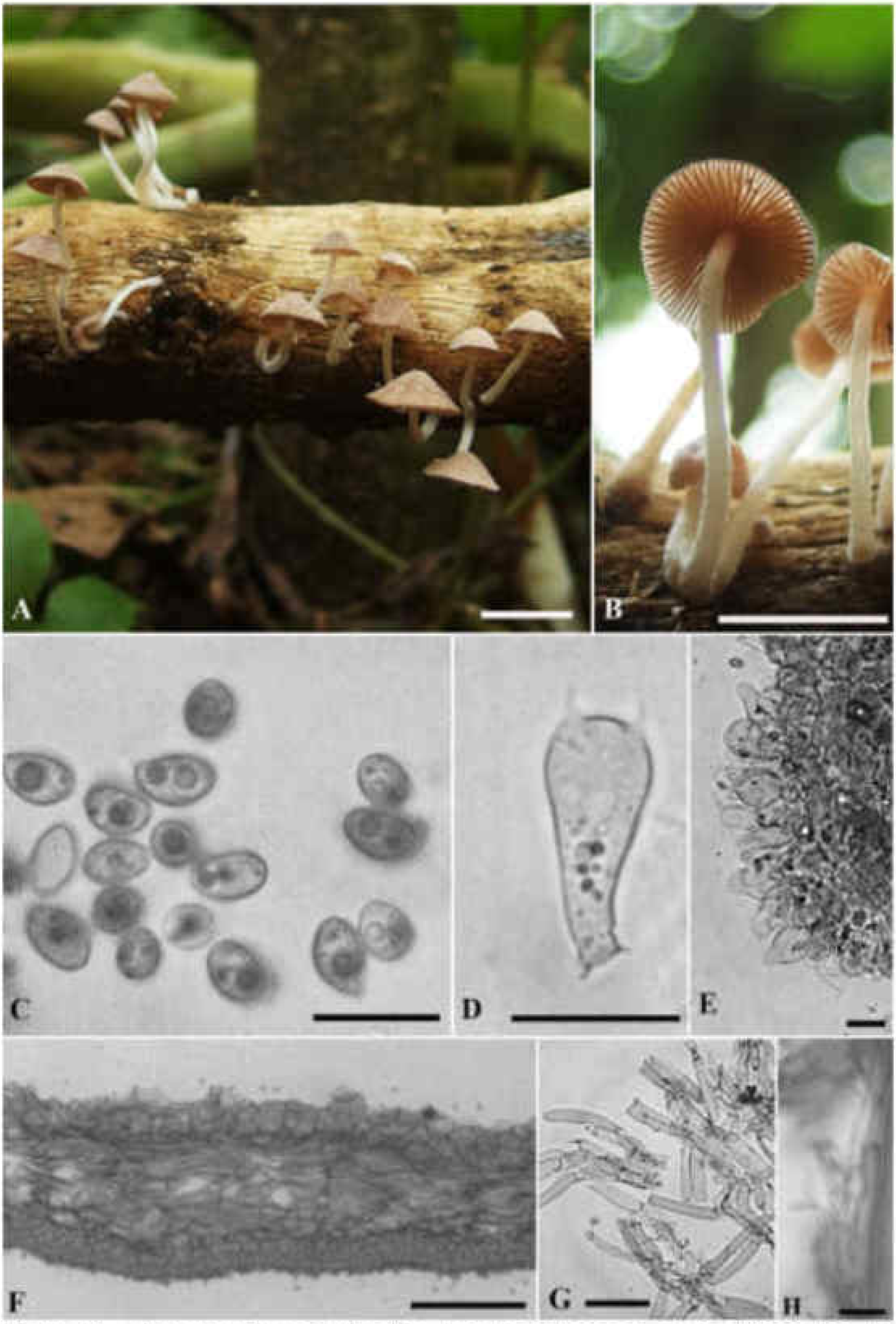

Plate 18. **A-H:** ***Coprinopsis fragilis*****. A-B.** Basidiocarps. **C.** Basidiospores. **D.** Basidium. **E.** Cheilocystidia. **F.** Pileipellis. **G.** Velar elements on the pileipellis. **H.** Stipitipellis. Scale Bars: **A-B** = 10 mm; **E** = 10 µm; **C & D** = 20 µm; **G & H**= 50 µm; **F** = 200 µm.

Coprinopsis* section *Xenobiae D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1244 (2020)

Basidiocarps small- to medium-sized. Veil present. Lamellae deliquescent. Basidiospores medium- to large-sized. Basidia 4-spored. Cheilocystidia utriform, clavate, subcylindrical. Pleurocystidia utriform to ellipsoid. Pileipellis with velar elements primarily composed of chains of branched, slightly diverticulate, hyaline to brownish, sometimes encrusted cells. Clamp connections present. Habitat terrestrial or fimicolous.

Type species: *Coprinopsis xenobia* (P.D. Orton) Redhead, Vilgalys & Moncalvo.

Only one species belonging to the section *Xenobiae* was discovered during the present study.

***Coprinopsis* species 2** **Plate 19.**

Description:—Basidiocarps small, fragile. Pileus initially 5–7 × 3–5 mm, finally up to 5–7 mm diam., cylindrical to paraboloid when young, becoming applanate with age; surface dark brown (6F6) at the centre and on the striations, white elsewhere, strongly glutinous, striate towards the margin when young, becoming radially rimose with a separable pellicle exposing the underlying tissue beneath, deliquescent; margin initially straight to incurved, inrolled at maturity. Lamellae free, crowded, partially deliquescent at maturity, edge not observed due to deliquescence. Stipe 30–35 × 2 mm, central, tapering towards the apex, hollow; surface white, slightly floccose towards the base; base slightly enlarged. Odour and taste not distinctive.

Basidiospores 8–9 × 5–6 × 5–6 µm, on an average 8.62 × 5.25 × 5.05 µm, Q_1 = 1.5–1.8, Q_{1avg} = 1.71, Q_2 = 1.5–1.8, Q_{2avg} = 1.64, lenticular, oblong in face view, oblong to oblong-ellipsoid in side view, with a truncate apex, dark brown to black, thick-walled, with a central germ-pore up to 2 µm wide. Basidia 8–24 × 6–9 µm, clavate to pedicellate-clavate, hyaline, slightly thick-walled, surrounded by 3–5 pseudoparaphyses, 4-spored; sterigmata up to 4 µm long. Pleurocystidia 28–32 × 16–22 µm, clavate, subglobose to oblong, hyaline, thin-walled. Lamella-edge sterile. Cheilocystidia 23–45 × 9–13 µm, subglobose to clavate often with a short pedicel, hyaline, thin-walled. Pileipellis a trichoderm composed of branched, chains of velar elements that form the pellicle, embedded in a gelatinised matrix when young, then the pellicle gets separated and becomes a cutis at maturity; hyphae 2–6 µm, hyaline, thin-walled; velar elements 15–34 × 5–17 µm, ellipsoid, cylindrical, rarely subglobose with finger-like projections, hyaline, thin-walled. Pileus trama subregular; hyphae 5–10 µm wide, with a brown encrusting wall pigment, slightly thick-walled. Stipitipellis a cutis with clusters of both thick- and thin-walled velar elements; hyphae; 7–10 µm, hyaline, thin-walled; velar elements 2–5 µm wide, hyaline. Clamp connections observed only at the base of cheilocystidia and on velar elements on the pileipellis.

Habit and Habitat:—Solitary or in small groups, on decaying elephant dung.

Collections examined:—INDIA. Kerala State, Ernakulam District, Dung samples collected from Thattekkad Forest and incubated in the lab: 29 October 2018, *K. G. Greeshma Ganga G293*; 01 November 2018, *K. G. Greeshma Ganga G294*.

Observations:—The present species is characterised by smaller basidiocarps with a glutinous pileus; free lamellae; a hollow stipe with a floccose surface; lenticular or oblong to ellipsoid basidiospores; 3–5 pseudoparaphyses surrounding each basidium; a hymenium with subglobose to clavate pleuro- and cheilocystidia; a trichoderm- to cutis-type pileipellis with branched, chains of velar elements; hyphae of pileus trama with encrusting pigments; a cutis-type stipitipellis with velar elements; clamped hyphae and a coprophilous habitat. Smaller basidiocarps, branched chains of velar elements on the pileipellis and a fimicolous habitat revealed that the present species belongs to the section *Xenobiae* (Wächter & Melzer 2020).

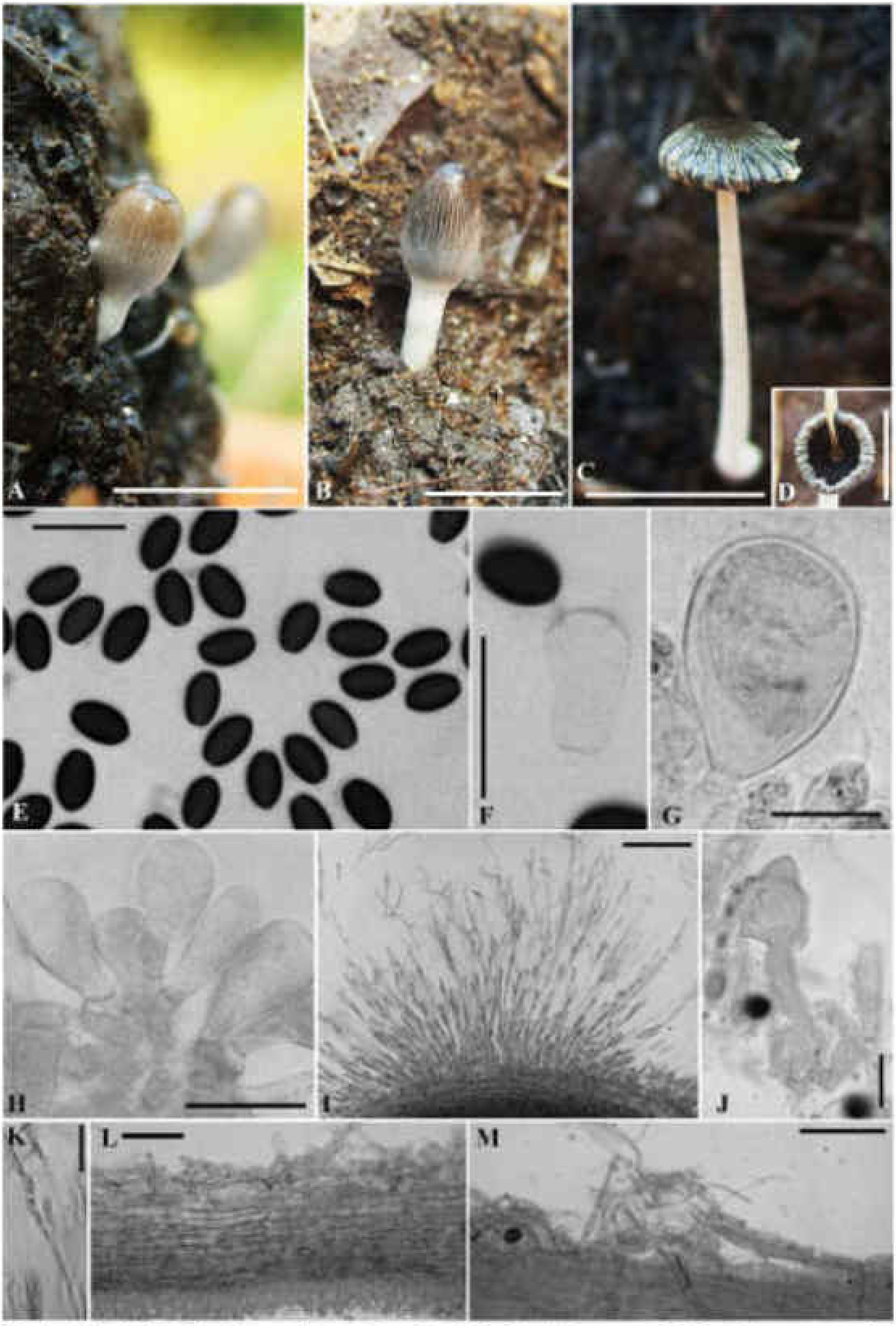

Plate 19. A-M: ***Coprinopsis*** **species 2. A-D.** Basidiocarps. **E.** Basidiospores. **F.** Basidium. **G.** Pleurocystidium. **H.** Cheilocystidia. **J.** Pileipellis when young. **J & K.** Velar elements on the pileipellis. **L.** Pileipellis at maturity. **M.** Stipitipellis. Scale Bars: **A-D** = 10 mm; **E-H, J & K** = 20 µm; **I** = 200 µm; **L & M** = 50 µm.

Coprinopsis candidolanata (Doveri & Uljé) Keirle, Hemmes & Desjardin, a species originally described from Italy (Keirle *et al*. 2004) and also reported from the Netherlands (Uljé 2005), resembles the present species in having similar-sized basidiocarps, a pileipellis with vertical hyphae and densely diverticulate elements with finger-like projections and a coprophilous habitat. However, *C. candidolanata* differs from the present species in having fibrous-woolly and snow-white velar remnants on the pileus, the absence of encrusting pigment in the pileus trama, non-gelatinised pileipellis with encrusted velar elements and the absence of clamp connections.

Coprinopsis xenobia (P. D. Orton) Redhead, Vilgalys & Moncalvo, a species reported from Scotland, Italy, Germany and the Netherlands (Uljé 2005), shows a few similarities with the present species in having diverticulate velar elements on the pileipellis, clamped hyphae and a coprophilous habitat. However, *C. xenobia* has larger basidiospores (9.5–14.5 × 5–8 µm), a hymenium with urtriform to ellipsoid cheilo- and pleurocystidia and the absence of gelatinisation on the pileipellis. *Coprinopsis luteocephala* (Watling) Redhead, Vilgalys & Moncalvo, a rare species known only from Scotland and Germany (Uljé 2005), shows some similarity with the present species in having oblong basidiospores with up to 2 µm wide germ-pore, a pileipellis with diverticulate velar elements, clamped hyphae and a habitat on dung. However, *C. luteocephala* has larger basidiocarps (pileus 8–18 × 6–16 mm and stipe (60 × 2–3 mm) with a yellow-coloured pileus, larger basidiospores (9.5–12 × 5.5–7 µm) and ellipsoid to utriform cheilo- and pleurocystidia.

The distinct status of the ITS (G293: 644 bp) and the nLSU (G293: 882 bp) sequences generated from the present *Coprinopsis* species was proved in the BLASTn searches. In a megablast search of the nucleotide database using the ITS sequence (644 bp), *Coprinopsis candidolanata* (JF907837: 96.73% identity) was the closest hit. A search with the nLSU sequence, *C. xenobia* (KF178384: 98.41% identity) resulted as the closest hit.

Uncertain infrageneric position

Coprinopsis species 3 Plate 20.

Description:—Basidiocarps small, fragile. Pileus 2–3 × 2–3 mm when young, 5–14 × 6–12 mm at maturity, initially convex to paraboloid, expanding to cylindrical or campanulate with age; surface dark brown (7F7) all over when young, becoming brown (7E6) or dark brown (7F6) at the centre and on the velar squamules, whitish towards the margin with age, initially appressed-velar squamules all over, becoming appressed- to recurved squamules on and around the centre, densely so at the centre, appressed-fibrillose towards the margin, deliquescent; margin initially straight, becoming upturned with age, at times fissile. Lamellae adnexed, crowded, initially white, becoming black with age; edge entire, concolourous with the sides. Stipe 16–33 × 1.5–2 mm, central, tapering towards the base, hollow; surface white, finely pruinose all over; base not enlarged, inserted. Odour and taste not distinctive.

Basidiospores 5–6 × 4–5 × 4–5 µm, on an average 5.77 × 4.1 × 4.05 µm, Q_1 = 1.2–1.5, Q_{1avg} = 1.45, Q_2 = 1.2–1.5, Q_{2avg} = 1.38, lenticular, subglobose to ellipsoid in face view, ellipsoid in side view, brown, thick-walled, with a central germ-pore up to 2 µm wide. Basidia 12–21 × 5–7 µm, clavate to pedicellate-clavate, hyaline, slightly thick-walled, surrounded by 3–5 pseudoparaphyses, 4-spored; sterigmata 3 µm long. Pleurocystidia 60–80 × 15–20 µm, abundant, cylindrical to subcylindrical, hyaline, thin-walled. Lamella-edge heterogeneous. Cheilocystidia 24–60 × 15–29 µm, abundant, subglobose, ovoid, clavate or cylindrical, hyaline, thin-walled. Pileipellis a cutis composed of elongate hyphae overlaid with patches of brown velar elements; hyphae 5–9 µm wide, with colourless granules scattered on the surface, hyaline, thin-walled; velar elements composed of short chains of hyphae, 20–40 × 6–14 µm, cylindrical to sausage-shaped, often with scattered, colourless granules on the surface, brown, thick-walled. Stipitipellis a cutis, almost similar to

Plate 20. A-L: *Coprinopsis* species 3. A. Basidiocarps. **B.** Basidiospores. **C.** Basidia. **D.** Pseudoparaphyses. **E.** Cheilocystidia. **F-I.** Pleurocystidia. **J.** Pileipellis. **K.** Stipitipellis hyphae with colourless granules. **L.** Velar elements on the pileipellis. Scale Bars: **A** = 10 mm; **B-D** = 20 µm; **E-L** = 50 µm.

pileipellis; hyphae 3–4 µm wide, branched or diverticulate, sometimes with colourless granules, hyaline, thin-walled. Clamp connections observed only at the base of basidia and on the hyphae of lamellar trama, stipitipellis and velar elements.

Habit and Habitat:—In large groups, among wood chips.

Collection examined:—INDIA. Kerala State, Malappuram District, Calicut University Campus: 12 July 2018, *K. G. Greeshma Ganga G271*.

Observations:—The present species is characterised by small basidiocarps, a paraboloid to campanulate pileus with brown velar squamules; adnexed, deliquescent lamellae; a pruinose stipe which is tapering towards the base; small, subglobose to ellipsoid basidiospores with a wide, central germ-pore; 3–5 pseudoparaphyses surrounding each basidium; abundant, cylindrical to subcylindrical pleurocystidia; a lamella-edge with abundant cheilocystidia; a cutis-type pileipellis with patches of brown velar elements and the presence of colourless granules scattered on the surface of velar elements, pilei- and stipitipellis hyphae. The morphological characters of the present species do not match those of any of the sections proposed so far under the genus *Coprinopsis* (Wächter & Melzer 2020). An ITS-based phylogenetic analysis of the genus *Coprinopsis* (Figure 5) performed as part of the present study showed that the present species nested in a distinct clade sister to the section *Coprinopsis*.

Coprinopsis fibrillosa (Berk. & Broome) Redhead, Vilgalys & Moncalvo, a species originally reported from Sri Lanka (Pegler 1986) and also from Uganda (Berkeley & Broome 1871; Pegler 1977), is strikingly similar to the present species in having an almost similar shape and colour of the basidiocarps and basidiospores, a pileus with brown squamules and slightly thick-walled velar elements on the pileipellis. However, *C. fibrillosa* differs from the present species in having a subumbonate, larger pileus (5–25 × 10–30 mm), ovoid to ellipsoid basidiospores, a lamella-edge devoid of cheilocystidia, a hymenium with a few pleurocystidia and the absence of colourless granules on the hyphae of pilei- and stipitipellis and velar elements. *Coprinopsis erythrocephala* (Lév.) Redhead, Vilgalys & Moncalvo, another species widespread in the Netherlands and also recorded from other countries of Europe (Uljé 2005), resembles the present species in having a pileus which is completely covered with brown or rust-coloured velar remnants when young and strong granular encrustations on the velar hyphae of the pileipellis. But *C. erythrocephala* has larger basidiocarps (pileus up to 30 mm diam. and stipe 100 × 2–4 mm), a stipe with a white basal mycelium and larger basidiospores (7.5–13 × 5–8 µm).

Coprinopsis ochraceolanata (Bas) Redhead, Vilgalys & Moncalvo*,* a species originally described from the Netherlands (Uljé & Bas 1993), seems to be close to the present species in having ochre-coloured squamules on the pileus, a pileipellis with granular, encrusted velar hyphae and a fasciculate habit and lignicolous habitat. However, the present *Coprinopsis* species can be distinguished from *C. ochraceolanata* in having larger basidiocarps (pileus up to 50 mm diam. and stipe 80 × 5.5 mm), basidiospores (8.5–13.5 × 5.5–7.7 µm), cheilo- (30–120 × 15–50 µm) and pleurocystidia (50–140 × 20–50 µm) and velar elements (45–200 × 7–20 µm). A pairwise comparison of the ITS sequence of the present species with that of *C. ochraceolanata* (HQ847051) showed only 94.69% sequence similarity.

Comparison of the ITS (652 bp) and the nLSU (875 bp) sequences of the present *Coprinopsis* species with those available in GenBank suggests that the present species has distinct ITS and nLSU sequences*. Coprinopsis urticicola* was the closest hit in a BLASTn search for the ITS (MN368600; identity 98.85%). While that nLSU, *C. ochraceolanata* (HQ847131; identity 98.83%) resulted as the closest hit. *Coprinopsis urticicola* (Berk. & Broome) Redhead, Vilgalys & Moncalvo, a species originally described from the Netherlands (Uljé & Bas 1993), resembles the present species in having smaller basidiocarps, a pileipellis with encrusted velar elements and a lignicolous habitat. However, *C. urticicola* has diverticulate velar elements on the pileipellis, larger basidiospores (5.5–9 × 4.5–6.5 µm) with a conical base and hyphae devoid of clamp connections.

5.1.2.4. ***HAUSKNECHTIA*** D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1234 (2020)

Basidiocarps small. Pileus surface fugacious, strikingly sulcate when young; margin splitting radially. Veil present. Lamellae deliquescent. Basidiospores medium-sized, subcylindrical, pale, germ-pore absent. Basidia 4-spored. Pleuro- and cheilocystidia absent. Pileipellis with velar elements consisting of subcylindrical, branched hyphae. Clamps connections present. Habitat terrestrial on sandy soil.

Type species: *Hausknechtia floriformis* (Hauskn.) Wächter & A. Melzer.

Only one species belonging to this genus was described during the present study.

Hausknechtia leucosticta (Pat.) Tkalčec, J.Q. Yan, C.F. Nie & C.K. Pradeep, in Nie, Wang, Tkalčec, Yan, Hu, Ge, Na, Zeng, Ding, Huo, Pošta, Pradeep & Mešić, Diversity 14 (699): 8 (2022) **Plate 21.**

Coprinus leucostictus Pat., Bull. Soc. mycol. Fr. 33: 61 (1917)

Description:—Basidiocarps small, fragile. Pileus 15–18 mm diam. at maturity, initially convex, becoming broadly campanulate at maturity; surface white on the velar remnants, brown (6E6) elsewhere when young, becoming light orange (5A4) at the centre and brown (6E6) at the middle and on the striations, brownish grey (6D2) elsewhere when mature, hygrophanous and becoming paler, mostly glabrous at the centre, rarely with small, floccose velar patches, plicate-striate towards the margin; margin initially straight, crenate when young, becoming upturned to revolute, often with rimose splitting when mature. Lamellae adnate, moderately crowded, initially white, becoming pale grey (6C1) with age, with lamellulae in 2 tiers; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 40–55 × 1.5–2 mm, central, terete, slightly tapering towards the apex, hollow; surface white, smooth all over; base slightly enlarged with rhizoids. Odour and taste not distinctive.

Basidiospores 9.5–13(14) × 5.5–7 × 6–6.5 µm, on an average 11.36 × 6.35 × 6.0 µm, Q_1 = 1.53–2.0, Q_{1avg} = 1.7, Q_2 = 1.66–2.0, Q_{2avg} = 1.86, lenticular, oblong in face view, ellipsoid in side view, dark brown, thick-walled, with a central germ-pore up to 2 µm wide. Basidia 19–26 × 13–14.5 µm, clavate to pedicellate-clavate, hyaline, thin-walled, 2–5-spored; sterigmata up to 5 µm long. Pleurocystidia absent. Lamella-edge heterogeneous. Cheilocystidia 36–47 × 10–15 µm, abundant, narrowly utriform to utriform, hyaline, slightly thick-walled. Pileipellis an epithelioid hymeniderm with scattered velar elements; epithelioid hymeniderm elements 24–39 × 20–28 µm, broadly clavate, hyaline, thin-walled; velar elements 3–15 µm wide, cylindrical, nodulose, diverticulate or rarely branched, hyaline, thick-walled. Stipitipellis a cutis disrupted by bunches of caulocystidia; hyphae 4–7 µm wide, hyaline, slightly thick-walled. Caulocystidia 48–142 × 16–25 µm, abundant, narrowly lageniform, hyaline, slightly thick-walled. Clamp connections observed only on velar elements on the pileipellis and hyphae of the stipitipellis, lamellar- and pileus trama.

Habit and Habitat:—In small groups, on humus rich soil.

Collections examined:—INDIA. Kerala State, Malappuram District, Calicut University Campus: 1 September 2016, *K. G. Greeshma Ganga G87*; 6 June 2018, *K. G. Greeshma Ganga G259*.

Observations:—*Hausknechtia leucosticta*, a species originally described from Vietnam and later from southern India and southern to southeastern China as *Coprinus leucostictus* (Nie *et al*. 2022), is characterised by small basidiocarps; a convex to broadly campanulate pileus with velar remnants and plicate-striations; adnate lamellae; a stipe with a slightly enlarged base and rhizoids; oblong basidiospores with a central germ-pore; a hymenium devoid of pleurocystidia; a

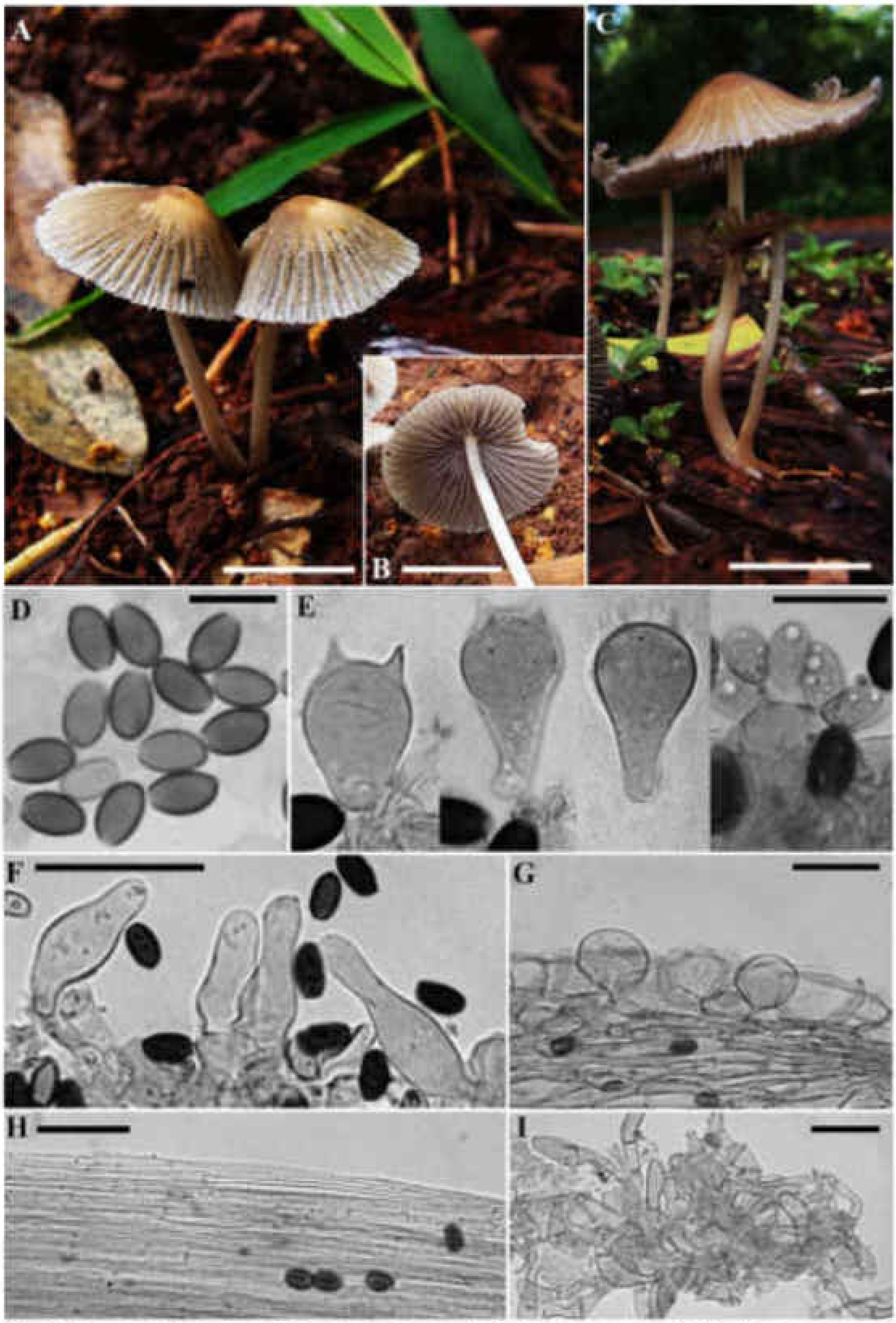

Plate 21. A-I: ***Hausknechtia leucosticta*****. A-C.** Basidiocarps. **D.** Basidiospores. **E.** Basidia. **F.** Cheilocystidia. **G.** Pileipellis. **H.** Stipitipellis. **I.** Velar elements on the pileipellis. Scale Bars: **A-C** = 10 mm; **D & E** = 20 µm; **F-I** = 50 µm.

lamella-edge with abundant cheilocystidia; an epithelioid hymeniderm-type pileipellis with velar elements and a cutis-type stipitipellis with caulocystidia.

Comparison of the ITS (G87: 669 bp) and the nLSU (G87: 871 bp) sequences of the present species with those available in GenBank revealed that the present species is *H. leucosticta*. A BLAST search using the ITS sequence showed an unpublished *Hausknechtia floriformis* (MK881745: 99.70% identity) as the closest hit followed by *H. leucosticta* (ON745618) with 99.40% identity. *Hausknechtia leucosticta* (ON745617: 99.89% identity) was the closest hit in a BLASTn search with the nLSU sequence.

5.1.2.5. ***NARCISSEA*** D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1203 (2020)

Basidiocarps small. Veil well-developed, granular. Basidiospores small to medium-sized, with a tri- to polygonal outline, laterally strongly flattened with a central germ-pore. Basidia mostly 4-spored. Pleurocystidia utriform. Cheilocystidia lageniform, utriform, interspersed with numerous sphaeropedunculate and clavate cells. Pileipellis with velar elements consisting of often incrusted globose elements and chains of subcylindrical cells. Pileipellis with velar elements, consisting of often incrusted globose elements and chains of subcylindrical cells. Pileocystidia absent. clamp Connections absent. Habitat fimicolous or on fertilized soil, sometimes on plant remnants.

Type species: *Narcissea patouillardii* (Quél.) D. Wächt. & A. Melzer.

During the present study, two species of the genus *Narcissea* were encountered.

Key to the species

1. Pileus ≥4 mm diameter; cheilocystidia without apical projections... ***Narcissea cordispora***

1. Pileus ≤4 mm diameter; cheilocystidia with apical projections... ***Narcissea* species 1**

Narcissea cordispora (T. Gibbs) D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1203 (2020) **Plate 22.**

Coprinopsis cordispora (T. Gibbs) Watling & M.J. Richardson, Edinb. J. Bot. 67 (3): 406 (2010)
Coprinus cordisporus T. Gibbs, Naturalist, Hull: 100 (1908)
Coprinus volvaceominimus Crossl., Naturalist 17 (209): 372 (1891)

Description:—Basidiocarps small, fragile. Pileus 3–10 × 3–5 mm when young, finally 5–20 mm diam. at maturity, initially ellipsoid to cylindrical, becoming broadly convex to applanate at maturity; surface yellowish grey (4B2) all over when young, becoming light brown (6D6) to dark brown (5F5) at the centre, white elsewhere with age, initially completely covered with a powdery veil, which later becomes granulose with erect, conical velar flocks at the centre, plicate-striate towards the margin, deliquescent; margin incurved, crenate. Lamellae free, L = 30–32, subdistant, initially white, becoming grey (6A5) with age, with lamellulae in 1 tier; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 10–50 × 0.5–1.5 mm, central, terete, equal, hollow; surface white, smooth, rarely with a tiny inferior annulus; base slightly enlarged. Odour and taste not distinctive.

Basidiospores 7–9 × 7–8 × 5–6 µm, on an average 8.02 × 7.42 × 5.75 µm, Q_1 = 1.0–1.21, Q_{1avg} = 1.09, Q_2 = 1.16–1.6, Q_{2avg} = 1.38, lenticular, rectangular-ellipsoid with an apical projection in face view, ellipsoid in side view, dark brown to black, thick-walled, with a central germ-pore up to 2 µm wide. Basidia 16–32 × 8–9 µm, clavate or pedicellate-clavate, hyaline, thin-walled, surrounded by 5–6 pseudoparaphyses, 4-spored; sterigmata up to 3 µm long. Pleurocystidia 44–77 × 17–25, abundant, subcylindrical or lageniform, hyaline, thin-walled. Lamella-edge heterogeneous. Cheilocystidia 39–72 × 17–23 µm, abundant, versiform: subglobose, ellipsoid, subcylindrical or lageniform, hyaline, thin-walled. Pileipellis an undifferentiated cutis overlaid with scattered or chains of ellipsoid to subglobose elements; hyphae 5–10 µm wide, hyaline, thin-walled; velar elements

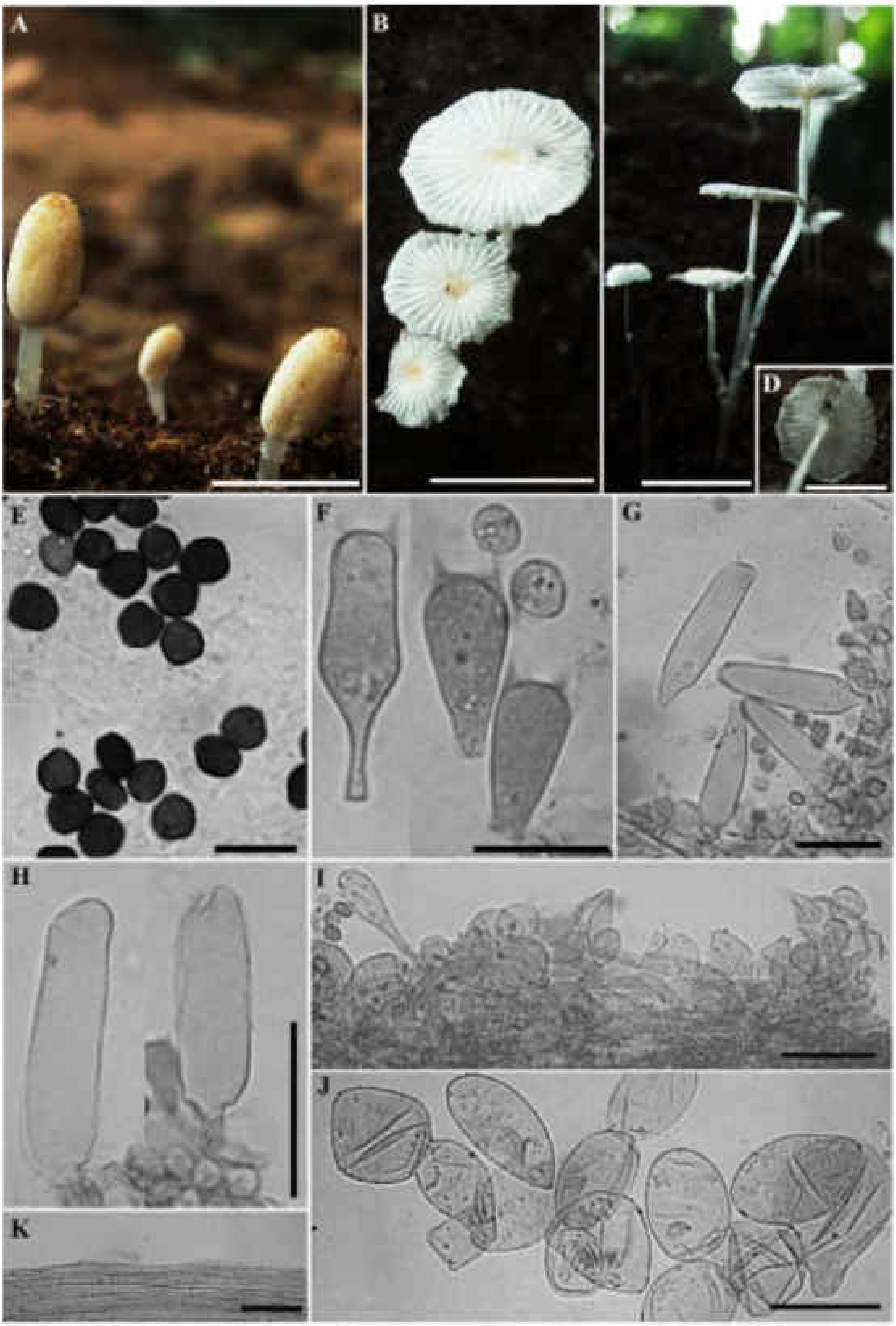

Plate 22. A-K: *Narcissea cordispora.* **A-D.** Basidiocarps. **E.** Basidiospores. **F.** Basidia. **G.** Cheilocystidia. **H.** Pleurocystidia. **I.** Pileipellis. **J.** Velar elements on the pileipellis. **K.** Stipitipellis. Scale Bars: **A-D** = 10 mm; **E-H & J** = 20 µm; **I & K** = 50 µm.

22–50 × 16–31 µm, hyaline or with a pale brown wall pigment and pale brown, granular encrustations, thin-walled. Stipitipellis a cutis rarely with scattered velar elements; hyphae 7–10 µm wide, hyaline, slightly thick-walled; velar elements 18–44 × 4–18 µm, ellipsoid, hyaline, thin-walled. Clamp connections not observed on any tissues.

Habit and Habitat:—In small groups, on decaying elephant dung and cow dung.

Collections examined:—INDIA. Kerala State, Wayanad District, Muthanga forest: 4 July 2017, *K. G. Greeshma Ganga G165*; Kannur District, Aarlam forest: 19 July 2017, *K. G. Greeshma Ganga G182*; Thrissur District, Punnayoorkulam: 7 August 2017, *K. G. Greeshma Ganga G194*; 5 October 2017, *K. G. Greeshma Ganga G225*.

Observations:—*Narcissea cordispora*, a species originally described from England as *Coprinus cordisporus* T. Gibbs (Gibbs 1908) and also reported from the Hawaiian Islands and India (Keirle *et al*. 2004; Amandeep *et al*. 2015c), has small basidiocarps; a broadly convex to applanate pileus with erect, conical velar flocks and plicate-striations; free lamellae; a stipe with a slightly enlarged base; rectangular-ellipsoid basidiospores with an apical projection; a hymenium with abundant pleurocystidia; a lamella-edge with versiform cheilocystidia; an undifferentiated cutis-type pileipellis with velar elements and a cutis-type stipitipellis with ellipsoid velar elements.

Comparison of the ITS and the nLSU sequences of the present collections with those available in GenBank database suggests that the present species is *N. cordispora*. A total of four ITS (G225: 632 bp; G165: 638 bp; G182: 646 bp; G194: 638 bp) and one nLSU (G225: 841 bp) sequences were generated from *N. cordispora.* A BLASTn search using the ITS (G225) sequence showed *Coprinus cordisporus* (presently as *Narcissea cordispora*) (AY461841) as the closest hit with 99.87% identity. While using the nLSU sequence, *Coprinus patouillardii* (presently as *Narcissea patouillardii*) (FN396195) resulted as the closest hit with 98.79% identity.

***Narcissea* species 1** **Plate 23.**

Description:—Basidiocarps very small, fragile. Pileus <1 mm diam. when young, finally 2–4 mm diam. at maturity, initially ellipsoid to cylindrical, becoming broadly convex to conical, sometimes with a shallow central depression at maturity; surface light brown (6D6) to yellowish brown (5D6) all over when young, becoming light brown (6D6) to dark brown (5F5) at the centre, grey (6C1) elsewhere when mature, initially completely covered with a powdery veil, which later becomes granulose with erect, velar conical flocks at the centre, plicate-striate towards the margin, deliquescent; margin incurved, crenate. Lamellae adnate to adnexed, L = 18–19, subdistant to distant, initially white, becoming grey (6A5) with age, with lamellulae in 1 tier; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 6–10 × 0.1–0.4 mm, central, terete, equal, filiform, hollow; surface translucent, smooth, often with a minute inferior annulus; base enlarged. Odour and taste not distinctive.

Basidiospores 6–8.5 × 6–8 × 4–5 µm, on an average 7.18 × 6.92 × 4.5 µm, Q_1 = 0.85–1.16, Q_{1avg} = 1.09, Q_2 = 1.2–2.0, Q_{2avg} = 1.52, lenticular, rounded-pentagonal often with an apical projection in face view, oblong or ellipsoid to rarely subcylindrical in side view, dark brown to black, thick-walled, with a central germ-pore up to 1.5 µm wide. Basidia 11–24 × 6–8 µm, clavate or pedicellate-clavate, hyaline, slightly thick-walled, surrounded by 3–5(6) pseudoparaphyses, 4-spored; sterigmata up to 3 µm long. Pleurocystidia 40–57 × 18–27, abundant, subcylindrical, lageniform or rarely clavate to sphaeropedunculate, hyaline, thin-walled. Lamella-edge heterogeneous. Cheilocystidia 20–26 × 10–12 µm, abundant, lageniform or clavate with cylindrical apical branches, hyaline, thin-walled. Pileipellis an undifferentiated cutis overlaid with scattered or chains of ellipsoid to subglobose velar elements; hyphae 6–20 µm wide, hyaline, thin-walled; velar

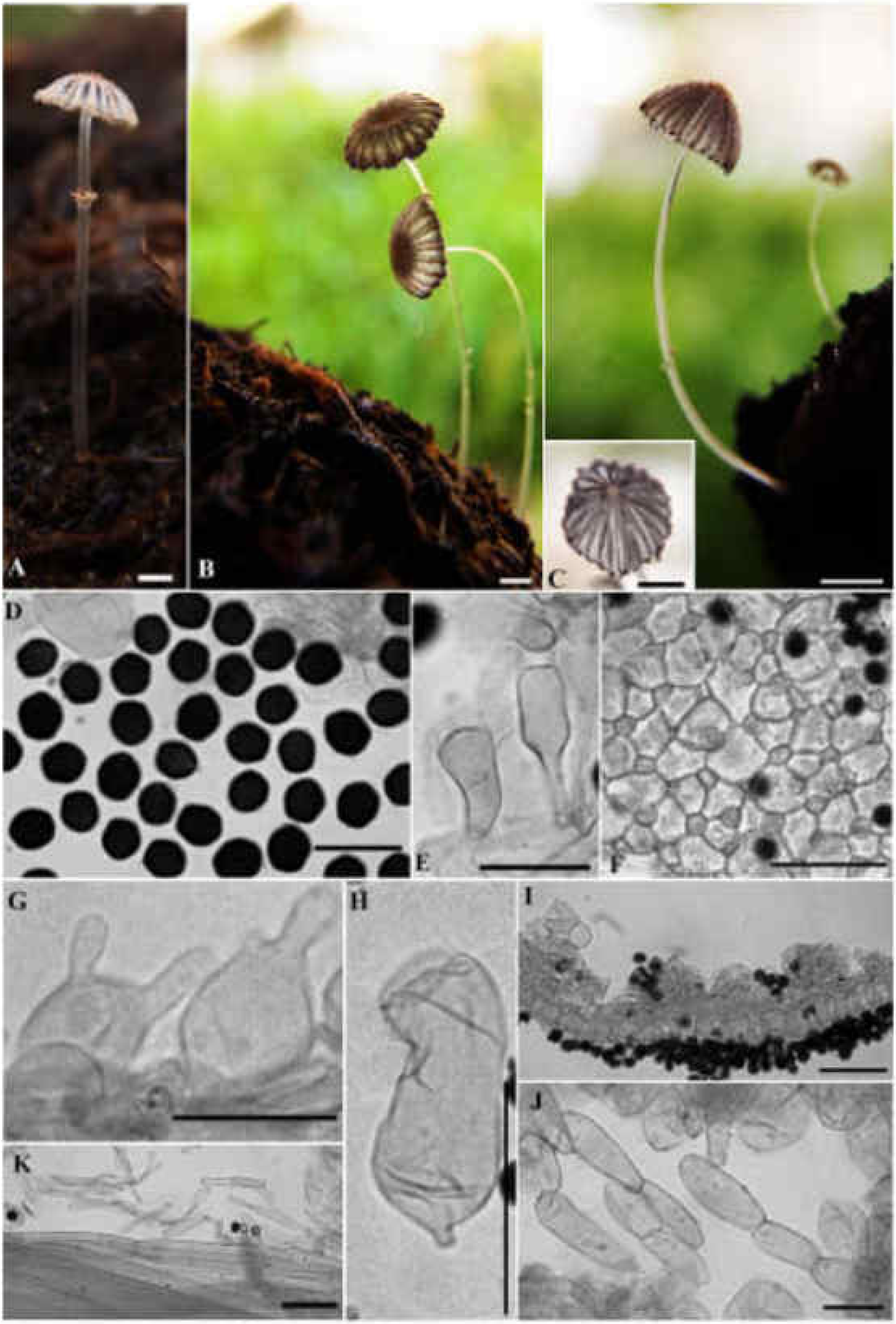

Plate 23. A-K: *Narcissea* species 1. A-C. Basidiocarps. **D.** Basidiospores. **E.** Basidia. **F.** psuedoparaphyses. **G.** Cheilocystidia. **H.** Pleurocystidium. **I.** Pileipellis. **J.** Velar elements on the pileipellis **K.** Stipitipellis. Scale Bars: **A-C** = 1 mm; **D, E, G, H & J** = 20 µm; **F, I & K** = 50 µm.

elements 25–76 × 6–26 µm, with a pale brown plasmatic pigment and hyaline, granular encrustations, dissolving in 3% KOH, thin-walled. Stipitipellis a cutis rarely with scattered velar elements; hyphae 20–25 µm wide, hyaline, slightly thick-walled; velar elements 10–52 × 4–7 µm, cylindrical, hyaline, thin-walled. Clamp connections not observed on any tissues.

Habit and Habitat:—In small groups, on decaying elephant dung.

Collections examined:—INDIA. Kerala State, Kozhikode District, substratum collected from Kakkayam forest incubated in the lab at University of Calicut: 7 October 2016, *K. G. Greeshma Ganga G111*; 8 October 2016, *K. G. Greeshma Ganga G112*; 27 October 2016, *K. G. Greeshma Ganga G124*.

Observations:—Very small basidiocarps; a broadly convex to conical pileus with erect, conical velar flocks and plicate-striations; adnate to adnexed lamellae; a stipe with an enlarged base; rounded-pentagonal basidiospores with an apical projection; a hymenium with abundant pleurocystidia; a lamella-edge with lageniform to clavate cheilocystidia with cylindrical apical branches; an undifferentiated cutis-type pileipellis with velar elements and a cutis-type stipitipellis with cylindrical velar elements are the characteristic features of the present species.

Narcissea cordispora, a species originally described from England as *Coprinus cordisporus* (Gibbs 1908) and also reported from the Hawaiian Islands and India (Keirle *et al.* 2004; Amandeep *et al.* 2015), resembles the present species in having fragile basidiocarps with granular velar remnants on the pileus, basidiospores of somewhat similar size and shape, a pileipellis with scattered or chains of ellipsoid to subglobose velar elements and the absence of clamp connections. However, *N. cordispora* can be distinguished from the present species in having larger basidiocarps (pileus >4 mm diam. and stipe 35–50 (–75) × 0.5–2 mm) with greater number (>20) of lamellae, a stipe with a pseudovolva, a lamella-edge with lageniform cheilocystidia and a pileipellis with smooth velar elements. *Narcissea cardiaspora*, a German species originally described as *Coprinus* *cardiasporus* (Enderle *et al.* 1986) and also recorded from the Netherlands (Uljé 2005), seems to be close to the present species in having delicate basidiocarps with granular velar remnants on the pileus, a translucent stipe with a slightly enlarged base, each basidium surrounded by 3–6 pseudoparaphyses and a pileipellis with encrusted velar elements. *Narcissea cardiaspora*, however, differs from the present species in having larger basidiocarps (pileus 10 mm diam. and stipe 15–35 × 0.8–1.5 mm), a stipe devoid of an inferior, complete or incomplete annulus, triangular to heart-shaped and narrow basidiospores (6–8.4 × 4–4.7 × 5.3–6 (6.5) µm) and a lamella-edge with subglobose to utriform cheilocystidia.

Narcissea patouillardii, a species originally described as *Coprinus patouillardii* from France (Orton & Watling 1979), shares a few characters such as delicate basidiocarps with granular velar remnants on the pileus, a translucent stipe with a slightly enlarged base and a pileipellis with granular, encrusted velar elements. However, *N. patouillardii* has larger basidiocarps (pileus 10–30 mm diam. and stipe 40–70 × 1–2.0 mm), a stipe devoid of an annulus, lageniform to globose cheilocystidia devoid of cylindrical apical branches and a habitat on vegetable refuse. Except for the description of *N. patouillardii* based on a collection from Germany (Enderle *et al.* 1986), any other descriptions available on *N. patouillardii,* including the description from the type material, do not mention the apical branches of cheilocystidia. However, the German collections differ from the present species in having a larger pileus (<20 mm wide pileus) and smooth velar elements on the pileipellis. The DNA sequences of the German collections of *N. patouillardii* are not available in GenBank for sequence comparison.

The distinctive status of the ITS (three ITS: G111: 646 bp; G124: 635 bp; G112: 584 bp) and the nLSU (one nLSU: G124: 878 bp) sequences of the present *Narcissea* species was confirmed in BLASTn searches. The closest hit with the ITS (G111) sequence was an unpublished *Coprinus cordisporus* (HM240520: 99.37% identity), followed by *C. bisporus* (presently as *Tulosesus bisporus* (AF345824: 99.21% identity) and *Coprinus patouillardii* (MH856581: 98.43% identity). However, *Tulosesus bisporus* (J.E. Lange) D. Wächt. & A. Melzer shows no macro- and micro-morphological similarities with the present *Narcissea* species and it differs in having larger basidiocarps, a pileus devoid of granular velar remnants, the presence of 2-spored basidia, ellipsoid basidiospores, clamped hyphae and pilei- and stipitipellis with pileo- and caulocystidia respectively. In addition, an ITS-based phylogenetic analysis (Figure 6) conducted as part of this study revealed that the present species formed a distinct group within the genus *Narcissea* with significant support. Except for one collection of *Tulosesus bisporus (*KACC49409: AF345824 whose country of origin is not available), which was positioned within the genus *Narcissea*, all other collections of this species (GU227705 from Sweden, KT804105 from Portugal, JN159517 and FN396107 whose country of origin is not available) were recovered in the genus *Tulosesus* and are phylogenetically distinct from *Narcissea.* It is possible that the sequence named as *Tulosesus bisporus* KACC49409 in GenBank represents a *Narcissea* species misidentified as *Tulosesus bisporus*.

In a BLASTn search with the nLSU sequence, the closest hit was *Coprinus patouillardii* (FN396195: 99.42% identity).

5.1.2.6. ***PARASOLA*** Redhead, Vilgalys & Hopple, Taxon 50 (1): 235 (2001)

Pileus membranous, strongly plicate, diaphanous. Veil absent. Lamellae non-deliquescent. Basidia irregularly di- to trimorphic. Pleurocystidia present. Pileipellis a smooth hymeniderm palisade, lacking pileocystidia, sometimes with brown setae at the centre of pileus. Stipitipellis without ozonium. Habitat terrestrial, frequently on lawns, in gardens and along forest trails.

Type species: *Parasola plicatilis* (Curtis) Redhead, Vilgalys & Hopple

Key to the sections of the genus *Parasola* described in this study

1. Basidiospores without an apical papilla; pileipellis with sclcerocystidia................ ....**Section *Auricomi***
1. Basidiospores with an apical papilla; pileipellis without sclcerocystidia. ....**Section *Parasola***

Parasola **section** ***Auricomi*** (Singer) D.J. Schaf. Field Mycology 11 (2): 51 (2010)

Pileus lacking veil. Pileipellis with long, narrow thick-walled setae. Pileocystidia absent.

Type species: *Parasola auricoma* (Pat.) Redhead, Vilgalys & Hopple

Three species of the section *Auricomi* were encountered in this study.

Key to the species

1. Pileus without plicate-striations; pleurocystidia absent... ***Parasola psathyrelloides***
1. Pileus with plicate-striations; pleurocystidia present **2**
2. Pileus with a central depression; habitat lignicolous............. ***Parasola auricoma***
2. Pileus without a central depression; habitat terrestrial..........***Parasola*** **species 1**

Parasola auricoma (Pat.) Redhead, Vilgalys & Hopple, in Redhead, Vilgalys, Moncalvo, Johnson & Hopple, Taxon 50 (1): 235 (2001)

Plate 24.

Agaricus subtilirugatus Secr., Mycogr. Suisse 1: 423 (1833)
Coprinus auricomus Pat., Tab. analyt. Fung. 5: 200 (1886)
Coprinus hansenii J.E. Lange, Dansk bot. Ark. 2 (3): 48 (1915)

Description:—Basidiocarps small, fragile. Pileus 11–16 ×10–15 mm when young, finally 22–23 mm diam. at maturity, initially subglobose to paraboloid, becoming broadly convex with a shallow central depression at maturity; surface light brown (6D7) to orange grey (6B2) all over when young, becoming light brown (6D7) at the centre and orange grey (5B2) towards the margin when mature, smooth at the centre, plicate-striate towards the margin; margin straight, crenate. Lamellae free

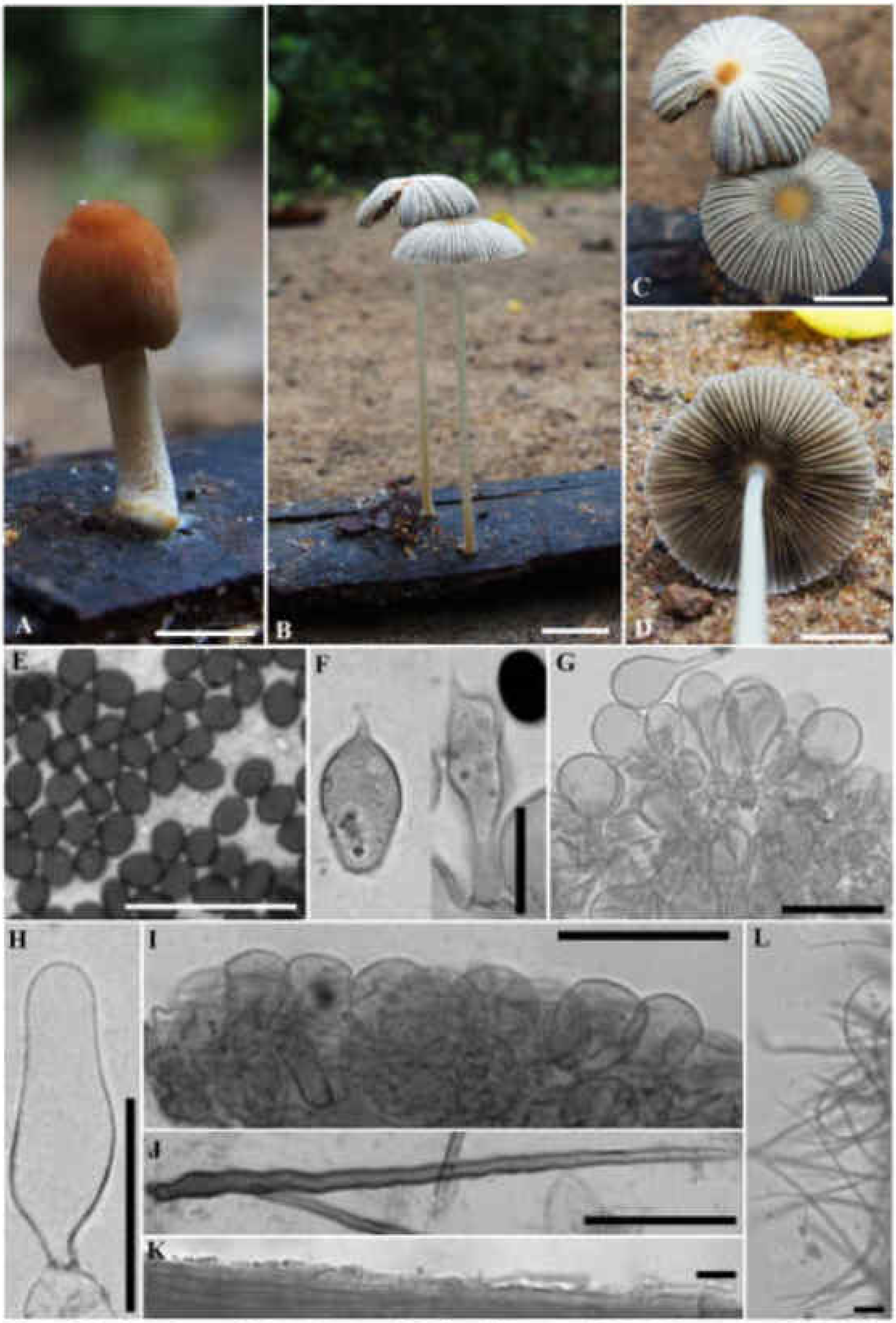

Plate 24. A-L: *Parasola auricoma.* A-D. Basidiocarps. **E.** Basidiospores. **F.** Basidia. **G.** Cheilocystidia. **H.** Pleurocystidium. **I.** Pileipellis. **J.** Sclerocystidium. **K.** Stipitipellis. **L.** Ozonium. Scale Bars: **A** = 1 mm; **B-D** = 10 mm **E-H** = 20 µm; **I-L** = 50 µm.

with a pseudocollarium, L = 34–36, close, initially white, becoming grey (5C1) with age, with lamellulae in 1 tier; edge pruinose, white. Stipe 57–60 × 1.5–2 mm, central, terete, slightly tapering towards the apex, hollow; surface white to off-white, smooth all over; base slightly enlarged, often with abundant hairs when young, disappearing at maturity. Odour and taste not distinctive.

Basidiospores 9–13 × 7–9 × 6–8 µm, on an average 10.5 × 8.3 × 7 µm, Q_1 = 1.11–1.57, Q_{1avg} = 1.30, Q_2 = 1.25–1.66, Q_{2avg} = 1.46, lenticular, ovo-ellipsoid or ellipsoid in face view, ellipsoid in side view, dark brown to black, thick-walled, with a central to slightly eccentric germ-pore up to 1.5 µm wide. Basidia 19–28 × 7–10 µm, clavate or pedicellate-clavate, hyaline, thin-walled, surrounded by 4–6 pseudoparaphyses, 1–4-spored; sterigmata up to 4 µm long. Pleurocystidia 52–102 × 18–27 µm, abundant, subutriform or lageniform, hyaline, thin-walled. Lamella-edge heterogeneous. Cheilocystidia 26–41 × 13–18 µm, abundant, versiform: subglobose, clavate, utriform or lageniform, hyaline, thin-walled. Pileipellis a hymeniderm composed of clavate elements, 45–55 × 20–25 µm, mostly hyaline, thin-walled, often with an intraparietal yellow wall pigment towards the base of the elements, intermixed with sclerocystidia; sclerocystidia 20–115 × 2–7 µm, abundant, narrowly lageniform, with a brown wall pigment, thick-walled. Stipitipellis a cutis often with abundant brown hairs restricted towards the base (ozonium); hyphae 3–4 µm wide, hyaline, slightly thick-walled. Ozonium >200 µm, abundant, with a brown wall pigment, thick-walled. Clamp connections observed on all tissues except at the base of pleurocystidia.

Habit and Habitat:—In small groups, on rotten wood remnants.

Collection examined:—INDIA. Kerala State, Thrissur District, Punnayoorkulam: 13 August 2017, *K. G. Greeshma Ganga G200*.

Observations:—*Parasola auricoma*, a widely distributed species *(*Uljé 2005; Schafer 2014*;* Hussain *et.al* 2018a), is characterised by small basidiocarps; broadly convex pileus with a shallow central depression and plicate-striations; free lamellae with a pseudocollarium; a stipe with a slightly enlarged base and abundant hairs; ovo-ellipsoid to ellipsoid basidiospores with a central to slightly eccentric germ-pore; a hymenium with pleurocystidia; a lamella-edge with abundant, versiform cheilocystidia; a hymeniderm-type pileipellis with sclerocystidia and a cutis-type stipitipellis with ozonium. The presence of sclerocystidia on the pileipellis indicates that the present species belongs to the section *Auricomi* (Schafer 2010).

Comparison of the ITS (688 bp) and the nLSU (872 bp) sequences of the present species with those available in GenBank revealed that the present species is *P. auricoma*. A BLAST search using the ITS and the nLSU sequences showed *P. auricoma* (MH855972, FM160723) as the closest hit with 98.40% and 99.43% identities respectively.

Parasola psathyrelloides K. G. G Ganga & Manim., *Phytotaxa* 405 (5): 257 (2019) **Plate 25.**

Description:—Basidiocarps small, psathyrelloid, delicate, not deliquescent. Pileus 2–9 × 1.5–8 mm when young, finally 16–20 mm diam, initially hemispherical to somewhat convex, expanding to almost conico-convex; surface light brown (6D8) when young, brownish orange (6C6) to light brown (6D6) all over when mature, glabrous, initially translucent-striate, becoming finely sulcate-striate up to the centre, finely tuberculate-punctate when mature, when young often with brown hairs that disappear as the pileus matures; margin straight, entire. Lamellae adnate, L = 19–20, almost close to close, initially white, becoming greyish brown (7E3), with lamellulae in 1-2 tiers; edge eroded, white; margin eroded, becoming paler when mature. Stipe 43–52 × 1.5–2 mm, central, equal, terete, hollow; white to off-white, smooth; base slightly enlarged, when young often with abundant hairs

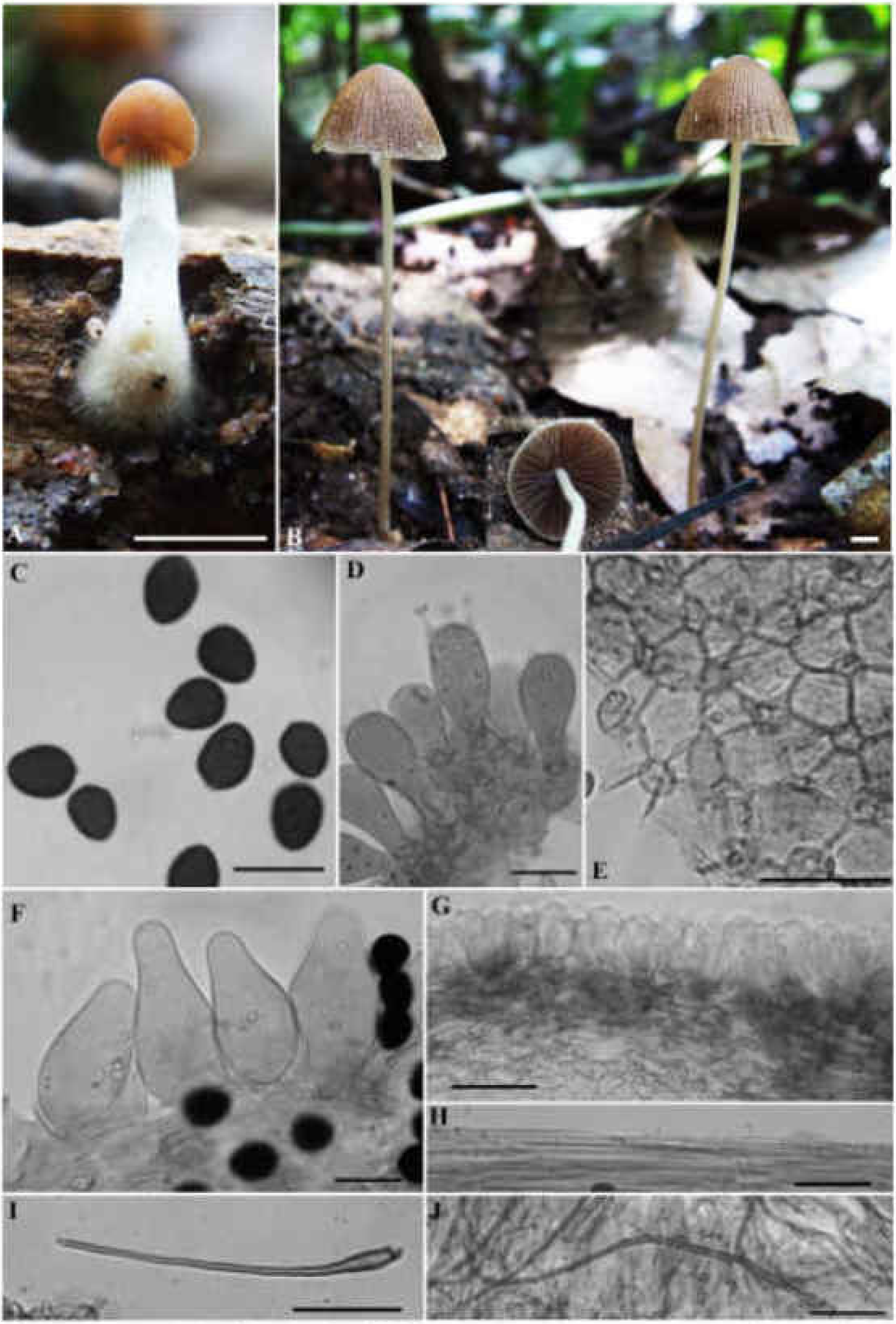

Plate 25. A-J: ***Parasola psathyrelloides***. **A-B**. Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Pseudoparaphyses. **F.** Cheilocystidia. **G.** Pileipellis. **H.** Stipitipellis **I.** Sclerocystidium. **J.** Ozonium. Scale Bars: **A-B** = 1 mm; **C, D & F** = 20 µm; **E, G-J** = 50 µm.

that disappear during the development of the stipe. Velar elements absent. Odour and taste not distinctive.

Basidiospores (8)9–12 × 7–9 × 6–7(8) µm, on an average 10.6 × 8.0 × 6.8 µm, Q1 = 1.12–1.50, Q1avg = 1.34, Q2 = 1.28–2.0, Q2avg = 1.54, lenticular, ovoid to ovo-ellipsoid in face view, often with 3–4 rounded angles, oblong to ellipsoid in side view, dark brown to black, thick-walled, with a central germ-pore up to 1 µm wide. Basidia 24–38 × 9–11 µm, clavate to pedicellate-clavate, hyaline, thin-walled, surrounded by 4–5 pseudoparaphyses, 4-spored; sterigmata up to 5 µm long. Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 27–47 × 18–23 µm, abundant, versiform: globose, subglobose, utriform, or lageniform, often with a short pedicel, hyaline. Pileipellis a hymeniderm composed of clavate elements, 27–43 × 7–23 µm, mostly hyaline, often with an intraparietal yellow pigment towards the base of the structure, mixed with sclerocystidia; sclerocystidia 103–250 × 5–7.5 µm, brown, thick-walled. Stipitipellis a cutis often with abundant, 300–700 µm long, thick-walled, brown hairs restricted towards the base (ozonium); hyphae 3–5 µm wide, thin-walled, hyaline or with a pale yellow intraparietal pigment. Clamp connections observed only on the hyphae of the stipitipellis.

Habit and Habitat:—In small group, on decaying twigs on the forest floor.

Collections examined:—INDIA. Kerala State, Wayanad District, Muthanga forest: 05 July 2017, *K. G. Greeshma Ganga G172* (AMH10120); Kollam District, Thenmala forest: 30 July 2017, *K. G. Greeshma Ganga G191* (CAL1753); Kozhikode District, Peruvannamuzhi forest: 28 September 2017, *K. G. Greeshma Ganga G221* (AMH10119).

Observations:—Psathyrelloid basidiocarps with a finely sulcate-striate pileus; adnate lamellae; a stipe with abundant hairs at the base; ovoid to ovo-ellipsoid basidiospores with 3–4 rounded angles; 4–5 pseudoparaphyses surrounding each basidium; absence of pleurocystidia; a lamellae-edge with versiform cheilocystidia; a hymeniderm-type pileipellis and a cutis-type stipitipellis are salient features of *P. psathyrelloides*. *Parasola psathyrelloides* belongs to the section *Auricomi* (Schafer 2010) because of the presence of sclerocystidia on the pileipellis. A detailed discussion, including the taxonomy and phylogeny of this species, has been provided in Ganga & Manimohan (2019).

***Parasola* species 1** **Plate 26.**

Description:—Basidiocarps small, fragile. Pileus 5–14 mm diam. at maturity, initially ellipsoid to paraboloid, becoming conical to broadly conical often with a small umbo at maturity; surface light brown (6D6) all over when young, becoming yellowish brown (5D6) to light brown (6D6) at the centre and brownish orange (5C5) towards the margin when mature, smooth at the centre, plicate-striate towards the margin; margin straight, crenate. Lamellae free, L = 38–40, close to moderately crowded, initially greyish orange (5B3), becoming black with age, with lamellulae in 1 tier; edge pruinose, white. Stipe 44–68 × 1–1.5 mm, central, terete, slightly tapering towards the apex, hollow; surface white to off-white, smooth all over; base slightly enlarged, often with abundant hairs when young, disappearing at maturity. Odour and taste not distinctive.

Basidiospores 10–13 × 8–10 × 6–8 µm, on an average 11.4 × 8.3 × 6.8 µm, Q_1 = 1.16–1.62, Q_{1avg} = 1.39, Q_2 = 1.42–1.84, Q_{2avg} = 1.65, lenticular, ovoid or ellipsoid with somewhat angular in face view, ellipsoid in side view, dark brown to black, thick-walled, with a central germ-pore up to 3 µm wide. Basidia 23–25 × 11–12 µm, clavate or pedicellate-clavate, hyaline, thin-walled, surrounded by 4–6 pseudoparaphyses, 4-spored; sterigmata up to 2 µm long. Pleurocystidia 38–74 × 19–29 µm, abundant, subutriform or lageniform, hyaline, thin-walled. Lamella-edge heterogeneous. Cheilocystidia 50–66 × 20–24 µm, abundant, utriform, sublageniform or subcylindrical, hyaline, thin-walled. Pileipellis a hymeniderm intermixed with sclerocystidia; hymeniderm elements 25–42 × 18–27 µm, clavate, mostly hyaline, often with an intraparietal yellow wall pigment towards the base of

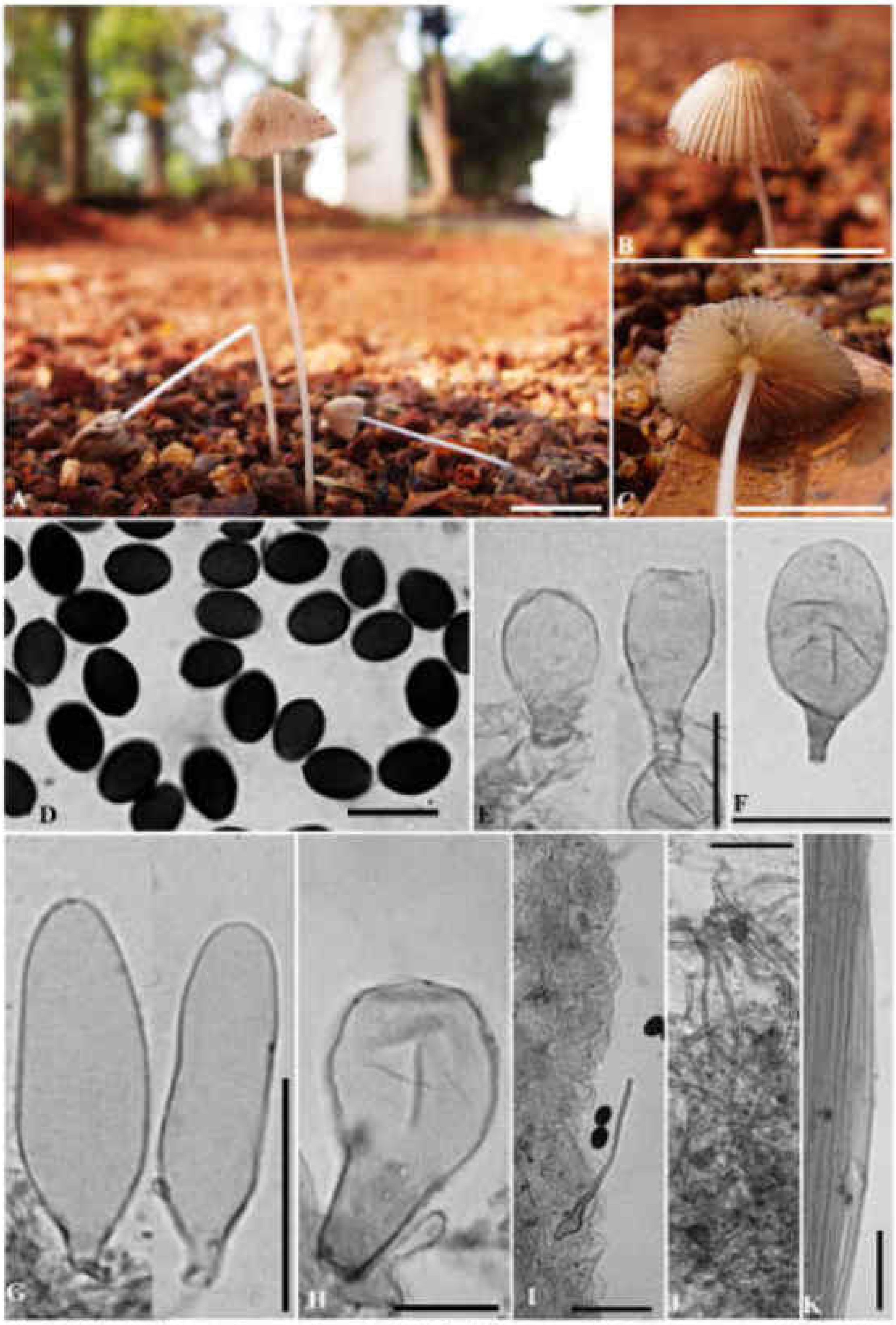

Plate 26. A-K. *Parasola* species 1 : A-C. Basidiocarps. **D.** Basidiospores. **E.** Basidia. **F.** Cheilocystidium. **G.** Pleurocystidia. **H.** Pileipellis element **I.** Pileipellis showing sclerocystidium. **J.** Ozonium. **K.** Stipitipellis. **A-C** = 10 mm; **D-H** = 20 µm; **I-K** = 50 µm

the element, thin-walled. Sclerocystidia 20–100 × 5–9 µm, abundant, narrowly lageniform, with a brown wall pigment, thick-walled. Stipitipellis a cutis often with abundant, brown hairs restricted towards the base (ozonium); hyphae 3–4 µm wide, hyaline, slightly thick-walled. Ozonium >200 µm, abundant, with a brown wall pigment, thick-walled. Clamp connections observed only on the hyphae of stipitipellis.

Habit and Habitat:—Scattered or in small groups, on soil.

Collection examined:—INDIA. Kerala State, Malappuram District, Calicut University Campus: 2 November 2016, *K. G. Greeshma Ganga G127.*

Observations:—The present species is characterised by smaller basidiocarps; conical to broadly conical pileus with an umbo and plicate-striations; free lamellae; a slightly enlarged stipe base with abundant hairs; ovoid to ellipsoid basidiospores with a central germ-pore; a hymenium with pleurocystidia; a lamella-edge with abundant cheilocystidia; a hymeniderm-type pileipellis with sclerocystidia and a cutis-type stipitipellis with an ozonium. A pileipellis with sclerocystidia leads the present species to the section *Auricomi* (Schafer 2010).

Parasola auricoma, a common species (Keirle *et.al* 2004; Uljé 2005; Schafer 2014; Hussain *et.al* 2018a), resembles the present species in having a plicate-striate pileus, a pileipellis with sclerocystidia and a stipitipellis with an ozonium. However, *P. auricoma* differs from the present species in having larger basidiocarps (pileus 13–60 mm diam. and stipe 1–3 mm diam.) with a dark reddish orange at the centre of the pileus, lamellae with a psuedocollarium, ellipsoid basidiospores with a central to slightly eccentric germ-pore and a lignicolous habitat.

Angular basidiospores with a central germ-pore of *Parasola setulosa* (Berk. & Broome) Redhead, Vilgalys & Hopple, in Redhead, Vilgalys, Moncalvo, Johnson & Hopple, a species originally described from Sri Lanka (Pegler 1986), seem to be close to the present collection. However, *P. setulosa* has smaller basidiospores (8–10.4 × 7.4–8.9 × 5.3–8.9 µm) with a narrow germ-pore (1.7–1.9 µm) and a lignicolous habitat. *Parasola psathyrelloides*, a species described during the course of this study (Ganga & Manimohan 2019), shows some similarity with the present species in having angular basidiospores with a central germ-pore and a lamella-edge with similar-sized cheilocystidia. However, *P. psathyrelloides* differs in having psathyrelloid basidiocarps with a smooth pileus, smaller basidiospores (8–12 × 7–9 × 6–8 µm), a hymenium devoid of pleurocystidia, a pileipellis with longer sclerocystidia (300–700 µm) and a lignicolous habitat.

Parasola malakandensis S. Hussain, Afshan & H. Ahmad, a species from Pakistan (Hussain 2017), shares some similarities with the present species in having almost similar-sized basidiocarps, a hymenium with lageniform to utriform pleurocystidia and a terrestrial habitat. *Parasola malakandensis* differs from the present species in having basidiocarps with an applanate to depressed pileus, lamellae with a psuedocollarium, larger basidiospores (11.5–19 × 10.5–16.5 × 9.5–14 µm) and a pileipellis with longer sclerocystidia (70–165 × 5–10 µm).

Comparison of the ITS (690 bp) and the nLSU (873 bp) sequences obtained from the present species with those available in the GenBank suggests that the present *Parasola* species has distinct ITS and nLSU sequences. The ITS and nLSU sequences of the present species showed *P. auricoma* (MH855972, 97.68%; FM160723, 99.08%) as the closest hit in BLASTn searches.

Parasola* section *Parasola Redhead, Vilgalys & Hopple, Taxon 50 (1): 235 (2001)

Pileus and stipe lacking veil. Pileipellis without setae. Pileocystidia absent.

Type species: *Parasola plicatilis* (Curtis) Redhead, Vilgalys & Hopple

Two species of the section *Parasola* were observed during the present study.

Key to the species

1. Basidiocarps small-sized; pileus violet brown or purplish brown...***Parasola parvula***
1. Basidiocarps medium-sized; pileus brownish yellow.............. ***Parasola lilatincta***

Parasola lilatincta (Bender & Uljé) Redhead, Vilgalys & Hopple**,** Taxon 50 (1): 236 (2001) **Plate 27.**

Coprinus lilatinctus Bender & Uljé, in Uljé & Bender, Persoonia 16 (3): 373 (1997)

Description:—Basidiocarps medium-sized, delicate. Pileus 3.5–12 × 2–5.5 mm when young, finally 20–30 mm diam., initially ellipsoid to cylindrical, expanding to broadly convex and finally applanate; surface brownish yellow (5C7) to light brown (6D7) with a lilac tinge when young, brownish yellow (5C7) to greyish orange (5B5) at the centre and paler towards the margin when mature, glabrous, strongly plicate-striate up to the centre; margin crenate. Lamellae free with a prominent pseudocollarium, L = 25–27, fairly crowded, initially white, becoming grey (5B1), with lamellulae in 1–2 tiers; edge even to the naked eye, finely torn under a lens, white. Stipe 70–112 × 1.5–4 mm, central, slightly tapering towards the apex, smooth, fragile at maturity, hollow, translucent-white; base slightly enlarged. Odour and taste not distinctive.

Basidiospores (11)12–16(16.5) × (10)12–14 × (7)8–10 µm, on an average 14.2 × 12.5 × 9.0 µm, Q1 = 1.07–1.25, Q1avg = 1.16, Q2 = 1.29–1.87, Q2avg = 1.55, lenticular, triangular or pentagonal often with an apical papilla in face view, ellipsoid in side view, dark brown to black, thick-walled, with an eccentric germ-pore up to 2 µm wide. Basidia 19–36 × 11–14 µm, clavate to pedicellate-clavate, hyaline, thin-walled, surrounded by 5–8 pseudoparaphyses, 4-spored; sterigmata up to 4 µm long. Pleurocystidia 55–83 × 23–47 µm, utriform or subcylindrical, often with a short pedicel, hyaline, thin-walled. Lamella-edge sterile. Cheilocystidia 42–62 × 21–50 µm, mostly utriform or subutriform, often with a short pedicel, rarely subglobose, hyaline, thin-walled. Pileipellis a hymeniderm; elements 23–55 × 10–15 µm, clavate, mostly hyaline, with a yellowish base in those at the centre of the pileus. Stipitipellis a cutis; hyphae 4–10 µm wide. Yellowish refringent granules present in almost all microscopic elements. Clamp connections observed only on the hyphae of pileus trama, pilei- and stipitipellis.

Habit and Habitat:—In small groups, on decaying elephant dung on the forest floor.

Collections examined:—INDIA, Kerala State: Kannur District, Aralam Forest: 14 July 2017, *K. G. Greeshma Ganga G180* (CAL 1668); Thiruvananthapuram District, Neyyar Forest: 21 October 2017, *K. G. Greeshma Ganga G229* (CAL 1671).

Observations:—*Parasola lilatincta* is characterised by a lilaceous tinge on the pileus of young basidiocarps with a strongly plicate-striate pileus; free lamellae with a prominent pseudocollarium; a stipe with a slightly enlarged base; broadly angular, rounded rhomboid or heart-shaped basidiospores with an apical papilla; presence of refringent granules in almost all elements; a hymenium with utriform or subcylindrical pleurocystidia; a lamella-edge with cheilocystidia; a hymeniderm-type pileipellis and a cutis-type stipitipellis. *Parasola lilatincta* lacks sclerocystidia on the pileipellis and hence belongs to the section *Parasola* (Redhead *et al*. 2001). The record of this species from Kerala State has been published during this study (Ganga & Manimohan 2018).

Parasola parvula K. G. G. Ganga & Manim., *Phytotaxa* 369 (4): 262 (2018)

Plate 28.

Description:—Basidiocarps very small, delicate. Pileus 3–11 mm diam., initially ovoid or ellipsoid, becoming hemispherical and finally applanate with a central depression; surface dark brown (9F4), violet brown (11F5) or purplish brown (12F4) at the centre, greyish brown (11D3) or greyish red (12D3) in the middle, and light

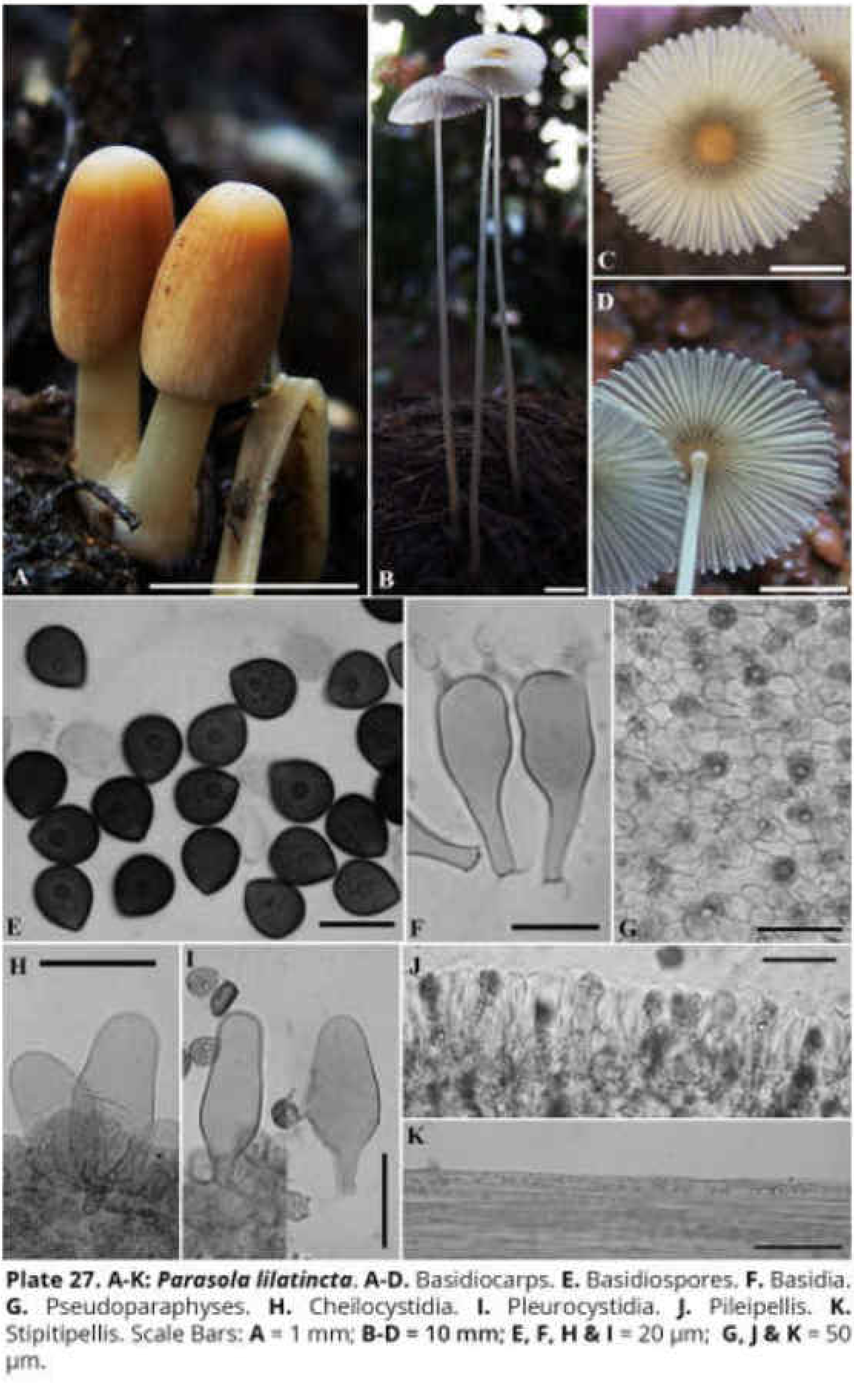

Plate 27. **A-K: *Parasola lilatincta***. **A-D.** Basidiocarps. **E.** Basidiospores. **F.** Basidia. **G.** Pseudoparaphyses. **H.** Cheilocystidia. **I.** Pleurocystidia. **J.** Pileipellis. **K.** Stipitipellis. Scale Bars: **A** = 1 mm; **B-D = 10 mm; E, F, H & I** = 20 µm; **G, J & K** = 50 µm.

brown (7D6) or reddish brown (8D5) at the margin, smooth, plicate-striate up to the centre; margin crenate, straight. Lamellae free with a prominent pseudocollarium, L = 19–20, close, initially pinkish (12A2), becoming reddish grey to grey, with lamellulae in 1 tier. Stipe 25–46 × 1 mm, central, equal, slender, hollow; surface translucent-white, pale purplish brown towards the base, smooth, finely pruinose towards the base. Odour and taste not distinctive.

Basidiospores 8–11 × (6)7–8(9) × (4)5–7 µm, on an average 9.2 × 7.9 × 5.7 µm, Q_1 = 1.0–1.37, Q_{1avg} = 1.15, Q_2 = 1.28–2.25, Q_{2avg} = 1.58, lentiform, limoniform or hexagonal with an apical papilla in face view, ellipsoid to subamygdaliform in side view, dark brown to black, thick-walled; germ-pore eccentric, 1–1.5 µm wide. Basidia 17–35 × 8–10 µm, surrounded by (3)4–5(6) pseudoparaphyses, clavate to pedicellate-clavate, hyaline, thin- to slightly thick-walled, 4-spored; sterigmata up to 4 µm long. Pleurocystidia 54–68 × 16–19 µm, scarce, utriform or cylindrical, often with a short pedicel, hyaline, thin-walled. Lamella-edge sterile. Cheilocystidia 25–44 × 15–20 µm, abundant, similar to pileipellis elements at the margin, versiform towards the stipe: subglobose, clavate, utriform, broadly lageniform or lageniform, often with a short pedicel, hyaline, thin-walled, collapsing at maturity. Pileipellis a hymeniderm; elements 22–73 × 7–22 µm, mostly clavate at the middle and margin of the pileus, clavate or rarely constricted and somewhat lecythiform or branched with a bulbous apex at the centre of the pileus, hyaline with a yellowish base at the margin and hyaline with a purplish black base at the centre of the pileus. Stipitipellis a cutis sometimes overlaid with clumps of branched diverticulate hyphae towards the base; hyphae 3–7 µm wide, hyaline, thin- to slightly thick-walled. Sclerocystidia absent. Clamp connections observed only on the hyphae of pilei- and stipitipellis.

Habit and Habitat:—Solitary or in small groups, on decaying elephant dung collected from the forest.

Collections examined:—INDIA, Kerala State: Substratum (elephant dung) collected from Thrissur District, Chimmini Forest, 07 July 2017; specimens collected from substratum incubated in the lab at Calicut University Campus, 23 July 2017, *K. G. Greeshma Ganga G157* (CAL 1667); 07 July 2017 *K. G. Greeshma Ganga G158* (CAL 1670).

Observations:—*Parasola parvula* is characterised by very smaller basidiocarps with a pileus that is violet brown at the centre, greyish red in the middle and brown at the margin; free lamellae with a prominent pseudocollarium; a pale purplish brown stipe with some pruinosity towards the base; limoniform or hexagonal basidiospores; a hymenium with utriform or cylindrical pleurocystidia; a lamella-edge with versiform cheilocystidia; a hymeniderm-type pileipellis and a cutis-type stipitipellis. *Parasola parvula* is assigned to the section *Parasola* due to the absence of sclerocystidia on the pileipellis (Schafer 2010). A detailed account of the taxonomy and phylogeny of this species is provided in Ganga & Manimohan (2018).

5.1.2.7. ***PSATHYRELLA*** (Fr.) Quél., Mém. Soc. Émul. Montbéliard, Sér. 25: 152 (1872)

Agaricus trib. *Psathyra* Fr., Syst. mycol. (Lundae) 1: 295 (1821)
Agaricus XXVIII *Psathyrella* Fr., Epicr. syst. mycol. (Upsaliae): 237 (1838)
Astylospora Fayod, Annls Sci. Nat., Bot., sér. 79: 376 (1889)
Drosophila Quél., Enchir. fung. (Paris): 115 (1886)
Gymnochilus Clem., in Pound & Clements, Bot. Surv. Nebraska 4: 23 (1896)
Hypholomopsis Earle, Bull. New York Bot. Gard. 5: 436 (1909)
Pluteopsis Fayod, Annls Sci. Nat., Bot., sér. 79: 377 (1889)
Psalliotina Velen., Novitates Mycologicae Novissimae: 155 (1939)
Psammocoparius Delile ex De Seynes, Essai Fl. mycol. Montpellier: 79 (1863)
Psathyra (Fr.) P. Kumm., Führ. Pilzk. (Zerbst): 20 (1871)
Psilocybe Fayod, Annls Sci. Nat., Bot., sér. 79: 377 (1889)

Basidiocarps minute to large, often fragile, short-lived. Pileus conical to campanulate or convex, typically thin, usually hygrophanous, mostly pale clay colour to deep liver brown. Lamellae narrowly adnexed to adnate, never free, pale

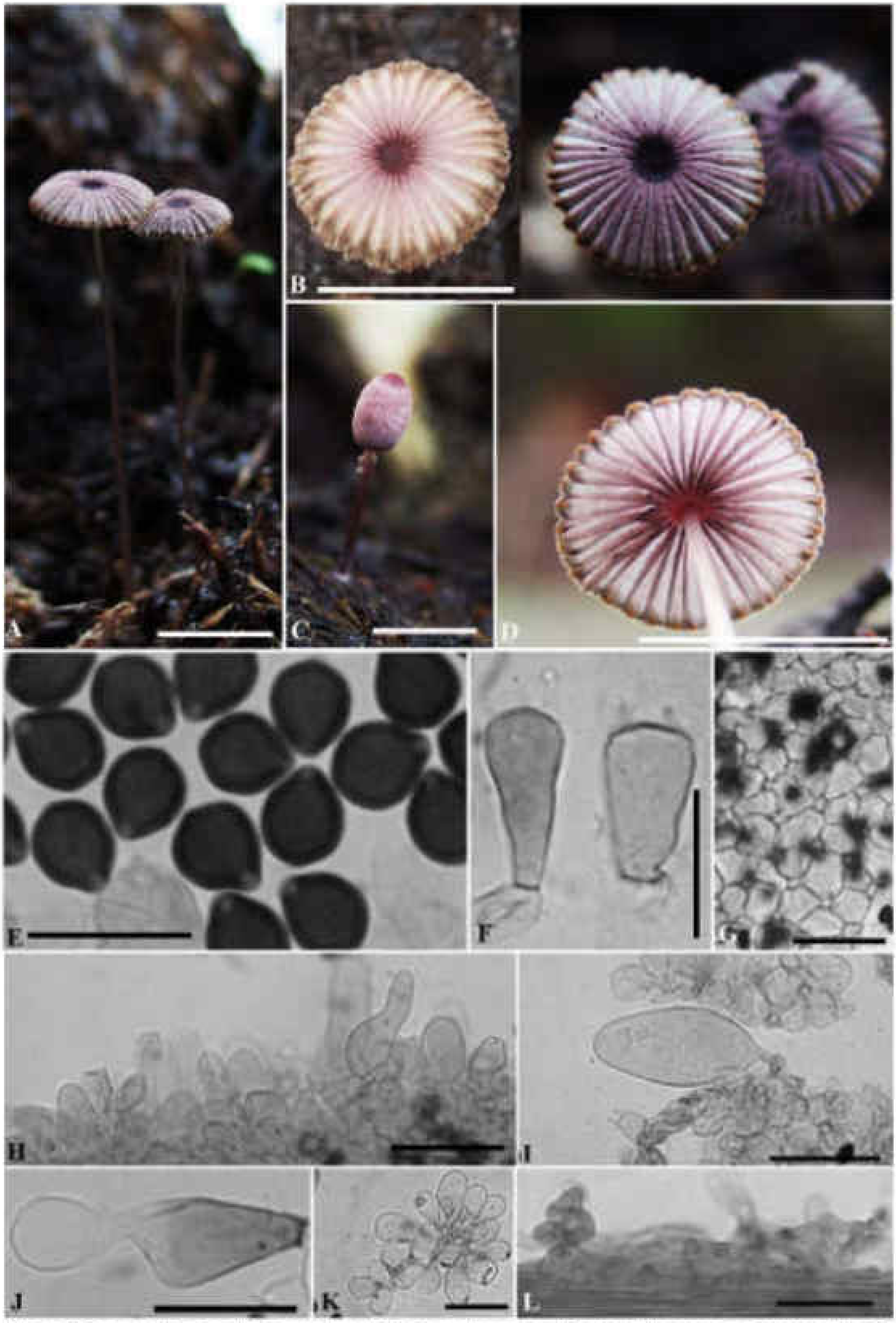

Plate 28. A-L: *Parasola parvula*. A-D. Basidiocarps. **E.** Basidiospores. **F.** Basidia. **G.** Pseudoparaphyses. **H.** Cheilocystidia. **I.** Pleurocystidium. **J & K.** Pileipellis elements. **L.** Stipitipellis. Scale Bars: **A-D** = 10 mm; **E, F, I, & J** = 20 µm; **G, H, K & L** = 50 µm.

soon darkening. Stipe central, well-developed, hollow, fragile. Veil present or absent, sometimes as a fibrillose pileal layer, occasionally as an annulus. Context thin, brittle; spore-print cocoa brown to black or dull brick red. Basidiospores small to large, mostly ovoid to ellipsoid, usually apically truncated by a germ-pore, russet to fuscous brown, opaque or translucent, smooth, with a complex wall. Basidia clavate or pedicellate, typically tetrasporic. Lamellae-edge sterile. Cheilocystidia always present. Pleurocystidia present or absent, occasionally metuloidal. Lamellar trama regular or nearly so, hyaline or pigmented. Pileipellis a true epithelium. Clamp connections present. Habitat terrestrial, lignicolous or coprophilous.

Type species: *Psathyrella gracilis* (Fr.) Quél.

Only one section of the genus *Psathyrella* was observed during the present study.

Psathyrella **section** ***Pygmaeae*** Romagn., Bull. trimest. Soc. mycol. Fr. 98 (1) (1982)

Basidiocarps small- to medium-sized. Veil sparsely developed. Basidiospores small to medium-sized, frontally ellipsoid, laterally phaseoliform, pale to medium dark-coloured, with a central germ-pore. Basidia 4-spored. Cheilocystidia mostly utriform, sometimes with thickened walls and crystalline deposits. Pleurocystidia similar to the cheilocystidia. Clamp connections present. Habitat terrestrial or lignicolous.

Type species: *Psathyrella pygmaea* (Bull. ex Schum.) Singer.

Two species of the section *Pygmaeae* were observed during this study.

Key to the species

1. Basidiocarps small-sized; pileus paraboloid; pleuro-, cheilo- and caulocystidia not muricate .... ***Psathyrella*** **species 1**
1. Basidiocarps medium-sized; pileus applanate; pleuro-, cheilo- and caulocystidia muricate .... ***Psathyrella*** **species 2**

***Psathyrella* species 1** **Plate 29.**

Description:—Basidiocarps small- to medium-sized, fragile. Pileus 27–49 mm diam. when mature, initially conico-convex to convex, expanding to applanate with age; surface white on velar remnants, light orange (5A5) to greyish orange (5B5) elsewhere, hygrophanous and becoming paler, with finely pruinose patches of velar remnants scattered over the surface, translucent-striate; margin decurved, eroded. Lamellae adnate, crowded, initially pale orange (5A3), becoming yellowish brown (5F7), with lamellulae in 4 tiers; edge finely pruinose, concolourous with the sides. Stipe 43–66 × 5–8 mm, central, terete, tapering towards the apex, hollow; surface white, floccose towards the base, pruinose at the apex; base enlarged, inserted. Odour and taste not distinctive.

Basidiospores 6–8 × 4–5 × 4 µm, on an average 7.12 × 4.55 × 4 µm, Q_1 = 1.2–1.75, Q_{1avg} = 1.53, Q_2 = 1.75–2.0, Q_{2avg} = 1.83, lenticular, ovo-ellipsoid, oblong or ellipsoid in face view, phaseoliform in side view, hilar appendix indistinct, dark brown, not opaque, thick-walled, with an indistinct germ-pore. Basidia 16–22 × 7–8 µm, clavate, hyaline, thin-walled, 4-spored; sterigmata up to 4 µm long. Pleurocystidia 42–57 × 11–16 µm, abundant, ventricose-utriform or subutriform, with a muricate apex, hyaline, thick-walled (up to 4 µm thick at the apex). Lamella-edge sterile. Cheilocystidia 34–55 × 11–20 µm, abundant, ventricose-utriform or subutriform, with a muricate apex, hyaline, thick-walled (up to 4 µm thick at the apex). Pileipellis a hymeniderm overlaid with velar hyphae; hymeniderm elements 41–73 × 28–46 µm, hyaline, thin-walled; velar hyphae 27–90 × 10–24 µm, long, branched, hyaline, thin-walled. Pileus trama loosely interwoven composed of barrel-shaped elements; elements 28–54 × 10–21 µm wide, hyaline, thin-walled. Stipitipellis a disrupted cutis with clumps of caulocystidia, more so towards the apex of the stipe; hyphae 3–5 µm, hyaline, slightly thick-walled. Caulocystidia 24–47 × 8–15 µm, abundant, ventricose-utriform or subutriform, hyaline, thick-walled (up

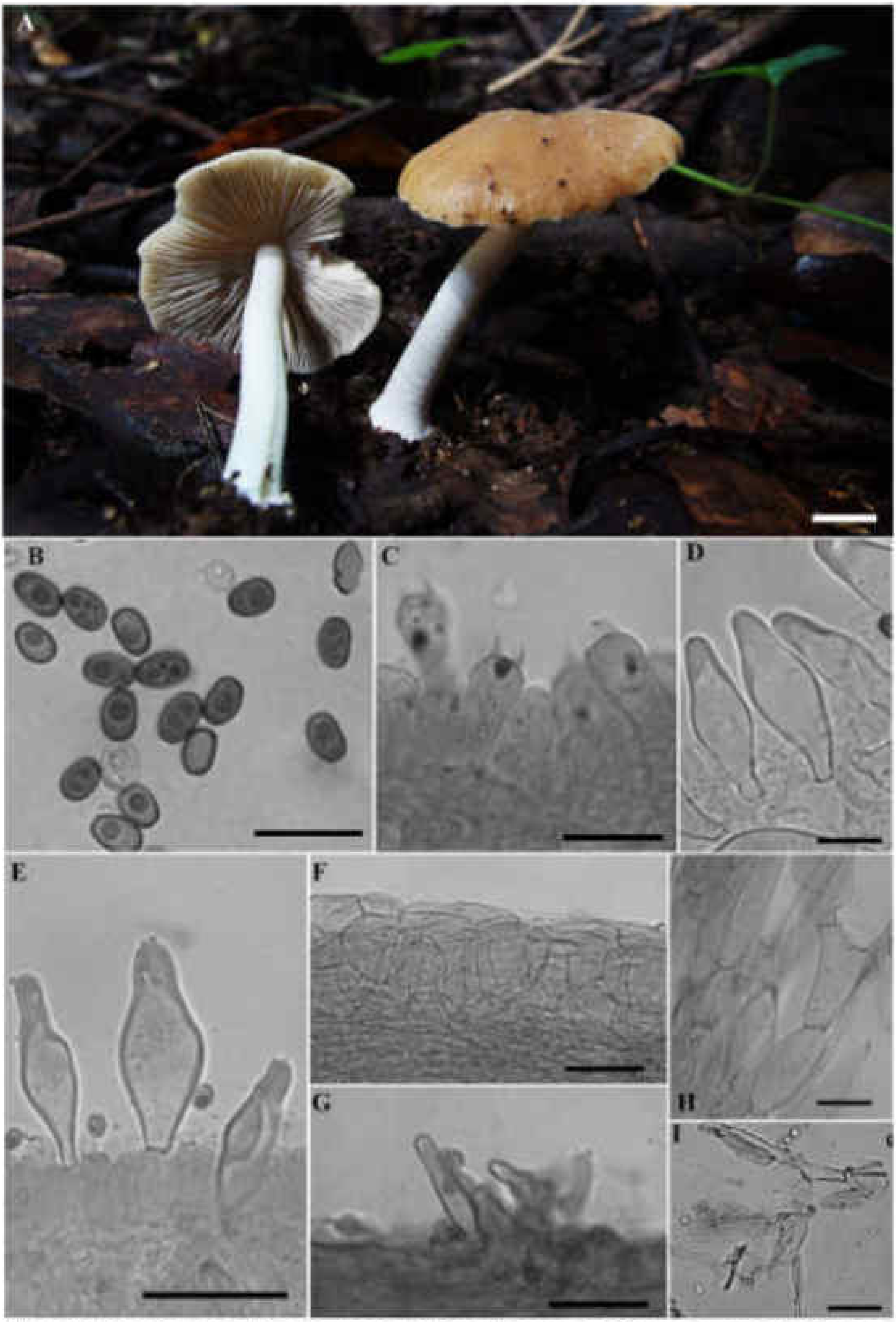

Plate 29. A-I: ***Psathyrella*** **species 1. A.** Basidiocarps. **B.** Basidiospores. **C.** Basidia. **D.** Cheilocystidia. **E.** Pluerocystidia. **F.** Pileipellis. **G.** Stipitipellis showing caulocystidia. **H.** Pileus trama. **I.** Velar elements on the pileipellis. Scale Bars: **A** = 10 mm; **B-E, H & I** = 20 µm; **F & G** = 50 µm.

to 4 µm thick). Clamp connections observed only on the hyphae of pileus trama and velar elements and at the base of caulocystidia.

Habit and Habitat:—Scattered or in small groups, on humus rich soil.

Collection examined:—INDIA. Kerala State, Kollam District, Thenmala forest: 28 July 2017, *K. G. Greeshma Ganga G186.*

Observations:—The present species is characterised by small- to medium-sized basidiocarps; a convex to applanate pileus with white velar remnants; adnate lamellae; a stipe with an enlarged base; ovo-ellipsoid, oblong or ellipsoid basidiospores with an indistinct germ-pore; a hymenium with muricate pleurocystidia; a lamella-edge with abundant, muricate cheilocystidia; a hymeniderm-type pileipellis with branched velar hyphae; a disrupted cutis-type stipitipellis with caulocystidia and a terrestrial habitat. Due to the presence of a sparsely developed veil on the pileus, ellipsoid basidiospores and a lamella-edge with muricate cheilocystidia, the present species belongs to the section *Pygmaea* (Wächter & Melzer 2020). *Psathyrella variata* A. H. Sm, a species originally reported from the Netherlands (Kits van Waveren 1985), shows some similarity with the present species in having basidiospores with an indistinct germ-pore, a hymenium with muricate pleurocystidia and a terrestrial habitat. However, *P. variata* differs from the present species in having a dark reddish brown pileus with a white, pruinose surface, basidiospores with a distinct hilar appendix, a hymenium with dimorphic pleurocystidia and a pileipellis with long and narrow hairs towards the margin of the pileus.

The muricate chielo- and pleurocystidia of *Psathyrella pygmaea* (Bull.) Singer, a species reported from France, the British Isles and the Netherlands (Kits van Waveren 1985), can be comparable with the present species. However, *P. pygmeae* has smaller basidiocarps (pileus 5–17 mm and stipe 10–20 × 1–1.5 mm) with a darker or ochreous colour at the centre of the pileus, basidiospores with a distinct germ-pore and hilar appendix and a gregarious habit and lignicolous habitat. *Psathyrella spadicea* (schaeff.) Sing., a species distributed in the Netherlands, France and Britain (Kits van Waveren 1985), is similar to the present species in having a hymenium with muricate cheilo- and pleurocystidia and basidiospores devoid of a germ-pore. However, *P. spadicea* has a dark reddish brown pileus devoid of a veil, larger basidiospores (7–10 × 4–5.5 µm) with a distinct hilar appendix, a caespitose habit and lignicolous habitat.

Psathyrella atricastanea, a species originally described from Cuba (Smith 1972), shares some similarities with the present species in having almost similar size and shape of the basidiocarps and ovo-ellipsoid basidiospores. However, *P. atricastanea* differs from the present species in having a lamella-edge with smooth and thin-walled cheilocystidia, a hymenium devoid of pleurocystidia and a lignicolous habitat.

Comparison of the ITS (645 bp) and the nLSU (845 bp) sequences derived from the present *Psathyrella* species with those available in the GenBank showed that the present *Psathyrella* species has distinct ITS and nLSU sequences. A megablast search using the ITS sequence showed *Psathyrella pygmaea* (DQ389718) as the closest hit with 95.34% identity. *Psathyrella atricastanea* (MW301083: 99.52% identity) resulted as the closest hit in a BLASTn search with the nLSU sequence.

***Psathyrella* species 2** **Plate 30.**

Description:—Basidiocarps small, fragile. Pileus 10–12 × 5–8 mm diam. when mature, initially ovoid to paraboloid, becoming campanulate to conico-campanulate with age; surface initially white on velar remnants, dark brown (7F8) to reddish brown (7D5) elsewhere, becoming light brown (6D4) to greyish brown (6D3) all over with age, hygrophanous and becoming paler, fibrillose when young, becoming translucent-striate towards the margin; margin decurved or straight, initially entire, wavy at maturity. Lamellae adnate, moderately crowded, initially

Plate 30. A-K: *Psathyrella* species 2. A-C. Basidiocarps. **D.** Basidiospores. **E.** Basidia. **F.** Cheilocystidia. **G.** pleurocystidium **H.** Pileipellis. **I.** Stipitipellis. **J.** pseudoparaphyses. **K.** Caulocystidium. Scale Bars: **A-C** = 10 mm; **D-G & K** = 20 µm; **H-J** = 50 µm.

white, becoming black, with lamellulae in 2 tiers; edge finely pruinose, concolourous with the sides. Stipe 15–40 × 1–1.5 mm, central, terete, slightly tapering towards the apex, hollow; surface orange white (6A2), pruinose; base enlarged. Context 1–1.5 mm wide, dark reddish brown. Odour and taste not distinctive.

Basidiospores 6–8(9) × 6–7 × 5–6 µm, on an average 7.17 × 6.15 × 5.5 µm, Q_1 = 1–1.3, Q_{1avg} = 1.2, Q_2 = 1–1.6, Q_{2avg} = 1.16, lenticular, pentagonal or triangular with a distinct apical papilla in face view, ellipsoid in side view, hilar appendix indistinct, dark brown to black, opaque, thick-walled, with a distinct germ-pore up to 3 µm wide. Basidia 12–16 × 8–9 µm, clavate or sphaeropedunculate, hyaline, slightly thick-walled, surrounded by 4–5 pseudoparaphyses, 4-spored; sterigmata up to 4 µm long. Pleurocystidia 29–38 × 9–13 µm, abundant, utriform or sublageniform, hyaline, thin-walled. Lamella-edge heterogeneous. Cheilocystidia 19–30 × 10–13 µm, abundant, utriform or lageniform, hyaline, thin-walled. Pileipellis an epithelioid hymeniderm; epithelioid hymeniderm elements 39–46 × 39–43 µm, broadly clavate, hyaline, thin-walled. Stipitipellis a disrupted cutis with clumps of caulocystidia; hyphae 2–5 µm, hyaline, slightly thick-walled. Caulocystidia 22–37 × 9–15 µm, abundant, utriform or subutriform, hyaline, thin-walled. Clamp connections observed only on the hyphae of stipitipellis.

Habit and Habitat:—Solitary, scattered or in small groups, on decaying elephant dung.

Collections examined:—INDIA. Kerala State, Kozhikode District, Kakkayam forest: 5 October 2016, *K. G. Greeshma Ganga G109, G110.*

Observations:—The present species is characterised by small basidiocarps with a campanulate to conico-campanulate pileus; adnate lamellae; a stipe with an enlarged base; pentagonal to triangular basidiospores with an apical papilla; a hymenium with abundant pleurocystidia; a lamella-edge with utriform to lageniform cheilocystidia; an epithelioid hymeniderm-type pileipellis; a disrupted cutis-type stipitipellis with caulocystidia and a coprophilous habitat. The present species could not be placed in any of the recognised sections of the genus *Psathyrella* to date (Wächter & Melzer 2020), as its morphological features do not fit into any of the sections. However, an ITS-based phylogenetic analysis of the genus *Psathyrella* conducted as part of the study (Figure 8) found that the members of the section *Pygmaeae* and the present species together formed a monophyletic group. Hence, *Psathyrella* species 2 is being treated under the section *Pygmaeae.*

Psathyrella saponacea F.H. Møller (previously treated as *Psathyrella coprophila* Watling), a species reported from the British Isles and Sweden (Kits van Waveren 1985; Larsson & Örstadius 2008), resembles the present species in having smaller basidiocarps with thick and dark reddish brown context, a hymenium with utriform or sublageniform cheilo- and pleurocystidia and a coprophilous habitat. However, *P. coprophila* has basidiocarps with a semiglobose to convex pileus, subdistant lamellae (L = 16–20) and ellipsoid to elongate-hexagonal and larger basidiospores (11–13(13.5) × 6.5–7 µm) with an eccentric and narrow germ-pore (1–1.5 µm wide). *Psathyrella obtusata* (Pers.) A.H. Sm, a species originally reported from Europe and also recorded from the United States, Canada and India (Smith 1972; Manjula 1983; Kits van Waveren 1985; Kaur *et al*. 2013b), seems to be close to the present species in having basidiocarps with an almost similar pileus surface, dark brown basidiospores and a solitary to gregarious habit. However, *P. obtusata* has larger basidiocarps (Pileus 10–25 diam. and stipe 20–75 × 2–3 mm) with a thin (<1 mm) context, purplish brown lamellae, oblong to ellipsoid and narrow basidiospores (7–9 × 4–4.5 µm), a lamella-edge with fusoid and clavate or saccate cheilocystidia with an obtuse apex and a lignicolous habitat.

Psathyrella melleipallida A.H. Sm., a species originally reported from North America (Smith 1972), has a comparable basidiocarp with an almost identical pileus to the present species. *Psathyrella melleipallida*, on the other hand, has ellipsoid to ovoid and larger basidiospores (8–10 × 5–6 µm) and a lignicolous habitat.

The distinctive status of the ITS (G110: 639 bp) and the nLSU (G110: 856 bp) sequences produced from the present *Psathyrella* species was confirmed by BLASTn searches. A megablast search using the ITS sequence showed *Psathyrella coprophila* (MH860434) as the closest hit with 95.50% identity. *Psathyrella melleipallida* (DQ986272: 99.53%) was the closest hit in a BLASTn search with the nLSU sequence.

Uncertain infrageneric position

***Psathyrella* species 3** **Plate 31.**

Description:—Basidiocarps small, fragile. Pileus 6–11 × 6–9 mm when young, finally 13–23 × 8–13 mm at maturity, initially convex to broadly paraboloid, expanding to broadly convex with age; surface white on velar remnants, brown (6D7) to light brown (6D6) elsewhere when young, becoming light brown (6D5) at the centre and greyish brown (6E3) towards the margin with age, hygrophanous and becoming paler, with somewhat squamulose to fibrillose patches of velar remnants scattered over the surface, translucent-striate towards the margin; margin incurved when young, becoming straight, first slightly appendiculate and becoming somewhat wavy at maturity. Lamellae adnate, moderately crowded, initially white, becoming greyish brown (6F3), with lamellulae in 2 tiers; edge finely pruinose, concolourous with the sides. Stipe 32–47 × 1.5–3 mm, central, terete, tapering towards the apex, hollow; surface white, pruinose all over, often with remnants of an inferior annulus close to the base; base enlarged, inserted. Odour and taste not distinctive.

Basidiospores 9–11(12) × 6–7(8) × 5–7 µm, on an average 9.8 × 7 × 5.35 µm, Q_1 = 1.25–1.66, Q_{1avg} = 1.43, Q_2 = 1.66–2.0, Q_{2avg} = 1.83, lenticular, ovoid to somewhat angular-ovate in face view, ellipsoid in side view, hilar appendix distinct, dark brown to black, opaque, thick-walled, with a distinct germ-pore up to 1.5 µm wide. Basidia 16–23 × 10–13 µm, elongate-clavate or sphaeropedunculate, hyaline, slightly thick-walled, 4-spored; sterigmata up to 4 µm long. Pleurocystidia 35–45 × 15–21 µm, abundant, cylindrical or utriform, often with amorphous materials at the apex, hyaline, thin-walled. Lamella-edge heterogeneous. Cheilocystidia 30–50 × 15–20 µm, abundant, utriform, often with amorphous materials at the apex, hyaline, thin-walled. Pileipellis an epithelioid hymeniderm with scattered velar elements; epithelioid hymeniderm elements 30–46 × 30–40 µm, hyaline, thin-walled; velar elements composed of thick-walled, inflated (8–30 µm wide) and thin-walled, narrow (2–4 µm wide) elements, hyaline. Stipitipellis a cutis disrupted with clusters of caulocystidia; hyphae 3–4 µm wide, hyaline, slightly thick-walled. Caulocystidia 33–55 × 9–18 µm, abundant, utriform or rarely lageniform, often with amorphous materials at the apex, hyaline, slightly thick-walled. Clamp connections observed only on the hyphae of velar elements and at the base of caulocystidia.

Habit and Habitat:—In small groups, on humus rich soil.

Collection examined:—INDIA. Kerala State, Thrissur District, Punnayoorkulam: 18 September 2018, *K. G. Greeshma Ganga G280.*

Observations:—Small basidiocarps; a broadly paraboloid to broadly convex pileus with white velar remnants; adnate lamellae; a stipe with remnants of an inferior annulus close to the base of the stipe; ovoid to somewhat angular-ovate basidiospores with a distinct germ-pore; a hymenium with cylindrical to utriform pleurocystidia with amorphous materials at the apex; a lamella-edge with abundant cheilocystidia; an epithelioid hymeniderm-type pileipellis with thick- and thin-walled velar hyphae; a cutis-type stipitipellis with caulocystidia and a terrestrial habitat are the diagnostic characters of the present species. The morphological

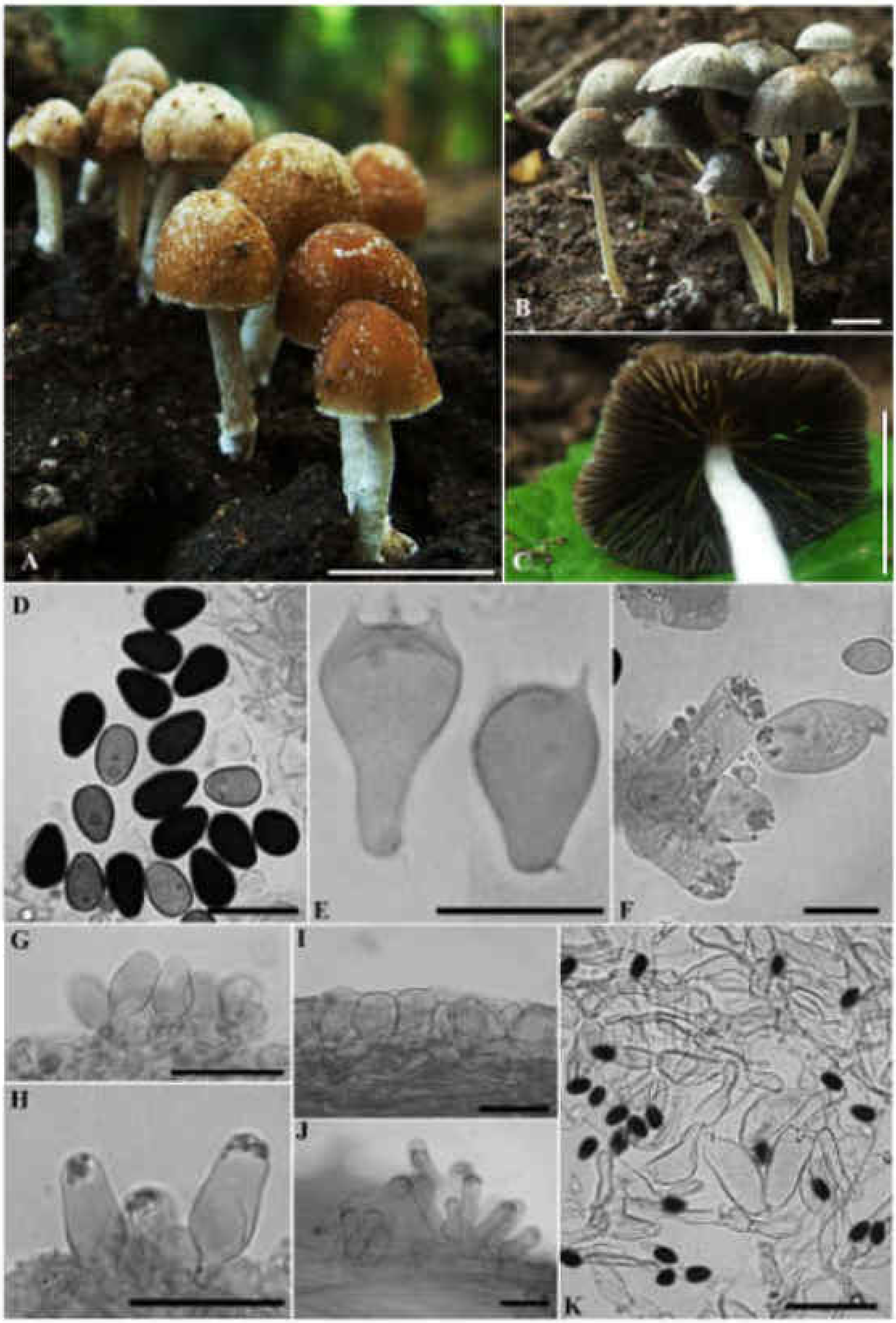

Plate 31. A-K: *Psathyrella* species 3. A-C. Basidiocarps. **D.** Basidiospores. **E.** Basidia. **F.** Cheilocystidia. **G.** Paracystidia. **H.** Pleurocystidia. **I.** Pileipellis. **J.** Stipitipellis showing caulocystidia. **K.** Velar elements on the pileipellis. Scale Bars: **A-C** = 10 mm; **D-F, H & K** = 20 µm; **G, I & J** = 50 µm.

characters of the present species could not be compared to those of any existing sections (Wächter & Melzer 2020) of the genus *Psathyrella*. This is also supported by the findings from the phylogenetic analysis of the genus *Psathyrella* (Figure 8) where the present species formed a distinct lineage from the members of the sections *Saponaceae* and *Pygmaeae*.

Psathyrella subnuda (P. Karst.) A.H. Sm., a North American species (Smith 1972; Voto *et al.* 2019), shows some resemblance with the present species in having ovoid to somewhat angular-ovate basidiospores, a lamella-edge with abundant para- and cheilocystidia and a terrestrial habitat. However, *P. subnuda* differs from the present species in having larger basidiocarps (pileus 25–40 mm diam. and stipe 40–60 × 2–3.5 mm), smaller basidiospores (8–10 × 4.5–5.5 × 5.5–7 µm) and a stipitipellis with larger caulocystidia (150 × 20 µm) devoid of amorphous materials at the apex. *Psathyrella spadiceogrisea* (Schaeff.) Maire, a species originally reported from Europe (Smith 1972; Kits van Waveren 1985), shares some similarities with the present species in having a brown to grey pileus with white velar remnants at the margin, a stipe with velar remnants close to the stipe base, basidiospores with a distinct germ-pore and a terrestrial habitat. However, *P. spadiceogrisea* has basidiocarps with an applanate, larger pileus (10–80 mm), ellipsoid and smaller basidiospores (7–10 × 4–5.5 µm) and a lamella-edge with numerous paracystidia.

The colour and shape of the basidiocarps and a pileus with patches of fibrillose velar remnants of *Psathyrella saponacea*, a species reported from the British Isles and Sweden (Kits van Waveren 1985; Larsson & Örstadius 2008), are similar to the present species. *Psathyrella saponacea,* however, differs from the present species in having larger basidiospores (11–13(13.5) × 6.5–7 µm) with a distinct, eccentric germ-pore, a hymenium with pleurocystidia devoid of amorphous materials at the apex and a coprophilous habitat.

Comparison of the ITS (636 bp) and the nLSU (772 bp) sequences derived from the present *Psathyrella* species with those available in the GenBank shows that the present *Psathyrella* species has distinct ITS and nLSU sequences. A megablast search using the ITS sequence showed *Psathyrella subnuda* (MF326000) as the closest hit with 96.86% identity. *Psathyrella saponacea* (MH155960: 99.74% identity) revealed as the closest hit in a BLASTn search using the nLSU sequence.

5.1.2.8. ***TULOSESUS*** D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1204 (2020)

Basidiocarps tiny to medium-sized. Veil sometimes present. Lamellae deliquescent or withering. Basidiospores mostly large-sized, occasionally medium-sized, rarely small, sometimes with a polygonal outline, germ-pore predominantly eccentric, rarely central. Basidia mostly 4-spored. Cheilocystidia mostly clavate and sphaeropedunculate, sometimes mixed with lageniform, rarely purely lageniform. Pleurocystidia present or absent. Pileipellis sometimes with velar elements, consisting of chains of diverticulate, subcylindrical cells, sometimes also mixed with subglobose, occasionally encrusted elements. Pileocystidia always present, often (sub-) capitate, sclerocystidia often present. Clamp connections present or absent. Habitat terrestrial, lignicolous, subfimicolous or fimicolous.

Type species: *Tulosesus callinus* (M. Lange & A.H. Sm.) Wächter & A. Melzer

Four species of the genus *Tulosesus* were encountered in this study.

Key to the species of the genus *Tulosesus* described in this study

1. Pleurocystidia present; pileipellis without velar elements .... ***Tulosesus brevisetulosus***
1. Pleurocystidia absent; pileipellis with velar elements... **2**
2. Pileus >6 mm in diameter; basidiospores >10 µm long, with a central germ-pore ....'***Coprinellus pseudodisseminatus'***

2. Pileus <6 mm in diameter; basidiospores <10 µm long, with an eccentric germ-pore **3**

3. Cheilocystidia lageniform; habitat terrestrial.......................... ***Tulosesus*** **species 1**

3. Cheilocystidia subglobose to ellipsoid; habitat lignicolous. ....
.... ***Tulosesus velatopruinatus***

`***Coprinellus pseudodisseminatus***´ T. Bau & M. Huang, in Huang & Bau, Phytotaxa 374 (2): 121 (2018) **Plate 32.**

Description:—Basidiocarps small, delicate. Pileus 3–4 × 2–3 mm when young, finally 5–4 × 2–5.5 mm at maturity, initially paraboloid, becoming broadly paraboloid to obtusely conical, often with an umbo with age; surface yellowish white (4A2) to white (4A1) when young, becoming grey (4B1) when mature, with fine glimmering hairs all over, plicate-striate towards the margin, deliquescent; margin straight, crenate. Lamellae adnate, L = 17–18, close, initially white, becoming grey (5D1), with lamellulae in 1 tier; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 15–22 × 0.5–1 mm, central, terete, slightly tapering towards the apex, hollow; surface white, pubescent all over; base slightly enlarged to subbulbous. Odour and taste not distinctive.

Basidiospores 6–9 × 3–5 × 3–4 µm, on an average 6.72 × 3.9 × 3.9 µm, Q_1 = 1.5–2.0, Q_{1avg} = 1.69, Q_2 = 1.55–2.0, Q_{2avg} = 1.77, lenticular, oblong-ellipsoid to oblong with a rounded base and apex in face view, ellipsoid in side view, dark brown, thick-walled, with a central germ-pore up to 1.5 µm wide. Mature basidia were not observed. Basidioles 18–22 × 6–7 µm, clavate, hyaline, thin-walled. Pleurocystidia absent. Lamella-edge heterogeneous. Cheilocystidia 13–25 × 10–16 µm, abundant, versiform: globose, subglobose, clavate or lageniform, hyaline, slightly thick-walled. Pileipellis an epithelioid hymeniderm disrupted by pileocystidia and scattered velar elements; epithelioid hymeniderm elements 25–40 × 23–34 µm, hyaline, thin-walled; velar elements 3–9 µm wide, short, branched, hyaline with scattered granules, thin-walled. Pileocystidia 47–200 × 21–33 µm, abundant, lageniform, hyaline, thin-walled. Stipitipellis a cutis disrupted by isolated or patches of caulocystidia; hyphae 4–15 µm wide, hyaline, slightly thick-walled. Caulocystidia 41–110 × 17–21 µm, abundant, subcylindrical to lageniform, hyaline, thin-walled. Clamp connections observed only at the base of cheilocystidia and on velar elements on the pileipellis.

Habit and Habitat:—In large groups or rarely scattered, on rotten twigs.

Collection examined:—INDIA. Kerala State, Thrissur District, Vazhachal Forest: 08 November 2017, *K. G. Greeshma Ganga G244*.

Observations:—'*Coprinellus pseudodisseminatus*', a species recently described from China (Huang & Bau 2018), is characterised by small basidiocarps; a paraboloid to obtusely conical pileus with plicate-striations; adnate lamellae; a stipe with a slightly enlarged base; oblong-ellipsoid to oblong basidiospores with a central germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; an epithelioid hymeniderm-type pileipellis with pileocystidia and scattered velar elements and a cutis-type stipitipellis with caulocystidia.

The closest hit in a BLASTn search using the ITS (654 bp) sequence was '*C. pseudodisseminatus*' (MH379151; 99.85% identity). While using the nLSU (892 bp) sequence, *Coprinellus subimpatiens* (MH868521; 99.22%) resulted as the closest hit. The macro- and microscopic characters of the present collection appear to be identical to those of '*C. pseudodisseminatus*' from China (Huang & Bau 2018). However, in the ITS-based molecular phylogenetic analysis (Figure 9) performed as part of the present study, the sequence of this Kerala collection was found to be nested within the genus *Tulosesus*, necessitating the transfer of the species from the genus *Coprinellus* to *Tulosesus*. *Tulosesus* is a recently established genus to accommodate the species that were previously treated under the clade

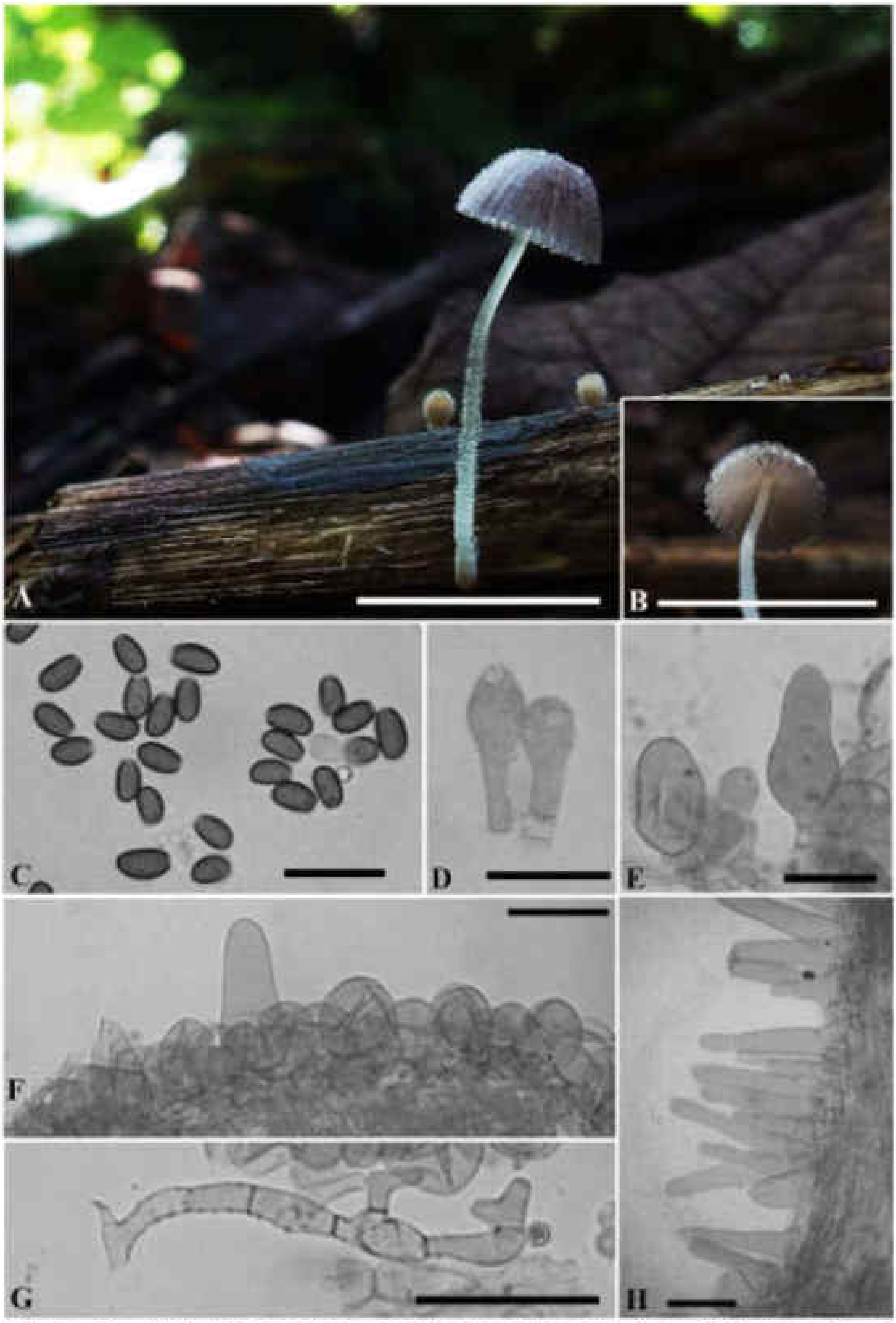

Plate 32. A-H: *'Coprinellus pseudodisseminatus'*. A-B. Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Cheilocystidia **F.** Pileipellis showing pileocystidia. **G.** Velar elemants on the pileipellis. **H.** Stipitipellis showing caulocystidia. Scale Bars: **A-B** = 10 mm; **C-E & G** = 20 µm; **F & H** = 50 µm.

/Coprinellus B of the genus *Coprinellus sensu lato*. Since there is no valid proposal available regarding the transfer of '*C. pseudodisseminatus*' to *Tulosesus*, the present study retained the name '*C. pseudodisseminatus*' but described and discussed it under the genus *Tulosesus*.

Tulosesus brevisetulosus (Arnolds) D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1209 (2020) **Plate 33.**

Coprinellus brevisetulosus (Arnolds) Redhead, Vilgalys & Moncalvo, in Redhead, Vilgalys, Moncalvo, Johnson & Hopple, Taxon 50 (1): 232 (2001)
Coprinus brevisetulosus Arnolds, Biblthca Mycol. 90 (3): 309 (1982)

Description:—Basidiocarps small, fragile. Pileus 2–4 × 4–6 mm when young, finally up to 10 mm diam. at maturity, initially subglobose to paraboloid, becoming applanate with age; surface yellowish grey (4B3) at the centre and greyish yellow (4B2) towards the margin when young, becoming yellowish brown (5D5) at the centre and grey (5E1) towards the margin when mature, finely velvety all over, plicate-striate towards the margin, deliquescent; margin initially crenate, becoming upturned, strongly fissile when mature. Lamellae adnexed, L = 26–28, close, initially white, becoming grey (5E1) to black at maturity, with lamellulae in 1 tier; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 13–30 × 1–1.5 mm, central, terete, slightly tapering towards the apex, hollow; surface white to off-white, pruinose all over; base slightly enlarged to subbulbous. Odour and taste not distinctive.

Basidiospores 8–11 × 4–6 × 4–5 µm, on an average 8.82 × 4.87 × 4.57 µm, Q_1 = 1.16–2.25, Q_{1avg} = 1.69, Q_2 = 1.5–2.5, Q_{2avg} = 1.85, lenticular, subcylindrical to rarely oblong in face view, ellipsoid in side view, dark brown to black, thick-walled, with a central germ-pore up to 1.5 µm wide. Basidia 13–19 × 8–9 µm, clavate to pedicellate-clavate, hyaline, thin-walled, surrounded by 4–5 pseudoparaphyses, 4-spored; sterigmata up to 4 µm long. Pleurocystidia 50–75 × 24–33, abundant, subcylindrical to cylindrico-clavate, hyaline, thin-walled. Lamella-edge sterile.

Cheilocystidia 18–35 × 16–25 µm, abundant, versiform: globose, subglobose, sphaeropedunculate, oblong or ellipsoid, often with a short pedicel, hyaline, thin-walled. Pileipellis an epithelioid hymeniderm disrupted by pileocystidia; epithelioid hymeniderm elements 21–27 × 18–23 µm, hyaline, thin-walled. Pileocystidia 33–60 × 8–10 µm, abundant, narrowly lageniform with a tapering apex, rarely with a short pedicel, hyaline, thin-walled. Stipitipellis a cutis disrupted by isolated or patches of caulocystidia; hyphae 2–6 µm wide, hyaline, slightly thick-walled. Caulocystidia 29–47 × 7–10 µm, abundant, narrowly lageniform with a tapering apex, hyaline, thin-walled. Clamp connections observed only on the hyphae of the stipitipellis.

Habit and Habitat:—In small groups, on decaying cow dung.

Collections examined:—INDIA. Kerala State, Thrissur District, Punnayoorkulam: 05 October 2016, *K. G. Greeshma Ganga G224*; Malappuram District, dung samples collected from Malappuram and incubated in the lab: 28 December 2017, *K. G. Greeshma Ganga G251*; 21 January 2018, *K. G. Greeshma Ganga G255.*

Observations:—*Tulosesus brevisetulosus,* a species originally described from the Netherlands as *Coprinellus brevisetulosus* (Prydiuk 2010), is characterised by small basidiocarps; a paraboloid to applanate pileus with translucent-striations; adnexed lamellae; a stipe with a slightly enlarged base; subcylindrical to rarely oblong basidiospores with a central germ-pore; a hymenium with subcylindrical to cylindrico-clavate pleurocystidia; a lamella-edge with abundant cheilocystidia; an epithelioid hymeniderm-type pileipellis with pileocystidia and a cutis-type stipitipellis with caulocystidia.

A total of four nucleotide sequences (Two ITS: G251: 661 bp, G224: 644 bp and two nLSU: G251: 914 bp, G224: 814 bp) were generated from the present species. The closest hits in BLASTn searches with the ITS (G251) and the nLSU (G224) sequences revealed *C. brevisetulosus* (presently as *T. brevisetulosus*)

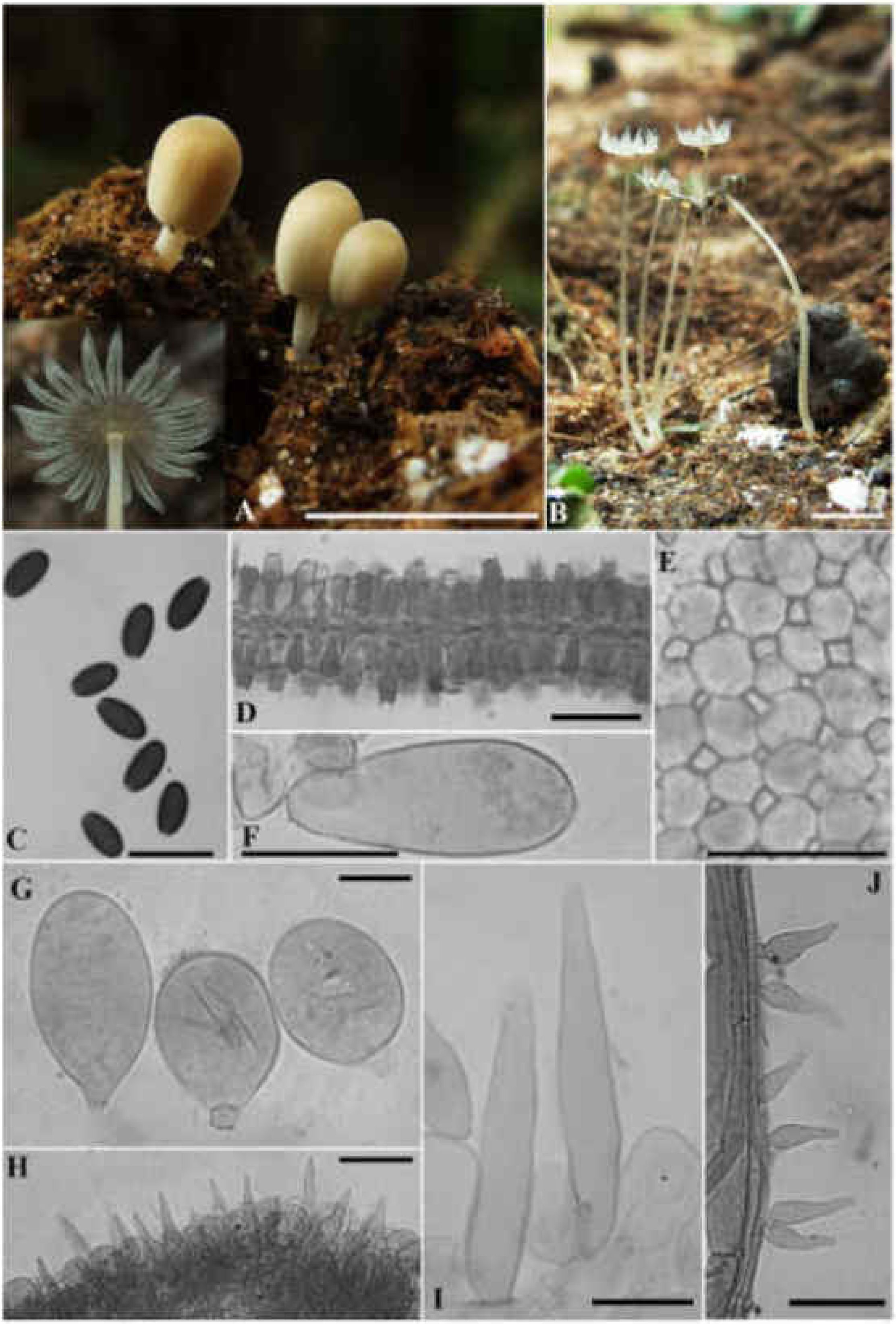

Plate 33. A-J: *Tulosesus brevisetulosus*. A-B. Basidiocarps. **C.** Basidiospores **D.** Basidia **E.** Pseudoparaphyses. **F.** Pleurocystidium **G.** Cheilocystidia. **H.** Pileipellis. **I.** Pileocystidia. **J.** Stipitipellis. Scale Bars: **A-B** = 10 mm; **C, F, G & I** = 20 µm; **D, E, H & J** = 50 µm.

(GU227711: 99.55% identity) and *C. pellucidus* (presently as *T. pellucidus*) (KR869761: 99.00% identity) respectively.

Tulosesus **species 1** **Plate 34.**

Description:—Basidiocarps small, fragile. Pileus 18–30 mm diam. at maturity, initially convex to paraboloid, expanding to applanate often with an umbo at maturity; surface yellowish brown (5E6) to brown (6E6) all over when young, becoming brownish orange (5C4) to greyish orange (5B3) at the centre and grey (4C1) towards the margin when mature, with fine glimmering hairs all over, plicate-striate towards the margin; margin straight, crenate. Lamellae adnate to adnexed, L = 19–20, close, initially white, becoming grey (5C1) with age, with lamellulae in 1 tier; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 33–45 × 1–2 mm, central, terete, slightly tapering towards the apex, hollow; surface white to off-white, finely pubescent all over; base slightly enlarged to subbulbous. Odour and taste not distinctive.

Basidiospores 10–12 × 6–7 × 5–6 µm, on an average 11.37 × 6.62 × 5.77 µm, $Q_1 = 1.57–2.0$, $Q_{1avg} = 1.75$, $Q_2 = 1.66–2.20$, $Q_{2avg} = 1.94$, lenticular, oblong or oblong-ellipsoid in face view, oblong in side view, dark brown to black, thick-walled, with an eccentric germ-pore up to 2 µm wide. Basidia 15–38 × 10–11 µm, clavate to pedicellate-clavate, hyaline, thin-walled, surrounded by 4–5 pseudoparaphyses, 4-spored; sterigmata up to 6 µm long. Pleurocystidia absent. Lamella-edge heterogeneous. Cheilocystidia 25–72 × 15–21 µm, abundant, mostly lageniform or rarely cylindrical, hyaline, thin-walled. Pileipellis an epithelioid hymeniderm disrupted by pileocystidia and scattered velar elements; epithelioid hymeniderm elements 23–32 × 24-37 µm, hyaline, thin-walled; velar elements 6–10 µm wide, subglobose, cylindrical or fusoid to clavate, branched, hyaline, thin-walled. Pileocystidia 73–138 × 14–37 µm, abundant, lageniform, rarely with a short pedicel, hyaline, thin-walled. Stipitipellis a cutis disrupted by isolated or bunches of caulocystidia; hyphae 3–15 µm wide, hyaline, thin-walled. Caulocystidia 43–104 ×

13–30 µm, abundant, lageniform to narrowly lageniform, hyaline, thin-walled. Clamp connections observed only on velar elements on the pileipellis and hyphae of the stipitipellis.

Habit and Habitat:—In small groups, on humus rich soil.

Collection examined:—INDIA. Kerala State, Thrissur District, Punnayoorkulam: 10 October 2016, *K. G. Greeshma Ganga G119*.

Observations:—Small basidiocarps; an applanate pileus with fine glimmering hairs; adnate to adnexed lamellae; a stipe with a slightly enlarged base; oblong or oblong-ellipsoid basidiospores with an eccentric germ-pore; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; an epithelioid hymeniderm-type pileipellis with pileocystidia and velar elements and a cutis-type stipitipellis with caulocystidia are the diagnostic characters of the present species.

Tulosesus heterothrix (Kühner) D. Wächt. & A. Melzer, a species common in Europe and also reported from America (Uljé 2005), shares a few characters with the present species in having almost similar colour, size and shape of the basidiocarps, a hymenium devoid of pleurocystidia and a lamella-edge with lageniform cheilocystidia. However, *T. heterothrix* differs from the present species in having a fibrillose pileus with visible velar remnants and ovoid and smaller basidiospores (5.8–8.8 × 3.8–4.4 (5) µm) with an almost central germ-pore.

Tulosesus allovelus (Uljé) D. Wächt. & A. Melzer, a species described from the Netherlands (Uljé 2005), resembles the present species in having basidiospores with an eccentric germ-pore, a hymenium devoid of pleurocystidia and a pileipellis with fusoid velar elements. However, *T. allovelus* has a smaller pileus (up to 12 mm wide) with visible velar remnants and subcylindrical and smaller basidiospores (9–11.5 × 5–5.5 µm). *Tulosesus hiascens* (Fr.) D. Wächt. & A. Melzer, a species common in Europe and also reported from America and Japan (Uljé 2005), seems to be

Plate 34. A-G: *Tulosesus* species 1. **A.** Basidiocarps. **B.** Basidiospores. **C.** Basidia. **D.** Cheilocystidia. **E.** Pileipellis showing pileocystidia.. **F.** Stipitipellis showing caulocystidia. **G.** Velar elements on the pileipellis. Scale Bars: **A** = 10 mm; **B, C & G** = 20 µm; **D-F** = 50 µm.

comparable with the present species in having basidiocarps with almost similar size, colour and shape, a hymenium devoid of pleurocystidia and habitat on the soil. *Tulosesus hiascens,* however, differs from the present species in having a fibrillose pileus with visible velar remnants, basidiospores with a central germ-pore and a pileipellis with tapering pileocystidia.

The distinctive status of the ITS (652 bp) and the nLSU (867 bp) of the present *Tulosesus* species was corroborated in BLASTn searches. A megablast search using the ITS sequence showed an unidentified species of *Tulosesus* from USA, *Tulosesus* 'IN01' (ON006924) as the closest hit with 99.38% identity. *Coprinellus subimpatiens* (presently as *Tulosesus subimpatiens*) (MH868521: 99% identity) resulted as the closest hit in a BLASTn search with the nLSU sequence. *Tulosesus subimpatiens* (M. Lange & A.H. Sm.) D. Wächt. & A. Melzer, a European species (Uljé 2005), shows some similarity with the present species in having basidiocarps of almost similar colour and shape, basidiospores with an eccentric germ-pore and similar morphology of pileocystidia. However, *T. subimpatiens* has ovoid and larger basidiospores (9.5–14 × 6–8 µm), a hymenium with pleurocystidia and a lamella-edge with globose cheilocystidia.

Tulosesus velatopruinatus (Bender) D. Wächt. & A. Melzer, Mycol. Progr. 19 (11): 1213 (2020) **Plate 35.**

Coprinellus velatopruinatus (Bender) Redhead, Vilgalys & Moncalvo, in Redhead, Vilgalys, Moncalvo, Johnson & Hopple, Taxon 50 (1): 235 (2001)
Coprinus velatopruinatus Bender, Beitr. Kenntn. Pilze Mitteleur. 5: 80 (1989)

Description:—Basidiocarps small, fragile. Pileus 9–17 ×5–11 mm when young, finally 10–38 mm diam. at maturity, initially ellipsoid to cylindrical, becoming broadly conical to applanate often with an umbo at maturity; surface brown (6E7) all over when young, becoming brown (6E7) at the centre and orange white (6B2) towards the margin when mature, with fine glimmering hairs all over, faintly plicate-striate towards the margin when young, becoming smooth on and around the centre and distinctly plicate-striate towards the margin, deliquescent; margin initially straight, becoming upturned to revolute when mature. Lamellae adnate, L = 23–31, close, initially white, becoming black with age, with lamellulae in 1 tier; edge even to the naked eye, finely pruinose under a lens, concolourous with the sides. Stipe 22–42 × 1–2 mm, central, terete, slightly tapering towards the apex, hollow; surface white to off-white, finely pubescent all over; base slightly enlarged to subbulbous. Odour and taste not distinctive.

Basidiospores (9)10–12(14) × 5.5–7 × 5–6 µm, on an average 11.17 × 6.32 × 5.7 µm, Q_1 = 1.57–2.33, Q_{1avg} = 1.86, Q_2 = 1.66–2.20, Q_{2avg} = 1.86, lenticular, ellipsoid to ovo-ellipsoid with a small apical papilla in face view, ellipsoid in side view, dark brown to black, thick-walled, with an eccentric germ-pore up to 2 µm wide. Basidia 13–27 × 8–10 µm, clavate to pedicellate-clavate, hyaline, thin-walled, surrounded by 3–5 pseudoparaphyses, 4-spored; sterigmata up to 5 µm long. Pleurocystidia absent. Lamella-edge sterile. Cheilocystidia 29–57 × 20–34 µm, abundant, mostly subcylindrical, rarely subglobose or ellipsoid to broadly utriform, hyaline, thin-walled. Pileipellis an epithelioid hymeniderm disrupted by pileocystidia and scattered velar elements; epithelioid hymeniderm elements 28–31 × 26–30 µm, hyaline, thin-walled; velar elements 2–5 µm wide, cylindrical or rarely branched, hyaline, thin-walled. Pileocystidia 121–167 × 22–31 µm, abundant, narrowly lageniform or rarely with a short pedicel, hyaline, slightly thick-walled. Stipitipellis a cutis disrupted by isolated or patches of caulocystidia; hyphae 6–11 µm wide, hyaline, slightly thick-walled. Caulocystidia 48–142 × 16–25 µm, abundant, narrowly lageniform, hyaline, slightly thick-walled. Clamp connections observed only on velar elements on the pileipellis and hyphae of the stipitipellis.

Habit and Habitat:—In small groups, on rotting *Musa* plant remains or coconut tree rachis.

Collections examined:—INDIA. Kerala State, Malappuram District, Chenakkal: 31 August 2016, *K. G. Greeshma Ganga G82*; Thrissur District, Punnayoorkulam: 15 October 2017, *K. G. Greeshma Ganga G227*.

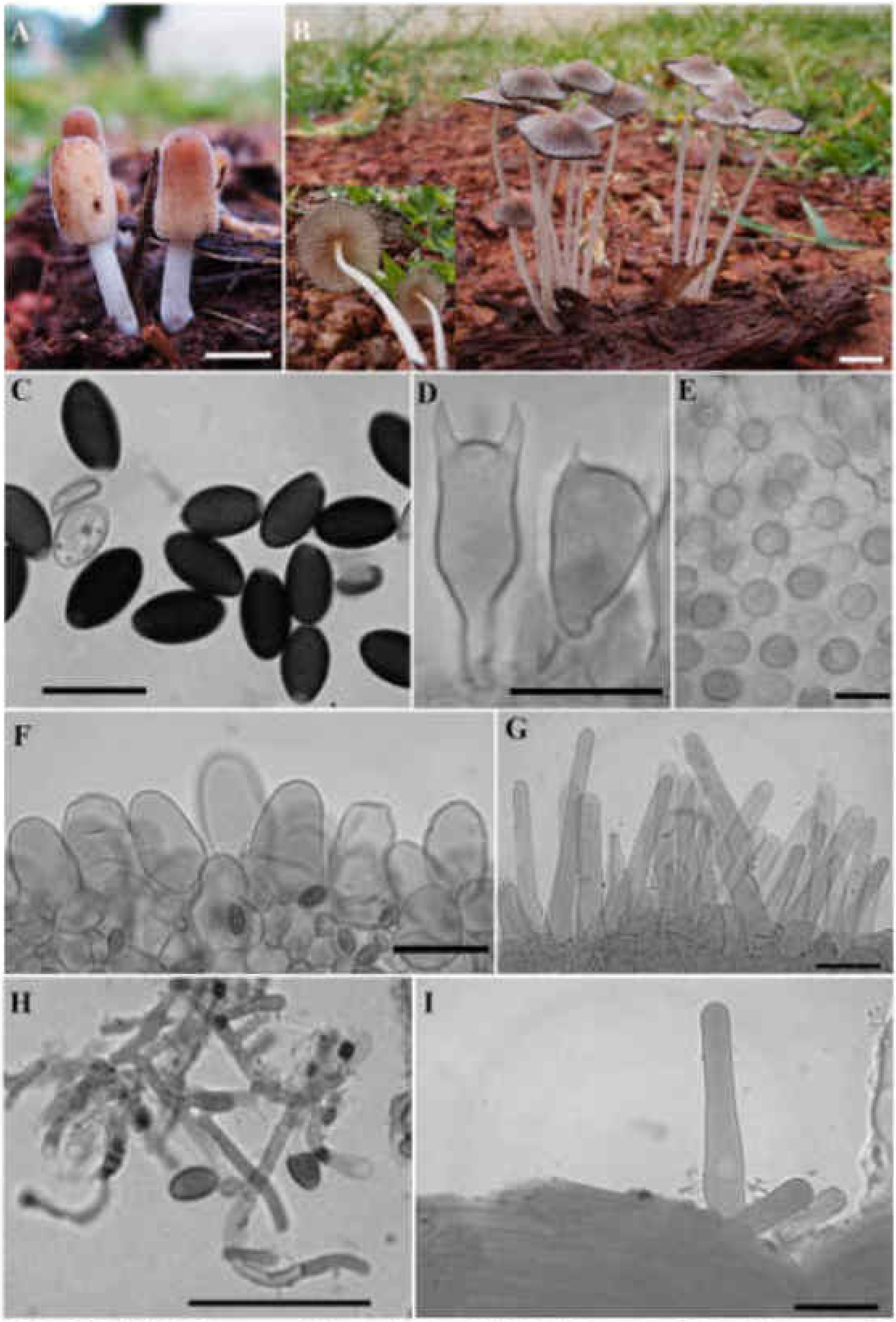

Plate 35. A-I: *Tulosesus velatopruinatus.* A-B. Basidiocarps. **C.** Basidiospores. **D.** Basidia. **E.** Pseudoparaphyses. **F.** Cheilocystidia. **G.** Pileipellis showing pileocystidia. **H.** Velar elements on the pileipellis. **I.** Stipitipellis showing caulocystidia. Scale Bars: **A-B** = 10 mm; **C-E & H** = 20 µm; **F, G & I** = 50 µm.

Observations:—*Tulosesus velatopruinatus*, a species previously reported from the Netherlands and Germany (Uljé 2005), is characterised by small basidiocarps; a broadly conical to applanate pileus with fine glimmering hairs and plicate-striations; adnate lamellae; a stipe with a slightly enlarged base; ellipsoid to ovo-ellipsoid basidiospores with a small apical papilla; a hymenium devoid of pleurocystidia; a lamella-edge with abundant cheilocystidia; an epithelioid hymeniderm-type pileipellis with pileocystidia and velar elements and a cutis-type stipitipellis with caulocystidia.

Two ITS (G82: 658 bp; G227: 655 bp) and two nLSU (G227: 928 bp; G82: 888 bp) sequences were generated from the present species. *Tulosesus velatopruinatus* (MT537093: 99.69% identity) and *Coprinellus subimpatiens* (presently as *Tulosesus subimpatiens,* MH868521: 99.77% identity) were the closest hits in BLASTn searches using the ITS (G227) and nLSU (G82) sequences respectively.

Chapter 6

Phylogenetic analyses

CHAPTER 6

PHYLOGENETIC ANALYSES

6.1. PHYLOGENETIC ANALYSIS OF THE COPRINOID AND PSATHYRELLOID AGARICS DISCOVERED DURING THIS STUDY

A Maximum Likelihood (ML) analysis based on ITS sequences was performed to elucidate the phylogenetic relationship of the coprinoid and psathyrelloid agarics described in this treatise. A total of thirty-five species representing two families (Agaricaceae and Psathyrellaceae) were described in this study. All the thirty-five species successfully yielded 52 ITS sequences, including those from additional collections. The family Agaricaceae in this study is represented by a single genus, namely *Coprinus,* with one species that yielded one ITS sequence. During the course of this study, eight genera of the family Psathyrellaceae were encountered, namely *Candolleomyces* (nine species), *Coprinopsis* (nine species), *Parasola* (five species), *Tulosesus* (four species), *Psathyrella* (three species), *Narcissea* (two species), *Coprinellus* (one species) and *Hausknechtia* (one species). The nine species of *Candolleomyces* yielded 13 ITS sequences. 10 ITS sequences were generated from the nine species of *Coprinopsis*. Five species of *Parasola* discovered during this study yielded 8 ITS sequences. 6 ITS sequences were obtained from four species of *Tulosesus* (including '*Coprinellus pseudodisseminatus*'). Two species of *Narcissea* described in the study produced 7 ITS sequences. From the genus *Psathyrella,* 3 ITS sequences representing three species were obtained. 4 ITS sequences were generated from two species of *Coprinellus*. Only one ITS sequence was produced from a single species of *Hausknechtia*. The phylogenetic tree (Figure 1) showed the overall relative placement of the two families, Agaricaceae and Psathyrellaceae, as well as the generic placement of the coprinoid and psathyrelloid species described in this study. The species of each family/genus/clade are colour-coded and the corresponding names are designated in Figure 1.

The phylogenetic tree revealed two distinct clades representing the two families, Psathyrellaceae (Clade I) and Agaricaceae (Clade II). Clade I, the larger clade with moderate (53% BS) bootstrap support, comprises the family Psathyrellaceae with 156 collections representing 107 species. This clade included the members of 16 genera, namely *Britzelmayria, Candolleomyces, Coprinellus*, *Coprinopsis*, *Cystoagaricus*, *Hausknechtia*, *Homophron*, *Kauffmania*, *Lacrymaria*, *Narcissea*, *Olotia*, *Parasola*, *Psathyrella*, *Punjabia*, *Tulosesus* and *Typhrasa*. Of these, eight genera (*Candolleomyces, Coprinellus*, *Coprinopsis*, *Hausknechtia*, *Narcissea*, *Parasola*, *Psathyrella* and *Tulosesus*) have species representation from the present study.

The genus *Coprinellus* formed a well-resolved monophyletic group with full (100% BS) bootstrap support. It accommodates 17 collections of *Coprinellus* representing nine species, including one species from the present study (*Coprinellus aureogranulatus* DED 8251 (SFSU), *C. curtus* SZMC-NL-1023, *C. deminutus, C. disseminatus* R175, *C. disseminatus* x-043, *C. disseminatus* CEQCA-M1203, *C. disseminatus* G134, *C. disseminatus* G228, *C. disseminatus* G292, *C. disseminatus* KACC500820, *C. flocculosus* SZMC-NL-1567, *C. heptemerus* X-22, *C. micaceus* BAFC 3218, *C. micaceus* CBM:FB-24398, *C. micaceus* KACC500403, *C. radians* F213 and *C. verrucispermus*). This clade was found to be sister to the clade representing the genus *Candolleomyces.*

The clade representing the genus *Candolleomyces,* contained 28 collections encompassing 14 species (*Candolleomyces cacao* SFSU: DED 8339, *C. candolleanus* 3-F7, *C. candolleanus* AMO, *C. candolleanus* BRPCL21, *C. candolleanus* BRPER4, *C. candolleanus* DOF-27, *C. candolleanus* G159, *C. candolleanus* G171, *C. candolleanus* G173, *C. candolleanus* LAS73030, *C. candolleanus* SZMC-NL-2145, *C. efflorescens* G130, *C. efflorescens* G270, *C. efflorescens* Pegler 2133, *Candolleomyces* species

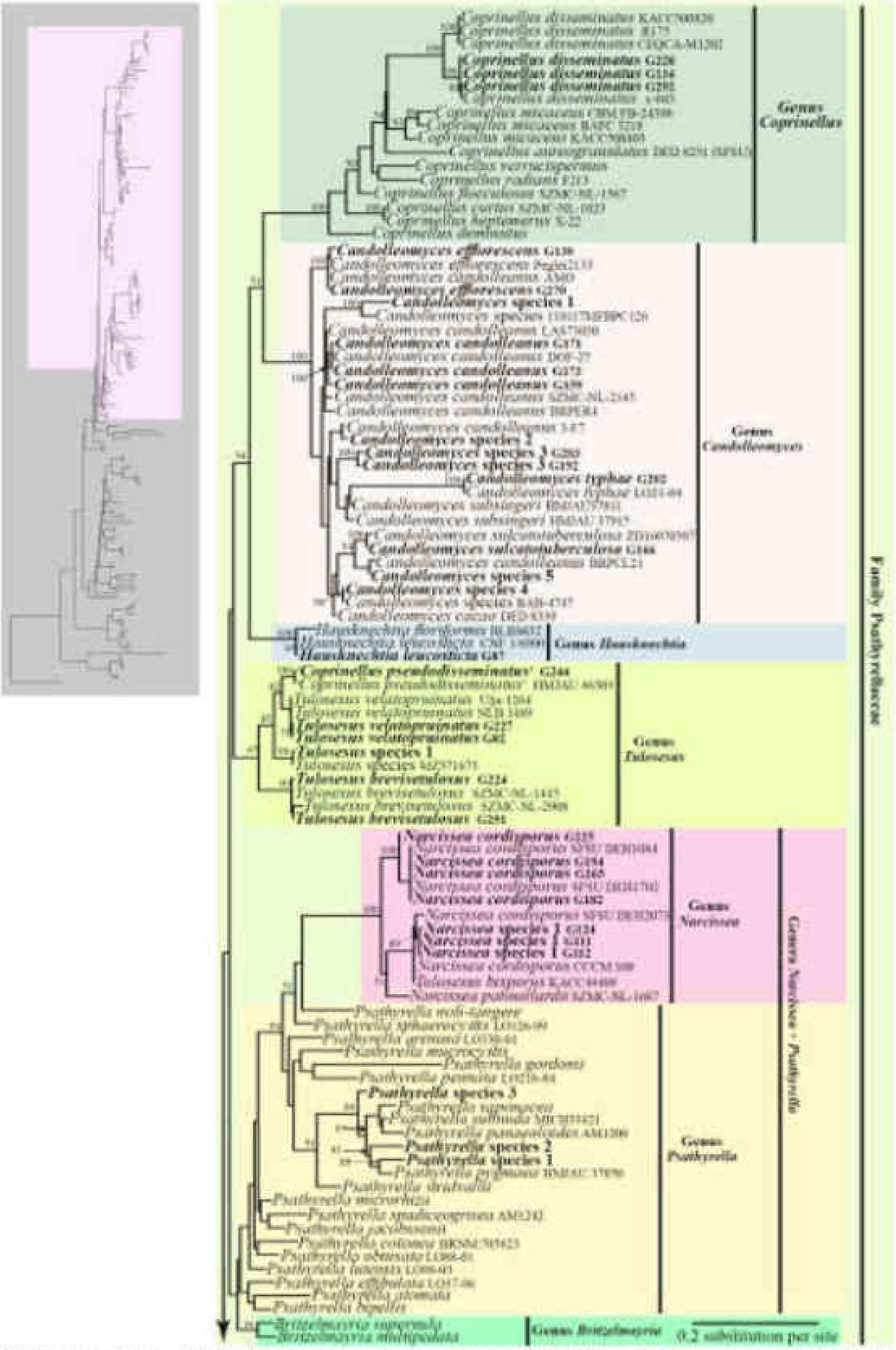

Figure 1. An ITS-based ML phylogenetic tree of coprinoid and psathyrelloid agarics showing the phylogenetic placement of thirty-five species under the families, Agaricaceae and Psathyrellaceae. The species described during the study are highlighted in bold font. Bootstrap values ≥ 50% are shown. *Amanita muscaria* was selected as an outgroup taxon.

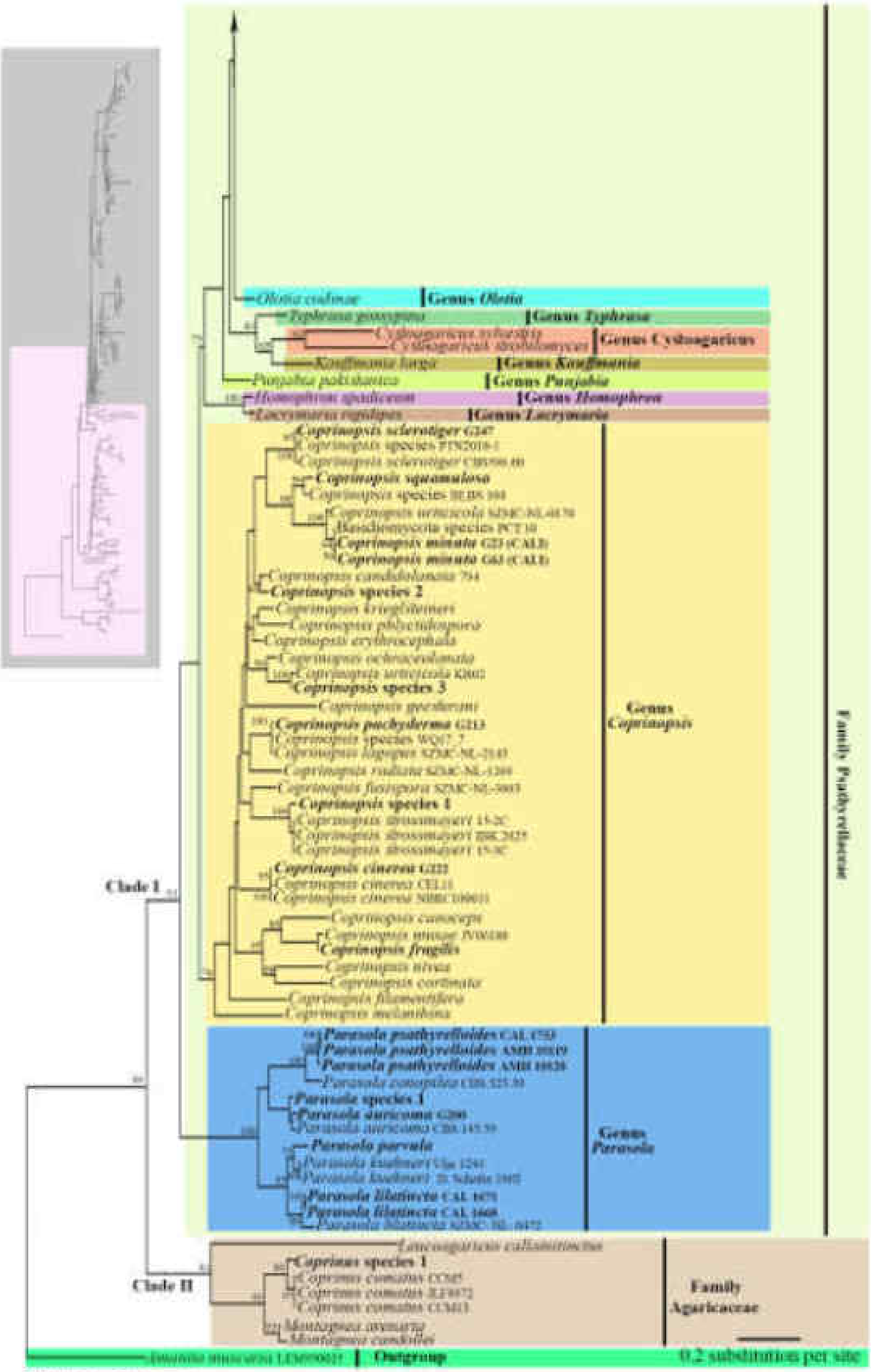

Figure 1. Continued

110117MFBPC126, *Candolleomyces* species 1, *Candolleomyces* species 2, *Candolleomyces* species 3 G192, *Candolleomyces* species 3 G203, *Candolleomyces* species 4, *Candolleomyces* species 5, *Candolleomyces* species BAB-4747*, C. subsingeri* HMJAU 37915, *C. subsingeri* HMJAU37811, *C. sulcatotuberculosa* G166, *C. sulcatotuberculosa* ZD16070507, *C. typhae* G202 and *C. typhae* LO21-04). Of these, nine species were from the present study, and this clade had maximum (100% BS) bootstrap support.

A small clade cladewith full (100% BS) bootstrap support, indicated the genus *Hausknechtia* and it comprised three collections representing two species, including one from the present study (*Hausknechtia floriformis* BLBS032, *H. leucosticta* CNF 1/6900 and *H. leucosticta* G87). This clade was found sister to the clade that, in turn, represented the members of the genera *Coprinellus* and *Candolleomyces*.

Twelve collections of *Tulosesus* that comprise four species of *Tulosesus* (*Tulosesus brevisetulosus* G224, *T. brevisetulosus* G251, *T. brevisetulosus* SZMC-NL-1445, *T. brevisetulosus* SZMC-NL-2908, *Tulosesus* species 1, *Tulosesus* species MZ571673, *T. velatopruinatus* Uljé 1264, *T. velatopruinatus* G227, *T. velatopruinatus* G82 and *T. velatopruinatus* NLB 1489)*,* including two collections of '*Coprinellus pseudodisseminatus'* ('*Coprinellus pseudodisseminatus*' G244 and '*C. pseudodisseminatus*' HMJAU 46303)*,* grouped together to form a strongly (97% BS) supported clade, representing the genus *Tulosesus*. The present study recommends the transfer of '*Coprinellus pseudodisseminatus*' to the genus *Tuloseus* as it is nested within the clade accommodating the members of *Tulosesus.*

A weakly supported clade, including the members of *Narcissea* and *Psathyrella* was also recognised, where the species of *Narcissea* formed a clear monophyletic group. However, the members of *Psathyrella* didn't appear to be a monophyletic group. With three species from the present study, the genus *Psathyrella* holds 23 collections representing 22 species of *Psathyrella* (*Psathyrella* *arenosa* LO330-01, *P. atomata, P. bipellis, P. cotonea* BRNM:705623, *P. effibulata* LO37-96, *P. gordonii, P. jacobssonii, P. lutensis* LO98-03, *P. microrhiza, P. mucrocystis, P. noli-tangere, P. obtusata* LO88-01, *P. panaeoloides* AM1200, *P. pennata* LO216-84, *P. pygmaea* HMJAU 37850, *P. saponacea*, *P. spadiceogrisea* AM1242, *Psathyrella* species 1, *Psathyrella* species 2, *Psathyrella* species 3, *P. sphaerocystis* LO126-99, *P. stridvallii* and *P. subnuda* MICH33421). The genus *Narcissea* accommodates 13 collections, which include three species of *Narcissea* (*Narcissea cordisporus* CCCM:108, *N. cordisporus* G165, *N. cordisporus* G182, *N. cordisporus* G194, *N. cordisporus* G225, *N. cordisporus* SFSU DEH1084, *N. cordisporus* SFSU DEH1702, *N. cordisporus* SFSU DEH2073, *N. patouillardii* SZMC-NL-1687, *Narcissea* species 1 G111*, Narcissea* species 1 G112, *Narcissea* species 1 G124) and one species of *Tulosesus* (*Tulosesus bisporus* KACC49409) together formed a distinct clade with maximum (100% BS) bootstrap support. Of these, seven collections representing two species of *Narcissea* were from the present study.

A clade with significant (76% BS) bootstrap support, comprising the genus *Coprinopsis,* was also nested within Clade I. This clade includes 37 collections encompassing 29 species of *Coprinopsis* (*Coprinopsis candidolanata* 794, *C. canoceps, C. cinerea* CEL11, *C. cinerea* G222, *C. cinerea* NBRC100011, *C. cortinata, C. erythrocephala, C. filamentifera, C. fragilis, C. fusispora* SZMC-NL-3863, *C. geesterani, C. krieglsteineri, C. lagopus* SZMC-NL-2143, *C. melanthina, C. minuta* G23 (CALI), *C. minuta* G63 (CALI), *C. musae* JV06180, *C. nivea, C. ochraceolanata, C. pachyderma* G213, *C. phlyctidospora, C. radiata* SZMC-NL-1269, *C. sclerotiger* CBS596.80, *C. sclerotiger* G247, *Coprinopsis* species 1, *Coprinopsis* species 2, *Coprinopsis* species 3, *Coprinopsis* species BLBS 104, *Coprinopsis* species PTN2018-1, *Coprinopsis* species WQ17_7, *C. squamulosa, C. strossmayeri* 15-2C, *C. strossmayeri* 15-3C, *C. strossmayeri* IBK 2625, *C. urticicola* KR02 and *C. urticicola* SZMC-NL-0170) and a collection labelled as ‘Basidiomycota species PCT.10’. Of these, nine species of *Coprinopsis* were from the present study.

The genus *Parasola* was represented as a monophyletic group with full bootstrap support (100% BS) within Clade I. This clade comprises 13 collections representing 7 species of *Parasola* (*Parasola auricoma* CBS:145.39, *P. auricoma* G200, *P. conopilea* CBS:325.39, *P. kuehneri* D. Schafer 1602, *P. kuehneri* Uljé 1241, *P. lilatincta* CAL 1668, *P. lilatincta* CAL 1671, *P. lilatincta* SZMC: NL: 0472, *P. parvula, P. psathyrelloides* AMH 10119, *P. psathyrelloides* AMH 10120, *P. psathyrelloides* CAL 1753 and *Parasola* species 1), of which five were from the present study.

The Clade II accommodates the members of the family Agaricaceae with strong (93% BS) bootstrap support. This clade includes seven collections representing five species of the family Agaricaceae (*Coprinus comatus* JLF8972, *C. comatus* CCM13, *C. comatus* CCM5, *Coprinus* species 1, *Leucoagaricus callainitinctus*, *Montagnea arenaria* and *M. candollei*). Within this clade, the only collection of the genus, *Coprinus* species 1, described during the present study, was nested.

The present phylogenetic analysis revealed the phylogenetic affinities of the coprinoid and psathyrelloid agarics represented by nine genera (*Coprinus, Candolleomyces, Coprinellus*, *Coprinopsis*, *Hausknechtia*, *Narcissea*, *Parasola*, *Psathyrella* and *Tulosesus*) belonging to the two families Agaricaceae and Psathyrellaceae. The tree also showed the overall outline of the taxonomic position of the 35 species collected during the study. In addition, this study provided evidence for the transfer of '*Coprinells pseudodisseminatus*' to the genus *Tulosesus*.

6.2. GENUS *COPRINUS*

The present analysis focuses on a single genus, *Coprinus,* with a single species (*Coprinus* species 1) from the family Agaricaceae that yielded only one ITS sequence. The phylogenetic tree constructed from ML analysis (Figure 2) for the genus *Coprinus* reveals the relative taxonomic position as well as the novelty of *Coprinus* species 1 collected during the study. The clade representing the genus *Coprinus* is colour-coded in Figure 2.

The phylogenetic tree recognised a well-resolved (100% BS) monophyletic group representing the genus *Coprinus*. This clade comprised 22 collections of *Coprinus,* namely *Coprinus comatus* 297310, *C. comatus* AH:45831, *C. comatus* AH: 44089, *C. comatus* CCM3, *C. comatus* YE19, *C. comatus* 11ZHONG, *C. comatus* CCM1, *C. comatus* CCM8, *C. comatus* CCM2, *C. comatus* AH:44095, *C. comatus* BUNS 12-00716, *C. comatus* JLF8972, *C. comatus* SAT-16-238-14, *C. comatus* KMCC04907, *C. comatus* CCM13, *C. comatus* YE23-01, *C. comatus* CCM10, *C. littoralis*, *C. pinetorum*, *Coprinus* species 1, *C. sterquilinus* and *C. vosoustii.* Within this clade, *Coprinus* species 1 formed a lineage distinct from the collections of *C. comatus* and *C. littoralis* with full (100% BS) bootstrap support.

The present phylogram confirmed the distinct position and novelty of *Coprinus* species 1 among other species of *Coprinus*.

6.3. GENERA *CANDOLLEOMYCES* AND *HAUSKNECHTIA*

A total of 10 species from two genera (*Candolleomyces* and *Hausknechtia*) were described in the present study. This includes nine species of *Candolleomyces* and a single species of *Hausknechtia*. The collected species of the genera *Candolleomyces* and *Hausknechtia* together yielded 14 ITS sequences. Of these, 13 ITS sequences were from *Candolleomyces* and one from *Hausknechtia*. An ITS-based phylogram inferred from the ML analysis is presented in Figure 3, which showed the relative taxonomic position of the nine species of *Candolleomyces* and the single species of *Hausknechtia*. The species of each genus/clade/lineage are named and colour-coded in Figure 3.

The phylogenetic tree recovered two major clades, Clade I and Clade II, representing the two genera, namely *Candolleomyces* and *Hausknechtia* respectively. Clade I formed a large monophyletic assemblage of the members of *Candolleomyces,* but with low bootstrap support. A total of 44 collections representing 24 species of *Candolleomyces* were included in Clade I, namely

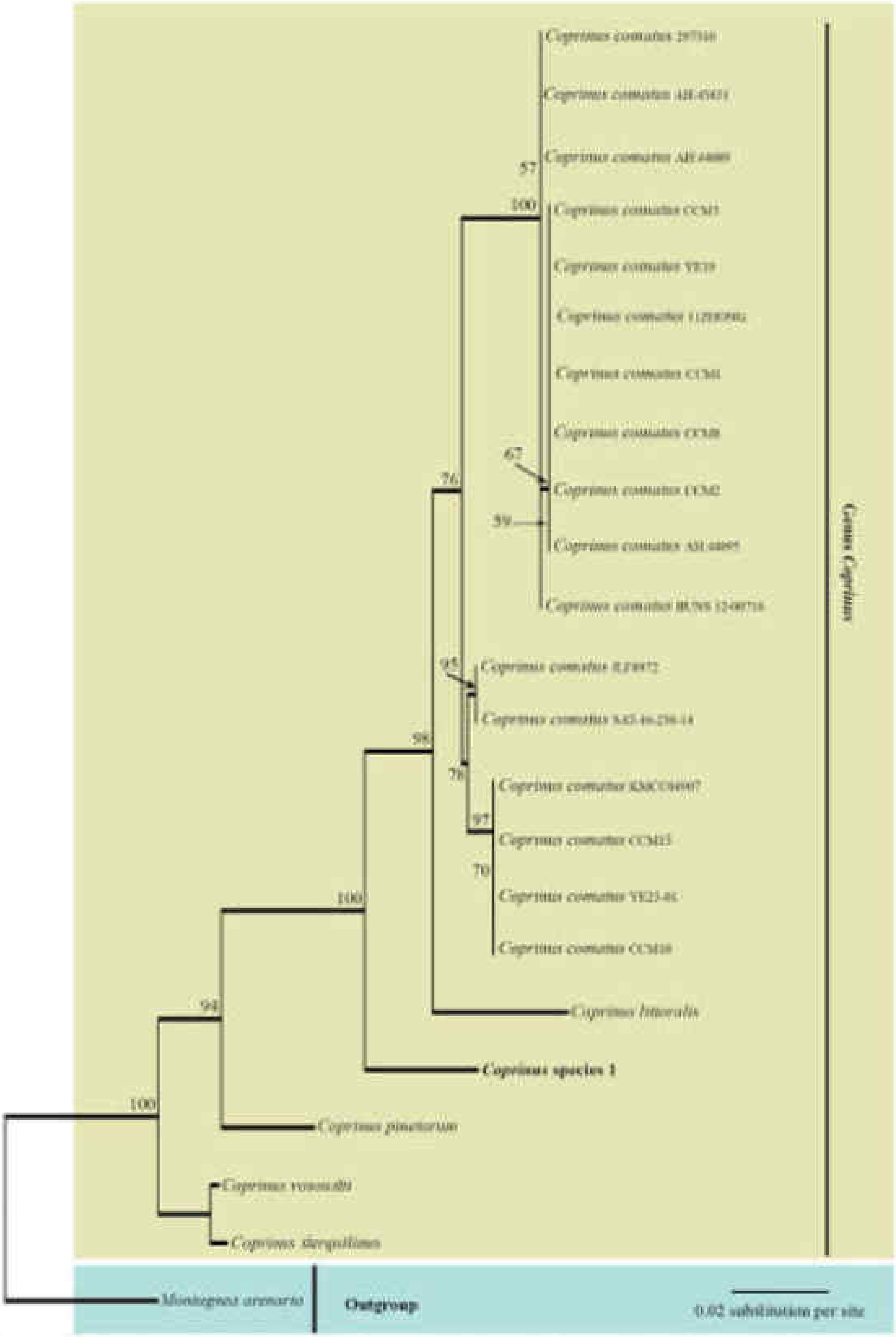

Figure 2. Maximum Likelihood phylogenetic tree of the genus *Coprinus* based on the ITS sequence data matrix. The species described during the study is highlighted in bold font. Bootstrap values ≥ 50% are shown. *Montagnea arenaria* was used as an outgroup taxon.

Candolleomyces aberdarensis, *C. badhyzensis*, *C. badiophylla*, *C. cacao* SFSU: DED 8339, *C. cacao* FP1R4, *C. candolleanus* 3-F7, *C. candolleanus* AMO, *C. candolleanus* BRPCL21, *C. candolleanus* DOF-27, *C. candolleanus* G159, *C. candolleanus* G171, *C. candolleanus* G173, *C. efflorescens* G130, *C. efflorescens* G270, *C. efflorescens* Pegler2133, *C. hymenocephala*, *C. leucotephrus*, *C. luteopallidus* HMJAU 5148, *C. luteopallidus* Sharp20863, *C. pseudocandolleanus*, *C. singeri*, *Candolleomyces* species 110117MFBPC126, *Candolleomyces* species 1, *Candolleomyces* species 2, *Candolleomyces* species 3 G192, *Candolleomyces* species 3 G203, *Candolleomyces* species 4, *Candolleomyces* species 5, *Candolleomyces* species BAB-4747, *C. subcacao* HMJAU37807, *C. subcacao* HMJAU37808, *C. subsingeri* HMJAU 37814, *C. subsingeri* HMJAU 37915, *C. sulcatotuberculosa* Battistin and Chiarello 07-10-2013, *C. sulcatotuberculosa* G166, *C. sulcatotuberculosa* GB:LO55-12, *C. sulcatotuberculosa* MCVE29112, *C. sulcatotuberculosa* ZD16070507, *C. trinitatensis*, *C. tuberculatus*, *C. typhae* BP23, *C. typhae* G202, *C. typhae* LO21-04 and *C. typhae* MJD10-17.

Clade I, in turn, consisted of 10 subclades/lineages, namely /aberdarensis, /cacao, Clade A, /leucotephra, /luteopallida, /singeri, /subsingeri, /sulcatotuberculosa, /tuberculata and /typhae. Of these 10 subclades/lineages, Clade A appears to be paraphyletic and further divided into five groups/lineages, namely /badhyzensis, /badiophylla, /candolleana sensu stricto, /efflorescens and /trinitatensis. The present phylogenetic analysis focuses mainly on /aberdarensis, /candolleana sensu stricto, /cacao, /efflorescens /subsingeri, /sulcatotuberculosa and /typhae, where the species of *Candolleomyces* described in this study were nested.

/candolleana sensu stricto of Clade A comprised eight collections representing five species of *Candolleomyces* (*Candolleomyces candolleanus* DOF-27, *C. candolleanus* G159, *C. candolleanus* G171, *C. candolleanus* G173, *C. hymenocephala*, *C. pseudocandolleanus*, *Candolleomyces* species 110117MFBPC126 and *Candolleomyces* species 1), which were found to be paraphyletic. Three collections of *Candolleomyces candolleanus* (*C. candolleanus* G159, *C. candolleanus* G171, *C. candolleanus* G173) from the present study and another collection of *C. candolleanus* (*C. candolleanus* DOF-27) from China appeared together and thereby formed a monophyletic group with moderate (57% BS) bootstrap support. *Candolleomyces* species 2, a species described during the study, was found to be clustered with an unpublished species, *Candolleomyces* species 110117MFBPC126 from China, with maximum (100% BS) bootstrap support.

The clade /efflorescens formed a distinct group in Clade A with full (100% BS) bootstrap support. It included four collections representing two species of *Candolleomyces* (a collection labelled as *Candolleomyces candolleanus* AMO, and three collections labelled as *C. efflorescens* G130, *C. efflorescens* G270 and *C. efflorescens* Pegler2133 respectively). The two collections of *C. efflorescens* from the present study were found to be nested within this clade. The sequence labelled as *Candolleomyces candolleanus* AMO nested in this clade is from India, and it seems to represent an as yet undescribed species misidentified in GenBank.

The clade /subsingeri contained six collections of *Candolleomyces* (*Candolleomyces candolleanus* 3-F7, *Candolleomyces* species 1, *Candolleomyces* species 3 G192, *Candolleomyces* species 3 G203, *C. subsingeri* HMJAU 37814 and *C. subsingeri* HMJAU 37915) with moderate (69% BS) bootstrap support. *Candolleomyces* species 1, another species described during this study, was found to be clustered with an unpublished collection of *C. candolleanus* (*C. candolleanus* 3-F7) from China, with 99% bootstrap support. The two collections of *Candolleomyces* species 3 (G192 and G203) appeared together with maximum (100% BS) bootstrap support.

A weakly-supported monophyletic group comprising six collections of *Candolleomyces* (*Candolleomyces* species 4, *Candolleomyces* species BAB-4747, *C. subcacao* HMJAU37807, *C. subcacao* HMJAU37808, *C. cacao* SFSU: DED 8339 and *C. cacao* FP1R4) represented the clade /cacao. *Candolleomyces* species 4, collected

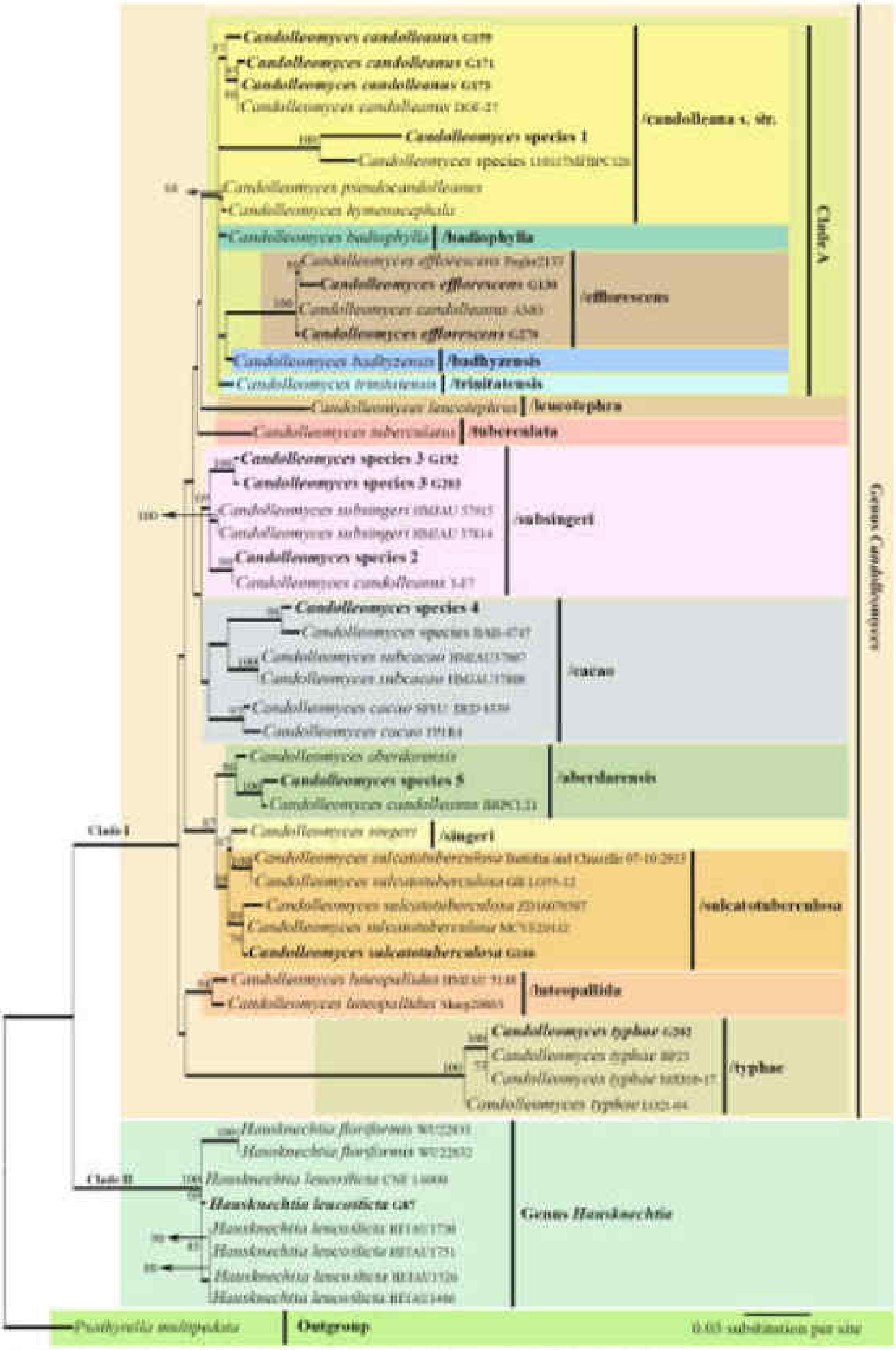

Figure 3. An ITS-based ML phylogeny of the genera *Candolleomyces* and *Hausknechtia*. The species described during the study are highlighted in bold font. Bootstrap values ≥ 50% are shown. *Psathyrella multipedata* was chosen as an outgroup.

during the present study, was found to be nested in this clade, where it grouped with an unidentified species of *Candolleomyces, Candolleomyces* species BAB-4747 from India, with high (96% BS) bootstrap support.

Three collections of *Candolleomyces,* including a collection from the present study (*Candolleomyces aberdarensis*, *C. candolleanus* BRPCL21 and *Candolleomyces* species 5) together formed a clade, /aberdarensis with strong (86% BS) bootstrap support. *Candolleomyces* species 5, a species from the study, clustered with a collection labelled as *C. candolleanus* BRPCL21 from China, with full (100% BS) bootstrap support.

The clade /sulcatotuberculosa and the lineage /*singeri* together represent a monophyletic group with strong (86% BS) bootstrap support. It includes five collections of *Candolleomyces sulcatotuberculosa* (*Candolleomyces sulcatotuberculosa* Battistin and Chiarello 07-10-2013, *C. sulcatotuberculosa* G166, *C. sulcatotuberculosa* GB: LO55-12, *C. sulcatotuberculosa* MCVE29112 and *C. sulcatotuberculosa* ZD16070507) and one collection of *C. singeri*. Inside this clade, *Candolleomyces sulcatotuberculosa* G166, a collection from the present study, was found clustered with other collections of *C. sulcatotuberculosa* (MCVE29112 from China and ZD16070507 from Italy) with significant (76% BS) bootstrap support.

The clade /typhae forms a well-supported monophyletic group with full (100% BS) bootstrap support. This clade contains four collections of *Candolleomyces typhae* (*Candolleomyces typhae* BP23, *C. typhae* G202, *C. typhae* LO21-04 and *C. typhae* MJD10-17). *Candolleomyces typhae* G202, a collection from the present study, was found to be grouped with other collections of *C. typhae* (BP23 from Philippines; LO21-04 from Sweden and MJD10-17 from China).

A well-resolved (100% BS) monophyletic group (Clade II) was recovered as a sister to the larger Clade I. The clade II holds the members of the genus *Hausknechtia*. This clade encompassed eight collections representing the only two species of *Hausknechtia,* namely *Hausknechtia floriformis* (WU22832, WU22833) and

H. leucosticta (CNF 1/6900, G87, HFJAU1486, HFJAU1526, HFJAU1730 and HFJAU1751). *Hausknechtia leucosticta* G87, a species described during the study, was clustered with other collections of *H. leucosticta* from China*,* indicating its identity.

The present phylogram supports the sister relationship of the two genera, *Candolleomyces* and *Hausknechtia*. The phylogenetic tree also confirmed the novelty of the five species of *Candolleomyces* labelled as *Candolleomyces* species 1, *Candolleomyces* species 2, *Candolleomyces* species 3, *Candolleomyces* species 4 and *Candolleomyces* species 5 and confirmed the taxonomic position and identity of four other species of *Candolleomyces* (*C. candolleanus*, *C. efflorescens*, *C. sulcatotuberculosa* and *C. typhae*) and one species of *Hausknechtia* as well.

6.4. GENUS *COPRINELLUS*

The genus *Coprinellus* was represented by a single species, *C. disseminatus,* in the present study. Altogether, three ITS sequences were obtained from *C. disseminatus,* including those from the additional collections. An ITS-based ML phylogram (Figure 4) of the genus *Coprinellus* inferred from ML analysis revealed the taxonomic position of *C. disseminatus* described in the present study. In Figure 4, each section/clade/lineage of the genus *Coprinellus* is colour-coded and the names are also indicated.

The phylogenetic tree identified a well-supported (100% BS) large clade that represents the genus *Coprinellus*. This includes 34 collections representing 12 species of *Coprinellus* (*Coprinellus aureogranulatus* CBS973.95, *C. aureogranulatus* DED 8251 (SFSU), *C. aureogranulatus* DZF4A, *C. curtus* SZMC-NL-1490, *C. curtus* SZMC-NL-2339, *C. deminutus*, *C. disseminatus* BAP 608 (SFSU), *C. disseminatus* CEQCA-M1203, *C. disseminatus* DWM51, *C. disseminatus* G134, *C. disseminatus* G228, *C. disseminatus* G292, *C. disseminatus* KACC500820, *C. disseminatus* KUC11047, *C. disseminatus* LE-BIN 2127, *C. disseminatus* olrim955 (SUAS), *C. disseminatus* PNB034A, *C. disseminatus* PNB034B, *C. disseminatus* PNB034D, *C. disseminatus* SZMC-NL-2337, *C. disseminatus* x-043, *C. flocculosus* SZMC-NL-0838, *C.*

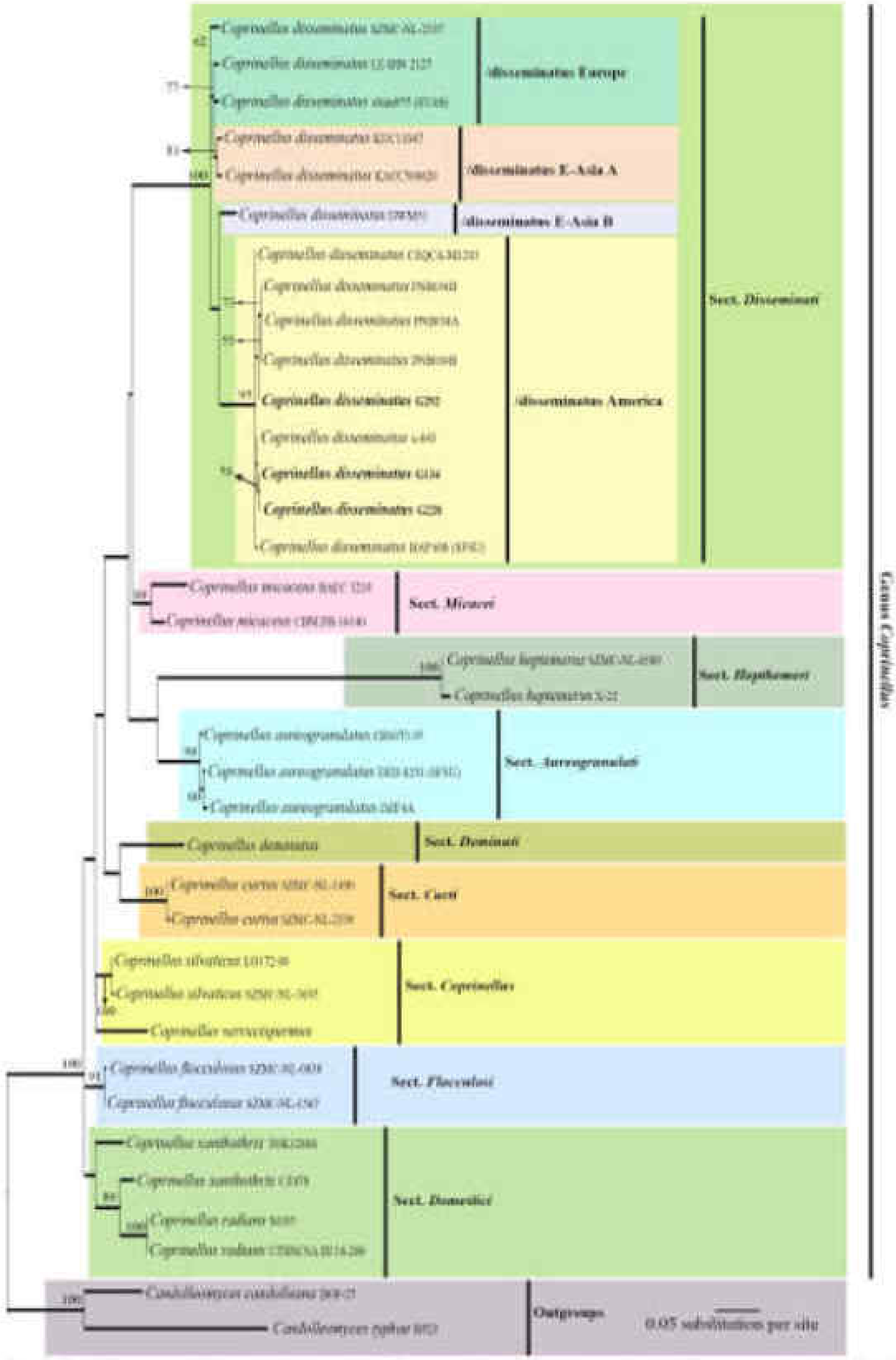

Figure 4. Maximum Likelihood phylogeny of the genus *Coprinellus* using the ITS sequence data matrix. The species collected during the study are highlighted in bold font. Bootstrap values ≥ 50% are shown. *Candolleomyces candolleana* and *C. typhae* were taken as outgroups.

flocculosus SZMC-NL-1567, *C. heptemerus* SZMC-NL-0589, *C. heptemerus* X-22, *C. micaceus* BAFC 3218, *C. micaceus* CBM: FB-16140, *C. radians* M105, *C. radians* UTHSCSA DI 14-208, *C. silvaticus* LO172-08, *C. silvaticus* SZMC-NL-3035, *C. verrucispermus*, *C. xanthothrix* CZ478 and *C. xanthothrix* TOK12808). Within this clade, nine sections were indicated, namely *Aureogranulati*, *Coprinellus*, *Curti*, *Deminuti*, *Disseminati*, *Domestici, Flocculosi*, *Hepthemeri* and *Micacei*. Among these sections, *C. disseminatus,* the species described under the genus *Coprinellus,* was found to be nested in the section *Disseminati.*

The section *Disseminati* formed a monophyletic group with maximum (100% BS) bootstrap support. This group comprised 15 collections of *Coprinellus disseminatus* (*Coprinellus disseminatus* BAP 608 (SFSU), *C. disseminatus* CEQCA-M1203, *C. disseminatus* DWM51, *C. disseminatus* G134, *C. disseminatus* G228, *C. disseminatus* G292, *C. disseminatus* KACC500820, *C. disseminatus* KUC11047, *C. disseminatus* LE-BIN 2127, *C. disseminatus* olrim955 (SUAS), *C. disseminatus* PNB034A, *C. disseminatus* PNB034B, *C. disseminatus* PNB034D, *C. disseminatus* SZMC-NL-2337 and *C. disseminatus* x-043). Within this section, four subclades/lineage, namely /disseminatus America, /disseminatus E-Asia A, /disseminatus E-Asia B and /disseminatus Europe, were recovered, similar to the phylogenetic results of Wächter & Melzer (2020). Surprisingly, three collections of *C. disseminatus* from the present study (*C. disseminatus* G134, *C. disseminatus* G228 and *C. disseminatus* G292) were found to be nested in one of the four subclades/lineage of the section *Disseminati,* /disseminatus America instead of /disseminatus E-Asia A and /disseminatus E-Asia B. The clade /disseminatus America represents a well-supported (95% BS) clade with nine collections of *C. disseminatus* (*Coprinellus disseminatus* BAP 608 (SFSU), *C. disseminatus* CEQCA-M1203, *C. disseminatus* G134, *C. disseminatus* G228, *C. disseminatus* G292, *C. disseminatus* PNB034A, *C. disseminatus* PNB034B, *C. disseminatus* PNB034D and *C. disseminatus* x-043). Apart from the collections of *C. disseminatus* from this study, all six other collections except for *C. disseminatus* x-043 (whose country of origin is not available) of this clade (*C. disseminatus* PNB034D (from Brazil), *C. disseminatus* PNB034A and PNB034B (from Peru), *C. disseminatus* BAP 608 (SFSU) (from West

Africa) and *C. disseminatus* CEQCA-M1203 (from Ecuador)) were previously reported from South American and West African regions. This indicates that the Indian collections of *C. disseminatus* are closer to the South American and African collections than the collections from Asia or Europe (/disseminatus E-Asia A, /disseminatus E-Asia B and /disseminatus Europe).

The present phylogram clearly indicated the identity and taxonomic position of *C. disseminatus* within the genus *Coprinellus*.

6.5. GENUS *COPRINOPSIS*

A total of nine species of the genus *Coprinopsis* are described in the present study. All these species of *Coprinopsis* together yielded 10 ITS sequences, including the sequences from the additional collections. The phylogram inferred from ML analysis is presented in Figure 5, which revealed the relative taxonomic position of these nine species within the genus *Coprinopsis*. The species of each section/clade of the genus *Coprinopsis* are named and colour-coded in Figure 5.

The phylogenetic tree yielded a large clade encompassing the genus *Coprinopsis*, but with low bootstrap support. This clade comprised species that belong to 13 different sections of the genus *Coprinopsis*, namely *Alopeciae, Canocipes, Cinereae, Coprinopsis, Filamentiferae, Lanatulae, Narcoticae, Niveae, Picaceae, Quartoconatae, Radiatae, Subniveae* and *Xenobiae*. In addition to these 13 sections, a distinct clade (Clade I) representing three species of *Coprinopsis* (*C. ochraceolanata*, *Coprinopsis* species 3 and *Coprinopsis urticicola* KR02) was also recovered.

The larger clade stands for the genus *Coprinopsis,* which includes a total of 80 collections representing 60 species of *Coprinopsis* (*Coprinopsis* aff. *lagopus, C. ammophilae, C. babosiae, C. bellula, C. bicornis, C. brunneistragulata, C. candidolanata* 794, *C. candidolanata* CAND1, *C. canoceps, C. cinerea* A767, *C. cinerea* CEL11, *C. cinerea* G222, *C. coniophora, C. cortinata, C. cothurnata, C. filamentifera, C. fluvialis, C.*

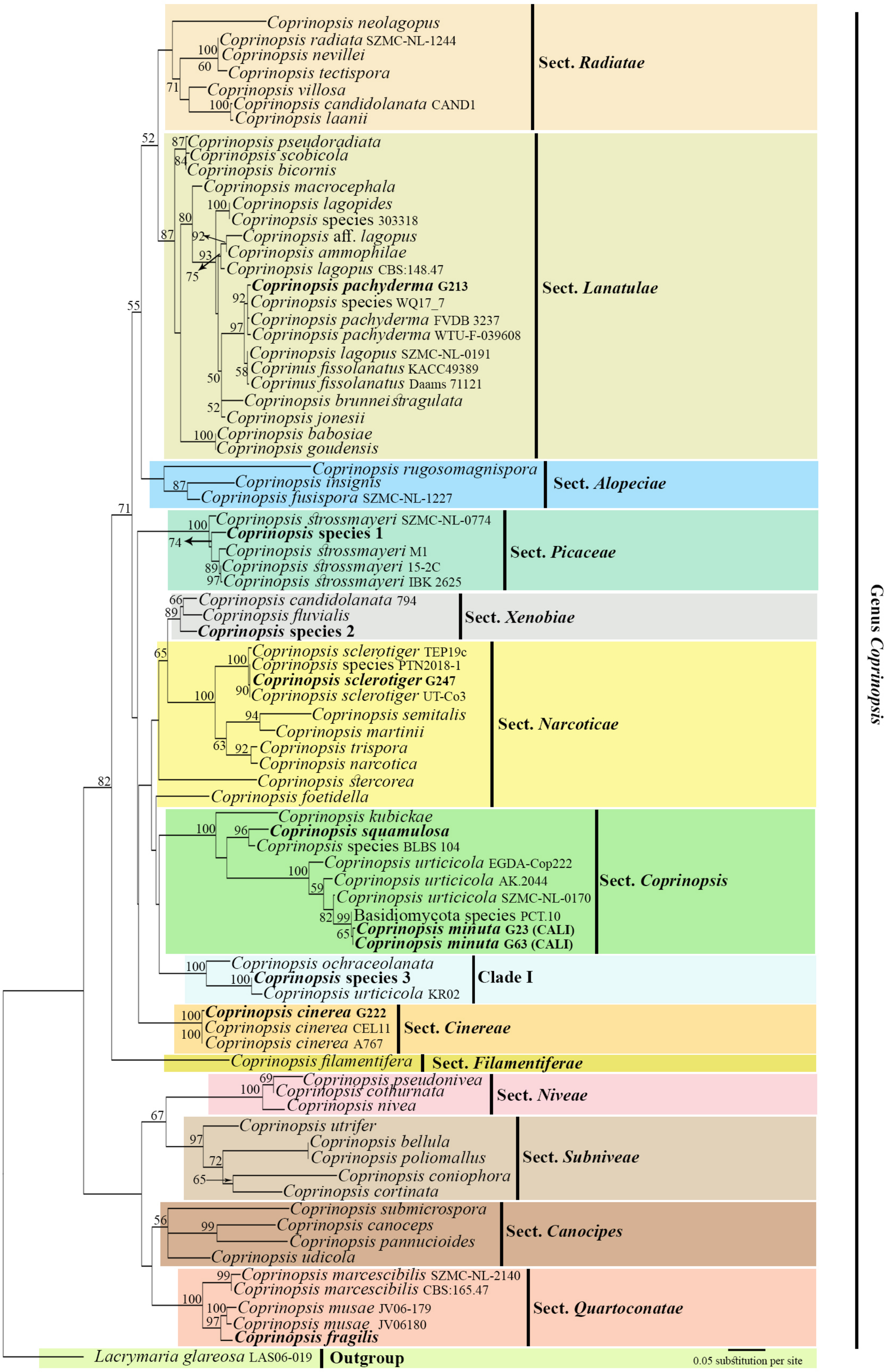

Figure 5. ML tree based on the ITS sequence data matrix for the genus *Coprinopsis*. The species described during the study are highlighted in bold font. Bootstrap values ≥ 50% are shown. *Lacrymaria glareosa* was used as an outgroup taxon.

foetidella, C. fragilis, C. fusispora SZMC-NL-1227, *C. goudensis, C. insignis, C. jonesii, C. kubickae, C. laanii, C. lagopides, C. lagopus* CBS:148.47, *C. lagopus* SZMC-NL-0191, *C. macrocephala, C. marcescibilis* CBS:165.47, *C. marcescibilis* SZMC-NL-2140*, C. martini, C. minuta* G23 (CALI), *C. minuta* G63 (CALI), *C. musae* JV06-179, *C. musae* JV06180, *C. narcotica, C. neolagopus*, *C. nevillei, C. nivea, C. ochraceolanata, C. pachyderma* FVDB 3237, *C. pachyderma* G213, *C. pachyderma* WTU-F-039608*, C. pannucioides, C. poliomallus, C. pseudonivea, C. pseudoradiata, C. radiata* SZMC-NL-1244, *C. rugosomagnispora, C. sclerotiger* G247, *C. sclerotiger* TEP19c*, C. sclerotiger* UT-Co3, *C. scobicola, C. semitalis, Coprinopsis* species 1, *Coprinopsis* species 2, *Coprinopsis* species 3, *Coprinopsis* species 303318, *Coprinopsis* species BLBS 104, *Coprinopsis* species PTN2018-1, *Coprinopsis* species WQ17_7, *C. squamulosa, C. stercorea, C. strossmayeri* 15-2C, *C. strossmayeri* IBK 2625, *C. strossmayeri* M1, *C. strossmayeri* SZMC-NL-0774, *C. submicrospora, C. tectispora, C. trispora, C. udicola, C. urticicola* AK.2044, *C. urticicola* EGDA-Cop222, *C. urticicola* KR02, *C. urticicola* SZMC-NL-0170, *C. utrifer* and *C. villosa*)*,* two collections of (KACC49389, Daams 71121) *Coprinus fissolanatus* (Later identified as *Coprinopsis lagopus* var. *vacillans,* but the name remained unchanged) and an unnamed taxon designated as ʽBasidiomycota species PCT.10ʼ. The present analysis centred mainly on seven sections (*Cinereae, Coprinopsis*, *Lanatulae*, *Narcoticae*, *Picaceae*, *Quartoconatae* and *Xenobiae*) and a distinct group formed within the larger clade of the genus *Coprinopsis*, where the species described in this treatise were nested.

A clade holding the members of the section *Lanatulae* was recovered with strong (87% BS) bootstrap support. It contains 20 collections of *Coprinopsis,* namely *Coprinopsis* aff. *lagopus*, *C. ammophilae*, *C. babosiae*, *C. bicornis*, *C. brunneistragulata*, *C. goudensis*, *C. jonesii*, *C. lagopides*, *C. lagopus* CBS:148.47, *C. lagopus* SZMC-NL-0191, *C. macrocephala*, *C. pachyderma* FVDB 3237, *C. pachyderma* G213, *C. pachyderma* WTU-F-039608, *C. pseudoradiata, C. scobicola*, *Coprinopsis* species 303318, *Coprinopsis* species WQ17_7, *Coprinus fissolanatus* KACC49389 and *C. fissolanatus* Daams 71121. *Coprinopsis pachyderma* G213, a species collected during the study, was grouped together with two other collections of *C. pachyderma* (WTU-F-039608 from USA and FVDB 3237 from North America) and an unidentified collection of *Coprinopsis* from China (*Coprinopsis* species WQ17_7) with strong (97% BS) bootstrap support.

The section *Picaceae* was recovered as a well-supported monophyletic group (100% BS). It includes five collections of *Coprinopsis*, namely *Coprinopsis* species 1, *C. strossmayeri* 15-2C, *C. strossmayeri* IBK 2625, *C. strossmayeri* M1 and *C. strossmayeri* SZMC-NL-0774. Within this clade*, Coprinopsis* species 1, a species encountered during the study, was differentiated well from the collections of *C. strossmayeri* (IBK 2625 whose locality is not available; 15-2C from Armenia and M1 from India) with 74% bootstrap support.

A well-supported (89% BS) clade that represents the members of the section *Xenobiae* was formed in this analysis. It comprises three species of *Coprinopsis* (*C. candidolanata* 794, *C. fluvialis* and *Coprinopsis* species 2). *Coprinopsis* species 2, another species described during this study, was found as a lineage distinct from the other two species of *Coprinopsis, C. candidolanata* 794 (from Italy) and *C. fluvialis* (whose country of origin is not available)*,* with strong (89% BS) bootstrap support.

The members of the section *Narcoticae* were found to be polyphyletic. Except for *C. stercorea* and *C. foetidella*, all other species of *Coprinopsis* (*C. martinii*, *C. narcotica, C. sclerotiger* G247, *C. sclerotiger* TEP19c, *C. sclerotiger* UT-Co3, *C. semitalis*, *C. trispora* and *Coprinopsis* species PTN2018-1) belonging to the section *Narcoticae* formed a distinct clade with full (100% BS) bootstrap support. *Coprinopsis sclerotiger* G247, a species collected and described as part of the present study, was nested within a group containing previously reported collections of *C. sclerotiger* (UT-Co3 from Iran and TEP19c whose country of origin is not available) and an unnamed *Coprinopsis* species from Vietnam (*Coprinopsis* species PTN2018-1) with strong (90% BS) bootstrap support.

Coprinopsis squamulosa and *C. minuta*, two species described and published during the course of the study (Ganga *et al.* 2022), were grouped in the clade representing the section *Coprinopsis*. This clade comprised nine collections, namely 'Basidiomycota species PCT.10', *C. kubickae*, *C. minuta* G23 (CALI), *C. minuta* G63 (CALI), *Coprinopsis* species BLBS 104, *C. squamulosa*, *C. urticicola* AK.2044, *C. urticicola* EGDA-Cop222 and *C. urticicola* SZMC-NL-0170. Within this clade, *Coprinopsis squamulosa* clustered with an unidentified collection of *Coprinopsis* from Brazil, *Coprinopsis* species BLBS 104, with (96% BS) bootstrap support. Two different collections of *C. minuta* (G23 (CALI), G63 (CALI)) and an unidentified 'Basidiomycota species PCT.10' together formed a distinct group with (99% BS) bootstrap support. Inside this group, *C. minuta* was found to be a distinct lineage sister to 'Basidiomycota species PCT.10' with high (99% BS) bootstrap support.

A distinct, well-supported clade (Clade I), sister to the section *Coprinopsis,* was recovered with maximum (100% BS) bootstrap support, which holds three species of *Coprinopsis*, namely *C. ochraceolanata* L173, *Coprinopsis* species 3 and *C. urticicola* KR02. Within this clade, *Coprinopsis* species 3 clustered with *C. urticicola* KR02 with full (100% BS) bootstrap support. In the previous phylogenetic analysis of the family Psathyrellaceae (Wächter & Melzer 2020), two collections of *C. ochraceolanata* formed a group within the genus *Coprinopsis,* which was then clustered among the members of section *Xenobiae,* representing a polyphyletic group. However, the morphological features of *C. ochraceolanata* are quite distinct from those of the members of the section *Xenobiae*. *Coprinopsis ochraceolanata* L173 and *Coprinopsis* species 3 have morphological characters that differ from members of both sections *Coprinopsis* and *Xenobiae*, supporting the distinct status of the clade. An unpublished collection of *Coprinopsis urticicola* KR02 from India was also found nested within this clade. But other collections of *C. urticicola* were grouped within the clade representing the section *Coprinopsis*. The identity of the sequence of *C. urticicola* (from India) nested within this clade is ambiguous and has to be verified.

Three collections of *C. cinerea* (*C. cinerea* G222, *C. cinerea* CEL11 and *C. cinerea* A767) together formed a monophyletic group representing the section *Cinereae,* with maximum (100% BS) bootstrap support. *Coprinopsis cinerea* G222, described during this study, was found to be conspecific with previously reported collections of *C. cinerea* (CEL11 from India and A767 whose locality is not available).

The members of the section *Quartoconatae* also formed a well-supported (100% BS) monophyletic group. This clade encompasses five collections of *Coprinopsis,* namely *C. fragilis, C. marcescibilis* CBS:165.47, *C. marcescibilis* SZMC-NL-2140, *C. musae* JV06-179 and *C. musae* JV06180. *Coprinopsis fragilis*, a species described and published during the present study (Crous *et al.* 2023), formed a lineage distinct from the two collections of *C. musae* from Denmark (JV06-179 and JV06180) with strong (97% BS) bootstrap support.

The present phylogenetic analysis clearly confirmed the novelty of six species of the genus *Coprinopsis* (*Coprinopsis* species 1, *Coprinopsis* species 2, *Coprinopsis* species 3, *C. fragilis*, *C. minuta* and *C. squamulosa*) discovered during this study. Of these six species, three were described and published during the course of this study. This study also ensured the relative taxonomic position and identity of *C. pachyderma, C. sclerotiger* and *C. cinerea* collected as part of the present study.

6.6. GENUS *NARCISSEA*

There were two species of the genus *Narcissea, N. cordispora* and *Narcissea* species 1, discovered during the course of the present study. A total of seven ITS sequences were successfully yielded from these two species. Figure 6 demonstrates the relative taxonomic position of the two species of *Narcissea* described in this study. The species of each genus/group/clade are colour-coded and named in Figure 6.

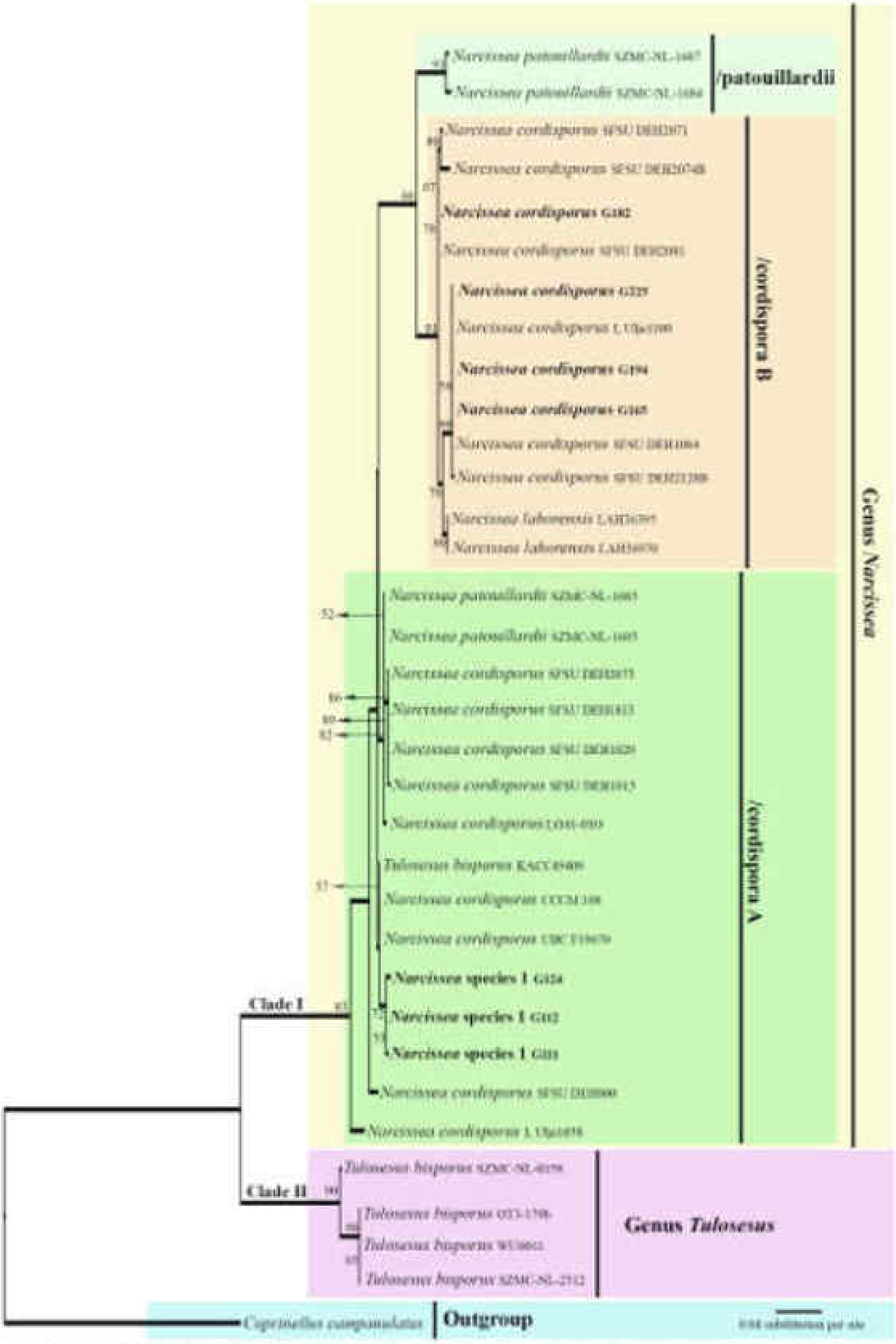

Figure 6. Maximum Likelihood phylogram of the genus *Narcissea* using the ITS sequence data matrix. The species described during the study are highlighted in bold font. Bootstrap values ≥ 50% are shown. *Coprinellus campanulatus* was selected as an outgroup.

The phylogenetic tree recognised two major clades: Clade I and Clade II, which represent two genera, namely *Narcissea* and *Tulosesus*. The two species of *Narcissea* collected during this study were nested within Clade I. This clade was found sister to Clade II, which accommodated the four collections of *Tulosesus bisporus* and had strong (83% BS) bootstrap support. Clade I comprised 23 collections, including one collection of *Tulosesus*, which were in turn distributed in /cordispora B, /patouillardii and /cordispora A. The present phylogenetic analysis focused primarily on /cordispora A and /cordispora B, where the species described in this study were nested.

A complex group (/cordispora A) formed within the genus *Narcissea* was found polyphyletic. This group comprised 15 taxa, which included 14 collections of *Narcissea* (*Narcissea cordisporus* CCCM:108, *N. cordisporus* L Uljé 1058, *N. cordisporus* LO41-01O, *N. cordisporus* SFSU DEH000, *N. cordisporus* SFSU DEH1813, *N. cordisporus* SFSU DEH1815, *N. cordisporus* SFSU DEH1829, *N. cordisporus* SFSU DEH2073, *N. cordisporus* UBC F19670, *N. patouillardii* SZMC-NL-1685, *N. patouillardii* SZMC-NL-1695, *Narcissea* species 1 G111, *Narcissea* species 1 G112 and *Narcissea* species 1 G124) and one collection of *Tulosesus* (*Tulosesus bisporus* KACC49409). The three collections of *Narcissea* species 1 (G124, G111 and G112), collected as part of the present study, together formed a distinct group and nested within /cordispora A with significant (72% BS) bootstrap support. Except for one collection of *Tulosesus bisporus* (*T. bisporus* KACC49409 nested in /cordispora A), all other collections of this species (SZMC-NL-0158 from Sweden, OT3-179b from Portugal and WU6011 and SZMC-NL-2512 whose localities are not available) were found to be clustered within Clade II with strong (90% BS) bootstrap support. This proved that the identity of the sequence denoted as '*T. bisporus* KACC49409' is a misidentification in GenBank and it in all probability belongs to the genus *Narcissea* as per the present analysis.

The clade /cordispora B was found as a well-resolved monophyletic group with 91% bootstrap support. This clade encompasses 12 collections representing two species of *Narcissea* (*Narcissea cordisporus* G165, *N. cordisporus* G182, *N. cordisporus* G194, *N. cordisporus* G225, *N. cordisporus* L Uljé 1100, *N. cordisporus* SFSU DEH1084, *N. cordisporus* SFSU DEH2071, *N. cordisporus* SFSU DEH2074B, *N. cordisporus* SFSU DEH2081, *N. cordisporus* SFSU DEH2128B, *N. lahorensis* LAH36395 and *N. lahorensis* LAH36970). Of these, four collections of *N. cordisporus* (G225, G165, G194 and G182) were from the present study. A pairwise alignment of the ITS sequences of these four collections showed 99.05% identity, confirming the conspecificity of these sequences.

The clade /patouillardii formed another well-resolved (91% BS) monophyletic group within Clade I, but with no species representation from the present study.

The present phylogenetic analysis confirmed the novelty and the taxonomic position of *Narcissea* species 1 and also ensured the identity of *N. cordisporus* collected during this study. According to the results of this analysis, the sequence labelled as '*T. bisporus* KACC49409' is a misidentification in GenBank and most likely it belongs to the genus *Narcissea*.

6.7. GENUS *PARASOLA*

The present study discovered five species belonging to two sections, *Auricomi* and *Parasola,* of the genus *Parasola.* The section *Parasola* includes 2 species and the remaining 3 species represent the section *Auricomi*. A total of 8 ITS sequences were generated from these five species, including those from the additional collections. The phylogenetic tree inferred from the ML analysis (Figure 7) depicted the taxonomic positions of the five species of *Parasola* described in the present study. The sections of the genus *Parasola* are colour-coded and named in Figure 7.

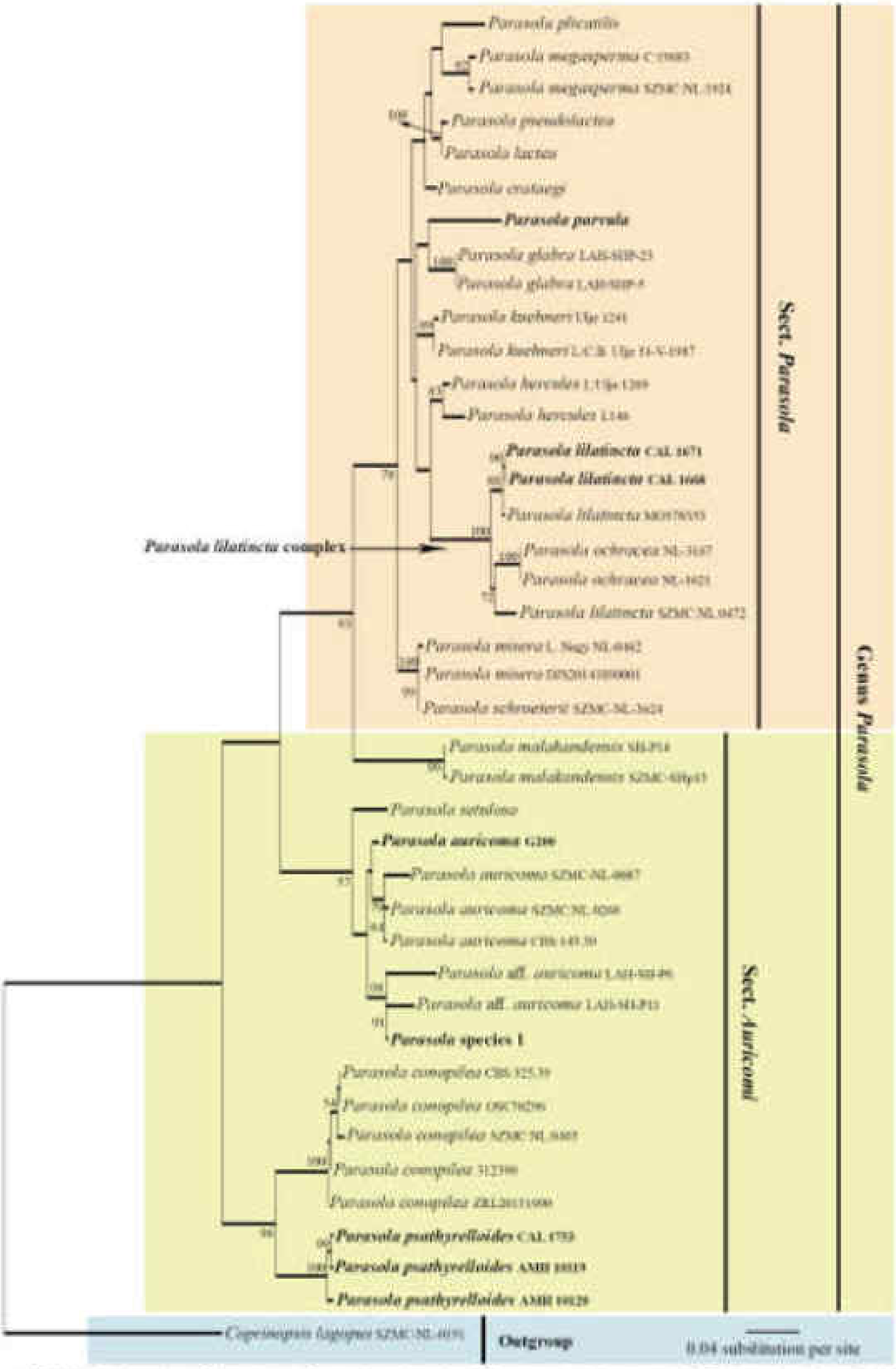

Figure 7. ML phylogram of the genus *Parasola* using the ITS sequence data matrix. The species described during the study are highlighted in bold font. Bootstrap values ≥ 50% are shown. *Coprinopsis lagopus* was used as an outgroup.

The phylogenetic tree recognised a distinct clade, representing the genus *Parasola*, but with low bootstrap support. Within this group, the monophyletic *Parasola* and the polyphyletic *Auricomi* sections were recovered. The monophyletic *Parasola* section comprises 22 collections representing 13 species of *Parasola,* namely *Parasola crataegi*, *P. glabra* LAH-SHP-23, *P. glabra* LAH-SHP-5, *P. hercules* L: Uljé:1269, *P. hercules* L146, *P. kuehneri* L: C.B. Uljé 31-V-1987, *P. kuehneri* Uljé 1241, *P. lactea*, *P. lilatincta* CAL 1668, *P. lilatincta* CAL 1671, *P. lilatincta* MO378353, *P. lilatincta* SZMC:NL:0472*, P. megasperma* C:19683, *P. megasperma* SZMC:NL:1924, *P. misera* DJS20141030001, *P. misera* L. Nagy NL-0462, *P. ochracea* NL-3621, *P. ochracea* NL-3167, *P. parvula*, *P. plicatilis*, *P. pseudolactea* and *P. schroeterii.* Within this clade, *P. parvula*, a species described and published during the present study (Ganga & Manimohan 2018), formed a lineage distinct from the collections of *P. glabra* from Pakistan (LAH-SHP-23 and LAH-SHP-5), but with low bootstrap support. *Parasola lilatincta,* another species published during the present study as a new record from India (Ganga & Manimohan 2018), was found to be nested in a well-supported (100% BS) clade within the section *Parasola,* named *Parasola lilatincta* complex. The *Parasola lilatincta* complex comprises the collections of *P. lilatincta* and *P. ochracea* (*Parasola lilatincta* CAL 1668, *P. lilatincta* CAL 1671, *P. lilatincta* MO378353, *P. lilatincta* SZMC:NL:0472, *P. ochracea* NL-3621 and *P. ochracea* NL-3167). Within this clade, the two collections of *Parasola lilatincta* collected as part of the present study (CAL 1668 and CAL 1671), together with the previously reported collection of the same (MO378353: USA), formed a distinct group with strong (88% BS) bootstrap support.

The section *Auricomi* formed within the genus *Parasola* was found to be polyphyletic. It includes 18 collections representing seven species of *Parasola,* namely *Parasola* aff. *auricoma* LAH-SH-P11, *Parasola* aff. *auricoma* LAH-SH-P6, *P. auricoma* CBS:145.39, *P. auricoma* G200, *P. auricoma* SZMC:NL:0268, *P. auricoma* SZMC-NL-0087, *P. conopilea* 312390, *P. conopilea* CBS:325.39, *P. conopilea* OSC50296, *P. conopilea* SZMC:NL:0465, *P. conopilea* ZRL20151990, *P.*

malakandensis SH-P14, *P. malakandensis* SZMC-SHp13, *P. psathyrelloides* AMH 10119, *P. psathyrelloides* AMH 10120, *P. psathyrelloides* CAL 1753, *P. setulosa* and *Parasola* species 1. A clade comprising four species of *Parasola,* including the additional collections (*P. auricoma* CBS:145.39, *P. auricoma* SZMC-NL-0087, *P. auricoma* SZMC:NL:0268, *P.* aff. *auricoma* LAH-SH-P6, *P.* aff. *auricoma* LAH-SH-P11, *P. setulosa* L32, *Parasola* species 1 and *P. auricoma* G200) was formed within the section *Auricomi,* with moderate (57% BS) bootstrap support. Inside this clade, *Parasola auricoma*, collected as part of the present study (*P. auricoma* G200), was grouped together with previously reported collections of *P. auricoma* (SZMC-NL-0087 and SZMC:NL:0268 from Hungary and CBS:145.39 whose locality is not available), but with low bootstrap support. However, a pair-wise comparison using the ITS sequence of *P. auricoma* G200 generated as part of the present study with those of the collections of *P. auricoma* available in the GenBank (CBS:145.39: MH855972; SZMC-NL-0087: JN943107; SZMC:NL.0268: FM163186) showed 98.40%, 98.08% and 93.5% similarities respectively. *Parasola* species 1, another species described during the study, was found to be nested in a group that comprised three collections of *Parasola* (*Parasola* aff. *auricoma* LAH-SH-P6 and LAH-SH-P11 from Pakistan and *Parasola* species 1 from India) with strong (98% BS) bootstrap support.

Another well-supported (96% BS) clade, which included two species of *Parasola*, *P. psathyrelloides* and *P. conopilea,* was also recovered in the section *Auricomi*. This clade contained eight collections of *Parasola,* namely *Parasola conopilea* 312390*, P. conopilea* CBS 325. 39, *P. conopilea* OSC50296*, P. conopilea* SZMC:NL:0465, *P. conopilea* ZRL20151990*, P. psathyrelloides* AMH 10119, *P. psathyrelloides* AMH 10120 and *P. psathyrelloides* CAL 1753. The three collections of *P. psathyrelloides* (*P. psathyrelloides* CAL 1753, *P. psathyrelloides* AMH 10119 and *P. psathyrelloides* AMH 10120), a species described and published during the course of this study (Ganga & Manimohan 2019), formed a distinct group within this clade with maximum (100% BS) bootstrap support.

The present phylogenetic analysis revealed the taxonomic position and confirmed the novelty of the three species of *Parasola* (*P. parvula*, *P. psathyrelloides* and *Parasola* species 1) collected during this study. It confirmed the identities of *P. lilatincta* and *P. auricoma* discovered during this study as well.

6.8. GENUS *PSATHYRELLA*

The genus *Psathyrella* was represented by three species in the present treatise: *Psathyrella* species 1, *Psathyrella* species 2 and *Psathyrella* species 3. All the three species successfully yielded DNA for sequencing, yielding one ITS sequence each. Figure 8 depicts the ML phylogram that showed the taxonomic positions of these three species within the genus *Psathyrella*. All the sections and the two lineages within the genus *Psathyrella* are colour-coded and named in Figure 8.

The phylogenetic tree recovered a large monophyletic group that stands for the genus *Psathyrella,* but with low bootstrap support. This clade included the members of 18 sections, namely *Arenosae, Atomatae, Confusae*, *Cystopsathyra, Hydrophilae*, *Jacobssoniorum*, *Lutenses*, *Microrhizae*, *Noli-tangere*, *Obtusatae, Pennatae, Psathyrella*, *Pseudostropharia*, *Pygmaeae*, *Saponaceae*, *Sinefibularum*, *Spadiceogriseae* and *Stridvalliorum*. In addition to these 18 sections, an independent lineage represented by a species of *Psathyrella* (*Psathyrella* species 3) discovered during the study was also recovered within this clade. The larger clade comprised a total of 48 collections representing 31 species of *Psathyrella,* including three species from the present study, namely *P. abieticola, P. arenosa* LO220-96, *P. arenosa* LO330-01*, P. conferta, P. cotonea* LO136-00*, P. cotonea* BRNM:705623*, P. effibulata* Herb.Orst. 99-11*, P. effibulata* LO37-96, *P. epimyces, P. fusca, P. gordonii, P. lutensis* HMJAU 37840*, P. lutensis* LO98-03*, P. microrhiza, P. noli-tangere, P. obtusata* CBS:166.72*, P. obtusata* LO88-01, *P. olympiana* LO32-02, *P. olympiana* SZMC-NL-2935, *P. panaeoloides* LO293-04*, P. panaeoloides* LO44-03, *P. pennata* LO216-84, *P. pennata* LO206-03*, P. piluliformis* HMJAU 37922, *P. piluliformis* WU:20516*, P. prona* 13147, *P. prona* JMT19678, *P. psammophila, P. pseudocorrugis, P. pseudogracilis*

LO287-06*, P. pseudogracilis* SZMC-NL-2142*, P. pygmaea* LO97-04, *P. pygmaea* SZMC-NL-2139*, P. pygmaea* SZMC-NL-2325*, P. saponacea*, *P. spadiceogrisea* AM1242, *P. spadiceogrisea* GENT JR3565*, Psathyrella* species 1, *Psathyrella* species 2, *Psathyrella* species 3, *P. sphaerocystis* Kew49734*, P. sphaerocystis* LO126-99*, P. stridvallii, P. sublatispora, P. subnuda* MICH33421*, P. subnuda* MICH5376, *P. tephrophylla* and *P. violaceopallens*. Except for the section *Pygmaeae* and an independent lineage within the larger clade, the rest of the sections have no species representation in the present study.

Psathyrella species 1, a species described during this study, was found nested in the section *Pygmaeae* where it formed a lineage distinct from the collections of *P. olympiana* (LO32-02 from Sweden and SZMC-NL-2935 whose locality is not available) with significant (72% BS) bootstrap support. *Psathyrella* species 2, another species nested in the section *Pygmaeae,* appeared as a lineage distinct from the members of the section *Pygmaeae* but with low bootstrap support. The macromorphological features of *Psathyrella* species 2 are in no way related to the members of the section *Pygmaeae.* However, as the species of the section *Pygmaeae* and *Psathyrella* species 2 have a common monophyletic lineage, *Psathyrella* species 2 is being treated under the section *Pygmaeae.*

Psathyrella species 3, yet another species described during this study, was not nested within any of the recognised sections of the genus *Psathyrella. Psathyrella* species 3 was figured as a discrete lineage (Lineage I), differentiated from the clade comprising the members of the sections *Pygmaeae* and *Saponaceae*, with significant (82% BS) bootstrap support.

The present phylogenetic analysis not only validated the novelty of three species of *Psathyrella* (*Psathyrella* species 1, *Psathyrella* species 2 and *Psathyrella* species 3) but also revealed their taxonomic position within the genus *Psathyrella*. The phylogram also showed that *Psathyrella* species 3 constitutes an independent

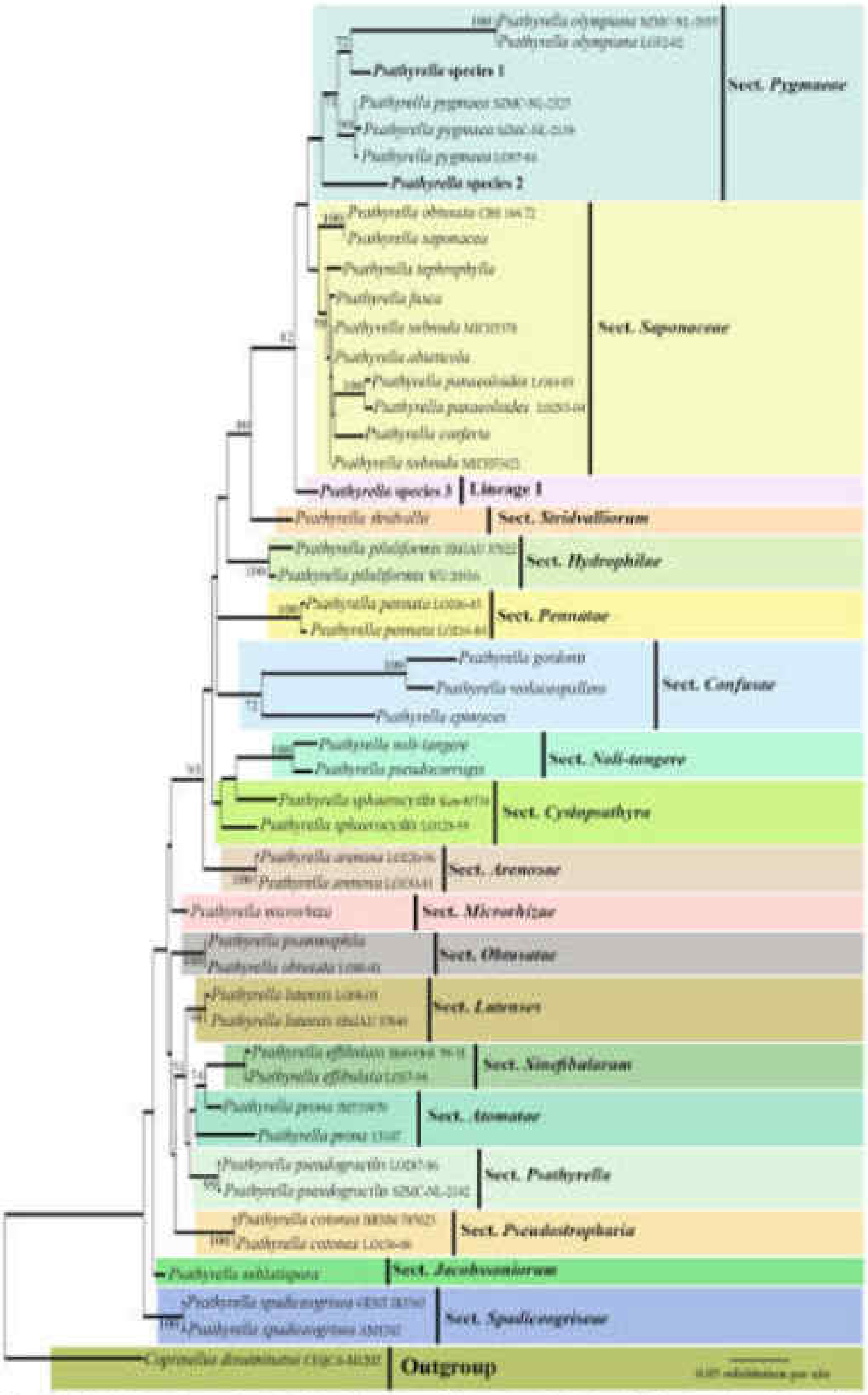

Figure 8. An ITS sequence-based ML phylogram of the genus *Psathyrella*. The species described during the study are highlighted in bold font. Bootstrap values ≥ 50% are shown. *Coprinellus disseminatus* was taken as an outgroup taxon.

lineage within the genus *Psathyrella* and does not belong to any existing sections of the genus *Psathyrella*.

6.9. GENUS *TULOSESUS*

The genus *Tulosesus* represents four species, including '*Coprinellus pseudodisseminatus*', in the present treatise. A total of six ITS sequences were generated from these four species of *Tulosesus* (including '*C. pseudodisseminatus*'), including their additional collections. The phylogram inferred from ML analysis revealed the relative taxonomic position of the species described within the genus *Tulosesus* and is presented in Figure 9. Also, all the clades/lineage recovered within the genus *Tulosesus* are colour-coded and named in Figure 9.

The phylogenetic tree identified 18 clades/lineage within the large clade representing the genus *Tulosesus,* namely /bisporus, /brevisetulosus, /callinus, /cinereopallidus, Clade 1, /congregates, /doverii, /heterosetulosus, /hiascens, /impatiens, /marculentus, /mitrinodulisporus, /pellucidus, /radicellus, /sabulicola, /sclerocystidiosus, /sp. and /velatopruinatus. Except for Clade 1, all other clades/lineage (17 clades/lineage) were recovered in the previous phylogenetic analysis of the genus *Tulosesus.*

The clade representing the genus *Tulosesus,* comprised a total of 42 collections containing 22 taxa, namely '*Coprinellus pseudodisseminatus*' HMJAU 46300, '*C. pseudodisseminatus*' HMJAU 46302, '*C. pseudodisseminatus*' HMJAU 46303, '*C. pseudodisseminatus*' G244, Fungal endophyte 4388, Fungal species E15613C, *Tulosesus bisporus* SZMC-NL-2512, *T. brevisetulosus* G224, *T. brevisetulosus* G251, *T. brevisetulosus* SZMC-NL-1445, *T. brevisetulosus* SZMC-NL-2908, *T. callinus* SZMC-NL-1931, *T. callinus* Uljé 1204, *T. cinereopallidus* Uljé 1163, *T. cinereopallidus* SZMC-NL-0177, *T. congregatus* SZMC-NL-1128, *T. congregatus* SZMC-NL-2138, *T. congregatus* Uljé 634, *T.* doverii, *T. heterosetulosus* SZMC-NL-1059, *T. heterosetulosus* Uljé 1284, *T. hiascens* Sieben96078, *T. hiascens* SZMC-NL-0628, *T. hiascens* SZMC-NL-0770, *T.*

hiascens SZMC-NL-1350, *T. impatiens*, *T. marculentus* SZMC-NL-1167, *T. marculentus* SZMC-NL-1471, *T. mitrinodulisporum*, *T. pellucidus* SZMC-NL-2344, *T. pellucidus* SZMC-NL-2928, *T. radicellus* SZMC-NL-0594, *T. radicellus* SZMC-NL-0957, *T. sabulicola*, *T. sclerocystidiosus*, *Tulosesus* species 1, *Tulosesus* species 'IN01', *Tulosesus* species MZ571673, *T. velatopruinatus* Uljé 1264, *T. velatopruinatus* G227, *T. velatopruinatus* G82 and *T. velatopruinatus* NLB 1489. The present study was limited to four clades (/brevisetulosus, Clade 1, /sp. and /velatopruinatus), within which the taxa described during the study were nested.

Clade 1, a small clade, comprised three species of *Tulosesus* (*Tulosesus* species 'IN01', *Tulosesus* species MZ571673 and *Tulosesus* species 1) and had strong (99% BS) bootstrap support. So far, no other clades corresponding to Clade 1 have been recognised in the previous phylogenetic study of the genus *Tulosesus* (Wächter & Melzer 2020). *Tulosesus* species 1, a species described during the present study, was found to be nested within this clade together with two unnamed species of *Tulosesus* from the USA (IN01'and MZ571673) with strong (99% BS) bootstrap support.

'*Coprinellus pseudodisseminatus*', a collection from the present study (G244,) and all other Chinese collections of the same (HMJAU 46303, HMJAU 46302 and HMJAU 46300) and an unidentified fungal species from New Guinea Island (Fungal endophyte 4388) together formed a distinct clade named as /sp. with full (100% BS) bootstrap support. Based on the present analysis, '*Coprinellus pseudodisseminatus*' was well nested within the /sp. of *Tulosesus,* which in turn suggests its transfer from the genus *Coprinellus* to *Tulosesus.*

The well-supported (93% BS) /velatopruinatus clade comprised four collections of *T. velatopruinatus* (G227, G82, NLB 1489 and Uljé 1264). *Tulosesus velatopruinatus* collected as part of the present study (G227 and G82) was grouped together with the other two collections of *T. velatopruinatus* (NLB 1489

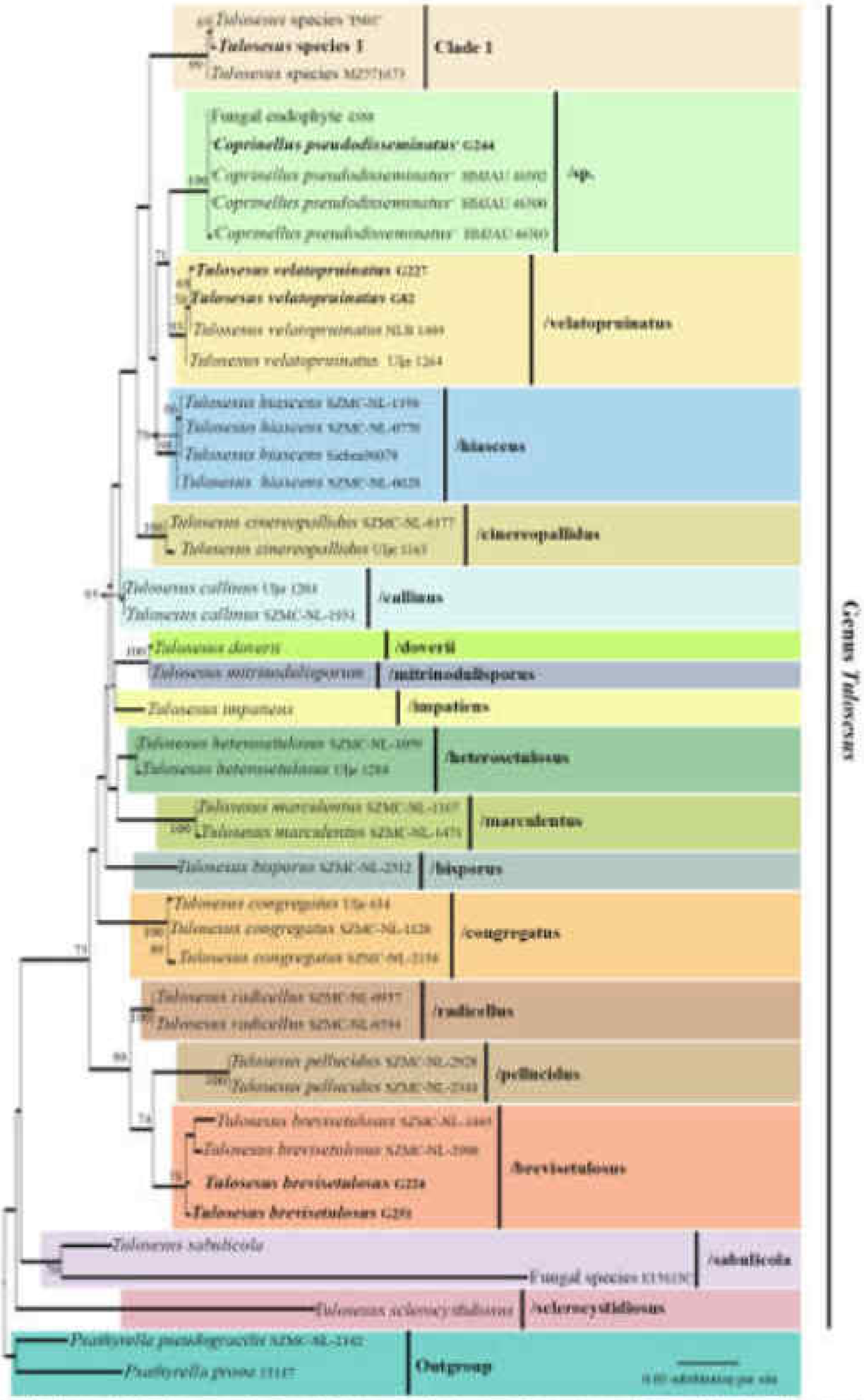

Figure 9. An ITS-based ML phylogenetic tree of the genus *Tulosesus*. The species described during the study are highlighted in bold font. Bootstrap values ≥ 50% are shown. *Psathyrella pseudogracilis* and *P. prona* were chosen as outgroups.

fromAustralia and Uljé 1264 whose locality is not available) with moderate (58% BS) bootstrap support.

The clade /brevisetulosus formed a group representing the collections of *T. brevisetulosus* with significant (79% BS) bootstrap support. Within this clade, the collections of *T. brevisetulosus* gathered during the present study (G251 and G224) along with other two collections of the same from Hungary (SZMC-NL-2908 and SZMC-NL-1445) were nested together.

The present phylogenetic tree confirmed the novelty as well as the taxonomic position of *Tulosesus* species 1. It also supported the identity and relative placement of the three species, namely *T. velatopruinatus* (G82, G227), *T. brevisetulosus* (G251, G224) and '*Coprinellus pseudodisseminatus*' G244 within the genus *Tulosesus*. In the present study, the collections of '*Coprinellus pseudodisseminatus*' were found to be nested within the large clade representing the genus *Tulosesus,* warranting its transfer into the genus *Tulosesus*.

Chapter 7

General observations and discussions

CHAPTER 7

GENERAL OBSERVATIONS AND DISCUSSIONS

7.1. FLORISTIC OBSERVATIONS

The present study is based on sixty-two collections of coprinoid and psathyrelloid agarics made from different parts of Kerala State during the period 2016-2019. The sixty-two collections include thirty-five species belonging to nine genera distributed in two families, namely Agaricaceae and Psathyrellaceae. Of these nine genera, except for the genus *Coprinus,* with a single species, that belongs to the family Agaricaceae, all other eight genera, namely *Candolleomyces*, *Coprinellus, Coprinopsis, Hausknechtia, Narcissea, Parasola, Psathyrella* and *Tulosesus,* together comprise thirty-four species belonging to the family Psathyrellaceae. Of these thirty-four species described, nine species each belong to the genera *Candolleomyces* and *Coprinopsis,* five to *Parasola*, four to *Tulosesus*, three to *Psathyrella*, two to *Narcissea* and one species each to the genera *Coprinellus* and *Hausknechtia.*

The thirty-five species of coprinoid and psathyrelloid agarics discovered and described during this study are listed below:

AGARICAEAE

Coprinus

1. *Coprinus* species 1

PSATHYRELLACEAE

Candolleomyces

2. *Candolleomyces candolleanus*
3. *Candolleomyces efflorescens*

4. *Candolleomyces* species 1
5. *Candolleomyces* species 2
6. *Candolleomyces* species 3
7. *Candolleomyces* species 4
8. *Candolleomyces* species 5
9. *Candolleomyces sulcatotuberculosus*
10. *Candolleomyces typhae*

Coprinellus

11. *Coprinellus disseminatus*

Coprinopsis

12. *Coprinopsis cinerea*
13. *Coprinopsis fragilis* (validly published during this study)
14. *Coprinopsis minuta* (validly published during this study)
15. *Coprinopsis pachyderma*
16. *Coprinopsis sclerotiger*
17. *Coprinopsis* species 1
18. *Coprinopsis* species 2
19. *Coprinopsis* species 3
20. *Coprinopsis squamulosa* (validly published during this study)

Hausknechtia

21. *Hausknechtia leucosticta*

Narcissea

22. *Narcissea cordispora*
23. *Narcissea* species 1

Parasola

24. *Parasola auricoma*

25. *Parasola lilatincta* (published during this study)
26. *Parasola parvula* (validly published during this study)
27. *Parasola psathyrelloides* (validly published during this study)
28. *Parasola* species 1

Psathyrella

29. *Psathyrella* species 1
30. *Psathyrella* species 2
31. *Psathyrella* species 3

Tulosesus

32. '*Coprinellus pseudodisseminatus*'
33. *Tulosesus brevisetulosus*
34. *Tulosesus* species 1
35. *Tulosesus velatopruinatus*

7.2. FLORISTIC NOVELTIES

Out of these thirty-five species of coprinoid and psathyrelloid agarics described in this treatise, 20 were found to be new to science. Among the remaining fifteen species, 9 were found to be new records for India and 11 were new to Kerala State. The newly discovered species described in this study included six species of *Coprinopsis*, five species of *Candolleomyces*, three species each from the genera *Parasola* and *Psathyrella* and one species each from the genera *Tulosesus*, *Narcissea* and *Coprinus* and are listed below:

1. *Candolleomyces* species 1
2. *Candolleomyces* species 2
3. *Candolleomyces* species 3
4. *Candolleomyces* species 4
5. *Candolleomyces* species 5

6. *Coprinopsis minuta* (validly published during this study)
7. *Coprinopsis fragilis* (validly published during this study)
8. *Coprinopsis* species 1
9. *Coprinopsis* species 2
10. *Coprinopsis* species 3
11. *Coprinopsis squamulosa* (validly published during this study)
12. *Coprinus* species 1
13. *Narcissea* species 1
14. *Parasola parvula* (validly published during this study)
15. *Parasola psathyrelloides* (validly published during this study)
16. *Parasola* species 1
17. *Psathyrella* species 1
18. *Psathyrella* species 2
19. *Psathyrella* species 3
20. *Tulosesus* species 1

The following nine species were found to be the first records for India in the present study:

1. *Candolleomyces sulcatotuberculosus*
2. *Candolleomyces typhae*
3. '*Coprinellus pseudodisseminatus*'
4. *Coprinopsis pachyderma*
5. *Coprinopsis sclerotiger*
6. *Parasola auricoma*
7. *Parasola lilatincta*
8. *Tulosesus brevisetulosus*
9. *Tulosesus velatopruinatus*

Eleven species identified during the study formed the first record from Kerala State:

1. *Candolleomyces sulcatotuberculosus*
2. *Candolleomyces typhae*
3. '*Coprinellus pseudodisseminatus*'
4. *Coprinopsis pachyderma*
5. *Coprinopsis sclerotiger*
6. *Coprinopsis cinerea*
7. *Narcissea cordispora*
8. *Parasola auricoma*
9. *Parasola lilatincta*
10. *Tulosesus brevisetulosus*
11. *Tulosesus velatopruinatus*

7.3. DIVERSITY AND DISTRIBUTION

Coprinoid and psathyrelloid agarics are frequently observed in humid environments such as forests, agricultural lands or farm yards with decaying dung. Therefore, coprinoid and psathyrelloid fungi have tremendous diversity in Kerala State. Several coprinoid and psathyrelloid agarics treated in this study were discovered from the Calicut University campus itself. Of the 8 species collected from the Calicut University campus, two new species of *Coprinopsis* (*Coprinopsis squamulosa* and *C. minuta*) were validly published during the course of this study (Ganga *et al.* 2022). In addition, a good number of coprinoid and psathyrelloid agarics were obtained from the southern parts of Kerala, such as the Thenmala (Kollam District) and Neyyar (Thiruvananthapuram District) regions. Despite excellent collections of coprinoid and psathyrelloid agarics in 2016-2017, with a high number of collections, especially during the July to September months, sightings of these agarics decreased in the subsequent years due to heavy flooding in Kerala State. As a result, the number of coprinoid and psathyrelloid agarics discovered in subsequent years has been modest.

Among the coprinoid and psathyrelloid agarics described in this study, the genera *Candolleomyces* and *Coprinopsis* showed excellent diversity in Kerala State. The present study described nine species each from these genera. Of these eighteen species, eleven species, comprising six species of *Coprinopsis* and five species of *Candolleomyces,* were found to be new to science. Similarly, the species of *Parasola* showed modest diversity in Kerala State. A total of five species of *Parasola* was described during the course of this study. Among these five species, three were identified as new to science (*Parasola parvula, P. psathyrelloides* and *Parasola* species 1) and one (*P. lilatincta*) was found to be a new record for India. The diversity of the genera *Coprinellus, Coprinus* and *Hausknechtia* was found less when compared to other genera of coprinoid and psathyrelloid agarics treated in this study, representing only a single species each from these genera. The author considers herself fortunate to have collected a coprinoid species (*Hausknechtia leucosticta*) from the campus of Calicut University (Malappuram District), one of the two species so far described under the genus *Hausknechtia*. '*Coprinellus pseudodisseminatus*', a species collected from the Vazhachal forest (Thrissur District), showed a close morphological similarity with *C. disseminatus,* originally described from China. However, DNA sequence and phylogenetic studies confirmed that this species has more affinity towards *Tulosesus,* another coprinoid genus described in this study.

Of the thirty-five species described in this study, three species, namely *Coprinellus disseminatus*, *Narcissea cordispora* and *Parasola psathyrelloides* were found to be widely distributed in Kerala State. The author collected these species from different localities in Kerala State: *Coprinellus disseminatus* from Edakkal caves (Wayanad District), Thattekkad (Ernakulam District) and Peruvannamuzhi

(Kozhikode District); *Narcissea cordispora* from Muthanga (Wayanad District), Aarlam (Kannur District) and Punnayoorkulam (Thrissur District) and *Parasola psathyrelloides* from Muthanga (Wayanad District), Thenmala (Kollam District) and Peruvannamuzhi (Kozhikode District).

7.4. ENVIRONMENTAL CONDITIONS AND FRUITING PATTERN

A wet and humid environment has been found to be ideal for the development of coprinoid and psathyrelloid agarics. As continuous and heavy rainfall will destroy the fragile fruit bodies, the sprouting of coprinoid and psathyrelloid agarics requires a moderate amount of rainfall at short intervals. The coprinoid and psathyrelloid agarics, like other agarics, are most commonly observed during the two monsoon seasons. However, even in the early summer, wet substrata such as herbivore dung in farm yards and irrigated agricultural lands can produce coprinoid and psathyrlloid agarics. It was found that incubating mycelium containing substrata such as herbivore dung and rotten plant remnants carefully collected from the natural environment can result in the development of coprinoid and psathyrelloid basidiocarps. With this insight, during the study, the development of coprinoid and psathyrelloid agarics was observed in the laboratory by providing suitable wet and humid environmental conditions.

The fruiting bodies of coprinoid and psathyrelloid agarics have a short lifespan. This is especially true for the basidiocarps of coprinoid agarics, which collapse within a few hours after reaching maturity. Unlike other agarics, the basidiocarps of some coprinoid species appear to open late night or early morning before sunrise. This makes collecting coprinoid fungi more difficult. Collecting deliquescent coprinoid fungi is a great challenge. Mycologists interested in coprinoid fungi have to observe their entire period of development, from the initial stage to maturity. The young specimens of coprinoid fungi have to be dried immediately before the onset of deliquescence. During this study, the author observed that most of the microscopic structures obtained from the mature fruit bodies collapsed due to this deliquescence, and these fruit bodies were found to be useful only for recording mature basidiospores. Except for the basidiospores, the microscopic characters of coprinoid fungi were observed and recorded from their young basidiocarps. Hence, it is critical to get a collection of coprinoid fungi that contains sufficient number of young basidiocarps along with mature ones.

7.5. HABITAT SPECIFICITY

The majority of the coprinoid and psathyrelloid species described in this study were found to grow on decaying plant remnants. Out of the thirty-five species, sixteen species (*Candolleomyces efflorescens*, *Candolleomyces* species 1, *Candolleomyces* species 3, *Candolleomyces* species 4, *Candolleomyces* species 5, *C. sulcatotuberculosus*, *C. typhae*, *Coprinellus disseminatus*, '*Coprinellus pseudodisseminatus*', *Coprinopsis cinerea*, *C. fragilis*, *C. minuta*, *Coprinopsis* species 3, *C. squamulosa*, *Parasola auricoma* and *P. psathyrelloides*) were seen on decaying plant remnants or wood. Ten species (*Coprinopsis pachyderma*, *C. sclerotiger*, *Coprinopsis* species 2, *Narcissea cordispora*, *Narcissea* species 1, *Parasola lilatincta*, *P. parvula*, *Psathyrella* species 2, *Tulosesus brevisetulosus* and *T. velatopruinatus*) were found to be growing on different kinds of herbivore dung. Nine species (*Candolleomyces candolleanus*, *Candolleomyces* species 2, *Coprinopsis* species 1, *Coprinus* species 1, *Hausknechtia leucosticta*, *Parasola* species 1, *Psathyrella* species 1, *Psathyrella* species 3 and *Tulosesus* species 1) were seen in humus rich soil. Coprophilous habitat is very common in coprinoid mushrooms. While psathyrelloid species are not frequently observed in herbivore dung and most of them are found in lignicolous habitat (Larsson & Örstadius 2008). However, *Psathyrella* species 2, a species discovered during the study, was found to be growing on decaying elephant dung. The coprinoid and psathyrelloid agarics collected from Kerala State were found to be scattered or in small groups. During the course of the study, only three species (*Coprinellus disseminatus*, *Candolleomyces candolleanus* and *C. efflorescens*) had a gregarious habit.

Except for *Coprinopsis cinerea, C. sclerotiger* and *Tulosesus brevisetulosus*, all other coprophilous species described in this study were collected from the dung of wild elephants. Wild elephant dung contains undigested hard plant remnants that will take almost a year to decay completely (Manimohan *et al*. 2007). All three collections of *Narcissea* species 1 were obtained from the undigested plant remnants in elephant dung that had been incubated in the lab. This species, therefore, is partly coprophilous and partly lignicolous.

7.6. MICROSCOPIC OBSERVATIONS

Thick gelatinisation was observed in the pileipellis of *Coprinopsis* species 2. A basidiocarp with a viscid pileus seems to be an unusual character in coprinoid and psathyrelloid agarics. There were no previous reports available regarding the viscid pileus of coprinoid and psathyrelloid agarics. The pileipellis of *Coprinopsis* species 2 was found to be a trichoderm composed of branched chains of velar elements that form the pellicle, embedded in a gelatinised matrix when young. As the pellicle gets separated, and the pileipellis becomes a cutis at maturity. The pileus of *Coprinopsis* species 2 in the young stage was smooth and slimy instead of having a floccose, squamulose, mealy, or granulose surface, as is common in *Coprinopsis* species.

A total of three species (*Parasola auricoma, P. psathyrelloides* and *Parasola* species 1) belonging to the section *Auricomi* of the genus *Parasola* were described in this study. Abundant hairs (ozonium) were observed in the stipitipellis obtained from the base of the stipe in all three species. Patouillard (1886) observed abundant thick-walled hairs as ozonium in the original description of *P. auricoma* (as *Coprinus auricomus*) and it was recorded in young basidiocarps. However, these hairs will soon disappear during the development of the stipe (Nagy 2010b). Except for *P. psathyrelloides*, which was described from India during the course of the study (Ganga & Manimohan 2019), there were no reports of true ozonium in any species of *Parasola.*

The presence of pseudoparaphyses surrounding the basidia was observed in *Psathyrella* species 2. Pseudoparaphyses are sterile basidioles that form a definite pattern around the basidia in coprinoid agarics. The number of pseudoparaphyses surrounding each basidium is usually used in discriminating coprinoid taxa. However, a psathyrelloid species with pseudoparaphyses that form a certain pattern around the basidia is an exceptional case. In addition, black, lenticular basidiospores with a papilla, which are common in coprinoid taxa, were discovered in *Psathyrella* species 2. *Parasola psathyrelloides,* a psathyrelloid species described during the study from Kerala (Ganga & Manimohan 2019), also showed pseudoparaphyses around the basidia. This taxon is most likely an evolutionary connecting link between the coprinoid and psathyrelloid taxa. A detailed study based on coprinoid and psathyrelloid agarics from all over the world will reveal a clear picture of the evolutionary relationship among this group of agarics in the future. A cutis-type pileipellis overlaid with a suprapellis composed of globose elements was observed in one of the psathyrelloid species, *Coprinopsis fragilis*. This species resembles the genus *Psathyrella* in having a similar pileipellis character.

7.7. DNA EXTRACTION

Dried specimens were used for DNA extraction in this study. A simple procedure for isolating mushroom DNA by Izumitsu *et al*. (2012) was adopted for this study. Although the technique was originally intended to isolate DNA from fresh samples, it has also been shown to be effective in isolating DNA from dried coprinoid and psathyrelloid agarics. Compared to the long series of steps using various chemicals as in the conventional CTAB method (Doyle & Doyle 1990), the present method appears to have the main advantage of requiring only a low quantity sample to isolate DNA. In terms of saving time, money and valuable specimens, this method has been found to be the most effective. The protocol was found extremely effective for tiny and delicate agarics as the majority of coprinoid and psathyrelloid agarics discovered during this study had very small and delicate basidiocarps. The isolation of DNA from these basidiocarps is very difficult using the conventional

CTAB method. The protocol of Izumitsu *et al*. (2012) was found to be nearly 100% successful in isolating DNA from coprinoid and psathyrelloid agarics collected during this study. All the thirty-five coprinoid and psathyrelloid agarics discovered during this study yielded ITS and nLSU sequences except for one species, *Candolleomyces* species 4, which failed to generate an nLSU sequence.

7.8. BLAST SEARCHES

The taxonomic reliability of GenBank nucleotide sequences used in BLASTn searches is critical to the phylogenetic analysis (Nilsson 2006). The DNA sequences of coprinoid and psathyrelloid agarics in GenBank are mainly from Europe and America. However, a small number of DNA sequences of these agarics are available from Asian regions. As the coprinoid and psathyrelloid agarics from India were so poorly documented, several previous molecular phylogenetic studies performed on this group have so far been unable to include any representation from India.

7.9. DNA SEQUENCES GENERATED DURING THIS STUDY

A total of 96 DNA sequences were generated as part of the present study (Table III). This includes 52 ITS and 44 nLSU sequences. All the thirty-five species described during the study yielded 52 ITS sequences, including sequences from additional collections. Except for one species, *Candolleomyces* species 4, thirty-four species successfully yielded 44 nLSU sequences, including those from additional collections. Of the 52 ITS sequences generated, 51 were obtained from eight genera in the family Psathyrellaceae. It includes 13 from 9 species of *Candolleomyces*, 3 from a single species of *Coprinellus*, 10 from 9 species of *Coprinopsis*, 1 from a single species of *Hausknechtia*, 7 from 2 species of *Narcissea*, 8 from 5 species of *Parasola*, 3 from 3 species of *Psathyrella* and 6 from 4 species of *Tulosesus*. Only one ITS sequence was produced from a single species of *Coprinus, Coprinus* species 1 belongs to the family Agaricaceae. The ITS sequences were obtained for all 35 species described in this study.

Among the 44 nLSU sequences produced, only one nLSU sequence was generated from a single species of *Coprinus*, *Coprinus* species 1, of the family Agaricaceae. The remaining 43 sequences were generated from thirty-three species belonging to the family Psathyrellaceae. It comprises 10 from 8 species of *Candolleomyces*, 2 from a single species of *Coprinellus*, 11 from 9 species of *Coprinopsis*, 1 from a single species of *Hausknechtia*, 2 from 2 species of *Narcissea*, 8 from 5 species of *Parasola*, 3 from 3 species of *Psathyrella* and 6 from 4 species of *Tulosesus*.

Of the 96 DNA sequences, 10 ITS (*Parasola parvula* (MH379796), *P. lilatincta* (MH379669, MH379670), *P. psathyrelloides* (MK682756, MK682752, MK682758), *Coprinopsis fragilis* (OP852345), *C. minuta* (OP549280, OP549038), *C. squamulosa* (OP549278)) and 10 nLSU (*Parasola parvula* (MH393599), *P. lilatincta* (MH393600, MH393601), *P. psathyrelloides* (MK682754, MK682759, MK682755), *Coprinopsis fragilis* (OP852344), *C. minuta* (OP549279, OP549277) *C. squamulosa* (OP549708)) sequences were deposited in the GenBank database and validly published (Ganga & Manimohan 2018, 2019; Ganga *et al.* 2022; Crous *et al.* 2023) during the course of this study. The remaining DNA sequence will be deposited in the GenBank soon after the successful completion of this study. The present work is the first attempt to study the molecular systematics of coprinoid and psathyrelloid agarics from India. The deposition of these sequences generated during this study will provide a major addition to the GenBank database. Furthermore, the deposition of these sequences generated as part of the present study in the GenBank, along with properly identified voucher specimens deposited in a recognised herbarium, will certainly be useful in future phylogenetic studies of coprinoid and psathyrelloid fungi as representations from the tropical regions.

Chapter 8

Recommendations

CHAPTER 8

RECOMMENDATIONS

Coprinoid and psatyhrelloid agarics are one of the most widely distributed groups of agarics. These agarics are abundant in the tropical countries, particularly India. The climate of Kerala State is highly favourable for the growth and development of coprinoid and pasthyrelloid agarics. The present study provides a detailed account of the coprinoid and psathyrelloid agarics found in Kerala State. This includes 35 species belonging to nine genera. Among these, 20 species were found to be new to science and nine species were new to the country. Further studies covering the unexplored regions of Kerala State and other parts of India will, in all probability, reveal several species new to the region and to science.

The short life span, fragility and deliquescence of the basidiocarps are the major challenges in collecting and describing coprinoid and psathyrelloid taxa in a humid tropical region like Kerala. This problem can be overcome to some extent by incubating the substratum containing the mycelium of the agarics in the lab itself. This practice was followed in this study, especially for extremely small and fragile species. A carefully collected substratum without damaging the mycelium is suitable for incubation. Any substrata, such as dung, decaying wood and plant remnants, or even the soil mixed with vegetable garbage, can be incubated in an open space by providing moisture. A large number of coprinoid agarics can be collected through this method before the onset of deliquescence.

Another hurdle faced during the study was the existence of ambiguous or misidentified DNA sequences of coprinoid and psathyreloid agarics in the GenBank database. For example, the phylogenetic analysis of the genus *Narcissea* conducted in the present study proved that '*Tulosesus bisporus* KACC49409', the closest taxon resulted in a BLASTn search of *Narcissea* species 1, was a misidentified/mislabelled sequence in the GenBank database and the present study revealed that it belongs to the genus *Narcissea*. Hence, it is highly recommended to consider the sequences from published works by reputed mycologists/mushroom taxonomists for the phylogenetic analysis.

As coprinoid and psatyhrelloid agarics were traditionally classified based on conventional morphology-based taxonomic systems, their ancestral/species relations could only be ascertained through macro- and micro-morphological characteristics. Now it became evident that the conventional systematics of all agarics would be drastically altered by molecular biology approaches. This is true in the case of coprinoid and psatyhrelloid agarics, where a number of new genera have recently been added to the family Psathyrellaceae based on multigene phylogenetic analyses. Most genera/species of the coprinoid and psatyhrelloid group can only be identified through DNA-based analysis. For instance, certain species of the genera *Candolleomyces, Coprinellus, Coprinopsis, Parasola, Psathyrella* and *Tulosesus* could not be correctly assigned to their respective genera without molecular evidence. Therefore, it is recommended that all future research on this particular group use DNA-based molecular techniques as well as macro- and micromorphological characteristics.

Several coprinoid and pasthyrelloid species are already well-known for their economic importance, including their use in medicine and food and as experimental models in research. More focused studies regarding the biochemical, biomedical, biotechnological aspects of the coprinoid and psathyrelloid agarics will definitely reveal more economic value of these fungi in the future.

Chapter 9
Summary

CHAPTER 9

SUMMARY

Coprinoid and psathyrelloid agarics are closely related groups of fungi with several similar features. They include a diverse group of species and often occupy similar ecological niches and play comparable roles in the ecosystem. Both groups are primarily decomposers, mostly saprophytic, contributing significantly to the decay of wood, dung, grassy debris and other types of forest litter.

Coprinoid mushrooms (inky-caps) are a fascinating group of agarics because their basidiocarps liquefy and convert into a black ink-like fluid within a few hours of maturity. Prior to the phylogenetic studies based on DNA comparisons, most of the autodigested species were classified as Coprinaceae, which included all inky-cap mushrooms. The type species of *Coprinus, C. comatus*, and a few additional species, however, were discovered to be more closely allied to Agaricaceae. Hence, these few species of *Coprinus* became the genus *Coprinus sensu stricto* which was transferred to the family Agaricaceae. The name "Coprinaceae" thus became a synonym of Agaricaceae. Most of the remaining species of *Coprinus sensu lato* and other genera of the previous Coprinaceae are now classified in the family Psathyrellaceae. According to the recent classification based on morphology and molecular phylogeny, the family Psathyrellaceae comprises 16 genera, namely *Britzelmayria*, *Candolleomyces*, *Coprinellus*, *Coprinopsis*, *Cystoagaricus*, *Hausknechtia*, *Homophron*, *Kauffmania*, *Lacrymaria*, *Narcissea*, *Olotia*, *Parasola*, *Psathyrella*, *Punjabia*, *Tulosesus* and *Typhrasa*.

The present study provides a detailed account of the diversity of the coprinoid and psathyrelloid agarics of Kerala State. This study forms the first attempt to document the diversity of the coprinoid and psathyrelloid agarics of this region and to analyse their phylogenetic relationships. The present study had three objectives: 1. to study the diversity of the coprinoid and psathyrelloid agarics of Kerala; 2. to prepare a systematic account of the discovered taxa with keys, detailed descriptions, photographs of microscopic structures and colour photographs of basidiocarps; 3. to study the evolutionary relationships of the discovered taxa using the method of molecular phylogenetics.

Conventional fungal taxonomic methods were adopted for morphological studies. The microscopic characters of the discovered species were examined with the aid of a light microscope. DNA was extracted from all the discovered species. PCR reactions were performed with primers ITS1 and ITS4 for the ITS and LROR and LR7 for the nLSU regions. Agarose gel electrophoresis technique was used to determine the quality and quantity of the amplified DNA. Amplified PCR products were sequenced at a commercial facility. The sequences thus generated were edited using BioEdit sequence alignment editor v.7.2.5. BLAST searches were performed using the newly generated sequences to find related species in the GenBank database.

The ITS sequences generated as part of this study were used for elucidating the phylogenetic relationship of the discovered species. Altogether, nine separate ITS data matrices were prepared. The first data matrix included all the coprinoid and psathyrelloid agarics described during this study. The remaining eight data matrices were constructed one each for the genera *Candolleomyces*, *Coprinellus*, *Coprinopsis*, *Coprinus*, *Hausknechtia*, *Narcissea*, *Parasola*, *Psathyrella* and *Tulosesus*. As the genus *Hausknechtia,* with only two species known so far, was found to be a sister to the genus *Candolleomyces*, the phylogenetic analysis of the genus *Hausknechtia* was performed along with that of the genus *Candolleomyces.* The data matrix was aligned using the MAFFT web tool (http://align.bmr.kyushu-u.ac.jp/mafft/online/server/) with default settings. The final data matrix was manually adjusted with the help of AliView v.1.2.7. The Maximum likelihood (ML) analyses were carried out using RAxML-HPC2 v.8.2.10 on the XSEDE platform as implemented in the CIPRES Science Gateway web server. The analyses were run employing the GTRGAMMA model with 1000 rapid ML bootstrap replicates and default settings for other options. FigTree v.1.4.3 was used to display the phylograms inferred from the ML analyses.

The present study described a total of 35 species representing 9 genera belonging to two families, namely Agaricaceae and Psathyrellaceae, which are fully described, discussed and illustrated. Except the genus *Coprinus*, which belongs to the family Agaricaceae, all other genera (*Candolleomyces*, *Coprinellus*, *Coprinopsis*, *Hausknechtia*, *Narcissea*, *Parasola*, *Psathyrella and Tulosesus*) belong to the family Psathyrellaceae. All the 35 species were identified based on the collections made from various localities of Kerala State during a four-year period (2016-2019). Artificial keys were prepared and provided, wherever applicable, to the families, genera, sections and species described in the present study. Synonyms, author citations, collection data and distribution details were supplemented along with the descriptions of the species treated in this study. Photographs of both the basidiocarps and the microscopic structures were also provided for all the species described in this study.

The present study discovered that out of the 35 species described, 20 species were new to science. The new species included six species of *Coprinopsis*, five species of *Candolleomyces,* three species of *Psathyrella*, three species of *Parasola*, one species each from *Narcissea, Coprinus* and *Tulosesus*. Two new species of *Parasola* (*Parasola psathyrelloides* and *P. parvula*) and three new species of *Coprinopsis* (*Coprinopsis fragilis*, *C. minuta* and *C. squamulosa*) were validly published during the course of this study. Of the 9 genera discovered, *Tulosesus* represents the first record of the genus from India. Only a single species of the genus *Parasola*, namely *P. plicatilis* was previously recorded from Kerala State. Among the previously known species depicted in this study, nine species were found to be the first records from India (*Candolleomyces sulcatotuberculosus, C.*

typhae, '*Coprinellus pseudodisseminatus*', *Coprinopsis pachyderma*, *C. sclerotiger, Parasola auricoma, P. lilatincta, Tulosesus brevisetulosus* and *T. velatopruinatus*) and 11 species formed the first records from Kerala (*Candolleomyces sulcatotuberculosus, C. typhae,* '*Coprinellus pseudodisseminatus*', *Coprinopsis pachyderma*, *C. sclerotiger, C. cinerea*, *Narcissea cordispora*, *Parasola auricoma*, *P. lilatincta*, *Tulosesus brevisetulosus* and *T. velatopruinatus*).

The phylogenetic analyses based on the nine data matrices resulted in nine phylograms. Of these nine phylograms, the first phylogram showed the overall placement of all the thirty-five species discovered and described during this study. The remaining eight phylogenetic trees illustrated the phylogenetic findings of the nine genera (*Candolleomyces, Coprinellus, Coprinopsis, Coprinus, Hausknechtia, Narcissea, Parasola, Psathyrella* and *Tulosesus*).

The present study suggests the transfer of '*Coprinellus pseudodisseminatus*' to *Tulosesus* as the taxon showed more affinity towards the genus *Tulosesus* than *Coprinellus* in the ITS-based phylogenetic analysis of the genus *Tulosesus*. The present study found that the sequence labelled as *Tulosesus bisporus* KACC49409 (AF345824) in the GenBank database was a misidentification. This sequence actually corresponds to a *Narcissea* species. The present study treated *Psathyrella* species 2 (a new species described in this treatise) in the section *Pygmaeae* based on the phylogenetic evidence. However, the macro- and micro-morphological features of *Psathyrella* species 2 completely differ from the characters of the section *Pygmaeae* or any other existing sections of the genus *Psathyrella.* This difference can be deciphered from the formation of an independent lineage of *Psathyrella* species 2 among the members of the section *Pygmaeae* within the larger monophyletic group representing the genus *Psathyrella*. In addition to the known sections of the genus *Psathyrella*, the present study identified an independent lineage (Lineage I) within which *Psathyrella* species 3 (a new species described in this treatise) was nested.

A distinct clade (Clade I), in addition to other identified clades, was recovered in the phylogenetic study of the genus *Coprinopsis* where *Coprinopsis* species 3 (a new species described in this treatise) and two other species of *Coprinopsis* belonging to the section *Xenobiae* were grouped. This finding echoed earlier phylogenetic observations that hinted at the non-monophyletic nature of species in the section *Xenobiae*. Similarly, the phylogenetic study of the genus *Tulosesus* found a distinct clade (Clade 1) that included *Tulosesus* species 1 (a new species described in this treatise) as well as two unnamed *Tulosesus* species. This clade was discovered besides the previously recognised clades and lineages of *Tulosesus*.

All the thirty-five species of coprinoid and psathyrelloid agarics collected during this study together yielded a total of 96 DNA sequences. These 96 DNA sequences contained 52 ITS and 44 nLSU sequences, including sequences from additional collections. One ITS sequence was obtained from the only species of the genus *Coprinus,* which belongs to the family Agaricaceae. Eight genera treated in the family Psathyrellaceae collectively generated 51 ITS sequences. It included 13 from 9 species of *Candolleomyces*, 3 from a single species of *Coprinellus,* 10 from 9 species of *Coprinopsis,* 1 from a single species of *Hausknechtia*, 7 from 2 species of *Narcissea*, 8 from 5 species of *Parasola*, 3 from 3 species of *Psathyrella* and 6 from 4 species of *Tulosesus*. All the 35 species described in this study successfully yielded ITS sequences.

A total of 43 nLSU sequences were obtained from Psathyrellaceae. This comprised 10 from 8 species of *Candolleomyces*, 11 from 9 species of *Coprinopsis*, 2 from a single species of *Coprinellus*, 1 from a single species of *Hausknechtia*, 2 from 2 species of *Narcissea*, 8 from 5 species of *Parasola*, 3 from 3 species of *Psathyrella* and 6 from 4 species of *Tulosesus*. Apart from this, a single nLSU sequence was generated from the only species of the genus *Coprinus* of the family Agaricaceae.

Among the 96 DNA sequences, 10 ITS (*Parasola parvula* (MH379796), *P. lilatincta* (MH379669, MH379670), *P. psathyrelloides* (MK682756, MK682752, MK682758), *Coprinopsis fragilis* (OP852345), *C. minuta* (OP549280, OP549038), *C. squamulosa* (OP549278)) and 10 nLSU (*Parasola parvula* (MH393599), *P. lilatincta* (MH393600, MH393601), *P. psathyrelloides* (MK682754, MK682759, MK682755), *Coprinopsis fragilis* (OP852344), *C. minuta* (OP549279, OP549277), *C. squamulosa* (OP549708)) sequences have been deposited in the GenBank database and published during the course of this study.

The thesis is arranged in the following order: Chapter 1 provides an introduction to the research topic, specifies the objectives of the present work and gives an overview of the contents of the thesis. A comprehensive review of the literature on the coprinoid and psathyrelloid agarics is given in Chapter 2. This chapter includes an account of the taxonomy of the coprinoid and psathyrelloid agarics, modern concepts based on recent phylogenetic studies, geographical distribution and characters used for the generic and infrageneric delimitation of the respective genera. The literature regarding the ecology and economic importance of the coprinoid and psathyrelloid agarics is also reviewed. Chapter 3 contains details regarding the physiography, vegetation and climate of Kerala State. A detailed account of the materials and methods followed in this study is given in Chapter 4 along with a distributional map and photographs showing major collection localities. Chapter 5 provides a systematic account of the coprinoid and psathyrelloid agarics found in Kerala State. Chapter 6 presents the results of the phylogenetic analyses. Some general observations and discussions on the coprinoid and psathyrelloid agarics based on the present study are provided in Chapter 7. Chapter 8 includes recommendations for future studies based on the findings of the present work. Chapter 9 provides a summary of the present study. All the literature cited in this thesis is listed at the end in the 'References' section, followed by the tables and appendices. Table I contains a list of the coprinoid and psathyrelloid species discovered in Kerala State so far. The species included in the phylogenetic analyses are listed in Table II and Table III represents a list of species, their collection localities and the ITS and nLSU sequences generated from them during the study. The appendices include the model data sheets used to document the macro- and microscopic characters (Appendix 1), major macroscopic characters studied (Appendix 2) and the major microscopic characters studied (Appendix 3). Appendix 4 shows the recipes of all stains, reagents, buffers and ingredients of the reaction mixture for PCR. A list of the articles published and presentations given during the course of the study is given in Appendix 5. The thesis ends with an index to the coprinoid and psathyrelloid taxa mentioned in this work.

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APPENDIX 1

Format of data sheet used to record macroscopic characters

Coll. No.:
Date :
Coll. by :
Locality :
Habitat :
Habit :

Determination:

Determiner :
Date :

Tentative Identification:

Digital photograph No.:
Culture :

MACROSCOPIC CHARACTERS :

BASIDIOME : Overall size: Aspect:
Odour :
Taste :
Latex :

PILEUS : Dimensions :
Shape :
Colour :
Surface Features :
Margin :
Flesh : Thickness: Colour:

STIPE : Dimensions:
Attachment : Consistency: Fibrous/Cartilaginous
Shape : { C.S.
L.S.
Solid/Hollow
Surface features:
Colour : Annulus: Volva
Base:

HYMENOPHORE: Lamellate/Tubulate/Poroid/Merulioid/Smooth
Attachment: Spacing: Colour:
Thickness: Lamellulai:
Lamella-edge:

MACROCHEMICAL TESTS:
Gum Guaiac: NH_3 : $FeSO_4$:
Guaiacol : KOH : Aniline:
Phenol: H_3SO_4 : An. $XHNO_3$
α-Naphthol: HNO_3 :

Format of data sheet used to record microscopic characters

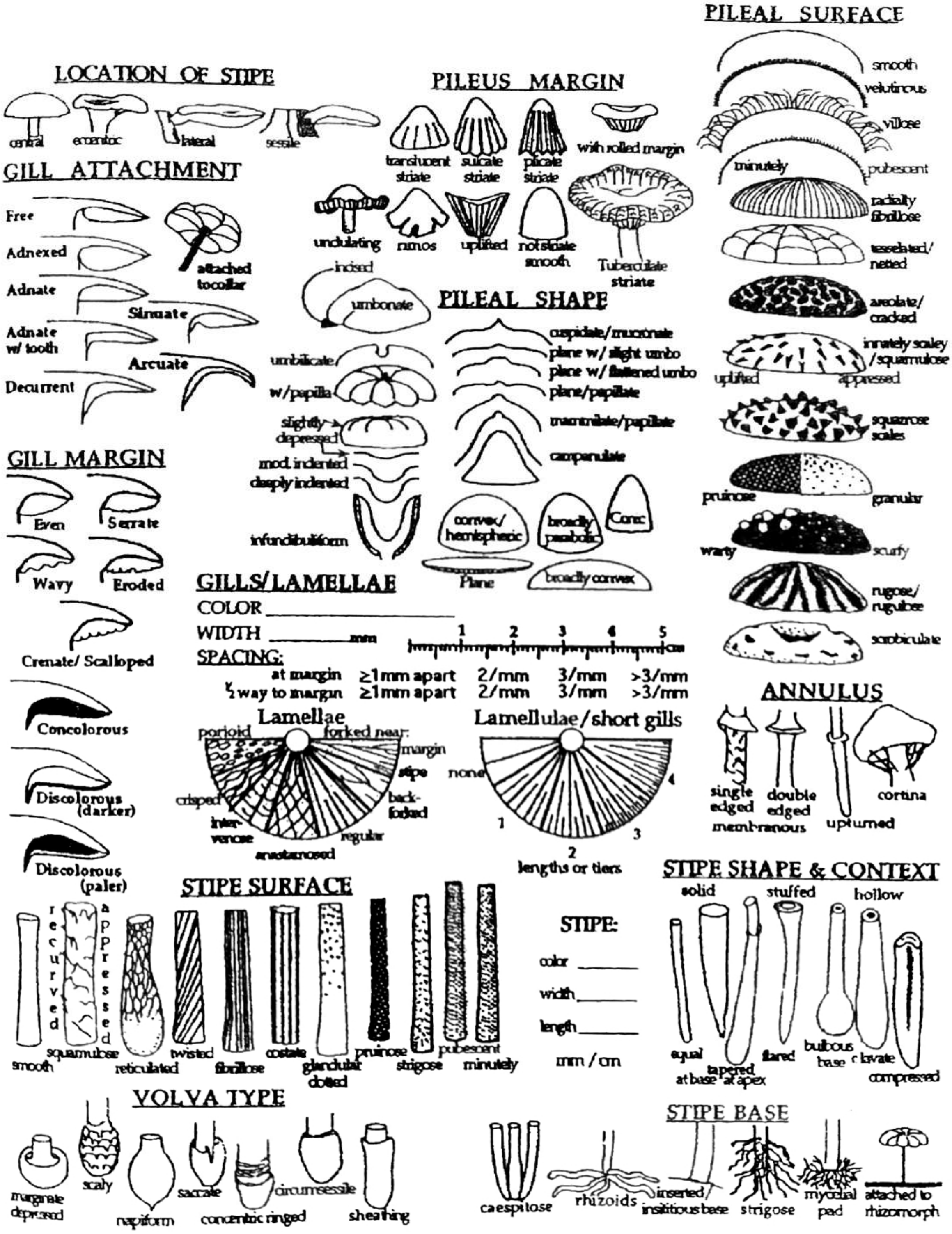
MICROSCOPIC CHARACTERS:

SPORES: Colour :
Dimensions:
Shape :
Face :
Pore:
Profile
Ornamentation:

Wall thickness:
BASIDIA:- spored
Dimensions:
Shape:
Colour:
Clamp-connections:
Contents:
PSEUDOPARAPHYSES:
Dimensions:
Shape:
Colour:
Clamp-connections:
Contents:
CHEILOCYSTIDIA: Frequency:
Dimensions:
Shape:
Colour:
Wall thickness:
Clamp-connections:
Contents:
LAMELLAR TRAMA:
Dimensions:
Melzers:
Colour:
Wall thickness:
Clamp-connections:
Subhymenium:
PLEUROCYSTIDIA: Frequency:
Dimensions:
Melzers:
Colour:
Wall thickness:
Clamp-connections:
Contents:
PILEUS TRAMA:
Dimensions:
Meizer's:
Colour:
Wall thickness:
Clamp-connections:
PILEIPELLIS : Type
Dimensions:
Wall thickness:
Pigment: Plasmatic/Membrane/Encrusting/Absent
Clamp-connections:
Pileocystidia: Present/Absent
Dimensions
Shape:
VELAR ELEMENTS:
Dimensions:
Shape:
Colour
Contents:
STIPITIPELLIS: Type:
Dimensions:
Wall thickness:
Pigment:
Clamp-connections:
Caulocystidia: Present/Absent
Dimensions:
Shape:

APPENDIX 2

Major macroscopic characters studied



APPENDIX 3

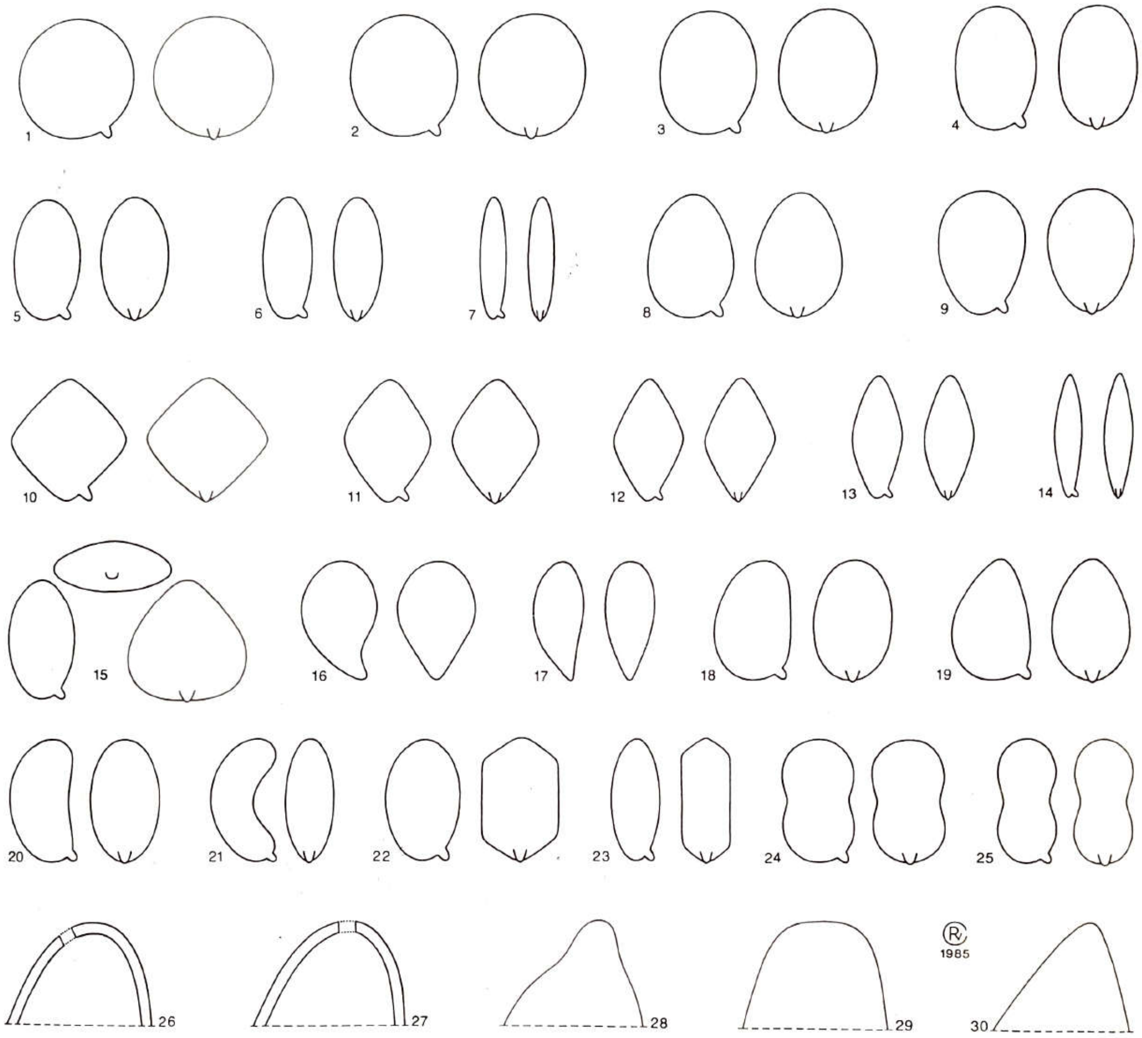
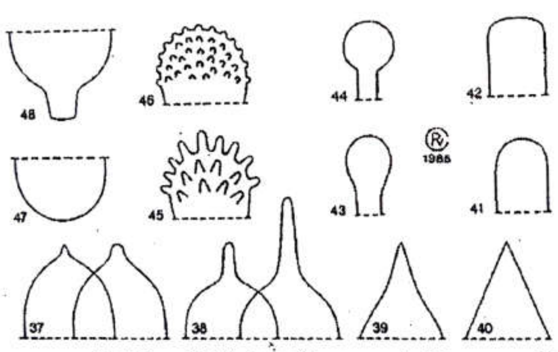


Fig. 33. Spores. – 1-25. *General shape:* 1. globose; 2. subglobose; 3. broadly ellipsoid; 4. ellipsoid; 5. oblong; 6. subcylindrical; 7. bacilliform; 8. ovoid; 9. obovoid; 10. quadrangular; 11. very broadly fusiform; 12. broadly fusiform; 13. fusiform. 14. narrowly fusiform; 15. oblong in side view, rounded triangular in frontal view, oblong in polar view; 16. lacrymoid (ellipsoid with suprahilar depression); 17. lacrymoid (subcylindrical with suprahilar depression); 18. amygdaliform in side view, ellipsoid in frontal view; 19. amygdaliform with acute apex in side view, ovoid in frontal view; 20. phaseoliform in side view, oblong in frontal view; 21. allantoid in side view, subcylindrical in frontal view; 22. oblong in side view, hexagonal in frontal view; 23. subcylindrical in side view, hexagonal in frontal view; 24. ellipsoid with median constriction; 25. oblong with median constriction. – 26-30. *Apex:* 26. with eccentric germ pore; 27. with central germ pore; 28. with apical papilla; 29. truncate; 30. acute.



Cystidia. – 37-44. *Apex:* 37. mucronate; 38. rostrate; 39. acuminate; 40. acute; 41. obtuse; 42. truncate; 43. subcapitate; 44. capitate. – 45-46. *Surface:* 45. diverticulate; 46. verrucose. – 47-48. Base: 47. sessile; 48. pedunculate or pedicellate.

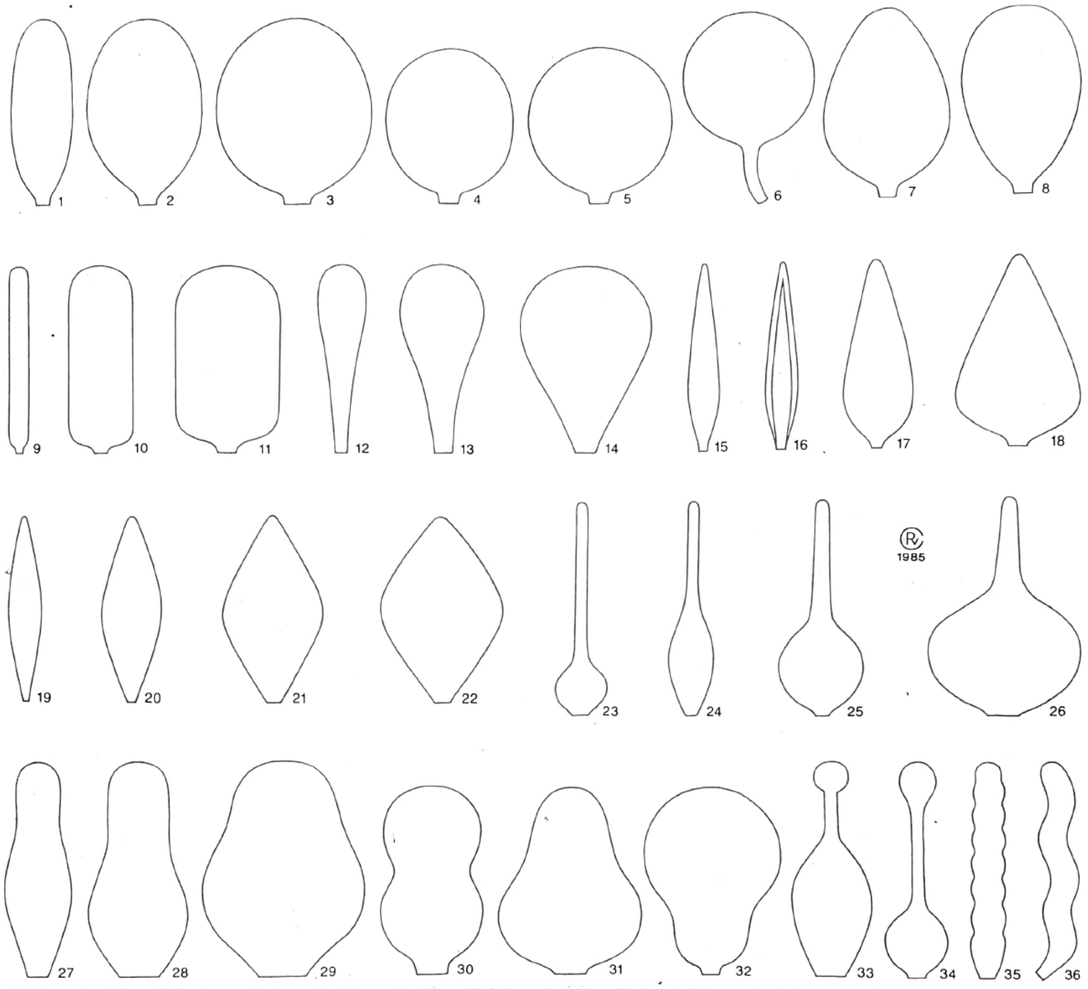


Fig. 34a. Cystidia. – 1-36. *General shape:* 1. oblong; 2. ellipsoid; 3. broadly ellipsoid; 4. subglobose; 5. globose; 6. spheropedunculate; 7. ovoid; 8. obovoid; 9. narrowly cylindrical; 10. cylindrical; 11. broadly cylindrical; 12. narrowly clavate; 13. clavate; 14. broadly clavate; 15. narrowly conical; 16. setiform; 17. conical; 18. broadly conical; 19. narrowly fusiform; 20. fusiform; 21. broadly fusiform; 22. very broadly fusiform; 23. nettle hair-shaped; 24. narrowly lageniform; 25. lageniform; 26. broadly lageniform; 27. narrowly utriform; 28. utriform; 29. broadly utriform; 30. with median constriction; 31. pyriform; 32. obpyriform; 33. lecythiform; 34. tibiiform; 35. moniliform; 36. flexuose.

APPENDIX 4

Recipe of Stains/reagents and buffers used:

1. Stains/reagents for Microscopic preparations

1. Congo red (1% aqueous solution)
   Congo red – 1 g
   H_2O – 99 ml
2. KOH (3% aqueous solution)
   KOH – 3 g
   H_2O – 97 ml

2. Buffers/gel/reagents used in Molecular works

1. EDTA (Ethylenediaminetetraacetic acid – 1 M)
   EDTA – 372. 24
   ddH_2O – 1000 ml
2. TE Buffer (Tris EDTA 1X in 250 ml)
   Tris – 2.5 ml (10 mM)
   EDTA – 0.5 ml (1 mM, pH 8.0)
   ddH_2O – 247 ml
3. TBE Buffer (Tris Boric acid EDTA 5X in 250 ml)
   Tris – 13.5 g
   Boric acid – 6.875 g
   EDTA – 5 ml (0.5 M, pH 8.0)
4. Agarose Gel (1%)
   Agarose – 0.23 g
   TBE – 23 ml (1X)
5. Reagents for PCR (final volume 30 μL)
   PCR Master Mix – 15 μL
   Forward Primer – 3 μL
   Reverse Primer – 3 μL
   Template DNA -3 μL
   ddH_2O – 6 μL (PCR grade)

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Table I. List of coprinoid and psathyrelloid species reported so far from Kerala State.

Sl No:	Name	Geographic location	Author & Year
1.	*Candolleomyces candolleanus*	Pukayilappara, Sholayar (Thrissur District)	Mohanan 2011 (as *Psathyrella candolleana*)
2.	*Candolleomyces efflorescens*	Irigolkavu (Ernakulam District)	Mohanan 2011 (as *Psathyrella efflorescens*)
3.	*Coprinellus disseminatus*	Thenmala (Kollam District), TBGRI campus (Thiruvananthapuram District), Nilambur (Malappuram District), Peechi-Vazhani Wildlife Sanctuary (Thrissur District)	Mohanan 2011; Vrinda & Pradeep 2014 (as *Coprinus disseminatus*)
4.	*Coprinellus micaceus*	TBGRI campus (Thiruvananthapuram District)	Vrinda & Pradeep 2014 (as *Coprinus micaceus*)
5.	*Coprinopsis clastophylla*	Thiruvananthapuram (Thiruvananthapuram District)	Vrinda *et al*. 2012 (as *Rhacophyllus lilacinus*)
6.	*Coprinopsis fibrillosa*	Nilambur (Malappuram District), Pukayilappara, Vazhachal (Thrissur District)	Mohanan 2011
7.	*Coprinopsis fragilis*	Thattekad (Ernakulam District)	Crous *et al*. 2023
8.	*Coprinopsis minuta*	Calicut University Campus (Malappuram District)	Ganga *et al*. 2022
9.	*Coprinopsis poliomalla*	Peechi-Vazhani Wildlife Sanctuary (Thrissur District), Mayiladumpara, (Palakkad District)	Natarajan & Raman 1983; Florence 2004 (as *Coprinus poliomallus*)
10.	*Coprinopsis squamulosa*	Calicut University Botanical Garden (Malappuram District)	Ganga *et al*. 2022
11.	*Coprinus comatus*	Muthanga (Wayanad District)	Varghese *et al*. 2010; Mohanan 2011
12.	*Hausknechtia leucosticta*	Thenmala, (Kollam District), Palode (Thiruvananthapuram District)	Nie *et al.* 2022
13.	*Homophron spadiceum*	Muthanga (Wayanad District)	Vrinda & Pradeep 2014 (as *Psathryrella spadicea)*
14.	*Lacrymaria lacrymabunda*	Idukki (Idukki District)	Vrinda *et al*. 2003 (as *Psathyrella velutina*)
15.	*Parasola conopilea*	Thiruvananthapuram (Thiruvananthapuram District)	Vrinda *et al*. 1999 (as *Psathyrella conopilea*)
16.	*Parasola lilatincta*	Aralam (Kannoor District), Neyyar (Thiruvananthapuram District)	Ganga & Manimohan 2018
17.	*Parasola parvula*	Chimmini (Thrissur District)	Ganga & Manimohan 2018
18.	*Parasola plicatilis*	Chinnakanal (Idukki District), Peechi-Vazhani Wildlife Sanctuary (Thrissur District)	Natarajan & Raman 1983; Florence 2004; Vrinda & Pradeep 2014 (as *Coprinus plicatilis*)
19.	*Parasola psathyrelloides*	Muthanga (Wayanad District), Thenmala (Kollam District), Peruvannamuzhi (Kozhikode District)	Ganga & Manimohan 2019

20.	*Psathyrella coprinoceps*	Thiruvananthapuram (Thiruvananthapuram District)	Vrinda *et al*. 2001
21.	*Psathyrella lithocarpi*	Kuruva (Wayanad District)	Mohanan 2011
22.	*Psathyrella lucipeta*	Irigolkavu (Ernakulam District)	Mohanan 2011
23.	*Psathyrella myceniformis*	Pothupara (Idukki District), Nelliyampathy (Palakkad District)	Mohanan 2011
24.	*Psathyrella trechispora*	Narikkundu (Wayanad District), Nadukani (Kottayam District), Nilambur (Malappuram District)	Pradeep *et al*. 1996; Mohanan 2011

Table II. Species included in the phylogenetic analyses (excluding the species from this study), their geographic location and the GenBank accession numbers of their ITS sequences.

Species	Geographic location	ITS
Amanita muscaria LEM950025	-	AB015700
Basidiomycota species PCT.10	-	HQ248225
Britzelmayria multipedata	-	GQ249282
Britzelmayria supernula	-	KC992867
Candolleomyces aberdarensis	Kenya	MH880928
Candolleomyces badhyzensis	-	KC992883
Candolleomyces badiophylla	-	FN430699
Candolleomyces cacao FP1R4	-	KU847452
Candolleomyces cacao SFSU: DED 8339	Africa	NR_148106
Candolleomyces candolleanus 3-F7	China	MW081329
Candolleomyces candolleanus AMO	India	MN809341
Candolleomyces candolleanus BRPER4	China	MT658071
Candolleomyces candolleanus DOF-27	-	KX611650
Candolleomyces candolleanus LAS73030	-	KM030175
Candolleomyces candolleanus SZMC-NL-2145	-	FM878001
Candolleomyces efflorescens Pegler2133	-	KC992941
Candolleomyces hymenocephala	-	FJ168609
Candolleomyces leucotephrus	-	KC992885
Candolleomyces luteopallidus HMJAU 5148	China	MG734736
Candolleomyces luteopallidus Sharp20863	-	KC992884
Candolleomyces pseudocandolleanus	China	KY120973
Candolleomyces singeri	China	MG734718
Candolleomyces species 110117MFBPC126	China	MW554230
Candolleomyces species BAB-4747	India	KR154976
Candolleomyces species BRPCL21	China	MT658050
Candolleomyces subcacao HMJAU37807	China	MW301064
Candolleomyces subcacao HMJAU37808	China	MW301065
Candolleomyces subsingeri HMJAU 37811	China	MG734715
Candolleomyces subsingeri HMJAU 37814	China	MG734714
Candolleomyces subsingeri HMJAU 37915	China	MG734742
Candolleomyces sulcatotuberculosa Battistin and Chiarello 07-10-2013	Italy	KJ138423
Candolleomyces sulcatotuberculosa GB: LO55-12	Germany	KJ138422
Candolleomyces sulcatotuberculosa MCVE29112	Italy	MF326002
Candolleomyces sulcatotuberculosa ZD16070507	China	MN523296
Candolleomyces trinitatensis	-	KC992882
Candolleomyces tuberculatus	-	KC992886
Candolleomyces typhae BP23	Philippines	MZ725485
Candolleomyces typhae LO21-04	Sweden	DQ389721
Candolleomyces typhae MJD10-17	China	JX077004
Coprinellus aureogranulatus CBS973.95	-	GQ249274
Coprinellus aureogranulatus DED 8251 (SFSU)	Africa	KX017206
Coprinellus aureogranulatus DZF4A	Sri Lanka	MF195026

Coprinellus campanulatus	-	MH753667
Coprinellus curtus SZMC-NL-1023	-	JN159568
Coprinellus curtus SZMC-NL-1490	-	JN159569
Coprinellus curtus SZMC-NL-2339	-	FM878016
Coprinellus deminutus	-	JN159572
Coprinellus disseminatus BAP 608 (SFSU)	West Africa	KX017207
Coprinellus disseminatus CEQCA-M1202	-	KC771476
Coprinellus disseminatus CEQCA-M1203	Ecuador	KC771477
Coprinellus disseminatus DWM51	-	KM357334
Coprinellus disseminatus KACC500820	-	AF345809
Coprinellus disseminatus KUC11047	South Korea	KJ714005
Coprinellus disseminatus LE-BIN 2127	Russia	MG722732
Coprinellus disseminatus olrim955 (SUAS)	Lithuania	AY787669
Coprinellus disseminatus PNB034A	Peru	KJ832004
Coprinellus disseminatus PNB034B	Peru	KJ832005
Coprinellus disseminatus PNB034D	Brazil	KJ832006
Coprinellus disseminatus R175	Lithuania	JN689938
Coprinellus disseminatus SZMC-NL-2337	-	FM878017
Coprinellus disseminatus x-043	China	MN209934
Coprinellus flocculosus SZMC-NL-0838	-	JN159573
Coprinellus flocculosus SZMC-NL-1567	-	FN430683
Coprinellus heptemerus SZMC-NL-0589	-	JN159553
Coprinellus heptemerus X-22	USA	KC176321
Coprinellus micaceus BAFC 3218	Argentina	FJ850970
Coprinellus micaceus CBM: FB-16140	Japan	AB597786
Coprinellus micaceus CBM: FB-24398	Japan	AB597785
Coprinellus micaceus KACC500403	-	AF345808
'Coprinellus pseudodisseminatus' HMJAU 46300	China	MH379148
'Coprinellus pseudodisseminatus' HMJAU 46302	China	MH379150
'Coprinellus pseudodisseminatus' HMJAU 46303	China	MH379151
Coprinellus radians F213	-	KM979913
Coprinellus radians M105	-	HM595561
Coprinellus radians UTHSCSA DI 14-208	-	KM272008
Coprinellus silvaticus LO172-08	-	KC992943
Coprinellus silvaticus SZMC-NL-3035	-	HQ846986
Coprinellus verrucispermus	-	AY521250
Coprinellus xanthothrix CZ478	China	FJ755223
Coprinellus xanthothrix TOK12808	-	JN159578
Coprinopsis aff. *lagopus*	-	HQ872014
Coprinopsis ammophilae	-	HQ847008
Coprinopsis babosiae	-	JX118684
Coprinopsis bellula SZMC:NL:2341	-	FM163176
Coprinopsis bicornis	-	JX118690
Coprinopsis brunneistragulata SZMC-NL-FVBD 3821	-	JX118724
Coprinopsis candidolanata 794	Italy	JF907837
Coprinopsis candidolanata CAND1	-	JX118682
Coprinopsis canoceps	-	KC992964
Coprinopsis cinerea A767	-	MK247764

Coprinopsis cinerea CEL11	India	MN173118
Coprinopsis cinerea NBRC100011	-	AB097563
Coprinopsis coniophora SZMC-NL-3414	-	FN396122
Coprinopsis cortinata	-	FN396121
Coprinopsis cothurnata	-	AY461833
Coprinopsis erythrocephala	-	JX118703
Coprinopsis filamentifera	-	HQ847035
Coprinopsis fluvialis	-	HQ847011
Coprinopsis foetidella	-	HQ847014
Coprinopsis fusispora SZMC-NL-1227	-	JX118740
Coprinopsis fusispora SZMC-NL-3863	-	JX118742
Coprinopsis geesterani	-	JX118699
Coprinopsis goudensis	-	FN396128
Coprinopsis insignis	-	JX118738
Coprinopsis jonesii	-	JX118726
Coprinopsis krieglsteineri	-	JX118701
Coprinopsis kubickae	Croatia	MH422562
Coprinopsis laanii	UK	MH859802
Coprinopsis lagopides	USA	KM373258
Coprinopsis lagopus CBS:148.47	France	MH856193
Coprinopsis lagopus SZMC-NL-0191	Hungary	JN943127
Coprinopsis lagopus SZMC-NL-2143	-	JX118727
Coprinopsis macrocephala	-	FN396126
Coprinopsis marcescibilis CBS:165.47	Portugal	MH856199
Coprinopsis marcescibilis SZMC-NL-2140	-	FM878020
Coprinopsis martinii	-	GU234126
Coprinopsis melanthina	-	KC992961
Coprinopsis musae JV06-179	Denmark	KC992965
Coprinopsis musae JV06180	Denmark	KC992966
Coprinopsis narcotica	-	MH855976
Coprinopsis neolagopus	-	AB097564
Coprinopsis nevillei	France	HM126488
Coprinopsis nivea	Italy	JF907848
Coprinopsis ochraceolanata	-	HQ847051
Coprinopsis pachyderma FVDB 3237	North America	JX118731
Coprinopsis pachyderma WTU-F-039608	USA	MK169350
Coprinopsis pannucioides	-	FN396143
Coprinopsis phlyctidospora	Japan	AB071615
Coprinopsis poliomallus	Hungary	FM163182
Coprinopsis pseudonivea	Hungary	FM163181
Coprinopsis pseudoradiata	-	JX118687
Coprinopsis radiata SZMC-NL-1244	-	HQ847024
Coprinopsis radiata SZMC-NL-1269	Hungary	JN943123
Coprinopsis rugosomagnispora	Poland	KX276859
Coprinopsis sclerotiger CBS596.80	-	GQ249277
Coprinopsis sclerotiger TEP19c	-	KR869759
Coprinopsis sclerotiger UT-Co3	Iran	MF161091
Coprinopsis scobicola	-	HQ847021

Coprinopsis semitalis	Iran	MH304260
Coprinopsis species 303318	China	MK894411
Coprinopsis species BLBS 104	Brazil	MK843958
Coprinopsis species PTN2018-1	Vietnam	LC425103
Coprinopsis species WQ17_7	China	MK894411
Coprinopsis stercorea	-	AF345817
Coprinopsis strossmayeri 15-2C	Armenia	FJ403471
Coprinopsis strossmayeri 15-3C	Armenia	FJ403472
Coprinopsis strossmayeri IBK 2625	-	MW616277
Coprinopsis strossmayeri M1	India	MG817404
Coprinopsis strossmayeri SZMC-NL-0774	-	HQ847048
Coprinopsis submicrospora	-	HQ847053
Coprinopsis tectispora	-	JX118665
Coprinopsis trispora	Germany	MN227299
Coprinopsis udicola	Germany	KC992967
Coprinopsis urticicola AK.2044	Turkey	MH748639
Coprinopsis urticicola EGDA-Cop222	Egypt	MW915588
Coprinopsis urticicola KR02	India	MN368600
Coprinopsis urticicola SZMC-NL-0170	-	HQ847015
Coprinopsis utrifer	-	FN396140
Coprinopsis villosa	-	HQ847031
Coprinus comatus 11ZHONG	China	MN022552
Coprinus comatus 297310	USA	MH817141
Coprinus comatus AH:44089	Spain	KU686914
Coprinus comatus AH:44095	Spain	KU686915
Coprinus comatus AH:45831	Spain	KU686918
Coprinus comatus BUNS 12-00716	Serbia	MG871207
Coprinus comatus CCM1	Poland	JQ901432
Coprinus comatus CCM10	Poland	JQ901441
Coprinus comatus CCM13	Poland	JQ901444
Coprinus comatus CCM2	Poland	JQ901433
Coprinus comatus CCM3	Poland	JQ901434
Coprinus comatus CCM5	Poland	JQ901436
Coprinus comatus CCM8	Poland	JQ901439
Coprinus comatus JLF8972	USA	MW989737
Coprinus comatus KMCC04907	South Korea	MN823158
Coprinus comatus SAT-16-238-14	USA	MW597169
Coprinus comatus YE19	China	MN043924
Coprinus comatus YE23-01	China	MN043925
Coprinus fissolanatus Daams 71121	-	JX118733
Coprinus fissolanatus KACC49389	-	AF345812
Coprinus littoralis	Spain	KU686920
Coprinus pinetorum	Spain	KU686927
Coprinus sterquilinus	Switzerland	MH854689
Coprinus vosoustii	Spain	KU686919
Cystoagaricus strobilomyces	-	AY176347
Cystoagaricus sylvestris	-	KC992949
Fungal endophyte 4388	New Guinea Island	KR015785

Fungal species E15613C	Ecuador	KM266141
Hausknechtia floriformis BLBS032	Brazil	MK881745
Hausknechtia floriformis WU22832	-	ON745613
Hausknechtia floriformis WU22833	-	JX968254
Hausknechtia leucosticta CNF 1/6900	India	ON745618
Hausknechtia leucosticta HFJAU1486	China	OL435561
Hausknechtia leucosticta HFJAU1526	China	OL435563
Hausknechtia leucosticta HFJAU1730	China	OL435562
Hausknechtia leucosticta HFJAU1751	China	OL435564
Homophron spadiceum	-	FN396132
Kauffmania larga	-	DQ389694
Lacrymaria glareosa	-	KC992954
Lacrymaria rigidipes	-	KC992953
Leucoagaricus callainitinctus	India	MT108797
Montagnea arenaria	Australia	OK159914
Montagnea candollei	Argentina	MH856879
Narcissea cordisporus CCCM:108	Canada	HM240521
Narcissea cordisporus L Ulje1058	Hawaiian Islands	AY461840
Narcissea cordisporus L Ulje1100	Hawaiian Islands	AY461841
Narcissea cordisporus LO41-01O	-	DQ389723
Narcissea cordisporus SFSU DEH000	-	AY461814
Narcissea cordisporus SFSU DEH1084	Hawaiian Islands	AY461816
Narcissea cordisporus SFSU DEH1702	Hawaiian Islands	AY461817
Narcissea cordisporus SFSU DEH1813	Hawaiian Islands	AY461819
Narcissea cordisporus SFSU DEH1815	Hawaiian Islands	AY461820
Narcissea cordisporus SFSU DEH1829	Hawaiian Islands	AY461821
Narcissea cordisporus SFSU DEH2071	Hawaiian Islands	AY461826
Narcissea cordisporus SFSU DEH2073	Hawaiian Islands	AY461827
Narcissea cordisporus SFSU DEH2074B	Hawaiian Islands	AY461829
Narcissea cordisporus SFSU DEH2081	Hawaiian Islands	AY461830
Narcissea cordisporus SFSU DEH2128B	Hawaiian Islands	AY461831
Narcissea cordisporus UBC F19670	Canada	HM240520
Narcissea lahorensis LAH36395	Pakistan	OK161263
Narcissea lahorensis LAH36970	Pakistan	OK161264
Narcissea patouillardii SZMC-NL-1684	-	FN430687
Narcissea patouillardii SZMC-NL-1685	-	FN396151
Narcissea patouillardii SZMC-NL-1687	Hungary	FM878009
Narcissea patouillardii SZMC-NL-1695	-	FN396152
Olotia codinae	-	MG696611
Parasola aff. *auricoma* LAH-SH-P11	Pakistan	KX212107
Parasola aff. *auricoma* LAH-SH-P6	Pakistan	KX212106
Parasola auricoma CBS:145.39	-	MH855972
Parasola auricoma SZMC:NL:0268	Hungary	FM163186
Parasola auricoma SZMC-NL-0087	Hungary	JN943107
Parasola conopilea 312390	USA	MH125285
Parasola conopilea CBS:325.39	-	MH856033
Parasola conopilea OSC50296	-	FJ899613
Parasola conopilea SZMC:NL:0465	Hungary	FM163223

Parasola conopilea ZRL20151990	-	LT716064
Parasola crataegi	Germany	KY928605
Parasola glabra LAH-SHP-23	Pakistan	KY621805
Parasola glabra LAH-SHP-5	Pakistan	KY621806
Parasola hercules L: Ulje:1269	Netherlands	FM163190
Parasola hercules L146	-	HQ847027
Parasola kuehneri D.Schafer 1602	UK	KY928609
Parasola kuehneri L: C.B. Ulje 31-V-1987	Netherlands	NR_175052
Parasola kuehneri Ulje 1241	-	HQ847026
Parasola lacteal	Hungary	KY928612
Parasola lilatincta MO378353	USA	MT551934
Parasola lilatincta SZMC:NL:0472	Hungary	FM163199
Parasola malakandensis SH-P14	Pakistan	KT343274
Parasola malakandensis SZMC-SHp13	Pakistan	KT343275
Parasola megasperma C:19683	Denmark	FM163206
Parasola megasperma SZMC:NL:1924	Hungary	FM163208
Parasola misera DJS20141030001	UK	OL630110
Parasola misera L. Nagy NL-0462	Hungary	KY928619
Parasola ochracea NL-3167	Norway	JN943136
Parasola ochracea NL-3621	Norway	JN943134
Parasola plicatilis	Hungary	FM163215
Parasola pseudolactea	-	KY461719
Parasola schroeterii	Norway	JN943135
Parasola setulose	-	HQ847030
Psathyrella abieticola	-	KC992891
Psathyrella arenosa LO220-96	Sweden	KC992895
Psathyrella arenosa LO330-01	-	KC992896
Psathyrella atomata	-	DQ389665
Psathyrella bipellis	-	FN396108
Psathyrella conferta GE2.007	-	KC992890
Psathyrella cotonea BRNM:705623	-	AM712283
Psathyrella cotonea LO136-00	-	KC992870
Psathyrella effibulata Herb.Orst. 99-11	-	KR261438
Psathyrella effibulata LO37-96	Sweden	DQ389672
Psathyrella epimyces	-	KC992928
Psathyrella fusca	-	KC992892
Psathyrella gordonii	-	KC992924
Psathyrella jacobssonii	Sweden	KC992855
Psathyrella lutensis HMJAU 37840	China	MG734748
Psathyrella lutensis LO98-03	-	DQ389685
Psathyrella microrhiza	-	AM712282
Psathyrella mucrocystis	-	DQ389700
Psathyrella multipedata LO237-04	-	KC992888
Psathyrella noli-tangere	-	DQ389713
Psathyrella obtusata CBS:166.72	England	MH860427
Psathyrella obtusata LO88-01	-	DQ389711
Psathyrella olympiana LO32-02	Sweden	DQ389722
Psathyrella olympiana SZMC-NL-2935	-	FN396103

Psathyrella panaeoloides AM1200	Germany	MK045663
Psathyrella panaeoloides LO293-04	-	KC992894
Psathyrella panaeoloides LO44-03	-	DQ389719
Psathyrella pennata LO206-03	-	DQ389710
Psathyrella pennata LO216-84	-	KJ939633
Psathyrella piluliformis HMJAU 37922	China	MG734716
Psathyrella piluliformis WU:20516	-	AM712272
Psathyrella prona 13147	-	KJ939634
Psathyrella prona JMT19678	US	FJ899618
Psathyrella psammophila Smith67836	-	KC992856
Psathyrella pseudocorrugis LO226-06	-	KC992917
Psathyrella pseudogracilis LO287-06	-	KC992853
Psathyrella pseudogracilis SZMC-NL-2142	-	FM878025
Psathyrella pygmaea HMJAU 37850	China	MG734744
Psathyrella pygmaea LO97-04	-	DQ389718
Psathyrella pygmaea SZMC-NL-2139	-	FM878010
Psathyrella pygmaea SZMC-NL-2325	-	FM878011
Psathyrella saponacea	UK	MH860434
Psathyrella spadiceogrisea AM1242	Germany	MK045696
Psathyrella spadiceogrisea GENT JR3565	Belgium	MK045679
Psathyrella sphaerocystis Kew49734	-	DQ389707
Psathyrella sphaerocystis LO126-99	-	DQ389709
Psathyrella stridvallii	Sweden	KC992926
Psathyrella sublatispora	Sweden	KC992854
Psathyrella subnuda MICH33421	USA	MF326000
Psathyrella subnuda MICH5376	USA	MF326005
Psathyrella tephrophylla AM1594	Germany	MK045664
Psathyrella violaceopallens LO96-11	-	KC992923
Punjabia pakistanica	-	KP012718
Tulosesus bisporus KACC49409	-	AF345824
Tulosesus bisporus OT3-179b	Portugal	KT804105
Tulosesus bisporus SZMC-NL-0158	Sweden	GU227705
Tulosesus bisporus SZMC-NL-2512	-	FN396107
Tulosesus bisporus WU6011	-	JN159517
Tulosesus brevisetulosus SZMC-NL-1445	Hungary	GU227710
Tulosesus brevisetulosus SZMC-NL-2908	Hungary	GU227711
Tulosesus callinus SZMC-NL-1931	-	FN396105
Tulosesus callinus Ulje 1204	-	JN159518
Tulosesus cinereopallidus SZMC-NL-0177	-	HQ847001
Tulosesus cinereopallidus Ulje 1163	-	JN159524
Tulosesus congregatus SZMC-NL-1128	-	JN159550
Tulosesus congregatus SZMC-NL-2138	-	GU227702
Tulosesus congregatus Ulje 634	-	JN159554
Tulosesus doverii	-	HQ846983
Tulosesus heterosetulosus SZMC-NL-1059	-	GU227708
Tulosesus heterosetulosus Ulje 1284	-	JN159519
Tulosesus hiascens Sieben96078	-	JN159528
Tulosesus hiascens SZMC-NL-0628	-	JN159530

Tulosesus hiascens SZMC-NL-0770	-	JN159529
Tulosesus hiascens SZMC-NL-1350	-	GU227720
Tulosesus impatiens	Hungary	JN943132
Tulosesus marculentus SZMC-NL-1167	Hungary	GU227706
Tulosesus marculentus SZMC-NL-1471	-	JN159543
Tulosesus mitrinodulisporum	Italy	HQ180171
Tulosesus pellucidus SZMC-NL-2344	-	GU227715
Tulosesus pellucidus SZMC-NL-2928	-	GU227714
Tulosesus radicellus SZMC-NL-0594	-	GU227716
Tulosesus radicellus SZMC-NL-0957	-	GU227718
Tulosesus sabulicola	-	JN159557
Tulosesus sclerocystidiosus	-	HQ846991
Tulosesus species 'IN01'	USA	ON006924
Tulosesus species MZ571673	USA	MZ571673
Tulosesus velatopruinatus PERTH: 8944237	Australia	MT537093
Tulosesus velatopruinatus Ulje 1264	-	JN159531
Typhrasa gossypina	-	KC992946

Table III. List of species, collection localities and ITS and nLSU sequences generated during the present study.

SL NO	Species	Geographic location	No. of sequences generated	
			ITS	nLSU
1.	*Candolleomyces candolleanus*	Mylanjivalavu (Malappuram District), Muthanga forest (Wayanad District)	G159: 671 bp; G171: 677 bp; G173: 683 bp	G171: 914 bp; G173: 873 bp
2.	*Candolleomyces efflorescens*	Mukkam (Kozhikode District), Calicut University Campus (Malappuram District)	G130: 676 bp; G270: 666 bp	G130: 841 bp
3.	*Candolleomyces* species 1	Thattekkad forest (Ernakulam District)	G291: 601 bp	G291: 873 bp
4.	*Candolleomyces* species 2	Calicut University Campus (Malappuram District)	G102: 681 bp	G102: 878 bp
5.	*Candolleomyces* species 3	Shendurney forest (Kollam District), Punnayoorkulam (Thrissur District)	G203: 669 bp; G192: 672 bp	G203: 868 bp; G192: 828 bp
6.	*Candolleomyces* species 4	Olavakkode (Palakkad District)	G206: 675 bp	-
7.	*Candolleomyces* species 5	Thattekkad forest (Ernakulam District)	G289: 683 bp	G289: 986 bp
8.	*Candolleomyces sulcatotuberculosa*	Muthanga forest (Wayanad District)	G166: 676 bp	G166: 870 bp
9.	*Candolleomyces typhae*	Punnayoorkulam (Thrissur District)	G202: 680 bp	G202: 863 bp
10.	*Coprinellus disseminatus*	Peruvannamuzhi forest (Kozhikode District), Edakkal Caves (Wayanad District), Thattekkad forest (Ernakulam District)	G134: 661 bp, G228: 619 bp, G292: 486 bp	G134: 894 bp G228: 874 bp
11.	*'Coprinellus pseudodisseminatus'*	Vazhachal Forest (Thrissur District)	G244: 654 bp	G244: 892 bp
12.	*Coprinopsis cinerea*	Punnayoorkulam (Thrissur District)	G222: 476 bp	G222: 916 bp
13.	*Coprinopsis fragilis*	Thattekkad forest (Ernakulam District)	OP852345 (G286 (CALI): 569 bp)	OP852344 (G286 (CALI): 888 bp)
14.	*Coprinopsis minuta*	Calicut University Campus (Malappuram District)	OP549038 (G23 (CALI): 676 bp) OP549280	OP549277 (G23 (CALI): 956 bp) OP549279

			G63 (CALI): 458 bp	G63 (CALI): 954 bp
15.	*Coprinopsis pachyderma*	Aralam Forest (Kannur District)	G213: 670 bp	G213: 888 bp
16.	*Coprinopsis sclerotiger*	Mongam (Kozhikode District)	G247: 674 bp	G247: 902 bp
17.	*Coprinopsis* species 1	Thenmala (Kollam District)	G268: 483 bp	G265: 873 bp; G268: 764 bp
18.	*Coprinopsis* species 2	Thattekkad Forest (Ernakulam District)	G293: 644 bp	G293: 882 bp
19.	*Coprinopsis* species 3	Calicut University Campus (Malappuram District)	G271: 652 bp	G271: 875 bp
20.	*Coprinopsis squamulosa*	Calicut University Campus (Malappuram District)	OP549278 G297 (CALI): 675 bp	OP549708 G297 (CALI): 920 bp
21.	*Coprinus* species 1	Muthanga forest (Wayanad District)	G164: 627 bp	G164: 870 bp
22.	*Hausknechtia leucosticta*	Calicut University Campus (Malappuram District)	G87: 669 bp	G87: 871 bp
23.	*Narcissea cordisporus*	Muthanga forest (Wayanad District), Aarlam forest (Kannur District), Punnayoorkulam (Thrissur District)	G225: 632 bp, G165: 638 bp, G182: 646 bp, G194: 638 bp	G225: 841 bp
24.	*Narcissea* species 1	Kakkayam forest (Kozhikode District)	G111: 646 bp; G112: 584 bp; G124: 635 bp	G124: 878 bp
25.	*Parasola auricoma*	Punnayoorkulam (Thrissur District)	G200: 688 bp	G200: 872 bp
26.	*Parasola lilatincta*	Aralam Forest (Kannur District), Neyyar Forest (Thiruvananthapuram District)	MH379669 (CAL 1668: 681 bp) MH379670 (CAL 1671: 684 bp)	MH393600 (CAL 1668: 915 bp) MH393601 (CAL 1671: 913 bp)
27.	*Parasola parvula*	Chimmini Forest (Thrissur District)	MH379796 (CAL 1667: 640 bp)	MH393599 (CAL 1667: 869 bp)
28.	*Parasola psathyrelloides*	Muthanga forest (Wayanad District), Thenmala forest (Kollam District), Peruvannamuzhi forest (Kozhikode District)	MK682752 (AMH 10119: 667 bp) MK682758 (AMH 10120: 518 bp) MK682756 (CAL 1753: 672	MK682759 (AMH 10119: 682 bp) MK682755 (AMH 10120: 980 bp) MK682754 (CAL 1753: 564

			bp)	bp)
29.	*Parasola* species 1	Calicut University Campus (Malappuram District)	G127: 690 bp	G127: 873 bp
30.	*Psathyrella* species 1	Thenmala forest (Kollam District)	G186: 645 bp	G186: 845 bp
31.	*Psathyrella* species 2	Thenmala forest (Kollam District)	G110: 639 bp	G110: 856 bp
32.	*Psathyrella* species 3	Punnayoorkulam (Thrissur District)	G280: 636 bp	G280: 772 bp
33.	*Tulosesus brevisetulosus*	Punnayoorkulam (Thrissur District), Malappuram (Malappuram District)	G224: 644 bp, G251: 661 bp	G224: 814 bp, G251: 914 bp
34.	*Tulosesus* species 1	Punnayoorkulam (Thrissur District)	G119: 652 bp	G119: 867 bp
35.	*Tulosesus velatopruinatus*	Punnayoorkulam (Thrissur District), Chenakkal (Malappuram District)	G227: 658 bp, G82: 655 bp	G227: 888 bp, G82: 928 bp