

**Systematic studies on the heterobasidiomycetes
(Agaricomycotina, Basidiomycota,
Fungi) of Kerala**

*Thesis submitted to the
UNIVERSITY OF CALICUT
in partial fulfillment for the requirements for
the award of the degree of*

Doctor of Philosophy in Botany

By

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August 2024



THE ZAMORIN'S GURUVAYURAPPAN COLLEGE

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August 2024

CERTIFICATE

This is to certify that the thesis entitled "**Systematic studies on the heterobasidiomycetes (Agaricomycotina, Basidiomycota, Fungi) of Kerala**", submitted to the University of Calicut by Ms. Anjitha Thomas, for the award of PhD. Degree in Botany is a record of Bonafide research work carried out by her under the supervision and guidance of Dr. Arun Kumar T. K., Assistant Professor, Post Graduate and Research Department of Botany of this College during the period 2018–2024.

Principal



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Dr. Arun Kumar T. K.



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(Head of the Department,
P.G. & Research Department of Botany)

DECLARATION

I hereby declare that the work presented in the thesis "**Systematic studies on the heterobasidiomycetes (Agaricomycotina, Basidiomycota, Fungi) of Kerala**" is based on the original work done by me under the guidance of Dr. Arun Kumar T. K., Assistant Professor, Post Graduate and Research Department of Botany and has not been included in any other thesis submitted previously for the award of any degree. The contents of the thesis are undergone plagiarism check using iThenticate software at C.H.M.K. Library, University of Calicut, and the similarity index found within the permissible limit. I also declare that the thesis is free from AI generated contents.

Place: Kozhikode
Date:

Anjitha Thomas

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ABSTRACT

Heterobasidiomycetes are a polyphyletic group of fungi having jelly-like basidiocarp, complex dolipore septum with parenthesomes, septate basidia, and basidiospores capable of producing secondary spores and/or yeast-like cells. Heterobasidiomycetes (Agaricomycotina) generally called as jelly fungi are distributed in the following classes: Agaricomycetes, Dacrymycetes, and Tremellomycetes. Heterobasidiomycetous fungi exhibit diversity in basidiocarp shape, size, colour and utilize various substrata. Ecological features of heterobasidiomycetes like habitat, mode of nutrition and associating organisms vary significantly in different classes and orders. Heterobasidiomycetes include economically important taxa with edibility and proven bioactivity.

From Kerala, Rangaswami *et al.* (1970) reported one species and Mohanan (2011) reported ten species of heterobasidiomycetes. Comprehensive studies of this group are lacking in Kerala State. Hence, a systematic study of the heterobasidiomycetes fungi of Kerala was attempted.

Specimens used in the study were collected from different localities of Kerala State during 2018-2024. Morphological and molecular characterizations were done. The newly generated sequences were deposited in GenBank (www.ncbi.nlm.nih.gov) database. Phylogenetic analysis to elucidate the relationships of taxa collected in the study was done. Pure cultures of 20 species were generated and maintained at Fungal Diversity laboratory of the Zamorin's Guruvayurappan College. All the collections (including holotype materials) have been deposited at the Zamorin's Guruvayurappan College herbarium (ZGC), Kozhikode.

The present systematic study on heterobasidiomycete documented 47 species belonging to 11 genera, 7 families, 4 orders. Detailed morphological descriptions, comprehensive taxonomic accounts, macroscopic and microscopic photographs, and keys to the heterobasidiomycetes group were prepared. Three species collected during the study have been formally proposed as new to science. Seven species were found as hitherto undescribed

and may represent species new to science (*Sebacina* species, *Dacrymyces* species 1, *Dacrymyces* species 2, *Tremella* species 1, *Tremella* species 2 and *Tremella* species 3 and *Vishniacozyma* species). Two taxa were identified only up to family level and belonged to Auriculariaceae, and Cryptococcaceae. These two taxa could not place in a genus because they exhibited phylogenetic distinction from all the heterobasidiomycete genera described so far. Fifty five molecular sequences were newly generated and phylogenetic analysis of Auriculariales, Sebacinales, Dacrymycetes, and Tremellomycetes were conducted for accurate identification of species.

This study forms the first phylogenetically supported comprehensive treatment of heterobasidiomycetes from India.

Key words: Auriculariales, Biodiversity, Dacrymycetes, Phylogeny, Sebacinales, Tremellomycetes

സംഗ്രഹം

ജെല്ലി സ്വഭാവമുള്ള ബസിഡിയോകാർപ്പ്, പാരന്തീസോമകളുള്ള ഡോളിപോർ സെപ്റ്റം, സെപ്റ്റേറ്റ് ബസിഡിയ, ദ്വിതീയ ബീജകോശങ്ങൾ (secondary spores), യീസ്റ്റ് പോലുള്ള കോശങ്ങൾ ഉത്പാദിപ്പിക്കാൻ കഴിവുള്ള ബസിഡിയോസ്പോറുകൾ എന്നിവ അടങ്ങിയിട്ടുള്ള ഫംഗസുകളുടെ ഒരു ഗ്രൂപ്പാണ് ഹെറ്ററോബസിഡിയോമൈസെറ്റുകൾ. അഗാരികൊമൈക്കോട്ടിനയിൽപ്പെട്ട ഹെറ്ററോബസിഡിയോമൈസെറ്റ് ടാക്സകളെ സാധാരണയായി ജെല്ലി ഫംഗസ് എന്ന് വിളിക്കുന്നു. അഗാരികൊമൈസെറ്റുകൾ, ഡാക്രിമൈസെറ്റുകൾ, ട്രൈമെല്ലോമൈസെറ്റുകൾ എന്നീ മൂന്നു ക്ലാസ്സുകളിലാണ് ഹെറ്ററോബസിഡിയോമൈസെറ്റ് ഫംഗസുകൾ അടങ്ങിയിട്ടുള്ളത്.

ഹെറ്ററോബസിഡിയോമൈസെറ്റ് ഫംഗസുകൾ ബസിഡിയോകാർപ്പ് ആകൃതിയിലും വലുപ്പത്തിലും നിറത്തിലും വൈവിധ്യം പ്രകടിപ്പിക്കുന്നു. ഹെറ്ററോബസിഡിയോമൈസെറ്റുകളിൽപ്പെട്ട ചില ഇനങ്ങൾ ഭക്ഷ്യയോഗ്യവും ഔഷധഗുണമുള്ളതും വാണിജ്യാടിസ്ഥാനത്തിൽ കൃഷി ചെയ്യുന്നവയുമാണ്. ചില ഇനങ്ങൾക്ക് തെളിയിക്കപ്പെട്ട ബയോആക്ടിവിറ്റിയും മൈക്കോറൈസൽ ഗുണങ്ങളുമുണ്ട്.

കേരളത്തിൽ നിന്ന്, രംഗസ്വാമി et al. (1970) ഒരു സ്പീഷിസും മോഹനൻ (2011) പത്ത് ഇനം ഹെറ്ററോബസിഡിയോമൈസെറ്റുകളും റിപ്പോർട്ട് ചെയ്തിട്ടുണ്ട്. ഈ ഗ്രൂപ്പിനെക്കുറിച്ചുള്ള സമഗ്രമായ പഠനങ്ങൾ കേരളത്തിൽ കുറവാണ്. അതിനാൽ, കേരളത്തിലെ ഹെറ്ററോബസിഡിയോമൈസെറ്റ് ഫംഗസുകളെ കുറിച്ച് ചിട്ടയായ പഠനം നടത്താൻ ശ്രമിച്ചു.

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ഹെറ്ററോബസിഡിയോമൈസെറ്റുകളെക്കുറിച്ചുള്ള ഈ പഠനത്തിൽ 11 ജനുസ്സുകൾ, 7 കുടുംബങ്ങൾ, 4 ഓർഡറുകൾ എന്നിവയിൽപ്പെട്ട 47 ഇനങ്ങളെ രേഖപ്പെടുത്തിയിട്ടുണ്ട്. വിശദമായ വിവരണങ്ങൾ, ടാക്സോണമിക് അക്കൗണ്ടുകൾ, മാക്രോസ്കോപ്പിക്,

മൈക്രോസ്റ്റോപ്പിക് ഫോട്ടോഗ്രാഫുകൾ, ഹെറ്ററോബസിഡിയോമൈസെറ്റ്സ് ഗ്രൂപ്പിന്റെ കീകൾ (Key) എന്നിവ തയ്യാറാക്കി. പഠനത്തിനിടെ ശേഖരിച്ച മൂന്ന് സ്പീഷീസുകൾ ശാസ്ത്രത്തിന് പുതിയതായി നിർദ്ദേശിച്ചിട്ടുണ്ട്. ഇതുവരെ വിവരിച്ചിട്ടില്ലാത്ത ഏഴ് ഇനങ്ങളെ കണ്ടെത്തി, അവ ശാസ്ത്രത്തിന് പുതിയ സ്പീഷീസുകളെ പ്രതിനിധീകരിക്കാം (സെബാസിന സ്പീഷീസ്, ഡാക്രിമൈസസ് സ്പീഷീസ് 1, ഡാക്രിമൈസസ് സ്പീഷീസ് 2, ട്രൈമെല്ല സ്പീഷീസ് 1, ട്രൈമെല്ല സ്പീഷീസ് 2, ട്രൈമെല്ല സ്പീഷീസ് 3, വിഷ്നിയാകോസിമ സ്പീഷീസ്). രണ്ട് ടാക്സകളെ കുടുംബ തലം വരെ മാത്രമേ തിരിച്ചറിഞ്ഞിട്ടുള്ളൂ, അവ ഓറിക്കലേറിയേസിയെ, ക്രിപ്റ്റോകോക്കേസിയെ എന്നിവയുടേതാണ്. ഇതുവരെ വിവരിച്ചിട്ടുള്ള എല്ലാ ഹെറ്ററോബസിഡിയോമൈസെറ്റ് ജനസ്സുകളിൽ നിന്നും ഫൈലോജെനെറ്റിക് വ്യത്യാസം പ്രദർശിപ്പിച്ചതിനാൽ ഈ രണ്ട് ടാക്സകൾക്കും ഒരു ജനസ്സിലും ഉൾപ്പെടുത്താനായില്ല. അൻപത്തിയഞ്ച് ഡി.എൻ.എ. സീക്വൻസുകൾ പുതുതായി സൃഷ്ടിക്കുകയും ഓറിക്കലേറിയേൽസ്, സെബാസിനേൽസ്, ഡാക്രിമൈസെറ്റ്സ്, ട്രൈമെല്ലോമൈസെറ്റ്സ് എന്നീ ഗ്രൂപ്പുകളുടെ ഫൈലോജെനെറ്റിക് വിശകലനം നടത്തുകയും ചെയ്തു.

ഇത് ഇന്ത്യയിൽ നിന്നുള്ള ഹെറ്ററോബസിഡിയോമൈസെറ്റുകളുടെ ഫൈലോജെനെറ്റിക് പിന്തുണയുള്ള ആദ്യത്തെ സമഗ്രമായ പഠനമാണ്.

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CONTENTS

| Chapter No. | Chapters | Page No. |
|-------------|--|-------------|
| 1. | INTRODUCTION | 1-5 |
| 2. | REVIEW OF LITERATURE | 7-81 |
| | 2.1. HETEROBASIDIOMYCETES | 7 |
| | 2.1.1. Class AGARICOMYCETES Doweld | 9 |
| | 2.1.1.2. Order AURICULARIALES Bromhead | 11 |
| | 2.1.1.2.1. Taxonomic characters of Auriculariales | 13 |
| | 2.1.1.2.2. Ecological and economic importance | 19 |
| | 2.1.1.2.3. Distribution | 19 |
| | 2.1.1.2.4. Family Auriculariaceae Fr. | 21 |
| | 2.1.1.2.4.1. Genus <i>Auricularia</i> Bulliard | 22 |
| | 2.1.1.2.4.1.1. Ecological and economic importance | 25 |
| | 2.1.1.2.4.1.2. Distribution | 26 |
| | 2.1.1.3. Order SEBACINALES M. Weiss, Seloosse, Rexer, A. Urb. and Oberw. | 26 |
| | 2.1.1.3.1. Taxonomic characters of Sebacinales | 28 |
| | 2.1.1.3.2. Ecological and economic importance | 31 |
| | 2.1.1.3.3. Distribution | 32 |
| | 2.1.1.3.4. Family Sebacinaceae K. Wells and Oberw. | 33 |
| | 2.1.1.3.4.1. Genus <i>Sebacina</i> Tul. and C. Tul. | 34 |
| | 2.1.1.3.4.1.1. Ecological and economic importance | 35 |
| | 2.1.1.3.4.1.2. Distribution | 36 |
| | 2.1.2. Class DACRYMYCETES Doweld | 36 |

| | |
|--|----|
| 2.1.2.1. Order DACRYMYCETALES Henn. | 38 |
| 2.1.2.1.1. Taxonomic characters of Dacrymycetales | 38 |
| 2.1.2.1.2. Ecological and economic importance | 44 |
| 2.1.2.1.3. Distribution | 45 |
| 2.1.2.1.4. Family Dacrymycetaceae J. Schröt. | 46 |
| 2.1.2.1.4.1. Genus <i>Calocera</i> Fr. | 49 |
| 2.1.2.1.4.1.1. Ecological and economic importance | 50 |
| 2.1.2.1.4.1.2. Distribution | 51 |
| 2.1.2.1.4.2. Genus <i>Dacrymyces</i> Nees | 51 |
| 2.1.2.1.4.2.1. Ecological and economic importance | 53 |
| 2.1.2.1.4.2.2. Distribution | 53 |
| 2.1.2.1.4.3. Genus <i>Dacryopinax</i> Martin | 53 |
| 2.1.2.1.4.3.1. Ecological and economic importance | 54 |
| 2.1.2.1.4.3.2. Distribution | 54 |
| 2.1.2.1.4.4. Genus <i>Dendrodacrys</i> J.C. Zamora, A. Savchenko, Gonz.-Cruz, Prieto-García, Olariaga and Ekman | 54 |
| 2.1.2.1.4.4.1. Ecological and economic importance | 55 |
| 2.1.2.1.4.4.2. Distribution | 55 |
| 2.1.2.1.4.5. Genus <i>Guepiniopsis</i> Patouillard | 56 |
| 2.1.2.1.4.5.1. Ecological and economic importance | 57 |
| 2.1.2.1.4.5.2. Distribution | 57 |
| 2.1.3. Class TREMELLOMYCETES Doweld | 57 |
| 2.1.3.1. Order TREMELLALES Fries | 60 |
| 2.1.3.1.1. Taxonomic characters of Tremellales | 61 |

| | |
|--|----|
| 2.1.3.1.2. Ecological and economic importance | 67 |
| 2.1.3.1.3. Distribution | 68 |
| 2.1.3.1.4. Family Bulleribasidiaceae X.Z. Liu, F.Y. Bai, M. Groenew. and Boekhout | 69 |
| 2.1.3.1.4.1. Genus <i>Vishniacozyma</i> X.Z. Liu, F.Y. Bai, M. Groenew. and Boekhout | 69 |
| 2.1.3.1.4.1.1. Ecological and economic importance | 70 |
| 2.1.3.1.4.1.2. Distribution | 70 |
| 2.1.3.1.5. Family Naemateliaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout | 71 |
| 2.1.3.1.5.1. Genus <i>Naematelia</i> Fries | 71 |
| 2.1.3.1.5.1.1. Ecological and economic importance | 72 |
| 2.1.3.1.5.1.2. Distribution | 73 |
| 2.1.3.1.6. Family Phaeotremellaceae Yurkov and Boekhout | 73 |
| 2.1.3.1.6.1. Genus <i>Phaeotremella</i> Rea | 74 |
| 2.1.3.1.6.1.1. Ecological and economic importance | 74 |
| 2.1.3.1.6.1.2. Distribution | 75 |
| 2.1.3.1.7. Family Sirobasidiaceae Lindau | 76 |
| 2.1.3.1.7.1. Genus <i>Sirobasidium</i> Lagerh. and Pat. | 76 |
| 2.1.3.1.7.1.1. Ecological and economic importance | 77 |
| 2.1.3.1.7.1.2. Distribution | 77 |
| 2.1.3.1.8. Family Tremellaceae Fries | 77 |
| 2.1.3.1.8.1. Genus <i>Tremella</i> Persoon | 78 |
| 2.1.3.1.8.1.1. Ecological and economic importance | 80 |
| 2.1.3.1.8.1.2. Distribution | 80 |

| | | |
|-----------|---|----------------|
| 3. | MATERIALS AND METHODS | 83-117 |
| | 3.1. Study area- Kerala State | 83 |
| | 3.2. Fields study and specimen collection | 87 |
| | 3.3. Morphological characterisation | 87 |
| | 3.4. Terminologies followed | 88 |
| | 3.5. Pure culture establishment | 91 |
| | 3.6. Molecular characterisation | 92 |
| | 3.7. Phylogenetic analyses | 93 |
| | 3.7. 1. Phylogenetic analysis of Auriculariales | 94 |
| | 3.7. 2. Phylogenetic analysis of Sebaciales | 101 |
| | 3.7. 3. Phylogenetic analysis of Dacrymycetes | 104 |
| | 3.7. 4. Phylogenetic analysis of Tremellomycetes | 109 |
| 4. | RESULTS AND DISCUSSION | 119-260 |
| | 4.1. Taxonomy | 122 |
| | 4.1.1. Taxonomic Key to the heterobasidiomycetes fungi in Kerala | 122 |
| | 4.2. Taxonomic descriptions | 127 |
| | 4.2.1. Taxonomic descriptions of Tremellales | 127 |
| | 4.2.2. Taxonomic descriptions of Dacrymycetales | 177 |
| | 4.2.3. Taxonomic descriptions of Auriculariales | 228 |
| | 4.2.4. Taxonomic descriptions of Sebaciales | 246 |
| | 4.3. Pure culture establishment | 249 |
| | 4.4. Molecular characterization | 250 |
| | 4.5. Phylogenetic analyses | 252 |
| | 4.5.1. Phylogenetic tree of Auriculariales | 252 |
| | 4.5.2. Phylogenetic tree of Sebaciales | 254 |
| | 4.5.3. Phylogenetic tree of Dacrymycetes | 255 |
| | 4.5.4. Phylogenetic tree of Tremellomycetes | 256 |
| 5. | SUMMARY | 261-262 |
| 6. | RECOMMENDATIONS | 263-264 |
| 7. | REFERENCES | 265-295 |
| | APPENDICES | 297-299 |
| | APPENDIX- I - List of figures | 297 |
| | APPENDIX- II - List of tables | 299 |

INTRODUCTION

Heterobasidiomycetes collectively refer to fungal taxa having jelly-like basidiocarp, complex dolipore septum with parenthesomes, septate basidia, and basidiospores capable of producing secondary spores and/or yeast-like cells (Webster and Weber 2007). The gelatinous consistency of basidiocarps helps them to survive under extreme environmental conditions (Wells 1994, Alvarenga and Xavier-Santos 2015). The heterobasidiomycetes taxa coming under Agaricomycotina Doweld are generally treated as 'jelly fungi' and are distributed within three classes, Agaricomycetes Doweld, Dacrymycetes Doweld, and Tremellomycetes Doweld (Alvarenga and Xavier-Santos 2015, Castro-Santiuste *et al.* 2017, Tederso *et al.* 2018, He *et al.* 2019).

Heterobasidiomycetous fungi exhibit diversity in basidiocarp shape, size, colour and utilize various substrata (Lowy 1952, Lowy 1971, Alexopoulos *et al.* 1996, Wells 1994, Looney *et al.* 2013, Alvarenga and Xavier-Santos 2015). Order Auriculariales Bromhead include corticioid, resupinate, effused-reflexed, foliose, cerebriform basidiocarps with gelatinous-waxy (*Auricularia* Bulliard, *Exidia* R.T. Moore, *Pseudohydnum* P. Karst.) or leathery (*Alloexidiopsis* L.W. Zhou, *Eichleriella* Bres. and *Heteroradulum* Lloyd ex Spirin and Malysheva) texture (Li *et al.* 2023a). Sebaciales M. Weiss, Selosse, Rexer, A. Urb. and Oberw. members are corticoid, pustulate, cushion-shaped, coralloid, infundibuliform, and stereoid (Oberwinkler *et al.* 2014). Dacrymycetales Henn. is characterised by basidiocarps that are pustular, cerebriform, foliose, clavarioid, spathulate, capitate, cupulate, resupinate forms with gelatinous (*Calocera* (Fr.) Fr., *Dacryopinax* G.W. Martin, *Dacrymyces* Nees, *Ditiola* Fr.) or non gelatinous (*Cerinomyces pallidus* G.W. Martin, *C. albosporus* Boidin and Gilles, *C. borealis* Miettinen, Spirin and A. Savchenko) texture (Savchenko *et al.* 2021). Order Tremellales Fr. contain taxa with pustulate, resupinate, cerebriform, foliose

basidiocarp morphology (Liu *et al.* 2015a). The colour of heterobasidiomycetes ranges from white, yellow, orange, red, pink, brown to black (Oberwinkler 1994, Shirouzu *et al.* 2009, Weiss *et al.* 2004, Liu *et al.* 2015a, Malysheva and Spirin 2017, Liu *et al.* 2022). Microscopically heterobasidiomycetes are characterised by different types of basidia like, transversely septate basidia (*Auricularia*), longitudinally septate basidia (*Exidia*, Sebacinales, Tremellales) or forked holobasidia (Dacrymycetales) (Alvarenga and Xavier-Santos 2015). The basidiospores are generally cylindrical to allantoid or subglobose to ovoid in shape without any ornamentation (Looney *et al.* 2013, Liu *et al.* 2015a).

Ecological features of heterobasidiomycetes like habitat, mode of nutrition and associating organisms vary significantly in different classes and orders. Auriculariales members are generally saprobic, growing on wood logs and have wood decomposing potential (Looney *et al.* 2013, Malysheva and Spirin 2017). Sebacinales members can live in soil, on mosses, pteridophytes, living plants, and they are well known for their ability to form endophytic and diverse types of mycorrhizal associations with plants and mosses (Oberwinkler *et al.* 2013, Weiß *et al.* 2016, Wartchow *et al.* 2017). Dacrymycetes members are wood decomposers and typically cause brown rot in coniferous and angiosperm wood (Oberwinkler 1994, Floudas *et al.* 2012, Zamora and Ekman 2020). Tremellomycetes include animal parasites, mycoparasitic and lichenicolous members (Webster and Weber 2007, Millanes *et al.* 2011, Liu *et al.* 2015a). Members of the genus *Tremella* Pers. are parasitic on fungal hosts that belong to Corticiales K.H. Larss., Dacrymycetales, Diaporthales Nannf., Pleosporales Luttr. ex M.E. Barr, Polyporales Gäum., Rhytismatales M.E. Barr ex Minter, Russulales Kreisel ex P.M. Kirk, P.F. Cannon and J.C. David, Trechisporales K.H. Larss. and Xylariales Nannf. (Diederich 1996, Chen 1998, Liu *et al.* 2015a, Malysheva *et al.* 2015, Zhao *et al.* 2019). Tremellaceous species inhabiting lichens are present in the orders Filobasidiales Jülich and Tremellales (Diederich *et al.* 2022). Unlike other heterobasidiomycetous taxa, most of the

members of Tremellomycetes are dimorphic in nature. They can exist in both filamentous and yeast stages. Tremellomyceteous yeasts can inhabit diverse habitats and have reported from extreme climatic conditions like Antarctic soils and hydrothermal oceanic vents (Weiß *et al.* 2014).

Heterobasidiomycetes include economically important taxa with edibility and proven bioactivity. *Auricularia* is the third most cultivated mushroom genus after *Lentinula* Earle and *Pleurotus* (Fr.) P. Kumm. (Royse *et al.* 2017, Bandara *et al.* 2019). Edible *Auricularia* can be processed into various value-added products, such as mushroom extracts, powders, and dietary supplements (Liu *et al.* 2019a, Chen *et al.* 2020). In addition to the unique flavour, *Auricularia* species are known for its therapeutic potential. Polysaccharides from *Auricularia* have anti-tumour, antioxidant, anti-coagulant, anti-hypercholesterolemic, hypoglycaemic, anti-viral, anti-bacterial and immunomodulating properties (Ma *et al.* 2018, Bandara *et al.* 2019). *Tremella fuciformis* Berk. has potential applications in dietary, pharmaceutical and cosmetic industry (Chen 2018, Ma *et al.* 2021). *Naematelia aurantialba* (Bandoni and M. Zang) Millanes and Wedin has been widely used in the medicinal preparations in China. Preparation of basidiocarps ground along with sugar is recommended for the treatment of lung fever, flu, asthma and hypertension (Liu and Bau 1980, Bandoni and Zang 1990). *Serendipita vermifera* (Oberw.) P. Roberts and *S. indica* (Sav. Verma, Aj. Varma, Rexer, G. Kost and P. Franken) M. Weiss, F. Waller, Zuccaro and Selosse are cultivable sebacinalean species with promising biocontrol and biofertilising activities on crop plants (Waller *et al.* 2008, Selosse *et al.* 2009, Weiß *et al.* 2011). Tremellomycetes yeasts are highly diverse with harmful animal and human pathogens as well as members with biotechnological applications. Pathogenic yeasts commonly infect immunocompetent and immunocompromised people. *Cryptococcus neoformans* (San Felice) Vuill. and *C. gattii* (Vanbreus. and Takashio) Kwon-Chung and Boekhout are the main infectious agents of cryptococcal meningitis

(Akapo *et al.* 2019). Tremellomycetous yeasts like *Cryptococcus terricola* T.A. Pedersen and *C. terreus* Di Menna are useful in the biodegradation of phenolic compounds (Weiß *et al.* 2014).

Heterobasidiomycetes have been documented world-wide (Martin 1936, 1945; Brasfield 1938, Kennedy 1958, Olive 1958, McNabb 1964, 1965a, 1965b, 1965c, 1965d, 1965e, 1966, 1969, 1973; Donk 1966, Lowy 1971, 1976; Reid 1974, Wells and Raitviir 1977, 1980; Bandoni 1987, Roberts and Spooner 1998, 2004; Roberts 2001a, 2001b, 2007; Dueñas 2005, Pippola and Kotiranta 2008, Shirouzu *et al.* 2009, Bandoni and Boekhout 2011, Malysheva and Bulakh 2014, Oberwinkler *et al.* 2014, Alvarenga and Xavier-Santos 2015, Malysheva *et al.* 2015, Castro-Santiuste *et al.* 2017, Malysheva and Spirin 2017, Bandara *et al.* 2017, Alvarenga *et al.* 2019, Spirin *et al.* 2019, Wu *et al.* 2021, Li *et al.* 2023a) and many species have cosmopolitan distribution. Floristic study of jelly fungi by Lowy (1971, 1976) revealed the diversity of jelly fungi in Neotropics. Alvarenga and Xavier-Santos (2015) produced a check-list of jelly fungi from Brazil. Roberts (2001b, 2003a, 2003b, 2006, 2008a, 2008b) have reported heterobasidiomycetes from Cameroon, Dominican Republic, Azore, Jamaica, Belize and British virgin islands.

Reports on jelly fungi of India are less when compared to reports world-wide. Studies concentrating on jelly mushrooms are few that of Nag Raj (1964), Mahamulkar *et al.* (2003), Patil *et al.* (2003), Das (2010), Kumari *et al.* (2013), Kakde and Gaikwad (2014), Prabhu *et al.* (2016), Singh (2008), Verma *et al.* (2019), Debnath *et al.* (2020).

From Kerala, Rangaswami *et al.* (1970) reported one species and Mohanan (2011) reported ten species of heterobasidiomycetes. Comprehensive studies of this group are lacking in Kerala State. Hence, a systematic study of the heterobasidiomycetes fungi of Kerala is attempted.

Objectives of the study

- 1) Preparation of a systematic account of the heterobasidiomycetes (Agaricomycotina, Basidiomycota, Fungi) of Kerala.
- 2) Morphological and molecular characterization of the documented taxa.
- 3) Elucidation of phylogenetic relationships of the heterobasidiomycetes fungi of Kerala.

REVIEW OF LITERATURE

2.1. HETEROBASIDIOMYCETES

Fries (1874) established the families of Basidiomycota based on basidiocarp morphology and hymenial configuration, with little importance for the basidial structure (Wells and Bandoni 2001). Subsequent workers like Tulasne brothers (1871, 1872), Patouillard (1887, 1900) and Brefeld (1888) modified Fries's (1874) classification by emphasising characters like basidial septations and basidiospore germination patterns. Brefeld (1888) subdivided the class Basidiomycetes into "*Autobasidiomyceten*" and "*Protobasidiomyceten*" for taxa with non-segmented and segmented basidia respectively. System of Brefeld (1888) was partially supported by Donk (1956, 1966) and Talbot (1968). Subsequently, Talbot (1968) proposed a classification with subdivision Basidiomycotina into three classes, Teliomycetes, Phragmobasidiomycetes and Holobasidiomycetes (Talbot 1968). Class Phragmobasidiomycetes included taxa which forming septate basidia. This proposal was widely accepted and followed by workers like Ainsworth *et al.* (1973) and Wells (1994). In the same time period of Brefeld (1888), Patouillard (1887, 1900) also classified Basidiomycetes into two groups "*homobasidiés*" and "*hétérobasidiés*" based on basidial septations. Martin (1945) accepted Patouillard's (1887, 1900) division of Basidiomycetes. According to Martin (1945), three or at the most four orders (Tremellales, Uridinales, Ustilaginales, Septobasidiales) were to be recognised under "Heterobasidiomycetes", characterised by septate basidia (Martin 1945) used the term "Heterobasidiomycetes" corresponding to the group "*hétérobasidiés*" of Patouillard (1887). Martin (1945) further considered order Tremellales to include families Auriculariaceae Fr., Ceratobasidiaceae G.W. Martin, Dacrymycetaceae J. Schröt, Hyaloriaceae Lindau, Phleogenaceae Weese, Sirobasidiaceae Lindau, Tremellaceae Fr. and Tulasnellaceae Juel. Lowy (1971)

proposed a new system where he divided Basidiomycetes into three subclasses (Heterobasidiomycetidae, Homobasidiomycetidae and Metabasidiomycetidae). Lowy (1971) recommended to retain Auriculariaceae, Hyaloriaceae, Phleogenaceae, Sirobasidiaceae and Tremellaceae under Eutremellales (subclass Heterobasidiomycetidae, class Basidiomycetes), and erected Metatremellales (subclass Metabasidiomycetidae, class Basidiomycetes) to incorporate Dacrymycetaceae, Tulasnellaceae and Ceratobasidiaceae.

Bandoni (1984) proposed an alternative classification for Auriculariales and Tremellales, and redefined the order Tremellales with taxa having dimorphic lifestyle, modified bifactorial compactibility system, septal pore apparatus with sacculate parenthesomes and tremelloid basidium. According to Bandoni (1984), Tremellales *s. str.* contained Tremellaceae, Sirobasidiaceae and Tetragoniomycetaceae Oberw. and Bandoni. Bandoni (1984) separated Auriculariaceae from Tremellales and redefined Auriculariales with simple septal pores, transversely or longitudinally septate basidia, haploid stages, continuous parenthesomes and dolipore septa (Weiß and Oberwinkler 2001).

According to *Index Fungorum*, Moore (1980) first used the rank Heterobasidiomycetes, without giving a proper diagnosis. Wells (1994) later provided a proper diagnosis for Heterobasidiomycetes and divided the class into two subclasses, Heterobasidiomycetidae and Tremellomycetidae based on septal pore ultrastructure and germination patterns. Wells and Bandoni (2001) redefined the class Heterobasidiomycetes as “those basidiomycetes with an interphase, biglobular spindle pole body and complex septal pore apparatus with imperforate, perforate, sacculate parenthesome or parenthesome lacking; basidiospores capable of forming secondary spores that may be ballistospores, blastospores or microconidia; and deeply septate, partially septate or nonseptate basidia”. Wells and Bandoni (2001) treated Ceratobasidiales Jülich, Tulasnellales Rea, Dacrymycetales and Auriculariales under subclass

Heterobasidiomycetidae, and Tremellales, Christianseniales F. Rath, Filobasidiales under subclass Tremellomycetidae.

Molecular phylogenetic analyses later revealed the heterobasidiomycetes to be an artificial group (Swann and Taylor 1993, Gargas *et al.* 1995, Begerow *et al.* 1997, Weiss *et al.* 2004). Based on molecular phylogenetic analyses, Weiss *et al.* (2004) proposed a systematic arrangement for heterobasidiomycetes. Weiss *et al.* (2004) included Urediniomycetes, Ustilaginomycetes, and some basal lineages of the Hymenomycetes in their study, and proposed a system where class Hymenomycetes were divided into two subclasses, (Subclass Tremellomycetidae *sensu* Swann and Taylor (1995) and subclass Hymenomycetidae *sensu* Swann and Taylor (1995)). Subclass Tremellomycetidae contained orders Tremellales and Cystofilobasidiales Fell, Roeljmans and Boekhout. Subclass Hymenomycetidae contained five orders, Auriculariales, Ceratobasidiales, Dacrymycetales, Sebaciniales and Tulasnellales. Bauer *et al.* (2006) elevated the status of class Hymenomycetes, Urediniomycetes and Ustilaginomycetes into subphyla and proposed Agaricomycotina, Ustilaginomycotina and Pucciniomycotina to accommodate them respectively.

Hibbett *et al.* (2007) established a system of classification, where three classes are considered under subphylum Agaricomycotina (Agaricomycetes, Dacrymycetes and Tremellomycetes). Tederso *et al.* (2018) and He *et al.* (2019), consider heterobasidiomycete members under three classes, Agaricomycetes, Dacrymycetes and Tremellomycetes.

2.1.1. Class AGARICOMYCETES Doweld

Class Agaricomycetes is one among the three classes under Agaricomycotina, which is monophyletic, with diverse morphological features and contains approximately one fifth of all known fungi (Kirk *et al.* 2008, Hibbett

et al. 2014, He *et al.* 2019). The class comprises Homobasidiomycetes *sensu* Hibbett and Thorn (2001) plus Auriculariales and Sebaciales (Hibbett *et al.* 2007). Agaricomycetes accommodate diverse morphological forms like gilled - mushrooms (Agarics), stinkhorns, corticioid fungi, coral fungi, bird's nest fungi, false truffle, morels and puffballs (Hibbett 2006).

Morphological, biochemical, cytological, ecological and cultural characters (Donk 1964, Oberwinkler 1977, Singer 1986, Hibbett *et al.* 2014) were used by taxonomists to formulate the phylogenetic relationships and classifications of Agaricomycetes. Ultrastructure of septal pore caps provided useful clues regarding the higher level taxonomy of Agaricomycetes long before the development of molecular characters. The presence of septal pore cap showed the close relationship of Agaricomycetes and Dacrymycetes when compared to Tremellomycetes which have septal pore composed of saccules. Monophyly of different orders of Agaricomycetes was revealed in different rRNA gene based studies (Binder and Hibbett 2002, Binder *et al.* 2005, Hibbett *et al.* 1997, Moncalvo *et al.* 2006). Matheny *et al.* (2007) conducted the first in-depth molecular phylogenetic analyses in Agaricomycetes with rRNA and protein coding genes, and the study suggested the paraphyletic assemblage of Sebaciales, Cantharellales Gäum., Auriculariales and Phallomycetidae K. Hosaka, Castellano and Spatafora within other Agaricomycetes members (Hibbett *et al.* 2014). Hibbett *et al.* (2007) studied the phylogenetic relationship within Agaricomycotina using multilocus dataset, and placed 17 orders under Agaricomycetes. Hibbett *et al.* (2007) divided Agaricomycetes to two subclasses (Agaricomycetidae and Phallomycetidae) and placed seven orders under these two subclasses. Remaining ten orders were treated under *incertae sedis*, including Auriculariales, Sebaciales, and few members of Cantharellales (Ceratobasidiaceae and Tulasnellaceae), which were previously classified under Heterobasidiomycetes. Phylogenomic analyses later provided resolution in the higher-level relationship of Agaricomycetes and confirmed some phylogenetic

aspects like monophyly of Agaricomycetidae, and its sister group relationship with Russulales.

According to He *et al.* (2019), Agaricomycetes comprises of 19 orders, Agaricales, Amylocorticiales K.H. Larss., Manfr. Binder and Hibbett, Atheliales Jülich, Auriculariales, Boletales E.-J. Gilbert, Cantharellales, Corticiales, Geastrales K. Hosaka and Castellano, Gloeophyllales Thorn, Gomphales Jülich, Hymenochaetales Oberw., Hysterangiales K. Hosaka and Castellano, Jaapiales Manfr. Binder, K.H. Larss. and Hibbett, Phallales E. Fisch., Polyporales, Russulales, Sebacinales, Thelephorales Corner ex Oberw. and Trechisporales. Among them, Auriculariales and Sebacinales contain heterobasidiomycetes (Alvarenga and Xavier-Santos 2015).

2.1.1.2. Order AURICULARIALES Bromhead

Auriculariales was erected for members possessing transversely septate basidia (Yuan *et al.* 2018), with *Auricularia* as the type genus (Liu *et al.* 2022). Bandoni (1984) proposed a classification system for Auriculariales and Tremellales by incorporating micromorphological, ultrastructural, developmental and ecological data and redefined Auriculariales with dolipore septa, transversely or longitudinally septate basidia, continuous parentheses and haploid hyphal stages (Weiß and Oberwinkler 2001). Many members of Auriculariales with gelatinous basidiocarp and four-celled basidia like *Exidia*, were traditionally treated under Tremellales (Olive 1954, Lowy 1971, Ye *et al.* 2020). Bandoni (1984) integrated them into Auriculariales. Later, Weiß and Oberwinkler (2001) confirmed the classification system of Bandoni (1984) using molecular phylogenetic studies with large subunit ribosomal RNA (LSU). Weiß and Oberwinkler (2001) revealed the clustering of these genera into different natural groups within Auriculariales clade.

The presence of diverse morphological features within Auriculariales makes the order taxonomically complex (Liu *et al.* 2022). Advanced studies covering all Auriculariales members are rare. In Auriculariales, species with stereoid morphology (having effused or cupulate with persistent basidiocarps), have been traditionally treated under *Eichleriella*, *Exidiopsis* (Bref.) A. Møller and *Heterochaete* Pat. (Burt 1915, Wells 1961, Wells and Raitviir 1966, 1980, Malysheva and Spirin 2017, Li *et al.* 2023a). Malysheva and Spirin (2017) re-evaluated Auriculariales with stereoid and corticoid basidiocarp, and reintroduced *Heteroradulum* and added two more new genera *Amphistereum* Spirin and Malysheva, and *Sclerotrema* Spirin and Malysheva. Subsequently, more phylogenetic studies were conducted in Auriculariales with stereoid morphology, and new genera like *Adustochaete* Alvarenga and K.H. Larss., *Alloexidiopsis*, *Crystallodon* Alvarenga, *Heterocorticium* S.H. He, T. Nie and Yue Li, *Metulochaete* Alvarenga, and *Proterochaete* Spirin and Malysheva were also added (Alvarenga *et al.* 2019, Li *et al.* 2023a). Spirin *et al.* (2019) studied Auriculariales members with effused basidiocarps and sphaeropedunculate basidia. According to them, *Myxarium* Wallr., *Myxariellum* Spirin and Malysheva, *Protodontia* Höhn., *Hydrophana* Malysheva and Spirin, *Protoacia* Spirin and Malysheva, *Gelacantha* Malysheva and Spirin and *Ofella* Spirin and Malysheva have sphaeropedunculate basidia (Spirin *et al.* 2019). Though order level comprehensive studies are rare in Auriculariales, taxonomic and phylogenic studies concentrating on different genera like *Basidi dendron* Rick (Spirin *et al.* 2020, 2021), *Exidia* (Spirin *et al.* 2018a), *Heterochaete* (Alvarenga *et al.* 2019), *Myxarium* (Spirin *et al.* 2018a), *Protohydnum* Möller (Malysheva *et al.* 2018) and *Pseudohydnum* (Spirin *et al.* 2023) has been conducted.

Genus *Exidia*, typified by *E. glandulosa* (Bull.) Fr., was accommodated under Tremellaceae of Tremellales for long considering the morphological similarity of basidiocarp and basidia with other members of Tremellaceae. Moore (1978) erected the family Exidiaceae R.T. Moore under Tremellales for

including the genus *Exidia*. Based on the morphological, ultrastructural, ecological and developmental data, Bandoni (1984) transferred *Exidia* to Auriculariaceae of Auriculariales. Phylogenetic study by Weiß and Oberwinkler (2001) confirmed the placement of *Exidia* under Auriculariaceae. Currently, Exidiaceae is considered as a synonym of Auriculariaceae (Spirin *et al.* 2018a, Ye *et al.* 2020).

Genus *Exidia* is polyphyletic within Auriculariales (Spirin *et al.* 2018a, Ye *et al.* 2020, Tohtirjap *et al.* 2023). *Exidia sensu lato* contain species with gelatinous basidiocarp, ellipsoid to subglobose, longitudinally septate basidia, and cylindrical to allantoid basidiospores. *Exidia sensu lato* include members from three genera, *Exidia*, *Myxarium*, and *Tremellochaete* Raitv. (Tohtirjap *et al.* 2023). Genus *Myxarium* belongs to Hyaloriaceae, and *Myxarium* is characterised by stalked basidia. *Exidia* and *Tremellochaete* belong to family Auriculariaceae. *Tremellochaete* is characterised by the presence of papillae on the hymenophore, which is absent in *Exidia*. But, the demarcation of these two genera is still not clear. Wang and Thorn (2021) treated these two genera as synonyms (Tohtirjap *et al.* 2023).

Currently, in Auriculariales two families, (Auriculariaceae, Hyaloriaceae) and 31 genera are kept under *incertae sedis* (He *et al.* 2019). Family Hyaloriaceae contain three genera, *Helicomysa* R. Kirschner and Chee J. Chen, *Hyaloria* Möller and *Myxarium*, while Family Auriculariaceae contain 17 genera (Liu *et al.* 2022).

2.1.1.2.1. Taxonomic Characters of Auriculariales

Traditional generic classification was based on the basidiocarp morphology, type of basidia, basidiospores, and presence of sterile hymenial cells.

Macroscopic characters

Auriculariales includes genera with diverse morphological features like corticoid, resupinate, stereoid, hydroid, poroid, effused-reflexed fungi (Malysheva and Spirin 2017, Liu *et al.* 2022). In Auriculariales, two types of basidiocarp morphologies are present that help these species to survive under extreme weather conditions. First type is gelatinous basidiocarps which can revive and dry out based on the availability of water. Genera like *Auricularia* and *Exidia* have this type of basidiocarps. Second type is the perennial, effused, stereoid basidiocarps which can resume their growth on suitable climatic conditions. Genera like *Eichleriella*, *Exidiopsis*, *Heterochaete*, *Alloexidiopsis* and *Amphistereum* have this type of basidiocarps (Malysheva and Spirin 2017).

Microscopic characters

Hymenium

Diverse hymenial construction like smooth, reticulate, hydroid and poroid can be seen in different Auriculariales members (Miettinen *et al.* 2012, Looney *et al.* 2013, Sotome *et al.* 2014, Yuan *et al.* 2018, Spirin *et al.* 2023). Genera like *Aporpium* Bondartsev and Singer, *Elmerina* Bres., and *Protodaedalea* Imazeki have poroid hymenium. Smooth and reticulate hymenium can be seen in different *Auricularia* species (Wu *et al.* 2021). *Eichleriella* possesses species with smooth and spiny hymenium (Liu *et al.* 2019b). *Protohydnum* and *pseudohydnum* have spiny hymenium (Malysheva *et al.* 2018, Spirin *et al.* 2023). *Exidia glandulosa* have sterile wart-like hyphal pegs on hymenium which results in a warted appearance (Gruffydd 1985, Aoki 1992).

Basidia

Auriculariales contain taxa with various basidial types (Weiß and Oberwinkler 2001, Weiss *et al.* 2004, McLaughlin and Spatafora 2014, Spirin *et al.* 2019). The major types are auricularioid, exidioid/tremelloid and myxarioid.

1. Transversely septate (auricularioid) basidia

Genus *Auricularia* is characterised by transversely three-septate, four celled cylindrical basidia. Each cells give raise to a long cylindrical epibasidium which grows up to hymenial surface and produce basidiospores from its sterigama on tip (Webster and Weber 2007)

2. Longitudinally septate (exidioid/tremelloid) basidia

Genera like *Exidia*, *Ductifera* Lloyd and *Basidiodendron* have globose, subglobose, ovoid to broadly suburniform or pear shaped, and longitudinally septate basidia without basal stalk (Wells 1958, Wells and Raitviir 1975, Weiß and Oberwinkler 2001, Spirin *et al.* 2021).

3. Sphaeropedunculate (myxarioid) basidia

Sphaeropedunculate (myxarioid) basidium consist 2-4 celled apical segments and a long enucleate stalk (Spirin *et al.* 2019). This type of basidia is characteristic of genera like *Myxarium*, *Myxariellum*, *Protodontia*, *Hyaloria*, *Hydrophane*, *Protoacia*, *Gelacantha* and *Ofella*. But genera with Sphaeropedunculate basidia are not phylogenticaly related (Weiß and Oberwinkler 2001, Wells *et al.* 2004, Spirin *et al.* 2018a, 2019, Malysheva *et al.* 2018).

Basidiospores

Auriculariales have colourless (hyaline), globose to cylindrical and broadly ellipsoid, smooth or ornamented basidiospores (Li *et al.* 2023a). Basidiospore ornamentation is a key morphological character in the species delimitation of *Basidiodendron* members, where some of them have smooth basidiospores and some have warted or spiny basidiospores (Spirin *et al.* 2021). Ability of basidiospores to form ballistoconidia (secondary basidiospores) is a key character of Auriculariales members. *Hyaloria pilacre* Möller, is an exception to this and all other species are ballistosporic (Hibbett *et*

al. 2014). Production of crescent-shaped microconidia on short sterigma-like projections from basidiospores, are also common in Auriculariales members (Ingold 1982, Hibbett *et al.* 2014).

Hyphal pegs

Hyphal pegs are defined as 'columns of skeletal or generative hyphae projecting above the hymenial layer but not covered with basidia or other hymenial cells' (Alvarenga *et al.* 2019). Genera like *Eichleriella*, *Heterochaete*, *Heteroradulum*, *Proterochaete*, *Hirneolina* (Pat.) Bres., *Tremellochaete*, *Adustochaete* and *Metulochaete* have hyphal pegs on hymenial surface (Bodman 1950, Malysheva and Spirin 2017, Alvarenga *et al.* 2019, Spirin *et al.* 2019, Li *et al.* 2022a,b). Hyphal pegs surrounded by crystals are the characteristic feature of monotypic genus *Crystalloodon* (Alvarenga and Gibertoni 2021).

Ultrastructure

All Auriculariales members have biglobular meiotic spindle pole bodies and dolipore septal pore apparatus with an imperforate parenthesome (Khan and Kimbrough 1980, Bandoni (1984), Wells 1994, Weiß and Oberwinkler 2001, Wells and Bandoni 2001). *Auricularia fuscosuccinea* (Mont.) Henn. is the first organism in which ultrastructural study of the septal pore apparatus and mitosis has been carried out (McLaughlin 1980, 1981; Lü and McLaughlin 1995). A special type of septal pore cap with an adseptal ribsome free zone, and membranous connections between the septal pore cap and plasma membrane of the septal cross walls, was identified in *A. auricula-judae* (Bull.) Qué. (Lü and McLaughlin 1991, 1995).

Ultrastructural features of Auriculariales members like *A. fuscosuccinea*, *Exidia candida* Lloyd, *E. crenata* (Schwein.) Fr., *Exidiopsis calcea* (Pers.) K. Wells, *Basidioidendron cinereum* (Bres.) Luck-Allen, *Elmerina caryae* (Schwein.) D.A. Reid,

Guepinia helvelloides (DC.) Fr., *Heterochaetella dubia* (Bourdot and Galzin) Bourdot and Galzin, *Heterorepetobasidium subglobosum* Chee J. Chen and Oberw. *Protodontia oligacantha* G.W. Martin and *Tremellodendropsis tuberosa* (Grev.) D.A. Crawford are available at the online public repository AFTOL Structural and Biochemical database (<https://aftol.umn.edu>) (Kumar *et al.* 2013).

Molecular characters

In the initial stages of molecular phylogenetic studies in Auriculariales, Weiß and Oberwinkler (2001) studied this group with large subunit ribosomal RNA (LSU) and confirmed the taxonomic rearrangements done by Bandoni (1984). Spirin *et al.* (2021) studied *Basidiodendron caesiocinereum* (Höhn. and Litsch.) Luck-Allen complex and revised its taxonomy based on LSU rDNA, ITS and *tef1* regions. In the multi-gene phylogenetic study of *Pseudohydnum*, Spirin *et al.* (2023) used ITS, LSU rDNA, *tef1*, *rpb1* regions. Series of studies were done by Spirin *et al.* (2018a, 2019, 2020, 2021) in different groups of Auriculariales and they used a combination of ITS, LSU, *rpb1* and *tef1* gene regions.

Genomic analysis of different *Auricularia* species were done by Dai *et al.* (2019), Yuan *et al.* (2019), Fang *et al.* (2020). Yuan *et al.* (2019) conducted genomic study in *A. heimuer* F. Wu, B.K. Cui and Y.C. Dai to find genes responsible for its wood degradation capacity and ability to produce secondary metabolite and polysaccharides.

Anamorphic members

Though anamorphic forms of different Auriculariales members have been established by researchers in cultural conditions, but its natural presence is comparatively rare (Olive 1952, Ingold 1991, Kirschner *et al.* 2010). The common anamorphic form in Auriculariales is that of micronematous conidiophores produced from germinating basidiospores or mycelia developed

from basidiospores, which producing allantoid conidia (Kisimova-Horovitz *et al.* 1997, 2000; Kirschner *et al.* 2012). In addition, pycnidia, sporodochia, bulbiferous and synnematos anamorphic structures have also been reported in Auricularials (Kirschner and Chen 2004, Kirschner *et al.* 2010, 2012).

Helicomysa everhartioides R. Kirschner and Chee J. Chen has an anamorphic form which is characterised by hyaline conidia that are hemi-circinate and hyphae with clamp-connections. They form sporodochia within which conidiospores and conidia are formed (Kirschner and Chen 2004). Kirschner and Chen (2004) erected genus *Helicomysa* to accommodate this anamorphic form *Helicomysa everhartioides*. *Ovipoculum album* Zhu L. Yang and R. Kirschner has gelatinous, cupulate conidiomata that produce bulbils from hyphae with clamp-connections. These bulbils are multicellular conidia developing on dense, branched and swollen hyphal cells. The fructifications show no differentiation as external cortex and inner medulla. *Ovipoculum album* is the first record in Auriculariales with the formation of bulbils (Kirschner *et al.* 2010). Kirschner *et al.* (2012) established a monotypic genus *Porpopycnis* to incorporate *Porpopycnis lubae* R. Kirschner. This species is characterised by conical pycnidia composed of hyphae with clamp-connections. Conidiophores and conidia are formed within these pycnidia. Morphological characters, ultrastructural features, and molecular data confirmed its relationship with Auriculariales members (Kirschner *et al.* 2012). Synnematos anamorph of *Exidia saccharina* Fr. was found in the galleries of bark beetles by Kirschner (2010). *Exidia saccharina* is characterised by cylindrical conidiospores. The hyphae have clamp-connections with a retrorse projection. One to three conidiogenous cells are formed from conidiophores (Kirschner 2010).

2.1.1.2.2. Ecological and economic importance

Auriculariales are ecologically important with their wood decomposing potential. They can inhabit hosts from tropics to the subarctic zone, and diverse climatic conditions like arid regions or dry habitats (Malysheva and Spirin 2017). In some genera like *Auricularia* and *Exidia*, the gelatinous nature of basidiocarp helps them to revive from dried state during rainy seasons. Members of some other genera with sterioid basidiocarps like *Amphistereum*, *Eichleriella*, *Exidiopsis*, *Heteroradulum* produce perennial basidiocarps and can resume their growth under favourable conditions (Malysheva and Spirin 2017). *Auricularia polytricha* (Mont.) Sacc. can form endomycorrhizal association with an achlorophyllous orchid, *Erythrorchis ochobiensis* (Hayata) Garay, which helped them to germinate in an experiment (Umata 1997).

Auricularia has edible and medicinal properties and is of high nutritional value. They are rich in proteins, carbohydrates, amino acids, trace elements and vitamins (Zeng *et al.* 2012, Wu *et al.* 2014). *Auricularia* mushrooms can be processed into various value-added products, such as mushroom extracts, powders, and dietary supplements (Liu *et al.* 2019a, Chen *et al.* 2020). Polysaccharides from *Auricularia auricula-judae* have biological functions, including anticoagulant, antitumor, and immune activities (Yoon *et al.* 2003)

2.1.1.2.3. Distribution

AFRICA: Cameroon (Wu *et al.* 2021), Ethiopia (Wu *et al.* 2021), Kenya (Duncan 1972, Wu *et al.* 2021), Morocco (Wells and Raitviir 1980), South Africa (Wu *et al.* 2021), Tanzania (Wu *et al.* 2021), Zambia (Wu *et al.* 2021). ASIA: China (Kirschner *et al.* 2010, Sotome *et al.* 2014, Wu *et al.* 2015a, Malysheva *et al.* 2018, Alvarenga *et al.* 2019, Liu *et al.* 2019a, Ye *et al.* 2020, Wang and Thorn 2021, Wu *et al.* 2021), India (Duncan 1972, Kumari *et al.* 2013), Indonesia (Sotome *et al.* 2014), Japan (Sotome *et al.* 2014, Wu *et al.* 2021), Korea (Cho *et al.* 2021),

Malaysia (Sotome *et al.* 2014), Philippines (Barrett 1910, Sotome *et al.* 2014), Singapore (Wu *et al.* 2021), Sri Lanka (Wu *et al.* 2021), Thailand (Kirschner and Chen 2004, Sotome *et al.* 2014, Bandara *et al.* 2015, Wu *et al.* 2021), Vietnam (Wells and Raitviir 1980, Wu *et al.* 2021), Uzbekistan (Wu *et al.* 2021). AUSTRALIA: Australia (Duncan 1972, Wu *et al.* 2021), New Zealand (Duncan 1972), Papua New Guinea (Sotome *et al.* 2014, Wu *et al.* 2021). EUROPE: Czech Republic (Wells and Raitviir 1977, Miettinen *et al.* 2012, Wu *et al.* 2015a, Wu *et al.* 2021), Denmark (Wells and Raitviir 1977, Hauerslev 1993, Wu *et al.* 2015b, Spirin *et al.* 2018a, 2019), Estonia (Wells and Raitviir 1977, Miettinen *et al.* 2012, Wu *et al.* 2015a, Wu *et al.* 2021), Finland (Spirin *et al.* 2018a, Miettinen *et al.* 2012), France (Wells 1961, Wells and Raitviir 1977, Wells and Raitviir 1980, Wu *et al.* 2015a), Wu *et al.* 2021), Georgia (Barrett 1910), Germany (Wells and Raitviir 1977, Kirschner 2010, Wu *et al.* 2021), Italy (Saitta 2015, Wu *et al.* 2015a, Wu *et al.* 2021), Netherlands (Spirin *et al.* 2018a), Norway (Miettinen *et al.* 2012, Spirin *et al.* 2018a, Alvarenga *et al.* 2019), Poland (Wells 1961, Wells and Raitviir 1980, Miettinen *et al.* 2012), Russia (Miettinen *et al.* 2012, Wu *et al.* 2015a), Spirin *et al.* 2018a, Alvarenga *et al.* 2019, Wu *et al.* 2021, Malysheva and Bulakh 2014, Wu *et al.* 2021), Sweden (Wells 1961, Wu *et al.* 2015a, Spirin *et al.* 2018a), Switzerland (Wu *et al.* 2015a, Wu *et al.* 2021), Ukrain (Wells and Raitviir 1977, Miettinen *et al.* 2012), United Kingdom (Wells and Raitviir 1977, Wells and Raitviir 1980, Roberts 1993, Wu *et al.* 2015a, Wu *et al.* 2021). NORTH AMERICA: Canada (Barrett 1910, Wells and Wong 1985, Alvarenga *et al.* 2019), Costa Rica (Wu *et al.* 2021), Cuba (Wells 1961), Jamaica (Wells 1961, Barrett 1910), Mexico (Wells 1961, Sierra *et al.* 2008, Malysheva *et al.* 2018, Alvarenga *et al.* 2019), Panamá (Wells 1961, Kirschner *et al.* 2012), USA (Barrett 1910, Duncan 1972, Wu *et al.* 2015a, Spirin *et al.* 2018a, 2019, Miettinen *et al.* 2012, Alvarenga *et al.* 2019, Miettinen *et al.* 2012, Wu *et al.* 2021), West Indies (Barrett 1910). SOUTH AMERICA: Brazil (Wells 1961, Wells and Raitviir 1980, Wu *et al.* 2015a, Malysheva *et al.* 2018, Alvarenga *et al.* 2019, Wu *et al.* 2021).

2.1.1.2.4. Family Auriculariaceae Fr.

Fries (1838) used the term 'Auricularini' for the first time (<https://www.indexfungorum.org>). Later, Lindau (Engler and Prantl 1897) established Auriculariaceae (<https://www.indexfungorum.org>) to accommodate basidiocarps with exposed hymenium and 'auricularioid' basidia (<https://en.wikipedia.org/wiki/Auriculariaceae>).

Auriculariales members have effused to effused-reflexed, tuberculate, pileate-stipitate, gelatinous to cartilaginous, tough, leathery to fleshy, gelatinous to cartilaginous basidiocarps that are hard and brittle when dry, and revive upon wetting. Hyphae are generally hyaline, and sometimes pigmented. Hymenium is amphigenous or unilateral, smooth, reticulate, poroid or with wart-like projections. Hyphal pegs, cystidia, and hyphidia may be present in the hymenium. Basidia are 2-4 celled. Transversely septate, cylindrical basidia or longitudinally septate, tremelloid basidia may be present. Basidiospores are thin-walled, smooth and hyaline, globose to cylindrical, allantoid, becoming septate in some species during the germination process. Germination may be by repetition, germ tube formation, or microconidia formation from spore wall (Wells *et al.* 2004, Li *et al.* 2023a).

Molecular and morphological studies (Weiß and Oberwinkler 2001, Wells *et al.* 2004) support the monophyly of the family Auriculariaceae, with *Auricularia*, *Exidia*, *Eichleriella* and *Exidiopsis*. Liu *et al.* (2022) recovered the monophyly of the family Auriculariaceae with 17 genera; *Auricularia*, *Adustochaete*, *Alloexidiopsis*, *Amphistereum*, *Aporpium*, *Crystallodon*, *Eichleriella*, *Elmerina*, *Exidia*, *Exidiopsis*, *Heterochaete*, *Heteroradulum*, *Hirneolina*, *Metulochaete*, *Protodaedalea*, *Sclerotrema* and *Tremellochaete*.

2.1.1.2.4.1. Genus *Auricularia* Bulliard

The genus *Auricularia*, was erected by Bulliard (1787), with *A. mesenterica* (Dicks.) Pers. as the type species. *Auricularia* has a world-wide distribution. Basidiocarps are substipitate, stipitate or resupinate, auriculiform to orbiculate, gelatinous and rubbery when fresh, which become translucent to opaque, thin and brittle when dry. Superior abhymenial surface of the basidiocarp is hairy, and inferior hymenial surface of the basidiocarp is smooth, folded to reticulate. Microscopically the basidiocarp has different zones of internal hyphae (*zona pilosa*, *zona compacta*, *zona subcompacta superioris*, *zona laxa superioris*, *medulla*, *zona laxa intermedia*, *zona laxa inferioris*, *zona subcompacta inferioris*, *hymenium*). Hymenium consists of basidia and paraphyses. Basidia are transversely three septate, cylindrical to clavate, with oil guttules and slender epibasidia. Basidiospores are inamyloid, transparent, cylindrical to allantoid (Lowy 1951, Montoya-Alvarez *et al.* 2011, Loony *et al.* 2013, Alvarenga *et al.* 2015)

Earlier attempts (Barret 1910, Kobayasi 1942) to classify *Auricularia* were based on variable features like colour, size of basidiocarp, appearance of dried specimen, abhymenial hair length and configuration of hymenial surface (Lowy 1951). To overcome the ambiguity resulting from such classifications, Lowy (1951, 1952) introduced a method based on internal stratification of hyphae and abhymenial hair length. According to Lowy (1951, 1952), different patterns of zonation are found and they were easily recognizable among the members of *Auricularia*. By making use of this pattern of zonation, Lowy (1952) described and classified taxa of *Auricularia* (Lowy 1951, Lowy 1952). The different zones described by Lowy (1951) are:

Zona pilosa: The sterile, superior zone which is composed of abhymenial hairs. Measurements of this zone vary among species, and the length of hairs is significant in species recognition. Hairs may be long or short, narrow or wide,

coloured or hyaline, pointed or blunted, making a dense mat or be more widely scattered.

Zona compacta: Narrow zone of hyphae from which abhymenial hairs arise. Composed of very compactly arranged, dense hyphae that surrounds the hair bases. They are perpendicularly oriented to the abhymenial surface and probably the darkest zone in section.

Zona subcompacta superioris: Composed of more loosely arranged hyphae than hyphae of *zona compacta*. Hyphae oriented perpendicularly to the surface.

Zona laxa superioris: The zone lies just above the medullary layer. Composed of loose, reticulately arranged hyphae with numerous anastomoses. Hyphae of this zone appear less dense towards the center of the section. This zone is absent in species which lack *medulla*.

Medulla: Central zone that may present or absent. They are characterized by the dense, transversely arranged pigmented hyphae parallel to the hymenial and abhymenial surface. Medullary layer separates the lax zone into superior and inferior.

Zona laxa intermedia: This zone is present only in those species which lack medullary layer. Separation of lax zone into superior and inferior is absent here and the loosely arranged central zone in between the compact zones is altogether termed as *zona laxa intermedia*.

Zona laxa inferioris: The zone lies below the medullary layer and *Zona subcompacta inferioris*. Hyphal nature and pattern are same as *zona laxa superioris*. This zone is absent in species which lack medulla.

Zona subcompacta inferioris: The zone lies above hymenial layer. Hyphal pattern looks similar to *zona subcompacta superioris*.

Hymenium: Fertile zone of the basidiocarp, which is located in the inferior position. This zone contains cylindrical basidia, which produces epibasidia from each of the four segments and eventually protrude out to produce cylindrical or allantoid basidiospores at its tip. Basidia, probasidia and highly branched paraphyses altogether give a dense composition to this layer.

Lowy's (1951, 1952) approach of using internal stratification are not always reliable and show variations in some conditions (Looney *et al.* 2013). Tissue structure and measurements of hyphal zones are extremely variable under environmental conditions. The age of the basidiocarp as well as the time period of tissue exposure in KOH also gives unreliable measurements of zones (Loony *et al.* 2013).

Molecular phylogenetic analyses in the genus *Auricularia* contributed data to resolve the taxonomic complexity within this genus. On the basis of phylogenetic informations from the ITS sequences, Montoya-Alvarez *et al.* (2011) reported five *Auricularia* species from Columbia and presented the monophyletic origin of this genus. Looney *et al.* (2013) revised the genus concepts in some *Auricularia* species using phylogenetic and morphological features. According to Looney *et al.* (2013), *A. delicata* (Mont. ex Fr.) Henn., which is characterized by reticulate hymenium is polyphyletic in nature. With the help of a new morphological character, 'schizomedulla' and molecular data, Looney *et al.* (2013) distinguished two novel species in the *A. delicata* complex. Wu *et al.* (2014) conducted phylogenetic study on Chinese *Auricularia* species, and erected a new species, *A. heimuer*, which was commercially using as edible *Auricularia* species in China. Malysheva and Bulakh (2014) conducted phylogenetic analyses to reveal the evolutionary relationships within the *Auricularia* species and species complexes in Russia. They described and phylogenetically placed seven *Auricularia* species from Russia and reported *A. villosula* Malysheva as new to science. Wu *et al.* (2015a) studied phylogeny and

diversity of *A. mesenterica* complex using samples from Europe, China and Brazil. Based on both molecular and morphological evidences, they erected two new species and reported them within the monophyletic *A. mesenterica* clade. Wu *et al.* (2015b) studied global diversity and taxonomy of *A. auricula-judae* by ITS sequences and combined ITS, LSU and *rpb2* sequences. The study delineated seven species from the complex and introduced three species new to science. Wu *et al.* (2021) studied the diversity and phylogeny of genus *Auricularia* based on ITS, LSU, *rpb1*, and *rpb2* sequences and resolved taxonomic uncertainty related to *Auricularia* species. According to the *Index Fungorum* (accessed on 01-08-2024), the genus currently contains 109 species.

2.1.1.2.4.1.1. Ecological and economic importance

Auricularia is economically important with members having culinary and medicinal properties. *Auricularia* members have an important place in traditional Asian medicine. The cultivation of *Auricularia* started 1300 years ago in China (Wu *et al.* 2014). Edible *Auricularia* members are rich sources of carbohydrates, proteins, fat, fibre, vitamins and minerals. *Auricularia* is the third most cultivated mushroom genus after *Lentinula* and *Pleurotus* (Fr.) P. Kumm. (Royse *et al.* 2017, Bandara *et al.* 2019). Gelatinous and crunchy texture of *Auricularia* and its unique flavour is the basis of high popularity and consumption rate in China and Southeast Asia (Misaki and Kakuta 1995, Cheung 2013, Jo *et al.* 2014, Bandara *et al.* 2019).

In addition to the food industry, *Auricularia* has potential to make therapeutic drugs. Polysaccharides from *Auricularia* are known for the anti-tumor, antioxidant, anti-coagulant, anti-hypercholesterolemic, hypoglycaemic, anti-viral, anti-bacterial and immunomodulating properties (Ma *et al.* 2018, Bandara *et al.* 2019).

2.1.1.2.4.1.2. Distribution

AFRICA: Kenya (Duncan 1972, Onyango *et al.* 2016, Wu *et al.* 2021), Uganda (Wu *et al.* 2021). ASIA: (Wu *et al.* 2021), China (Bandara *et al.* 2015, Du *et al.* 2016, Wu *et al.* 2014, 2015b, 2021), India (Duncan 1972, Kumari *et al.* 2013), Japan (Shirouzu *et al.* 2018), Korea (Cho *et al.* 2021), Thailand (Bandara *et al.* 2015, 2017). AUSTRALIA: Duncan 1972, Loony *et al.* 2013, Wu *et al.* 2021, New Zealand (Duncan 1972), Papua New Guinea (Wu *et al.* 2021). EUROPE: Czech Republic (Wu *et al.* 2015b, 2021). Denmark (Wu *et al.* 2015b, Wu *et al.* 2021), France (Wu *et al.* 2015b, Wu *et al.* 2021), Germany (Wu *et al.* 2015b, Wu *et al.* 2021), Russia (Malysheva and Bulakh 2014, Wu *et al.* 2015b, Wu *et al.* 2021), Switzerland (Loony *et al.* 2013), UK (Wu *et al.* 2015b, Wu *et al.* 2021). NORTH AMERICA: Canada (Loony *et al.* 2013, Barrett 1910), Costa Rica (Loony *et al.* 2013), Cuba (Loony *et al.* 2013), Jamaica (Duncan 1972, Loony *et al.* 2013), Mexico: (Sierra *et al.* 2008, Loony *et al.* 2013), USA (Barrett 1910, Duncan 1972, Loony *et al.* 2013, Wu *et al.* 2015a, Wu *et al.* 2021). SOUTH AMERICA: Argentina (Loony *et al.* 2013), Brazil (Alvarenga *et al.* 2015, Wu *et al.* 2015b, Wu *et al.* 2021). Peru (Loony *et al.* 2013), Columbia (Barrett 1910, Montoya-Alvarez *et al.* 2011).

2.1.1.3. Order SEBACINALES M. Weiss, Seloese, Rexer, A. Urb. and Oberw.

Weiss *et al.* (2004) established the order Sebacinales to accommodate the family Sebacinaceae K. Wells and Oberw. Sebacinales members are characterised by the presence of imperforate parentheses at the septal pores, longitudinally septate (exidioid) basidia, ability of basidiospores to produce ballistoconidia (secondary spores), thick hyphal walls in substrate hyphae, lack of clamp-connections and cystidia (Wells and Bandoni 2001, Weiss *et al.* 2004, Murphy *et al.* 2014, Hibbett *et al.* 2014).

Sebacinales contain both basidiocarp forming and basidiocarp lacking members. Different types of basidiocarp morphology like corticoid (*Sebacina* Tul. and C. Tul.), pustulate (*Efibulobasidium* K. Wells), cushion shaped (*Craterocolla* Bref.), coralloid (*Tremellodendron* G.F. Atk.), infundibuliform (*Tremelloscypha* D.A. Reid) and stereoid (*Tremellostereum* Ryvarden) forms can be seen in Sebacinales. Molecular phylogenetic analyses suggest that basidiocarp morphology is a poor marker for generic delimitations in Sebacinales (Weiß *et al.* 2016). Weiss *et al.* (2004) identified two groups (named group A and group B) in Sebacinales based on the molecular phylogeny (Murphy *et al.* 2014). Subsequent workers named Group A as Sebacinaceae (Oberwinkler *et al.* 2014) and Group B as Serendipitaceae M. Weiss, F. Waller, Zuccaro and Selosse (Weiß *et al.* 2016). Sebacinaceae contains basidiocarp forming members, which develop as root endophytes, ectomycorrhiza, and orchid mycorrhiza (on partially or fully mycoheterotrophic orchids) (Weiß *et al.* 2016, Fritsche *et al.* 2021).

Group B or Serendipitaceae lack macroscopically visible basidiocarps and they can form different types of mycorrhizal associations compared to Sebacinaceae. Oberwinkler (1964) described the first Serendipitaceae member and named it *Sebacina vermifera* Oberw. which is characterised by longitudinally septate basidia and worm-like basidiospores. Later, isolates with similar characters were reported from terrestrial Australian orchids (Warcup and Talbot 1967, Warcup 1988). Roberts (1993) erected the genus *Serendipita* P. Roberts to accommodate taxa which lack macroscopically visible basidiocarp, exceptionally thin branched hyphae, formation of single basidia or basidial clusters from a common sub-basidial cell, lack of hyphidia, globose basidia with short sterigmata and elongated basidiospores. Roberts (1993) designated *Serendipita vermifera* as the type species of genus *Serendipita*. Genus *Piriformospora* Sav. Verma, Aj. Varma, Rexer, G. Kost and P. Franken was introduced by Verma *et al.* (1998) to accommodate anamorphic taxa,

Piriformospora indica, collected from soil, which easily colonises plant roots. Weiß *et al.* (2016) conducted molecular phylogenetic studies in Sebaciales and found that *Piriformospora* (based on the anamorphic stage) and *Serendipita* (based on the teleomorphic stage) can not be separated taxonomically. Weiß *et al.* (2016) merged *Piriformospora* with *Serendipita* and proposed two combinations *S. indica* (from *P. indica*) and *S. williamsii* (Zuccaro and M. Weiss) M. Weiss, F. Waller, Zuccaro and Selosse (from *P. williamsii*). Currently, family Serendipitaceae is monotypic (He *et al.* 2019) with genus *Serendipita* having 23 species records (www.indexfungorum.org accessed on 01-08-2024).

2.1.1.3.1. Taxonomic characters of Sebaciales

Macroscopic characters

Basidiocarp morphology of Sebaciales ranges from microscopic to pustulate, resupinate, erect or branching with amphigenous hymenia, and flabellate to infundibuliform with unilateral hymenia (Oberwinkler 1964, Wells and Oberwinkler 1982). Basidiocarps have cartilaginous to rubbery or gelatinous consistency (Sesli 2021). In contrast to other sebacinean species which grows on soil, *S. dimitica* Oberw. grows on the bark (Oberwinkler *et al.* 2014).

Microscopic characters

Basidia

Sebacineae members have ovate to pyriform basidia without basal clamp-connections. They are longitudinally cruciate septate which giving rise to long sinuous epibasidia (Selosse *et al.* 2007, Sesli 2021).

Hyphidia/Dikaryophyses

Hyphidia are sterile terminal hyphae with protective function present in all sebacinean species except *S. allantoidea* R. Kirschner and Oberw.

(Oberwinkler *et al.* 2014). Hyphidia are present in the hymenium along with basidia. They may be simple to little branched, apically short branched to nodulose, sometimes forming a palisade like layer covers young and mature basidia in the hymenium (Wells and Oberwinkler 1982). Encrusted hyphidia are present in *Ditangium* P. Karst. species (Oberwinkler *et al.* 2014). Apically ramified hyphidia are present in *Efibulobasidium* species.

Basidiospores

Basidiospores of Sebacinales range from broadly ovate, ellipsoid, oblong to short cylindrical or allantoid. They are capable of germinating by repetition (Wells 1975, Wells and Oberwinkler 1982). *Serendipita* members have long and narrow, filiform or slightly curved basidiospores (Oberwinkler 1964, Oktalira *et al.* 2021).

Resting spores

Resting spores are thick-walled spores with irregular spore wall. Developments of "star-like" resting spores are reported from secondary spores of *S. epigaea* (Berk. and Broome) Bourdot and Galzin *s.str.* Although resting spore formation from basidiospores are not reported anywhere, Oberwinkler *et al.* (2014) predicted that there is possibility for such development.

Hyphae

Most of the members of Sebacinales have monomitic hyphal system, whereas, all *Tremellodendron* species and *S. dimitica*, have dimitic hyphal system (Oberwinkler *et al.* 2014). Presence of thick-walled hyphae in the central region supports the upright growth pattern of *Tremellodendron* species. Heavily gelatinising hyphal walls are present in species like *E. rolleyi* (L.S. Olive) K. Wells, *S. epigaea s.str.* (Oberwinkler *et al.* 2014). Finely encrusted hyphae are present in the genus *Ditangium* (Oberwinkler *et al.* 2014).

Anamorphic members

Sebacinales contains anamorphic taxa belonging to different genera like *Serendipita*, *Chaetospermum* Sacc. and *Ditangium* (Kirschner and Oberwinkler 2009, Wells and Bandoni 2001). Fruiting structures are totally absent in *Serendipita* and majority of *Serendipita* members are anamorphic in nature (Oberwinkler *et al.* 2014). Members of the genus *Chaetospermum* produce anamorphic fructifications which are characterised by gelatinous conidiomata, cylindrical, non-septate conidia with tubular appendages, and holoblastic sympodial conidiogenesis (Sutton 1980, Nag Raj 1993). Genus *Ditangium* also produces anamorphic fructifications and sometimes both anamorphic and teleomorphic fruiting bodies grow together (Oberwinkler *et al.* 2014, Malysheva *et al.* 2018). The name *Craterocolla* was previously used to the teleomorphic forms and *Ditangium* was used for the anamorphic forms. Malysheva *et al.* (2018) replaced the younger name *Craterocolla* as later homonym of *Ditangium*. *Ditangium* produces crater-like fructifications in anamorphic forms, and pustulate or cerebriform basidiocarps (Malysheva *et al.* (2018).

Molecular characters

Molecular data was the basis of separation of Sebacinaceae from Auriculariales (Weiß and Oberwinkler 2001, Oberwinkler *et al.* 2013). Weiss *et al.* 2004 erected order Sebacinales based on the D1/D2 gene regions of ribosomal large subunit. Hibbett *et al.* (2007) used LSU, SSU, 5.8S, *rpb2*, *tef1* gene regions of Sebacinales members when they proposed the phylogenetic classification of kingdom Fungi. A combination of ITS and LSU sequences was used by Garnica *et al.* (2013) in the phylogenetic study of sebacinoid fungi associated with different plant communities. Reiss *et al.* (2013) found that *rpb2* and *atp6* genes show high interspecific synonymous polymorphism in the genus *Sebacina*. Oberwinkler *et al.* (2014) used ITS and the LSU regions in their combined morphological and molecular study on the Sebacinales. Garnica *et al.* (2016)

used the combination of 18S, ITS, 28S, *rpb1* and *atp6* to study the divergence times and phylogenetic patterns of Sebaciales. ITS and *tef1* gene regions are used by Malysheva *et al.* (2019) in their study on the genus *Ditangium*.

Ultrastructure

Sebaciales has dolipore septa with continuous parentheses (Khan and Kimbrough 1980, Oberwinkler 1985, Oberwinkler *et al.* 2013). In *Serendipita vermifera*, continuous parentheses are associated with a strand of unmodified endoplasmic reticulum (Muller *et al.* 1998, Wells and Bandoni 2001). Williams and Thilo (1989) compared the ultrastructure of some *Rhizoctonia* DC. species with four Sebaciales members (*Sebacina calcea* (Pers.) Bres., *S. grisea* Bres., *S. umbrina* D.P. Rogers and *Serendipita vermifera*), and observed their similarity in the septal pore parentheses features. Ultrastructural details of *Sebacina calcea*, *S. grisea*, *S. umbrina* and *Serendipita vermifera* are available at the online public AFTOL Structural and Biochemical database (<https://aftol.umn.edu>) (Kumar *et al.* 2013).

2.1.1.3.2. Ecological and economic importance

Sebaciales have diverse associations with roots of land plants (Weiss *et al.* 2004, Weiß *et al.* 2016, Garnica *et al.* 2013, Oberwinkler *et al.* 2013, Oktalira *et al.* 2021) and exhibits saprotrophic, endophytic and mycorrhizal nutritional modes (Weiß *et al.* 2016).

Early diverging genera of family Sebacinaceae, like *Paulisebacina* Oberw., Garnica and K. Riess, *Craterocolla*, *Efibulobasidium*, *Chaetospermum* and *Globulisebacina* Oberw., Garnica and K. Riess are saprobic (Rungjindamai *et al.* 2008). Sebaciales members can form symptomless endophytic relationship with bryophytes, pteridophytes, and angiosperms (Selosse *et al.* 2009, Weiß *et al.* 2011, 2016; Murphy *et al.* 2014, Garnica *et al.* 2016, Fritsche *et al.* 2021). *Serendipita indica* and *S. williamsii* are cultivable Serendipitaceae species.

Their genetic tractability, availability of genome and broad host plant range makes them good model organism for studying plant-fungal interactions (Hibbett *et al.* 2014, Weiß *et al.* 2016). *Serendipita vermifera* and *S. indica* are promising biocontrol and biofertilising agents for crop plants (Waller *et al.* 2008, Selosse *et al.* 2009, Weiß *et al.* 2011).

Sebacinales can form different types of mycorrhizal interactions like ectomycorrhizal association with herbs and trees, ericoid mycorrhiza with Ericaceae members, orchid mycorrhiza with photoautotrophic and heterotrophic orchids, and mycorrhiza-like interactions with liverworts (Garnica *et al.* 2013, Oberwinkler *et al.* 2013, Weiß *et al.* 2016). Genera like *Helvellosebacina* Oberw., Garnica and K. Riess, *Sebacina*, *Serendipita* and *Tremelloscypha* contain species having ectomycorrhizal (ECM) associations (Weiß *et al.* 2016). Sebacinaceae is the most species rich group with abundant nonspecific ECM members from temperate and tropical regions (Tedersoo and Nara 2010, Moyersoen and Weiß 2014, Toju *et al.* 2016, Weiß *et al.* 2016).

2.1.1.3.3. Distribution

Sebacinales members have world-wide distribution (Weiß *et al.* 2011, Garnica *et al.* 2016, Fritsche *et al.* 2021) AFRICA: Egypt (Weiß *et al.* 2011), Ethiopia (Weiß *et al.* 2011), Namibia (Weiß *et al.* 2011), South Africa (Weiß *et al.* 2011), Sudan (Weiß *et al.* 2011). ANTARCTICA: (Newsham and Bridge 2010). ASIA: India (Wakefield 1922, Nag Raj 1964, Rajeshkumar *et al.* 2010), Russia (Malysheva *et al.* 2019), Taiwan (Kirschner *et al.* 2017). AUSTRALIA: Phillips *et al.* (2016), Ruibal *et al.* (2014). EUROPE: Austria (Weiß *et al.* 2011), Czech Republic (Malysheva *et al.* 2019), England (McNabb 1969, Roberts 1993), France (Weiß *et al.* 2011), Finland (Malysheva *et al.* 2019), Germany (Kirschner and Oberwinkler 2002, Weiß *et al.* 2011, Riess *et al.* 2013, Garnica *et al.* 2013, Malysheva *et al.* 2019), Iceland (Weiß *et al.* 2011), Italy (McNabb 1969, Weiß *et al.* 2011), Norway (Malysheva *et al.* 2019), Slovenia (Weiß *et al.* 2011), Switzerland (Weiß *et al.*

2011), Turkey (Sesli 2021), Ukraine (Malysheva *et al.* 2019). NORTH AMERICA: Jamaica (Wells and Oberwinkler 1982), Panama (Kirschner *et al.* 2017), U.S.A (McNabb 1969, Weiß *et al.* 2011). SOUTH AMERICA: Brazil (Fritsche *et al.* 2021), Ecuador (Weiß *et al.* 2011, McNabb 1969, Setaro *et al.* 2006), Guyana (Henkel *et al.* 2004), Venezuela (Moyersoen and Weiß 2014).

2.1.1.3.4. Family Sebacinaceae K. Wells and Oberw.

The family Sebacinaceae was erected by Wells and Oberwinkler (1982) based on micromorphological features, like longitudinally septate basidia, absence of clamp-connections, and often thick-walled hyphae, particularly within the substratum. Wells and Oberwinkler (1982) included four genera (*Sebacina*, *Tremellodendron*, *Tremelloscypha* and *Efibulobasidium*) within Sebacinaceae. Study of Oberwinkler *et al.* (2014) merged genus *Sebacina* with *Tremellodendron*, since *Tremellodendron* clusters within *Sebacina* *s. str.* in the phylogenetic analysis. Same study erected three more genera *Globulisebacina*, *Helvellosebacina* and *Paulisebacina* under Sebacinaceae (Oberwinkler *et al.* 2014). Currently, the family Sebacinaceae contains eight genera, *Chaetospermum*, *Ditangium*, *Efibulobasidium*, *Globulisebacina*, *Helvellosebacina*, *Paulisebacina*, *Sebacina* and *Tremelloscypha* (He *et al.* 2019).

The genus *Chaetospermum* was erected by Saccardo (1892) based on *Tubercularia chaetospora* Pat. (Rajeshkumar *et al.* 2010). *Chaetospermum* is characterised by gelatinous conidiomata, conidia with tubular appendages, and holoblastic sympodial conidiogenesis (Rajeshkumar *et al.* 2010, Tan *et al.* 2014). Currently, the genus *Chaetospermum* contain ten members (<https://www.indexfungorum.org> accessed on 01-08-2024). The genus *Ditangium* was treated as a heterotypic synonym of *Craterocolla* (Malysheva *et al.* 2019). Studies of Weiss *et al.* (2004) and Oberwinkler *et al.* (2014), has noticed the placement of *Craterocolla* members within the order Sebaciales. Later, Malysheva *et al.* (2019) re-introduced *Ditangium* (Karsten 1867) to replace the

older name *Craterocolla* (Brefeld 1888). Crater-like young basidiocarps, presence of both anamorphic and telomorphic fruitifications together, lack of clamp-connections are the characteristic features of *Ditangium* (Malysheva *et al.* 2019). Currently, the genus contains five members (<https://www.indexfungorum.org> accessed on 01-08-2024). Wells (1975) erected the genus *Efibulobasidium*, with two members, *E. rolleyi* and *E. albescens* (Sacc. and Malbr.) K. Wells, and placed *E. albescens* as the type species (Kirschner *et al.* 2017). Both *E. rolleyi* and *E. albescens* have small gelatinous basidiocarps which coalesce when mature (Oberwinkler *et al.* 2014). According to Oberwinkler *et al.* (2014), *E. rolleyi* lacks the *Chaetospermum* conidial stage and is phylogenetically not related to the *E. albescens* or *Chaetospermum* clade. So, a new genus *Globulisebacina* was erected by Oberwinkler *et al.* (2014) to include *E. rolleyi*. At present, the genus *Efibulobasidium* contains three species (<https://www.indexfungorum.org> accessed on 01-08-2024). The genus *Helvellosebacina* is characterised by resupinate to upright merulioid–helvelloid basidiocarp and simple to rarely branching hyphidia (Oberwinkler *et al.* 2014). *Helvellosebacina* is comprised of three members (<https://www.indexfungorum.org> accessed on 01-08-2024). *Paulisebacina* is a monotypic genus with *P. allantoidea* R. Kirschner and Oberw. The genus is characterised by extremely thin basidiocarp without hyphidia (Oberwinkler *et al.* 2014). Genus *Tremelloscypha* was erected by Reid (1979) with *T. australiensis* D.A. Reid as the type species. *Tremelloscypha* currently includes 4 species (<https://www.indexfungorum.org> accessed on 01-08-2024).

2.1.1.3.4.1. Genus *Sebacina* Tul. and C. Tul.

Tulasne and Tulasne (1871) erected the genus *Sebacina* to accommodate *S. incrustans* (Pers.) Tul. and C. Tul. (Tulasne and Tulasne 1871, Oberwinkler *et al.* 2013). *Sebacina incrustans* was originally described as *Corticium incrustans* (Persoon 1796). Since *S. incrustans* has longitudinally septate basidia and

Corticium Pers. members have holobasidia, Tulasne and Tulasne (1872) transferred *Corticium incrustans* into *S. incrustans* (Weiß *et al.* 2016).

All resupinate forms of fungi with cruciate septate basidia and gelatinous texture were treated under the genus *Sebacina* (Ervin 1957). *Sebacina* is a heterogenous group with resupinate basidiocarp, smooth or undulate hymenium, and tremellaceous basidia (Ervin 1957). Ervin (1957) studied the genus *Sebacina* in detail and supported the derivation of four genera (*Bourdotia*, *Exidiopsis*, *Heterochaetella* and *Sebacina*) from *Sebacina sensu* McGuire (1941) and Martin (1944). Phylogenetic studies using the nuclear ribosomal DNA regions later confirmed the placement of *Bourdotia* (Bres.) Bres. and Torrend, *Exidiopsis* and *Heterochaete* in the Auriculariales (Weiß and Oberwinkler 2001).

Sebacina incrustans is the type species of the genus *Sebacina* (Reiss *et al.* 2013). The polyphyletic nature of *Sebacina* and the diversity of molecular data in sebacinalean species complexes were noticed by many workers (Weiss *et al.* 2004, Reiss *et al.* 2013, Murphy *et al.* 2014, Oberwinkler *et al.* 2014, Weiß *et al.* 2016). Oberwinkler *et al.* (2014) emended the genus *Sebacina* to include *Tremellodendron*, on the basis of the scattered clustering of *Tremellodendron* species within other *Sebacina* clades in the phylogenetic analysis. According to Oberwinkler *et al.* (2014), the upright growth pattern of basidiocarp, which is characteristic of *Tremellodendron* may be a result of convergent evolution.

Sebacina is characterized by longitudinally septate basidia, imperforate parentheses and absence of clamp-connections (Selosse *et al.* 2007, Ray and Craven 2016).

2.1.1.3.4.1.1. Ecological and economic importance

Sebacina forms different types of mycorrhizal associations like ectomycorrhiza, ectendomycorrhiza, ericoid mycorrhiza, jungermannioid

mycorrhiza and cavendishoid mycorrhiza with different land plants (Selosse *et al.* 2002, 2007; Weiss *et al.* 2004, Weiß *et al.* 2016, Garnica *et al.* 2013, Oberwinkler *et al.* 2013, Kühdorf *et al.* 2014, Oktalira *et al.* 2021).

2.1.1.3.4.1.2. Distribution

AUSTRALIA: Ruibal *et al.* (2014), Phillips *et al.* (2016). EUROPE: Germany (Kirschner and Oberwinkler 2002, Oberwinkler *et al.* 2014), Italy (McNabb 1969), Spain (Martínez 1992, Dueñas 2005). NORTH AMERICA: Costa Rica (Kühdorf *et al.* 2014), USA (McNabb 1969). SOUTH AMERICA: Brazil (Wartchow *et al.* 2017), Ecuador (McNabb 1969), Venezuela (Moyersoen and Weiß 2014). Tahiti (Olive 1958), Belize (Roberts 2008a).

2.1.2. Class DACRYMYCETES Doweld

Dacrymycetes (Agaricomycotina, Basidiomycota, Fungi) is a well defined monophyletic clade with unique basidial morphology and ultrastructure (Zamora and Ekman 2020). Dacrymycetes is characterised by long, bifurcating (forked) holobasidia (Hibbett *et al.* 2007, Zamora and Ekman 2020), and continuous parentheses covering the dolipore-type septa (Oberwinkler 1994, Wells 1994, Wells and Bandoni 2001, Shirouzu *et al.* 2013a).

According to Oberwinkler (2014), Dacrymycetales is a natural order with shared common characters. The pigmentation of basidiocarps (*Cerinomyces* G.W. Martin members and *Ditiola haasii* Oberw. are exceptions with unpigmented basidiocarps), ontogeny and morphology of the basidium, morphology and the germination patterns of basidiospores, characteristics of septal pore apparatus, and the predominantly brown rot type of wood decay are common characters among the dacrymycetoid members. Phylogenetic studies suggest that the ancestors of Dacrymycetes were most likely the early divergent wood decomposers in Basidiomycota (Floudas *et al.* 2012, Shirouzu *et al.* 2013a, Zhao *et al.* 2017, Varga *et al.* 2019).

In the taxonomic history, Martin (1945) segregated basidiomycetes into two groups. "Heterobasidiomycetes" and "Homobasidiomycetes". Martin (1945) treated the family Dacrymycetaceae under Tremellales along with other Heterobasidiomycetes members by considering the epibasidium of Dacrymycetaceae as a part of the basidia rather than part of sterigma (Talbot 1973, Wells 1994). Later, Talbot (1954, 1968, 1973) and Donk (1958) divided basidiomycetes into three classes based on the type and structure of basidia: Teliomycetes, Phragmobasidiomycetes and Holobasidiomycetes. They treated dacrymycetoid fungi under Holobasidiomycetes along with species having aseptate basidia (Castro-Santiuste *et al.* 2017).

Based on molecular phylogenetic analyses, Hibbett (2006) and Hibbett *et al.* (2007) considered Dacrymycetes under Agaricomycotina, as a sister group to Agaricomycetes and Tremellomycetes. Hibbett *et al.* (2007) treated two families Cerinomycetaceae Jülich and Dacrymycetaceae under the order Dacrymycetales. Traditionally, Dacrymycetes was comprised of a single order Dacrymycetales. This classification system remained unaltered for a long time (Brasfield 1938, Kobayasi 1939a,b; Kennedy 1958, Reid 1974, Oberwinkler 1994). Shirouzu *et al.* (2013a) showed the clustering of *Dacrymyces unisporus* (L.S. Olive) K. Wells as a sister clade to remaining Dacrymycetes members. *Dacrymyces unisporus* was specially characterised by non-bifurcate cylindrical basidia and subglobose to ovoid basidiospores with transverse and longitudinal septa. Along with molecular data, electron microscopic studies conducted by Shirouzu *et al.* (2013a) also supported the independent lineage of *D. unisporus* within Dacrymycetes. As a result, they erected another order Unilacrymales Shirouzu, Tokum. and Oberw. and family Unilacrymaceae Shirouzu, Tokum. and Oberw. to accommodate this species. In the multilocus phylogeny of Zamora and Ekman (2020), they observed the separation of Dacrymycetes as four different lineages, the already existing Cerinomycetaceae, Dacrymycetaceae, Unilacrymaceae and an additional lineage. This additional lineage was later

formally erected to the level of a family, Dacryonaemataceae J.C. Zamora and Ekman, to accommodate its three species. The order level placement of the family is uncertain. Currently, the class Dacrymycetes contains two orders, four families and 13 genera (Alvarenga and Gibertoni 2022).

2.1.2.1. Order DACRYMYCETALES Henn.

Dacrymycetales is the largest order in the class Dacrymycetes with two families, Dacrymycetaceae and Cerinomycetaceae. The families were separated based on basidiocarp morphology (Shirouzu *et al.* 2013a). The family Dacrymycetaceae contained members with pulvinate to dendroid basidiocarps. The family Cerinomycetaceae included resupinate basidiocarps (Shirouzu *et al.* 2013a).

Cerinomycetaceae is a monotypic family with *Cerinomyces* as the only genus. According to McNaab (1964), Cerinomycetaceae is characterised by corticioid, resupinate, typically ochraceous to buff basidiocarps with waxy gelatinous or cartilaginous texture and bifurcating basidia. Taxonomic position of the *Cerinomyces* in Dacrymycetales has been in controversy due to its varied micromorphological features (McNabb 1964). Savchenko *et al.* (2021) conducted revision with detailed phylogenetic analysis of *Cerinomyces* and suggested that the genus is not limited to the corticioid members, but includes members with a combination of hyphal clamp-connections, mostly aseptate thin-walled basidiospores, and low content of carotenoid pigments.

2.1.2.1.1. Taxonomic characters of Dacrymycetales

Dacrymycetales members are easily distinguishable from other fungal groups by their gelatinous texture, wood habiting nature, mostly bright yellowish to orange basidiocarps and unique basidial ontogeny and morphology (Oberwinkler 2014). Morphology of basidiocarp, hymenial position, growth pattern, hyphal structure, wall thickness, and shape of marginal hyphae

are the important taxonomic characters used in generic delimitation (Brasfield 1938, McNabb and Talbot 1973, Zamora and Ekman 2020). For species delimitation, characteristics of internal hyphae, presence of clamp-connections, size, shape and number of septations of basidiospores, characters of conidia have been used. Although the characters can be easily observed, the lack of variation among these characters makes genus level identification difficult (Shirouzu *et al.* 2007, Savchenko *et al.* 2022).

Macroscopic characters

Basidiocarp morphology of the Dacrymycetales varies from corticoid, resupinate, pustulate, pulvinate, cerebriform, turbinate, cupulate, cyphelloid, simple or branching clavarioid, stalked spathulate or capitate to sessile discoid (Reid 1974, Oberwinkler 1994, Wells 1994, Shirouzu *et al.* 2009). The members of *Cerinomyces* have a corticoid to resupinate habit. Basidiocarps of *Ditiola*, *Heterotextus* Lloyd, *Femsjonia* Fr., *Guepiniopsis* Pat., and *Dacryopinax* have cupulate, turbinate or spathulate morphology. Members of *Dacryonaema* Nannf. have capitate basidiocarps with globose fertile head. *Calocera* members have simple to forked, clavarioid basidiocarps and *Dacryomitra* Tul. and C. Tul have stalked basidiocarp with morcheloid head (Oberwinkler 2014).

Basidiocarps of Dacrymycetales have a gelatinous to waxy, or fleshy cartilaginous texture depending on the gelatinisation of the hyphal walls and water content. The colour of basidiocarp varies from hyaline to bright yellow and orange (Reid 1974, Oberwinkler 1994, Wells 1994, Shirouzu *et al.* 2009). According to Brasfield (1938), colour of basidiocarp can be used as a taxonomic character, but it should be used with caution, since colour may change due to the exposure to sun or prolonged soaking. Absence of colour or semitransparent nature is also common in Dacrymycetales members, especially when growing in darkness (Vail and Lilly 1968, Savchenko *et al.* 2021). *Dacryonaema rufum* (Fr.) Nannf. (dark brown to dark reddish brown) and *Ditiola*

haasii Oberw. (hyaline) are exceptional species that consistently lack yellow or orange coloured basidiocarps (Oberwinkler 2014, Zamora and Ekman 2020). Discoloured basidiocarps are also present in *Cerinomyces* members like *C. cokeri* (McNabb) A. Savchenko and J.C. Zamora and *C. tortus* (Willd.) Miettinen, J.C. Zamora and A. Savchenko (Savchenko *et al.* 2021).

Microscopic characters

Hymenium

Hymenial surface is generally smooth. Position of hymenium varies among different species. In *Dacrymyces spathularia* (Schwein.) Alvarenga, hymenium is unilateral (limited to one side of the basidiocarp) (McNabb 1965b). Members like *D. stillatus* Nees has amphigenous hymenium hymenium covered all around the fertile part of basidiocarp, except the stipe or portion attaching to the substratum (Reid 1974, Kennedy 1958). In *Guepiniopsis*, which has cupulate basidiocarp, the hymenium is limited to the interior of the cup (McNabb 1965c). Hyphidia is present in between basidia in the hymenium.

Basidia

Probasidia of Dacrymycetales members are cylindrical to clavate in nature and expand apically into two long cylindrical epibasidia. Sterigma develops at the tip of each epibasidia, on which basidiospores will develop (Kennedy 1958, Oberwinkler 2014).

Basidiospore

Basidiospores are curved-cylindrical to allantoid, which become transversely septate soon after discharge. *Dacrymyces ovisporus* Bref. and *Guepiniopsis chrysocoma* (Bull.) Brasf. produce subglobose, and ovate to broadly elliptic basidiospores respectively. The number and thickness of septations are species specific (Kennedy 1958, Reid 1974, Wells 1994, Wells and Bandoni 2001). In some *Cerinomyces* members like *C. crustulinus* (Bourdot and Galzin) G.W. Martin, *C. canadensis* (H.S. Jacks. and G.W. Martin) G.W. Martin, and *C.*

pallidus G.W. Martin, spores are exceptionally aseptate (Oberwinkler 2014). Basidiospores with oblique to muriform septations are present in *D. ovisporus* and *G. chrysocoma* (Reid 1974, Oberwinkler 2014).

The basidiospores of Dacrymycetales do not produce secondary ballistospores but form microconidia, or germinate directly (Reid 1974, Wells 1994). The shape and size of microconidia produced by germinating basidiospores can help in species recognition (Oberwinkler 2014).

Hyphidia/Dikaryophyses

Hyphidia are sterile elements present in hymenium in between basidia. They may vary in shape and size among different members. Commonly, hyphidia are narrower than basidium, aseptate or septate, with or without clamp-connections, and grow up to the length of basidium or longer (Kennedy 1958). Slender unbranched hyphidia are present in *D. estonicus* Raitv., *D. pachysporus* Shirouzu and *D. stenosporus* Shirouzu and in many more Dacrymycetales members (Oberwinkler 2014, Shirouzu *et al.* 2017). Weakly branched hyphidia can be seen in *Cerinomyces* members.

Tramal hyphae

Tramal hyphae of Dacrymycetales members are gelatinised (Kennedy 1958). This feature helps them to survive through desiccation. Wall thickness and carotenoid pigmentation varies from species to species (Oberwinkler 2014). Both thick-walled and thin-walled hyphae with or without clamp-connections can be seen. The presence of clamp-connections can be used for species delimitation (Oberwinkler 2014). Normal clamp-connections and medallion clamp-connections (clamp-connection where there is a gap between main hyphae and the hook) are present within the order (Savchenko 2023). Tramal hyphae may be smooth or roughened due to gelatinised layer (Figure: 27) (Savchenko *et al.* 2022).

Terminal cells of cortical/ marginal hairs

Abhymenial surface of Dacrymycetales members are covered with specialised hyphal end cells called marginal hairs or cortical hairs, which have been used for traditional generic delimitation in this group (Oberwinkler 2014).

Members of the family Dacryonaemataceae have branched and frequently anastomosing cortical hairs, which was one of the key family characters used by Zamora and Ekman (2020). *Heterotexus* members have thick-walled, apically blunt, and basically swollen marginal hairs. This type of marginal hair is also reported in *Dacrymyces suecicus* MacNabb, indicating its relatedness with *Heterotexus* (McNabb 1973, Oberwinkler 2014). The genus *Guepiniopsis* is characterized by thick-walled, layered, catenulate or capitate, or obpyriform marginal hairs (Kennedy 1958, Reid 1974, Oberwinkler 2014). Based on the presence of marginal hairs, Dueñas (2005) transferred *D. estonicus* Raitv. to *Guepiniopsis*. *Dacryonaema rufum* have thin and strongly ramified marginal hairs (Oberwinkler 2014).

Dacryopinax elegans (Berk. and M.A. Curtis) G.W. Martin have thick-walled, cylindrical fascicle of marginal hairs. In *D. indacocheae* Lowy, *D. lowyi* S. Sierra and Cifuentes and *D. primogenitus* D.J. McLaughlin and E.G. McLaughlin, bulbous abhymenial hairs are present (McLaughlin *et al.* 2016, Alvarenga and Gibertoni 2022).

Anamorphic members

In genera like *Cerinomyces*, *Dacrymyces*, *Ditiola*, and *Femsjonia*, microconidia developing from basidiospores or hyphae, and the development of yeast colonies in cultural conditions are anamorphs (Ingold 1983, Maekawa 1987, De Hoog 1993, Oberwinkler 1994, Kirschner and Yang 2005). Genus *Dacryoscyphus*, erected by Kirschner and Yang (2005) contain anamorphic members. *Dacryoscyphus chrysochilus* R. Kirschner and Zhu L. Yang, type species

of *Dacryoscyphus* is characterised by cupulate conidiomata and staurosporous conidia, which grow on dead twigs of *Rhododendron* species (Kirschner and Yang 2005, Oberwinkler 2014). Based on morphological and molecular similarities, Kirschner *et al.* (2010) transferred two species *Dacrymyces pinacearum* Shirouzu and Tokum. and *D. subarcticus* Shirouzu and Tokum. to *Dacryoscyphus* (Shirouzu *et al.* 2009). Currently, the genus *Dacryoscyphus* contains three members (<https://www.indexfungorum.org> accessed on 01-08-2024).

Ultrastructure

Ultrastructural details of septa are highly significant in this group as phylogenetic markers (Grand and Moore 1971, Lü and McLaughlin 1991, Wells 1994, Sierra *et al.* 2013). Dacrymycetales members consistently show dolipore septa with continuous parenthesomes, or rarely with a tiny central pore (Oberwinkler 1994, Wells 1994, Shirouzu *et al.* 2013a, McLaughlin *et al.* 2016). In addition to the septal pore features, ultrastructural features of basidiospores have also some relevance. Sierra *et al.* (2013) noted that the ultrastructural features of basidiospores like spore septal pore and lateral wall layers of spores, as species specific. A biglobular spindle pole body has been reported in *D. stillatus* (Wells and Bandoni 2001).

Wells (1994) studied the ultrastructural features of *Cerinomyces altaicus* Parmasto, *Dacrymyces stillatus*, *Guepiniopsis chrysocoma*. McLaughlin *et al.* (2016) detailed the ultrastructural features in *Dacryopinax primogenitus* and presented the characters of septal pore apparatus and the endogenous origin of epibasidia. Available ultrastructural data that is of taxonomic relevance has been compiled and made available at the online public repository AFTOL Structural and Biochemical database (<https://aftol.umn.edu>) (Kumar *et al.* 2013).

Molecular characters

Molecular phylogenetic studies support the monophyletic origin of Dacrymycetales. Different combinations of gene regions were used in the molecular studies of Dacrymycetales. Earlier, either ITS or LSU alone (Kirschner and Yang 2005, Shirouzu *et al.* 2007, 2009, Wu *et al.* 2011, Shirouzu *et al.* 2013a, Hanif and Khalid 2015), or combination of these two were commonly used (McLaughlin *et al.* 2016, Shirouzu *et al.* 2017, Shirouzu and Sanjo 2018, Fan *et al.* 2021a, Lian *et al.* 2022, Alvarenga and Gibertoni 2022). A combination of LSU, 18S, ITS, *rpb2* were used by Shirouzu *et al.* (2013a). In the multigene molecular phylogenetic studies, different combinations of primers like SSU, ITS, LSU, *tef1- α* , *rpb1*, *rpb2*, 12S and *atp6* were observed as useful in the Dacrymycetales taxonomy (Zamora and Ekman 2020, Savchenko *et al.* 2021, 2022, Zamora *et al.* 2022). The first whole genome study in this group was conducted by McLaughlin *et al.* (2016) which described a new species *Dacryopinax primogenitus*.

2.1.2.1.2. Ecological and economic importance

All Dacrymycetales members are decomposers of coniferous and angiosperm wood (Oberwinkler 1994, Worrall *et al.* 1997, Floudas *et al.* 2012, Zamora and Ekman 2020). The study conducted by Seifert (1983) is an exception that proved that few dacrymycetoid fungi can cause both white rot and brown rot. Seifert (1983) noted that two *Calocera* members, *C. lutea* (Massee) McNabb and *C. viscosa* (Pers.) Bory can cause white rot and some other *Dacrymyces* species can cause brown rot and lignin degradation.

Dacrymyces spathularia is known for its edibility and mycochemical compositions. Kumar *et al.* (2018) reported the presence of tannins, saponins, alkaloids, flavonoids and phenolics in *D. spathularia* which have potential antibacterial activity. The long-chain glycolipids isolated from *D. spathularia*

(AM-1) are used as a food additive in certain beverages (EFSA Panel on Food Additives and Flavourings (FAF) *et al.* 2021).

2.1.2.1.3. Distribution

Dacrymycetales have a worldwide distribution.

AFRICA: (Brasfield 1938), Ethiopia (Savchenko *et al.* 2021), Kenya (Savchenko *et al.* 2021), Madagascar (Savchenko *et al.* 2021). ASIA: China (Brasfield 1938, McNabb 1965a, Liu *et al.* 1988, Liu and Fan 1989, Peng *et al.* 1992, Fan *et al.* 2021a, Savchenko *et al.* 2021), Japan (Kobayasi 1939a, Shirouzu *et al.* 2009, Shirouzu *et al.* 2013b, Shirouzu and Hosoya 2017, Savchenko *et al.* 2021), Nepal (Savchenko *et al.* 2021), Pakistan (McNabb 1965c, Ahmad *et al.* 1997, Hanif and Khalid 2015), Russia (Malysheva 2013, Zamora and Ekman 2020, Savchenko *et al.* 2021), Taiwan (Shirouzu *et al.* 2009, Wu *et al.* 2011, Savchenko *et al.* 2021), Tibet (McNabb 1965a). AUSTRALIA: Australia (McNabb 1965a), New Zealand (McNabb 1965a, 1965b; Shirouzu *et al.* 2017, Savchenko *et al.* 2021), Tasmania (McNabb 1965a). EUROPE: Britain (Reid 1974), Cyprus (Savchenko *et al.* 2021), Czechoslovakia (McNabb 1965a, Reid 1983), Czech Republic (Savchenko *et al.* 2021), Denmark (Mathiesen 1992), Estonia (Savchenko *et al.* 2021), Finland (McNabb 1965a, Zamora and Ekman 2020, Savchenko *et al.* 2021), France (Brasfield 1938, McNabb 1965b, Savchenko *et al.* 2021), Germany (McNabb 1965a, 1965b), Netherlands (Savchenko *et al.* 2021), Norway (Zamora and Ekman 2020, Savchenko *et al.* 2021), Spain (Savchenko *et al.* 2021), Sweden (Brasfield 1938, Nannfeldt 1947, McNabb 1965a, Zamora and Ekman 2020, Savchenko *et al.* 2021), Ukraine (Savchenko *et al.* 2021). NORTH AMERICA: (Brasfield 1938), Belize (Savchenko *et al.* 2021), Canada (Zamora and Ekman 2020, Savchenko *et al.* 2021), Costa Rica (Lowy 1971, McLaughlin *et al.* 2016), Jamaica (Lowy 1971), Mexico (Lowy 1971, Castro-Santiuste *et al.* 2017), Panama (Lowy 1971, Savchenko *et al.* 2021), USA (McNabb 1965b, Zamora and Ekman 2020, Savchenko *et al.* 2021). SOUTH AMERICA: (Brasfield 1938), Argentina (Lowy 1971, Savchenko *et al.* 2021), Bolivia (McNabb 1965b, Lowy 1971), Brazil

(Lowy 1971, Shirouzu *et al.* 2013a, Alvarenga and Xavier-Santos 2015, Savchenko *et al.* 2021, Alvarenga and Gibertoni 2022), Colombia (Savchenko *et al.* 2021), Ecuador (McNabb 1965a, Savchenko *et al.* 2021), Venezuela (Lowy 1971).

2.1.2.1.4. Family Dacrymycetaceae J. Schröt.

Family Dacrymycetaceae was erected by Schröter (1889) as *Dacryomycetini* (Shirouzu *et al.* 2009, www.indexfungorum.org accessed on 01-08-2024). However, in Brasfield's (1938) view, Dacrymycetaceae was erected by Brefeld (1888) with the concept of gelatinous fungi with cylindrical forked basidia. Dacrymycetaceae is the largest family within Dacrymycetes, with taxa having pustulate, resupinate to clavarioid basidiocarp (Shirouzu *et al.* 2013a).

Family concepts and generic treatment under Dacrymycetaceae varies considerably (Table1). Establishment of proper generic boundaries was difficult due to varied basidiocarp morphology which evolved multiple times independently within the family (Shirouzu *et al.* 2013a, Zamora and Ekman 2020, Savchenko 2023).

Currently, 10 genera are accepted under Dacrymycetaceae, based on the latest phylogenetic treatment (Alvarenga and Gibertoni 2022). They are, *Calocera*, *Dacrymyces*, *Dacryomitra*, *Dacryopinax*, *Dacryoscyphus*, *Dendrodacrys* J.C. Zamora, A. Savchenko, Gonz.-Cruz, Prieto-García, Olariaga and Ekman, *Ditiola*, *Femsjonia*, *Guepiniopsis* and *Heterotextus*.

The genus *Dacryomitra* was erected by Tulasne (1872) to accommodate small morel-like fungus with a sterile stalk and a morchelloid hymenium. *Dacryomitra* is typified with *D. pusilla* Tul. and C. Tul. Due to the similarity of *Dacryomitra* and *Calocera* in the stipitate and pileate nature, Brasfield (1938), McNabb (1965a), Donk (1966), and Reid (1974) did not accept *Dacryomitra*. But Oberwinkler (2014) supported the generic treatment of *Dacryomitra*.

Table 1: Generic concept of Dacrymycetataceae according to different workers

| Brefeld (1888) | Neuhoff (1936) | Kennedy (1958) | McNabb and Talbot (1973) | Oberwinkler (2014) | He <i>et al.</i> (2019) | Alvarenga and Gibertoni (2022) |
|--------------------|-------------------|---------------------|--------------------------|----------------------|-------------------------|--------------------------------|
| <i>Calocera</i> | <i>Calocera</i> | <i>Arrhytidia</i> | <i>Cerinomyces</i> | <i>Arrhytidia</i> | <i>Calocera</i> | <i>Calocera</i> |
| <i>Dacrymyces</i> | <i>Dacrymyces</i> | <i>Cerinomyces</i> | <i>Calocera</i> | <i>Calocera</i> | <i>Cerinosterus</i> | <i>Dacrymyces</i> |
| <i>Dacryomitra</i> | | <i>calocera</i> | <i>Dacrymyces</i> | <i>Cerinomyces</i> | <i>Dacrymyces</i> | <i>Dacryomitra</i> |
| <i>Guepinia</i> | | <i>Dacrymyces</i> | <i>Dacryopinax</i> | <i>Dacrymyces</i> | <i>Dacryonaema</i> | <i>Dacryopinax</i> |
| | | <i>Dacryopinax</i> | <i>Ditiola</i> | <i>Dacryonaema</i> | <i>Dacryopinax</i> | <i>Dacryoscyphus</i> |
| | | <i>Ditiola</i> | <i>Dacryonaema</i> | <i>Dacryomitra</i> | <i>Dacryoscyphus</i> | <i>Dendrodacrys</i> |
| | | <i>Dacryonaema</i> | <i>Femsjonia</i> | <i>Dacryopinax</i> | <i>Ditiola</i> | <i>Ditiola</i> |
| | | <i>Femsjonia</i> | <i>Guepiniopsis</i> | <i>Dacryoscyphus</i> | <i>Femsjonia</i> | <i>Femsjonia</i> |
| | | <i>Guepiniopsis</i> | <i>Heterotextus</i> | <i>Ditiola</i> | <i>Guepiniopsis</i> | <i>Guepiniopsis</i> |
| | | | | <i>Femsjonia</i> | <i>Heterotextus</i> | <i>Heterotextus</i> |
| | | | | <i>Guepiniopsis</i> | | |
| | | | | <i>Heterotextus</i> | | |

The genus *Ditiola* was erected by Fries (1822) to include four species. He described the genus as having basidiocarps with tuberculate form covered by white, floccose veil, development of head when mature, and the rooting base (Kennedy 1964). However, his descriptions were highly similar to that of other genera such as *Helotium* and *Peziza*. Tulasne (1853), Donk (1931), and Neuhoff (1936) don't consider *Ditiola* under Dacrymycetaceae (Kennedy 1958, Lowy 1971). Lindau (1894) accepted *Ditiola* and illustrated *D. radicata* (Alb. and Schwein.) Fr. Kennedy (1958) later redefined *Ditiola* and restricted the genus with heterogeneously constricted basidiocarps. McNabb (1966) studied *Ditiola* in detail and described a new combination of *Ditiola* and two varieties of *D. radicata*. Lowy (1971) incorporated *Ditiola* in his monograph on neotropical Tremellales and described a new species (*D. coccinea* Lowy) and *Ditiola radicata*.

The genus *Heterotextus* was erected by Lloyd (1921) to accommodate distinct members of the *Dacrymyces* and *Guepinia*. The genus was distinguished from other Dacrymycetaceae by their globose bottle shape or cylindrical cells. Lloyd (1921) described a single species under *Heterotextus* and transferred three *Guepinia* members to this genus. Martin (1936b) later reduced *Heterotextus* as a synonym of *Guepiniopsis*. Though most workers (Kennedy 1958, Reid 1974) supported this synonymy, Donk (1964) and McNabb (1965d) did not follow this placement. Oberwinkler (1994, 2014) and Shirouzu *et al.* (2009, 2017) who worked on molecular aspects of this group is of view that *Heterotextus* is a distinct genus. Phylogenetic analysis conducted by Shirouzu *et al.* (2017) showed separate clustering of *Heterotextus* within Dacrymycetaceae and it revealed its distinction with *Guepiniopsis*.

The genus *Femsjonina* was erected by Fries (1849) based on the turbinate, pezizoid, or shallow cupulate basidiocarps, thick-walled marginal hyphae, and internal hyphae with clamp-connections (McNabb 1965e). Phylogenetic analysis

done by Shirouzu *et al.* (2017) observed a weakly supported relationship between *Femsjonia* and *Ditiola*.

Genus *Dacryoscyphus* was erected by Kirschner and Yang (2005) based on *D. chrysochilus*. *Dacryoscyphus* includes the anamorphic members of Dacrymycetaceae. *D. chrysochilus* is characterised by cupulate conidiomata and staurosporous conidia, which grows on dead twigs of *Rhododendron* species (Kirschner and Yang 2005, Oberwinkler 2014). Based on morphological and molecular similarities, Kirschner *et al.* (2010) transferred two species which were originally described under *Dacrymyces* (*D. pinacearum* and *D. subarcticus*) (Shirouzu *et al.* 2009) to *Dacryoscyphus*. Currently, the genus *Dacryoscyphus* contains three members (<https://www.indexfungorum.org> accessed on 01-08-2024).

2.1.2.1.4.1. Genus *Calocera* (Fr.) Fr.

The genus *Calocera* was erected by Fries (1821), as a subgenus of *Clavaria*. He described six species under this genus without designating a type specimen. According to Brasfield (1938), *C. cornea* Batsch serves as the type specimen. McNabb (1965a), Lowy (1971) and Reid (1974) treated *C. viscosa* (Pers.) Fries as the type specimen of the genus.

For many years, species currently treated under *Calocera* were considered under *Clavaria* because of the clavarioid morphology. Later, Tulasne brothers (1853, 1871) noticed their similarity to *Dacrymyces* in their hymenial structure. Brefeld (1888) studied and illustrated the characteristic internal organisation of these members (McNabb 1965a). Later, Fisher (1931) and Nannfeldt (1947) described the compactly arranged strand of thin-walled hyphae at the middle of the basidiocarp, surrounded by a zone of loosely arranged hyphae and hymenial layer as an outer covering. On the basis of Brefeld's (1888) discussion on *Calocera*, and personal observations on *C. cornea*

and *C. viscosa*, Kennedy (1958) prepared the generic concept of *Calocera*. The characteristic features were cylindrical attenuate basidiocarp, internal organisation of the basidiocarp with three well distinguished zones, and bifurcate basidia.

McNabb (1965a) studied the genus *Calocera* in detail and broadened the generic concept to include some little known species with morphological variations. McNabb (1965a) incorporated spathulate, flabelliform, forked or profusely branched, palmately lobed and stipitate basidiocarps within *Clavaria*. McNabb (1965a) included more microscopic features like hyphal composition, clamp-connection, hyphidia, probasidia, basidial septation and germination in his concept. According to McNabb (1965a) distinction of the internal zones vary with age of the basidiocarps. McNabb (1965a) treated the genera *Corynoides* S. F. Gray, *Dacryomitra*, *Calopposis* Lloyd as synonyms to *Calocera*.

Lowy (1971) listed three *Calocera* species (*C. coralloides* Kobayasi, *C. cornea* and *C. macrospora* Brasf.) in his book "Flora Neotropica". Lowy (1971) was also of the opinion that the genera *Corynoides*, *Dacryomitra* and *Calopposis* are synonyms of *Calocera*. Reid (1974) agreed with Lowy (1971) in treating these genera as synonyms of *Calocera*. Reid (1974) reported five *Calocera* species including one new species (*C. pallidospatulata* D.A. Reid) from Britain.

Phylogenetic analysis of Wu *et al.* (2011) showed that the species of *Calocera* with clamp-connections are more closely related to each other than with species without clamp-connections. Shirouzu *et al.* (2017) studied the phylogenetic relationship among different Dacrymycetaceae members and they found that *Calocera* is polyphyletic.

2.1.2.1.4.1.1. Economic and ecological importance

Calocera cornea and *C. viscosa* have wood degrading potential (Seifert 1983, Worrall *et al.* 1997) and can break down both cellulose and lignin (Seifert

1983, Shirouzu *et al.* 2013a). *Calocera viscosa* can cause heart rot in stumps of *Pseudotsuga menziesii* (Siepmann 1977, 1979) and *Larix deciduas* (Pawsey 1971).

Basidiocarps of *Calocera*, and its *in vitro* cultures serve as valuable sources of antioxidants like β -Carotene (Muszynska *et al.* 2012). Mycochemical analyses revealed the presence of alkaloids, tannins, flavanoids, sterols, glycosides, terpenoids and phenols in *C. viscosa*. Antibacterial studies using *Calocera* proved its antibiotic potential with an appreciable zone of inhibition (Naik *et al.* 2019).

2.1.2.1.4.1.2. Distribution

According to Brasfield (1938), *Calocera* species (*C. cornea* and *C. viscosa*) are cosmopolitan in distribution.

ASIA: China (Liu *et al.* 1988, Liu and Fan 1989; Peng *et al.* 1992), Japan (Kobayasi 1939a), Pakistan (McNabb 1965a, Ahmad *et al.* 1997, Hanif and Khalid 2015), Philippine (McNabb 1965a), Russia (Malysheva 2013), Tibet (McNabb 1965a), Taiwan (Wu *et al.* 2011). EUROPE: Czechoslovakia (McNabb 1965a), Denmark (Mathiesen 1992), Finland (McNabb 1965a), France (McNabb 1965a), Germany (McNabb 1965a), Italy (McNabb 1965a), Norway (McNabb 1965a), Sweden (McNabb 1965a). AUSTRALIA: Australia (McNabb 1965a), New Zealand (McNabb 1965a), Tasmania (McNabb 1965a). NORTH AMERICA: (Brasfield 1938), Mexico (Castro-Santiuste *et al.* 2017), USA (McNabb 1965a). SOUTH AMERICA: Brazil (Shirouzu *et al.* 2013a, Alvarenga and Xavier-Santos 2015).

2.1.2.1.4.2. Genus *Dacryomyces* Nees

Nees (1816) erected the genus "*Dacryomyces*" to accommodate a single species *D. stillatus*. Later, Fries (1822), modified the name "*Dacryomyces*" to *Dacryomyces* and redefined the genus concept to include members with fleshy or gelatinous basidiocarp having homogenous consistency, composed of

interwoven hyphae, and spore production from all sides of the basidiocarp (McNabb 1973). Nauhoff (1936) considered *Dacrymyces* in a wide concept with only two genera under Dacrymycetaceae (*Dacrymyces* and *Calocera*). Martin (1952) followed comparatively narrow concept of the genus with ten other genera under Dacrymycetaceae. Kennedy (1958) followed Martin's concept and extended it to include part of the genus *Arrhytidia* and some stipitate members which were placed under *Dacryomitra*. Kobayasi (1939a) established two subgenera under *Dacrymyces*; *Eudacrymyces* and *Turbinaster*. *Eudacrymyces* was characterised by non-turbinate basidiocarps with an amphigenous hymenium. *Turbinaster* was characterised by members having a hymenium confined to the surface of the top portion of turbinate or pezizoid basidiocarps, and with cortex composed of thin or thick-walled hairs (McNabb 1973).

According to modern concept, *Dacrymyces* has diverse basidial morphology, and includes about half of the members of class Dacrymycetes (Reid 1974, Shirouzu *et al.* 2009, 2017, Zamora *et al.* 2022). The generic limits of *Dacrymyces* are not well defined (Zamora *et al.* 2022). In the phylogenetic studies, *Dacrymyces* was revealed as polyphyletic (Shirouzu *et al.* 2007, 2013a, 2017, Zamora and Ekman 2020, Savchenko *et al.* 2021, Zamora *et al.* 2022). A new genus *Dendrodacrys* was established to accommodate species with pulvinate to depressed basidiocarps having highly branched hyphidia, and up to 3-septate basidiospores, which formed a separate group within *Dacrymyces sensu lato* (Zamora *et al.* 2022).

Alvarenga and Gibertoni (2022) emended the genus concept of *Dacrymyces* based on their phylogenetic study to include two species *Dacryopinax maxidorii* Lowy and *Dacryopinax spathularia* having spathulate to flabellate basidiocarps with superior or unilateral hymenium.

2.1.2.1.4.2.1. Economic and ecological importance

Dacrymyces members are wood decomposers, and species like *Dacrymyces stillatus*, *D. capitatus* Schwein, *D. dictyosporus* G.W. Martin exhibit both brown and white rot capabilities (Seifert 1983).

Studies conducted by Goodwin (1953) found the presence of polyenes like phytofluene, α -carotene, β -carotene, ζ -carotene, torulene, cryptoxanthin and zeaxanthin in *D. stillatus*, and β -carotene as the major pigment in *D. stillatus*. Food additives have been isolated from *Dacrymyces spathularia* and is commercially used (EFSA Panel on Food Additives and Flavourings (FAF) *et al.* 2021).

2.1.2.1.4.2.2. Distribution

ASIA: China (Kennedy 1958, Lian *et al.* 2022), Japan (Kennedy 1958, Shirouzu *et al.* 2017, Shirouzu and Sanjo 2018). EUROPE: England (Kennedy 1958), Finland (Kennedy 1958), France (Kennedy 1958, McNabb 1973), Germany (Kennedy 1958, McNabb 1973, Weiß and Oberwinkler (2001), Greece (Kennedy 1958) Sweden (Kennedy 1958), Ukraine (Malysheva and Akulov 2011). AUSTRALIA: (Kennedy 1958). NORTH AMERICA: Canada (Kennedy 1958), Colombia (Kennedy 1958), Mexico (Castro-Santiuste *et al.* 2017), Panama (Kennedy 1958), United States (Kennedy 1958, McNabb 1973). SOUTH AMERICA: Brazil (Kennedy 1958, Alvarenga and Gibertoni 2022).

2.1.2.1.4.3. Genus *Dacryopinax* Martin

The genus *Dacryopinax* was erected by Martin (1948) for three species which were previously classified under *Guepinia*. Genus *Guepinia* is currently invalid because it is a later homonym of the plant genus *Guepinia* Bastard (Cruciferae). Donk (1941) noted the similarity of *D. spathularia* (currently *Dacrymyces spathularia*) with *Calocera* members and suggested treating *Dacryopinax* members under *Calocera*. Nannfelt (1947) considered *Dacryomitra*

and *Calocera* as separate genera although they have anatomical similarities (McNabb 1965b).

Members of the genus can be easily identified with basidiocarp morphology and hymenial position. Basidiocarps are stipitate, spatulate, obliquely cupulate or flabelliform with unilateral inferior hymenium and unspecialised cortical hairs (McNabb 1965b). According to *Index fungorum* (accessed on 01-08-2024), the genus currently consists of 22 species.

2.1.2.1.4.3.1. Ecological and economic importance

Dacryopinax primogenitus have high hemicellulolytic ability which proves its wood decaying capacity (Floudas *et al.* 2012, Tulsani *et al.* 2022).

2.1.2.1.4.3.2. Distribution

ASIA: China (Mu 1985), India (Bera *et al.* 2018, Joshi *et al.* 2021), Japan (Shirouzu *et al.* 2009), Java (McNabb 1965b). EUROPE: France (Courtecuisse and Lowy 1990). NORTH AMERICA: Costa Rica (McLaughlin *et al.* 2016), Mexico (Pérez-Silva and Esqueda 1992, Sierra and Cifuentes 2005, Castro-Santiuste *et al.* 2017, Castro-Santiuste *et al.* 2020), USA (McNabb 1965b, Lowy 1971). SOUTH AMERICA: Bolivia (Lowy 1959, McNabb 1965b, Lowy 1971), Brazil (Lowy 1981, Lowy 1987), Colombia (Lowy 1971), Venezuela (McNabb 1965b, Lowy 1971).

2.1.2.1.4.4. Genus *Dendrodacrys* J.C. Zamora, A. Savchenko, Gonz.-Cruz, Prieto-García, Olariaga and Ekman

Dendrodacrys is a recently erected monophyletic genus in the Dacrymycetaceae, with *D. ellipsosporum* J.C. Zamora, A. Savchenko, Gonz.-Cruz, Prieto-García, Olariaga and Ekman as the type species. The members of this genus have pustulate, cerebriform, or stipitate basidiocarps of yellow to dark brown colours, hyphal septa are with or without clamp-connections, hyphidia are branched and basidiospores are 3 septate (Savchenko *et al.* 2022). According to *Index fungorum*, (accessed on 01-08-2024) the genus currently consists of 11 species (*D. brasiliense* (Lloyd) A. Savchenko, Shirouzu and J.C.

Zamora, *D. ciprense* J.C. Zamora, *D. concrescens* J.C. Zamora and Ekman, *D. dendrocalami* (Oberw.) A. Savchenko and J.C. Zamora, *D. elliposporum*, *D. kennedyae* A. Savchenko, *D. laetum* A. Savchenko, *D. oblongisporum* J.C. Zamora and Ekman, *D. paraphysatum* (L.S. Olive) J.C. Zamora and A. Savchenko, *D. pezizoideum* (Henn.) A. Savchenko and Alvarenga, *D. rigoratum* A. Savchenko and J.C. Zamora) (Savchenko *et al.* 2022, Zamora *et al.* 2022).

While erecting the genus *Dendrodacrys*, Zamora *et al.* (2022) included only European taxa. In the same year itself, Savchenko *et al.* (2022) expanded the species composition of the genus to include tropical and subtropical representatives.

2.1.2.1.4.4.1. Ecological and economical importance

All members of *Dendrodacrys* are saprobic, found growing on decaying wood logs (Savchenko *et al.* 2022, Zamora *et al.* 2022). *Dendrodacrys elliposporum* is always associated with *Juniperus*. *Dendrodacrys elliposporum* is xerotolerant, and can withstand repeated dry and wet conditions (Zamora *et al.* 2022).

2.1.2.1.4.4.2. Distribution

AFRICA: Kenya (Savchenko *et al.* 2022). ASIA: Japan (Shirouzu *et al.* 2013b, Savchenko *et al.* 2022), Taiwan (Savchenko *et al.* 2022). AUSTRALIA: French Polynesia (Savchenko *et al.* 2022), New Zealand (McNabb 1973), Tahiti (McNabb 1973). EUROPE: Cyprus (Zamora *et al.* 2022), Norway (Zamora *et al.* 2022, Savchenko *et al.* 2022), Spain (Savchenko *et al.* 2022, Zamora *et al.* 2022), Sweden (Savchenko *et al.* 2022, Zamora *et al.* 2022), Ukraine (Zamora *et al.* 2022). NORTH AMERICA: Panama (Savchenko *et al.* 2022), Puerto Rico (Savchenko *et al.* 2022). SOUTH AMERICA: Brazil (Savchenko *et al.* 2022), Guyana (Savchenko *et al.* 2022), Venezuela (Savchenko *et al.* 2022).

2.1.2.1.4.5. Genus *Guepiniopsis* Patouillard

Patouillard (1883) erected this genus with *Guepiniopsis tortus* Pat. as the type species. Kennedy (1958) argued that it was a misidentification and proposed *G. buccina* (Pers.) L.L. Kenn. as the correct type species. Patouillard (1883) originally described the genus with members having stipitate and cupulate basidiocarp with a lining of hymenium in the interior area. Later, Patouillard (1887) broadened the concept and added stipitate forms with cupulate or spathulate pileus. After a few years, Patouillard (1900) again emended the genus concept and added unilateral hymenia and continuous or septate abhymenial hairs. Martin (1936b) redefined the genus concept of *Guepiniopsis* with species having inflated cortical cells (McNabb 1965c).

According to McNabb (1965c), two different genera in the Dacrymycetaceae, *Heterotextus* and *Guepiniopsis*, have thick-walled cortical hairs. In McNabb's (1965d) view, *Heterotextus* is characterised by the thick-walled, inflated, beaked cells, each of which arises from a single terminal cell (McNabb 1965d). Whereas, *Guepiniopsis* is characterised by simple or branched, cylindrical septate hyphae, the individual cells in the hyphae may get inflated to oval or subglobose shapes (McNabb 1965c, Delivorias 2012). Kennedy (1958) and Reid (1974) did not consider these characters as valid diagnostic features of these genera. Oberwinkler (1994) was of the view that both genera are valid and that the layered cell walls of marginal hairs in *G. buccina*, and lack of clamp-connections are valid distinguishing characters (Delivorias 2012). According to *Index Fungorum*, (accessed on 13-05-24) *Guepiniopsis* has 18 species.

The clustering of sequences of *G. buccina* within other *Dacrymyces* members like *D. stillatus*, *D. pezizoides* Kobayasi, *D. subantarcticensis* Burds. and Laursen have already been revealed by molecular phylogenetic studies (Shirouzu *et al.* 2007, 2009, Zamora and Ekman 2020, Alvarenga and Gibertoni 2022, Zamora *et al.* 2022) suggesting synonymy. Lack of sequence from the type species (*G. torta* Pat.) remains an impediment in confirming the relation

(Alvarenga and Gibertoni 2022). At present, *Guepiniopsis* is a valid genus (Shirouzu *et al.* 2013a, Alvarenga and Gibertoni 2022, Zamora *et al.* 2022).

2.1.2.1.4.5.1. Ecological importance

All *Guepiniopsis* members are wood inhabiting species that may be of the brown rot type (Seifert 1983, Oberwinkler 2014).

2.1.2.1.4.5.2. Distribution

ASIA: Japan (Kobayasi 1939a), Iran (Asef 2010). AUSTRALIA: (Saccardo 1890), New Zealand (McNabb 1965c). EUROPE: Czechoslovakia (Pilát 1957), Estonia (Raitviir 1967), France (Bourdot and Galzin 1928, McNabb 1965c), Germany (Brefeld 1888, McNabb 1965c), Greece (Delivorias 2012), Spain (Dueñas 2005), Sweden (Neuhoff 1936, Dueñas 2005), Portugal (Dueñas 2005). NORTH AMERICA: Canada (Martin 1952), U.S.A. (Martin 1952, McNabb 1965c). SOUTH AMERICA: Argentina (Lowy 1982), Ecuador (McNabb 1965c).

2.1.3. Class TREMELLOMYCETES Doweld

Tremellomycetes encompasses a variety of fungi, which show variations in lifestyle, morphology, nutritional mode, and pathogenicity (Millanes *et al.* 2011, Weiß *et al.* 2014). Most of the species are dimorphic in nature, with a unicellular yeast stage and a dikaryotic filamentous stage. They are nutritionally heterogenous with saprotrophs, animal parasites, fungicolous and lichenicolous members (Millanes *et al.* 2011). In the teleomorphic groups, the dikaryotic hyphal stage usually develops from mature compatible yeast cells (Boekhout *et al.* 2011), and they produce basidia in gelatinous basidiocarps or in gall formations on other fungi or lichen (Millanes *et al.* 2011).

The genus *Tremella* was erected by Persoon in 1794. Later, Fries (1821) established the family Tremellaceae (as Tremellini) and the order Tremellales (as Tremellinae) to accommodate this genus (Weiß *et al.* 2014). In the

taxonomic history of Basidiomycetes, the names associated with *Tremella* (Tremellineae, Tremellales, Tremelleae, Tremellaceae) were widely used for hymenomycetes with longitudinally septate basidia (Brefeld 1888, Bandoni 1984, Weiß *et al.* 2014). This concept of using Tremellales for all taxa with longitudinally septate basidia was redefined by Bandoni (1984). According to him, ultrastructural characters, haploid status and trophic strategies are more significant characters in Tremellales than basidial morphology. Later, Swann and Taylor (1995) introduced Tremellomycetidae as one of the two subclasses (the other being Hymenomycetidae) under the class Hymenomycetes based on 18S gene sequence analysis. They placed Filobasidiales, Tremellales and *Trichosporon cutaneum* (Beurm., Gougerot and Vaucher bis) M. Ota under Tremellomycetidae. Molecular studies conducted by Swann and Taylor (1995), Weiß and Oberwinkler (2001), Hibbett *et al.* (2007) supported Bandoni's (1984) concept of treating Tremellales as the taxa with the *Tremella* type septal pore complex and unicellular haploid stages.

Based on the results inferred from molecular data, morphological and physiochemical features, Liu *et al.* (2015a) updated the classification of Tremellomycetes with five orders, 17 families and 54 genera. Irwin *et al.* (2021) introduced one more order Chionasterales N. A. T. Irwin, C. S. Twynstra, V. Mathur, P. J. Keeling to accommodate *Chionaster nivalis* (Bohlin) Wille. Currently, class Tremellomycetes contain six orders, Order Chionasterales, Order Cystofilobasidiales, Order Filobasidiales, Order Holtermanniales Libkind, Wuczkowski, Turchetti and Boekhout, Order Trichosporonales Boekhout and Fell and Order Tremellales (Irwin *et al.* 2021).

The order Chionasterales and family Chionasteraceae was erected based on the genus *Chionaster* Wille (Irwin *et al.* 2021). *Chionaster nivalis* is commonly observed and widely distributed in the high alpine and arctic regions consisting of extreme low temperature. Since the discovery of *C. nivalis* in 1893

(Bohlin 1893), they remain taxonomically and phylogenetically distinct (Irwin *et al.* 2021). Morphologically, *C. nivalis* is characterised by three to four thick radiating extensions with rounded ends, and a central condensed cell. In phylogenetic analysis, *C. nivalis* formed a distinct clade within Tremellomycetes (Irwin *et al.* 2021).

The order Cystofilobasidiales was erected to incorporate teleomorphic yeasts with teliospores, holobasidia, and dolipore septa without parenthesomes (Weiß *et al.* 2014). Wells and Bandoni (2001) considered the family Cystofilobasidiaceae K. Wells and Bandoni within Filobasidiales. Liu *et al.* (2015b) elevated this group as an order and emended the family Cystofilobasidiaceae to incorporate *Cystofilobasidium* clade. In the same study, a new family, Mrakiaceae Liu, Bai, Groenew and Boekhout was proposed to incorporate the monophyletic clade comprising *Mrakia* Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout, *Phaffia* M.W. Mill., Yoney. and Soneda, *Udeniomyces* Nakase and Takem., *Itersonilia* Derx, *Tausonia* Babeva and huempii group, which clustered along with *Cystofilobasidium* (Liu *et al.* 2015b). Currently, the order Cystofilobasidiales contains two families: Cystofilobasidiaceae and Mrakiaceae. All of the members of this order are yeasts and basidiocarps are absent.

The order Filobasidiales was established for yeasts lacking basidiocarps and having holobasidia with passively released basidiospores (Jülich 1981, Liu *et al.* 2015a). Wells and Bandoni (2001) treated this family with Filobasidiaceae L.S. Olive, Cystofilobasidiaceae and Rhynchogastremaceae Oberw. and B. Metzler. Liu *et al.* (2015b) recircumscribed the order with two families; Filobasidiaceae and Piskurozymaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout, and seven genera. Filobasidiaceae have members with gelatinous to waxy basidiocarps. They are lichenicolous with clamp-connections and haustorial branches. Piskurozymaceae have no basidiocarps. They possess pseudohyphae

and true hyphae with occasional presence of clamp-connections (Liu *et al.* 2015b).

Order Holtermanniales was proposed by Wuczkowski *et al.* (2011) to include the teleomorphic genus *Holtermannia* Sacc. and Traverso, and anamorphic genus *Holtermanniella* Libkind, Wuczk., Turchetti and Boekhout. *Holtermannia corniformis* Kobayasi has small clavarioid and anatomically complex basidiocarp similar to *Calocera* members with tremelloid basidia (Bandoni and Boekhout 2011, Weiß *et al.* 2014). Liu *et al.* (2015b), confirmed the order as a distinct lineage. Currently, Holtermanniales contains two genera *Holtermannia* and *Holtermanniella* (Liu *et al.* 2015b).

Order Trichosporonales is an anamorphic order which was initially erected to include species which are known to be arthroconidia-producing (*Trichosporon* Behrend) and lacking yeast stage (Fell *et al.* 2000, Weiß *et al.* 2014). Most of the members of this group are associated with human infections or allergic diseases. Liu *et al.* (2015b), accepted two families (Trichosporonaceae Nann. and Tetragoniomycetaceae Oberw. and Bandoni) and ten genera in this order, and emended the order concept to also consider members of non-arthrospore producing genera like *Bullera* Derx and *Cryptococcus* Vuill. (Takashima *et al.* 2001, Fungsin *et al.* 2006, Boekhout *et al.* 2011, Weiß *et al.* 2014, Liu *et al.* 2015b).

2.1.3.1. Order TREMELLALES Fries

Tremellales is the largest order in the Tremellomycetes having members with different life cycles and morphology (Weiß *et al.* 2014). Fries (1821) described Tremellales to incorporate the genus *Tremella*. Recently, on the basis of phylogenetic and ultrastructural data, the concept of Tremellales has been refined (Liu *et al.* 2015a). Currently, the order Tremellales is limited to taxa which have yeast-like haploid state, longitudinally septate basidia, dikaryotic hyphae with dolipore septum and sacculate parentheses which is

invaginated towards the septal pore (Berbee and Wells 1988, Webster and Weber 2007).

Based on extensive multi-gene phylogeny, and Phylogenetic Rank Boundary Optimisation (PRBO) test, Liu *et al.* (2015b) rearranged the order with eleven families and 28 genera. Among these families, only the Bulleraceae Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout, Naemateliaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout, Phaeotremellaceae Yurkov and Boekhout, Sirobasidiaceae and Tremellaceae contain basidiocarp forming members (Liu *et al.* 2015a).

2.1.3.1.1. Taxonomic characters of Tremellales

Macroscopic characters

Basidiocarp produced by members of Tremellales are distinguishable by their jelly-like texture. There are many members that are parasitic and produce basidiocarps on tissue of other fungal groups (Weiß *et al.* 2014).

Morphology of basidiocarps varies from pustulate, cushion-shaped, lobose-cerebriform, and foliose (Weiß *et al.* 2014, Liu *et al.* 2015a). *Phaeotremella foliacea* (Pers.) Wedin, J.C. Zamora and Millanes and *T. fuciformis* has foliose basidiocarps and *T. mesenterica* Retz. has lobose to cerebriform basidiocarps. *Naematelia encephala* (Pers.) Fr. have globose cerebriform basidiocarp with a solid core composed of host hyphae (Bandoni 1987, Weiß *et al.* 2014). Lichenicolous taxa like *Tremella* and *Syzygospora* G.W. Martin are capable of forming conspicuous galls or deformations on the lichen hosts (Millanes *et al.* 2011).

The size of basidiocarps varies greatly among the basidiocarp forming members of the Tremellales. Basidiocarp may be produced as a layer on the mycelium of hosts to large-sized structures ranging several centimeters

(Webster and Weber 2007). The interior of basidiocarps may be hollow, solid, or stuffed with host hyphae (Bandoni 1987). The genus *Naematelia* Fr. has heterogenous basidiocarp contrasting with the other tremellacious members. In *N. encephala*, the inner core of basidiocarp is stuffed with fleshy host hyphae surrounded by the gelatinous hyphae of *Neamatelia* (Bandoni 1961, Roberts 1999).

Colour of basidiocarp is variable with taxa. Colour ranges from hyaline, whitish, yellowish, brown, to black. Colour varies significantly based on environmental factors like exposure to sunlight, seasonal changes and pigmentation of host organism (Bandoni and Boekhout 2011). Basidiocarps with more exposure to sunlight become brighter in colour than those in shady areas (Wong *et al.* 1985). *Tremella moriformis* Sm. and Sowerby and *T. exigua* Desm. contain pigments, which are products of its host organism (Bandoni 1987).

The gelatinous consistency of basidiocarp of the Tremellales helps them survive through desiccation, revive growth, and produce spores (Wells and Bandoni 2001). The gelatinous nature varies with the level of hydration, age of basidiocarp, and the amount of host hyphae within the basidiocarp (Bandoni 1987).

Microscopic characters

Hymenium

Basidiocarps have an amphigenous hymenium composed of basidia and hyphidia. In some taxa, conidiogenous cells are also present along with basidia in the hymenial region (Bandoni 1987).

Basidia

Basidial morphology is an important taxonomic character in Tremellales. Various basidial morphologies like *Tremella*-type longitudinally septate basidia

(*Bulleromyces* Boekhout and Á. Fonseca, *Tremella*, *Cuniculitrema* J.P. Samp. and R. Kirschner), holobasidia (*Cryptococcus* Vuill.) and transversely septate basidia (*Auriculibuller* J.P. Samp. and Fonseca, *Papiliotrema* J.P. Samp., M. Weiss and R. Bauer) are present in Tremellales (Boekhout *et al.* 2011). Longitudinally cruciate septate (tremelloid basidia) with 2–4 compartments is most common basidial type with shapes varies from globose, subglobose to ellipsoid, fusiform, pyriform to capitate (Bandoni 1987, Chen 1998). In *Sirobasidium*, basidia are chained catenulate. Shape of basidia in the basidial chain varies from fusiform, subglobose or cylindrical in different *Sirobasidium* species (Bandoni 1957, Yamada *et al.* 2022). In the tremella-type basidia, septation may be longitudinal, transverse or oblique. In some taxa, all these three types may be present in a single basidiocarp (Chen 1998). Long cylindrical epibasidia will develop from each compartment and will penetrate through the hymenium. At the tip of each epibasidia, basidiospores develop and get discharged with maturity (Weiß *et al.* 2014).

Basidiospores

Basidiospores germinate by repetition, budding, and by germ tube formation. Basidiospores frequently undergo budding and act like conidiogenous cells by forming numerous blastoconidia leading to a haploid yeast state. When the compatible yeast cells come in contact with each other they will undergo fusion and will re-establish the dikaryotic phase (Webster and Weber 2007). Dikaryotic hyphae will grow and form the basidiocarp (Weiß *et al.* 2014).

Swollen cells

Swollen cells are commonly present in some families of Tremellales like Naemateliaceae, Phaeotremellaceae and Tremellaceae (Chen 1998, Malysheva *et al.* 2015, Spirin *et al.* 2018a). They may be present in trama, basal part

towards substratum, subhymenium and hymenial region (Chen 1998, Zhao *et al.* 2019). Formation of swollen cells may be terminal, subterminal or lateral. In some taxa, swollen cells are capable of partial germination with hyphal formation (Chen 1998).

The shape of swollen cells varies from globose to subglobose, ovate, citriniform, broadly pyriform with short stalk, clavate and ventricose. Swollen cell may be thick-walled or thin-walled (Chen 1998). Some species possess two types of swollen cells in a basidiocarp. For example, in *T. mesenterica*, there are big sized swollen cells (26–37 × 13–22 µm), which vary from globose to oval, citriform, or pyriform, and small sized terminally swollen cells (3–9 × 3–8 µm), which are globose to ellipsoid. In *T. australiensis* Lloyd, conidial formation has also been reported from the swollen cells (Chen 1998).

Vesicles

The shape of vesicles varies from ellipsoid, ovoid, lanceolate, clavate, cylindrical to versiform. Vesicles are thick-walled, sometimes formed as chain of cells, and commonly present in subhymenium and hymenium (Chen 1998).

Hyphae

Clamp-connections are commonly present within Tremellomycetales members but, some exceptional species like *Phaeotremella simplex* (Jacks. and Martin) Millanes and Wedin and *T. pyrenophila* Tray. and Migl. lack clamp-connections (Bandoni 1987). *Tremella mesenterica* produces dikaryotic conidia directly from hyphae in cultural conditions (Bandoni 1987).

Haustoria

Tremella exhibits a mycoparasitic mode of nutrition, which is mediated through modified hyphae called tremelloid haustoria or haustorial branches (Olive 1947, Chen 1998, Boekhout *et al.* 2011). Haustorial branches are attached

to a swollen segment called haustorium from which one or more haustorial branches arise. The basal haustorial cell is usually subtended by clamp-connections (Bandoni 1987). When the haustorial filament comes in contact with hyphae of a suitable host, the host wall dissolves and a micropore is formed, which make direct cytoplasmic connection between host and the filament (Webster and Weber 2007). Tremelloid haustorium is observed within different genera of the Tremellales, like, *Auriculibuller* (Sampaio *et al.* 2004), *Bulleromyces* (Boekhout *et al.* 1991), *Cuniculitrema* (Kirschner *et al.* 2001), *Bulleribasidium* J.P. Sampaio. emend. X.Z. Liu, F.Y. Bai, M. Groenew. and Boekhout and *Papiliotrema* (Sampaio *et al.* 2002).

Yeast stage

Majority of tremellaceous haploid yeasts look similar in morphology and colony characters (Weiß *et al.* 2014). Generally, the yeast colonies are slimy, and whitish or cream in colour. Yeast cells are globose to ellipsoid and encapsulated, They bud polarly and may form annetate apiculus on maturity (Bandoni 1987). *Trimorphomyces papilionaceus* Bandoni and Oberwinkler is an exception with both dikaryotic and monokaryotic yeast stages (Bandoni 1987). Dikaryotic yeast cells of *T. papilionaceus* have “butterfly” shape and they multiply by budding. They can produce ballistoconidia that are morphologically and functionally same as basidiospores. *Carcinomyces* have elongated yeast cells (Weiß *et al.* 2014).

Ultrastructure

Tremellales members have dolipore septa, which are surrounded by sacculate parenthesomes in hemispherical model. In the cross or oblique section of the septum, these finger-like extensions look like saccules with abseptal opening. Endoplasmic reticulum is continuous with the outer limiting membrane of each saccule (Khan 1976, Berbee and Wells 1988, Weiß *et al.*

2014). Each cupulate unit is similar to the parenthesome found in other basidiomycetes and hence the *Tremella* type parenthesome is a compound rather than a fragmented unit (Moore and Marchant 1972, Khan 1976). Patrignani *et al.* (1983, 1984) studied the septal pore apparatus features in *Tremella* members and observed that septal pore features are not consistent in different hyphae of same species. Sacculate parenthesomes were absent at the septum at basidial base of *T. mesenterica* and *T. foliacea* (*Phaeotremella foliacea*). In the ultrastructural studies in *T. globispora* D.A. Reid, biglobular spindle pole bodies were observed during prophase and are a characteristic feature of Agaricomycotina (Berbee and Wells 1988, Weiß *et al.* 2014).

Molecular characters

Molecular markers have helped to clarify the taxonomic uncertainties in Tremellomycetes (Liu *et al.* 2015a, 2015b, Wang and Wang 2015, Li *et al.* 2022c). A combination of gene regions has been traditionally used in molecular phylogenetic studies of Tremellales.

Sequences of the combined internal transcribed spacer (ITS) rRNA and the D1/D2 domains of the large subunit (LSU or 26S) rRNA gene regions are widely accepted in the phylogentic studies of Tremellales (Chen 1998, Malysheva *et al.* 2015, Khunnamwong *et al.* 2019, Fan *et al.* 2021c). In the modern era with multi-gene phylogeny, different combination of gene regions like the small subunit (SSU or 18S) rRNA gene regions, ITS, LSU, *rpb1* and *rpb2*, *tef1*- α and *cytb* are also proven as useful in the phylogenetic studies of this group (Findley *et al.* 2009, Millanes *et al.* 2011, Liu *et al.* 2015a, 2015b, Spirin *et al.* 2018a, Li *et al.* 2020, Fan *et al.* 2021b, Yamada *et al.* 2022). Genomic level studies have been conducted on *N. encephala* (Mondo *et al.* 2017), *Cryptococcus* species (Chen *et al.* 2019), *N. aurantialba* (Sun *et al.* 2021), *T. mesenterica* (Tagirdzhanova *et al.* 2021), *T. yokohamensis* (Alshahni *et al.* 2011) Yurkov (Chiku *et al.* 2022), and *T. fuciformis* (Li *et al.* 2023b).

2.1.3.1.2. Ecological and economic importance

Mycoparasitic nature is a characteristic feature of many Tremellales members. *Tremella* species like *T. obscura* (L.S. Olive) M.P. Christ., *T. penetrans* (Hauerslev) Jülich, and *T. giraffa* Chee J. Chen, form mycoparasitic associations with Dacrymycetaceae. *Tremella giraffa* parasitise and produce their basidia and conidia on the hymenium of its host organism, *Dacrymyces stillatus* (Chen 1998, Bandoni and Boekhout 2011). The basidiocarp of *T. moriformis* develops around its host, *Peniophora* species.

Yeast stages are present in diverse habitats like terrestrial and aquatic ecosystems including extremely cold habitats and hydrothermal oceanic vents (Weiß *et al.* 2014). Different yeast collections have been isolated from diverse sources like surface of land plants, flowers, tree bark, water samples from natural sources, clinical specimens and from animals or their wastes (Kurtzman *et al.* 2011, Weiß *et al.* 2014). Tremellales contains root associated microorganisms which enhances plant performance and productivity. Members of the *Dioszegia* species are known for their abundance in plant root microbiome (Banerjee *et al.* 2019).

Tremellomycetes contain harmful human pathogens like *Cryptococcus neoformans* and *C. gattii*. They are opportunistic in immunocompromised animals and human beings, which start a local infection and then invade into other organs, mainly central nervous system (Weiß *et al.* 2014, Akapo *et al.* 2019, Chen *et al.* 2019).

Tremella fuciformis, commonly known as 'silver ear fungus' has commercial value, and it has been cultivated in China for about 200 years (Miles and Chang 2004). It is one of the major delicacy mushrooms in China (Chen 2018). Commercial cultivation of *T. fuciformis* is by the dual culture method, where both the host (*Annulohyphoxylon archeri* (Berk.) Y.M. Ju, J.D. Rogers and

H.M. Hsieh) and parasite are cultured together in the same test tube or Petri plate. Although monoculture of *T. fuciformis* is possible, the rate of production is lesser compared to the dual culture method (Chen 2018).

2.1.3.1.3. Distribution

AFRICA: Cameroon (Roberts 2001b, 2003a). ASIA: China (Bandoni and Zang 1990, Zhao 2019, Khunnamwong *et al.* 2019, Li *et al.* 2019, Sun *et al.* 2020, Yuan *et al.* 2020, Fan *et al.* 2021a,b,c), Japan (Kobayasi 1939b, Bandoni 1961, Krieglsteiner 2000, Li *et al.* 2020, Yamada *et al.* 2022), Russia (Malysheva *et al.* 2015, Spirin *et al.* 2018b), Thailand (Chen 1998, Chen *et al.* 1999, Khunnamwong *et al.* 2016, Li *et al.* 2020). AUSTRALIA: Australia (Martin 1936). EUROPE: (Bandoni 1961), Austria (Dämon and Hausknecht 2002, Döbbeler 2019), Bulgaria (Denchev and Assyov 2010), Czech Republic (Spirin *et al.* 2018b), Estonia (Raitviir 1967, Diederich *et al.* 2020), Finland (Pippola and Kotiranta 2008, Lindgren *et al.* 2015, Spirin *et al.* 2018b), France (Maire 1945, Döbbeler 2019), Germany (Spirin *et al.* 2018b, Döbbeler 2019, Rödel 2019, Li *et al.* 2020), Ireland (Diederich 2007, Döbbeler 2019), Macaronesia (Kout *et al.* 2015), Netherlands (Li *et al.* 2020), Norway (Diederich 2007, Sprin *et al.* 2018b), Portugal (Dueñas 2002, Diederich *et al.* 2020, Li *et al.* 2020), Scotland (Reid 1974), Spain (Dueñas 2002, Kout *et al.* 2015, Zamora *et al.* 2017, Diederich *et al.* 2020), Sweden (McNabb 1973, Millanes *et al.* 2012, Zamora *et al.* 2017, Sprin *et al.* 2018b, Diederich *et al.* 2020), Switzerland (Li *et al.* 2020), Ukraine (Malysheva and Akulov 2011), United Kingdom (Roberts 1995, 1999, 2001a, 2007; Overall 2017, Sprin *et al.* 2018, Diederich *et al.* 2020). NORTH AMERICA: Canada (Bandoni 1961, Diederich 2007, Lindgren *et al.* 2015, Li *et al.* 2020), Costa Rica (Bandoni *et al.* 1996, Kisimova-Horovitz *et al.* 2000), Guatemala (Lowy 1971), Mexico (Lowy 1971, Diederich 2007, Diederich *et al.* 2020), Jamaica (Lowy 1971), Panama (Lowy 1976), U.S.A (Bandoni 1961, Damon and Hausknecht

2002, Diederich 2007, Millanes *et al.* 2012, Lindgren *et al.* 2015, Spirin *et al.* 2018, Diederich *et al.* 2020, Li *et al.* 2020). SOUTH AMERICA: Argentina: (Lowy 1971), Brazil: (Lowy 1971, Lowy 1982), Colombia (Lowy 1971), Ecuador (Bandoni *et al.* 2011).

Available records of Tremellales from India are those of Kundalkar and Patil (1986), Mahamulkar *et al.* (2003), Swapna *et al.* (2008), Saluja *et al.* (2007), Das (2010), Prabhu *et al.* (2016), Pandey and Veena (2012), Devi *et al.* (2013), Kakde and Gaikwad (2014), Verma *et al.* (2019), Bera *et al.* (2018), and Debnath *et al.* (2020).

From Kerala, only four Tremellaceae members have been reported to date (Mohanani 2011, Kumar *et al.* 2019, Thomas and Kumar 2023, 2024).

2.1.3.1.4. Family Bulleribasidiaceae X.Z. Liu, F.Y. Bai, M. Groenew. and Boekhout

The family Bulleribasidiaceae is named based on the type genus *Bulleribasidium*. The family comprises of the genera, *Bulleribasidium*, *Derxomyces* F.Y. Bai and Q.M. Wang, *Dioszegia* Zsolt, *Hannaella* F.Y. Bai and Q.M. Wang, *Nielozyma* Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout and *Vishniacozyma* Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout (Liu *et al.* 2015). Most of the members of the family lack basidiocarps. Pseudohyphae, true hyphae and basidia formation may occur in cultural conditions (Liu *et al.* 2015). Basidia may be cylindrical, or occasionally globose, 2-celled, and produce globose basidiospores.

2.1.3.1.4.1. Genus *Vishniacozyma* X.Z. Liu, F.Y. Bai, M. Groenew. and Boekhout

The genus *Vishniacozyma* was erected by Liu *et al.* (2015b) based on the molecular distinction of few taxa belonging to *Cryptococcus*, *Bullera* and *Trimorphomyces* Bandoni and Oberw. Earlier, Boekhout *et al.* (2011) and Liu *et al.* (2015a) also had made similar observations on the clustering together of

these taxa that showed close phylogenetic relationship with *Tremella* members. The new genus, *Vishniacozyma* initially included 11 species with *Vishniacozyma carnescens* (Verona and Luchetti) X.Z. Liu, F.Y. Bai, M. Groenew. and Boekhout as the type species. The genus currently contains 25 accepted species (Zhu *et al.* 2023, <https://www.indexfungorum.org/Names/Names.asp>). Among them, *V. nebularis* (R. Kirschner and Chee J. Chen) Yurkov and *V.* species (CBS 200.94) are teleomorphic, with gelatinous pustulate basidiocarps and rest of them were yeast species. The yeast members of this genus are commonly associated with plant materials (Liu *et al.* 2015b).

2.1.3.1.4.1.1. Ecological and economic importance

Vishniacozyma ellesmerensis M. Tsuji, Y. Tanabe, W.F. Vincent and Mas. Uchida is psychrophilic in nature, and they can grow at sub-zero temperatures and in vitamin-free medium (Tsuji *et al.* 2019). Members of the genus *Vishniacozyma* have potential for exopolysaccharides production. *Vishniacozyma victoriae* (M.J. Montes, Belloch, Galiana, M.D. García, C. Andrés, S. Ferrer, Torr.-Rodr. and J. Guinea) Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout produces high molecular weight hetero-mannan and β -glucan type exopolysaccharides (Rusinova-Videva *et al.* 2022). *Vishniacozyma victoriae* have proven biocontrol activity against post harvest pathogenic fungi like *Botrytis cinerea* that affect kiwi fruits and organic pears (Gorordo *et al.* 2022, Nian *et al.* 2023).

2.1.3.1.4.1.2. Distribution

ASIA: China (Nian *et al.* 2023, Zhu *et al.* 2023), South Korea (Maeng *et al.* 2022), Taiwan (Chang *et al.* 2021). NORTH AMERICA: Canada (Tsuji *et al.* 2019). SOUTH AMERICA: Brazil (Felix *et al.* 2020).

2.1.3.1.5. Family Naemateliaceae Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout

The family Naemateliaceae was erected by Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout in 2015 to accommodate *Naematelia* and a monotypic genus *Dimennazyma* X.Z. Liu, F.Y. Bai, M. Groenew. and Boekhout (Liu *et al.* 2015a). In the genus *Tremella*, Chen (1998) introduced various groups based on morphological and molecular evidence. The *aurantia* group was one among the five groups in *Tremella*. Later, in the phylogenetic analysis of Tremellomycetes the *aurantia* group clustered differently from other *Tremella sensu stricto* members. Liu *et al.* (2015b) transferred *aurantia* group members to genus *Naematelia*. A single species of *Cryptococcus cisti-albidi* Á. Fonseca, J. Inácio and Spenc.-Mart. also segregated along with the members of the *aurantia* group, and was accommodated in a new genus *Dimennazyma*.

2.1.3.1.5.1. Genus *Naematelia* Fries

The genus *Naematelia* was erected by Fries (1818) to incorporate tremellaceous species with heterogenous basidiocarps (Bandoni and Zang 1990). The presence of host hyphae in the core of basidiocarp make the basidiocarp heterogenous in constitution, and this served as the key character to distinguish *Naematelia* members from other tremellaceous species. Fries (1818) treated two species, *N. encephala* based on *Tremella encephala*, and a new species *N. tubiformis* under this genus. Since Fries (1818) did not designate type specimen to this genus, the valid lectotypification was done by Clements and Shear (1931) by choosing *N. encephala* as the type species.

Bandoni (1961) identified the mycoparasitic nature of *N. encephala*. Study conducted by Chen (1998) revealed the polyphyletic nature of the genus *Tremella*. Chen (1998) divided the non-lichenicolous *Tremella* members into five

groups, *mesenterica* group, *fuciformis* group, *indecorata* group, *foliacea* group and *aurantia* group based on both morphological and molecular data. The multi-gene phylogenetic study of Tremellomycetes by Liu *et al.* (2015b) recognised the separation of *aurantia* group *sensu* Chen (*T. aurantia* (Schwein.) Burt, *T. aurantialba* (Bandoni and M. Zang) Millanes and Wedin, *T. encephala* and *T. microspora* (Lloyd) Millanes and wedin) as a unique clade in Tremellomycetes. Liu *et al.* (2015b) accommodated these species in the genus *Naematelia* (Liu *et al.* 2015b).

According to *Index Fungorum* (<https://www.indexfungorum.org/> accessed on 06-06-2023), the genus *Naematelia* includes eighteen species. Among them, only four species have been studied adequately because of the lack of voucher materials for few specimens and due to the uncertainty regarding taxonomic descriptions (Bandoni 1961), and have been partially represented in molecular phylogenetic studies (Liu *et al.* 2015a, 2015b).

2.1.3.1.5.1.1. Ecological and economic importance

Naematelia aurantialba has been widely used in medicinal preparations in China. The special preparation of ground basidiocarps along with sugar is recommended for the treatment of lung fever, flu, asthma and hypertension (Liu and Bau 1980, Bandoni and Zang 1990). *Naematelia aurantialba* is popular in China because of its unique flavour and high nutritional value with anti oxidant, anti inflammatory, anti tumor, and immunomodulatory activities. *Naematelia aurantialba* is a rich source of diverse polysaccharides, active proteins, terpenoids, phenolic compounds and flavanoids (Sun *et al.* 2022). Polysaccharides from *N. aurantialba* are also good for enhancing glucose tolerance (Zhang *et al.* 2010). In a study conducted in diabetic mice, the extracts of *N. aurantialba* successfully reduced the rate of diabeties (Wei *et al.* 2012).

Naematelia aurantialba also helps for quality improvement of fermented soybean beverages. It is observed that nutrient composition and antioxidant activity of soybean beverages increased significantly after fermenting with *N. aurantialba* (Sun *et al.* 2022)

2.1.3.1.5.1.2. Distribution

ASIA: China (Bandoni and Zang 1990), Japan (Kobayasi 1939b, Bandoni 1961, Krieglsteiner 2000), Taiwan (Chen 1998). EUROPE: (Bandoni 1961), England (Roberts 1999), Finland (Pippola and Kotiranta 2008), Japan (Bandoni 1961). NORTH AMERICA: Canada (Bandoni 1961), USA (Bandoni 1961). SOUTH AMERICA: Argentina (Lowy 1971).

2.1.3.1.6. Family Phaeotremellaceae Yurkov and Boekhout

Family Phaeotremellaceae was erected by Yurkov and Boekhout (Liu *et al.* 2015b) to incorporate the genus *Phaeotremella* Rea and genus *Gelidatrema* Yurkov, Xin Zhan Liu, F.Y. Bai, M. Groenew. and Boekhout (Liu *et al.* 2015a). In the phylogenetic analysis of Tremellomycetes, *foliacea* clade of *Tremella sensu* Chen (1998) together with a single-species, *Cryptococcus spencermartinsiae* V. de García, Brizzio, Boekhout, Theelen, Libkind and Van Broock, formed a monophyletic clade (Liu *et al.* 2015a). Based on phylogenetic analysis and physiological features, Liu *et al.* (2015b) introduced genus *Gelidatrema* to incorporate *C. spencermartinsiae*, and genus *Phaeotremella* for *foliacea* clade of *Tremella*.

Basidiocarp formation is not known in the genus *Gelidatrema* till date. At present *Gelidatrema* contains 2 species, *G. psychrophila* Tsuji and *G. spencermartinsiae*. *Gelidatrema psychrophila* is a cold adapted yeast species, which was isolated from a melt-pool microbial mat community in Canada (Tsuji *et al.* 2017). Currently, the family Phaeotremellaceae comprises of two genera, *Gelidatrema*, *Phaeotremella* (Liu *et al.* (2015b).

2.1.3.1.6.1. Genus *Phaeotremella* Rea

Rea (1912) erected the genus *Phaeotremella* with *P. pseudofoliacea* (= *Tremella foliacea*) as the type species. *Phaeotremella* was considered as a synonym of genus *Tremella* because of morphological similarities (Donk 1966, Chen 1998, Roberts 1999, Yuan *et al.* 2020). In the phylogenetic studies of Liu *et al.* (2015b), polyphyletic nature of the genus *Tremella* became evident and species similar to *T. foliaceae* clustered distinctly. Liu *et al.* (2015b) emended this genus to include *foliacea* clade of *Tremella*.

Along with the emendment of *Phaeotremella*, 6 new combinations of *Phaeotremella* based on the phylogenetic analysis have been listed in Liu *et al.* (2015a). Four of them were *Tremella* species and two of them were *Cryptococcus* species. Wedin *et al.* (2016) transferred *Tremella foliacea* Pers. to *P. foliacea* *comb. nov.* Spirin *et al.* (2018b) proposed *P. eugeniae* and three new combinations of *Phaeotremella* from the genus *Tremella*. Li *et al.* (2019) described *P. lacus* based on phylogenetic and phenotypic characterisation. Li *et al.* (2020) proposed *P. lactea* and *P. ovata* based on the study of diversity and phylogeny of basidiomycetes yeasts. Fan, Wu and Dai described another new species, *P. yunnanensis* into this genus (Yuan *et al.* 2020). At present 21 species are listed in *Index Fungorum*, (www.indexfungorum.org, 01-08-2024) under *Phaeotremella*.

2.1.3.1.6.1.1. Ecological and economic importance

Phaeotremella comprises both teleomorphic and anamorphic species (Sun *et al.* 2020). Among the teleomorphic members, most are mycoparasitic on either ascomycetous or basidiomycetous hosts (Spirin *et al.* 2018b, Sun *et al.* 2020). *Phaeotremella translucens* (H.D. Gordon) M. Yamada, Endoh et Degawa forms parasitic relationship with an ascomycete member *Lophodermium* species whereas, *P. mycetophiloides* (Kobayasi) Millanes et Wedin, *P. mycophaga*

(G.W. Martin) Millanes et Wedin, and *P. simplex* (H.S. Jacks. et G.W. Martin) Millanes et Wedin parasitize basidiomycetous *Aleurodiscus* species (Kobayasi 1939b, Martin 1940, Bandoni and Ginns 1993, Yamada *et al.* 2022). *Phaeotremella fimbriata* ((Pers.) Spirin and Malysheva), *P. foliacea* ((Pers.) Wedin, J.C. Zamora and Millanes), *P. frondosa* ((Fr.) Spirin and Malysheva), and *P. fuscossuccinea* (Chen) Spirin and Yurkov have similar ecology and they are associated with *Stereum* species (Sun *et al.* 2020). *Phaeotremella roseotincta* (Lloyd) Malysheva and *P. eugeniae* Malysheva grow on deciduous trees, but details of their fungal host species are still not known (Spirin *et al.* 2018b).

The anamorphic members of the genus *Phaeotremella* inhabit a wide range of habitats and environmental conditions. Yeast species of *Phaeotremella* can exist in water, soil, plant materials and mushrooms (Sun *et al.* 2020). *Phaeotremella lacus* Li, Jia and Zhou was described from freshwater of crater lake located in the Arxan–Chaihe volcanic field (ACVF) in East China with subarctic climatic conditions (Li *et al.* 2019). *Phaeotremella lactea* Q.M. Wang, F.Y. Bai and A.H. Li and *P. ovata* Q.M. Wang, F.Y. Bai and A.H. Li were isolated from leaves of an unidentified plant in China. *Phaeotremella skinneri* (Phaff and Carmo Souza) Yurkov and Boekhout is reported from an Acid Mine Drainage with low pH (2.7–3.4) and very high iron (up to 2700 mg l⁻¹) and arsenic (up to 350 mg l⁻¹) concentrations (Delavat *et al.* 2013). The same species *P. skinneri* is reported from insect frass under bark of *Tsuga heterophylla* in Oregon, USA (Fonseca *et al.* 2011).

2.1.3.1.6.1.2. Distribution

ASIA: China (Li *et al.* 2019, Sun *et al.* 2020, Yuan *et al.* 2020), Japan (Yamada *et al.* 2022), Russia (Spirin *et al.* 2018b). EUROPE: Czech Republic (Spirin *et al.* 2018), Finland (Spirin *et al.* 2018), Germany (Spirin *et al.* 2018), Norway (Spirin *et al.* 2018), Sweden (Spirin *et al.* 2018), United Kingdom (Spirin *et al.* 2018). NORTH AMERICA: USA (Spirin *et al.* 2018).

2.1.3.1.7. Family Sirobasidiaceae Lindau

The family Sirobasidiaceae was erected by Möller (1895), and Lindau (Engler and Prantl 1897) later validated the family with *Sirobasidium* Lagerh. and Pat. as the type species (Liu *et al.* 2015b). Now Sirobasidiaceae contains two genera, *Sirobasidium* and *Fibulobasidium* Bandoni (Liu *et al.* 2015b). Sirobasidiaceae is characterised by linearly arranged chains (*Sirobasidium*) or clusters of basidia (*Fibulobasidium*). In the phylogenetic studies of Tremellomycetes (Liu *et al.* 2015b), *Fibulobasidium* species formed a well supported cluster within Tremellales. Whereas, *Sirobasidium* species scattered as divergent lineages within Tremellales (Liu *et al.* 2015b). Currently, Sirobasidiaceae have 2 genera and 14 species according to *Index Fungorum* (www.indexfungorum.org, accessed on 01-08-2024).

2.1.3.1.7.1. Genus *Sirobasidium* Lagerh. and Pat.

Lagerheim and Patouillard (1892) proposed the genus *Sirobasidium* with two species, *S. albidium* Lagerh. and Pat. and *S. sanguineum* Lagerh. and Pat. *Sirobasidium* members are similar to the *Tremella* members in basidiocarp morphology, and in production of budding cells in cultures (Chen 1998).

Serial arrangement of the basidia on the end of hyphae is the characteristic feature of the genus *Sirobasidium* (Damon and Hausknecht 2002). In addition to the catenulate basidia, the genus was first described with fusiform basidiospores which eventually become detached. Later, researchers found that the fusiform structures were epibasidia and typical apiculate, globose to subglobose basidiospores differentiated from these fusiform structures (Bandoni 1957).

Möller (1895), Bandoni (1957) and Kobayasi (1962) were of the opinion that *Tremella* basidium evolved from the *Sirobasidium* type. According to Bandoni (1984), during the course of evolution, hymenium and basidial

structures of *Tremella* adapted for aerial dispersal evolved from relatively inefficient *Sirobasidium* type hymenium and basidia. However, Olive (1958) and Chen (1998) were of the opinion that *Sirobasidium* type basidium evolved from *Tremella* type. Chen (1998) studied the genus *Sirobasidium* in detail and believed that basidia in chain are more efficient way to simultaneously produce more basidiospores and to protect the lower basidia from desiccation.

2.1.3.1.7.1.1. Ecological and economic importance

Sirobasidium members have been found to be associated with Pyrenomycetes, especially Xylariales and *Hypoxyton* species (Chen 1998). Although haustorial structures were not reported from the basidiocarps of any Sirobasidiaceae species (Bandoni 1984, Wells 1994, Chen 1998), Yamada *et al.* (2022) reported the formation of tremelloid haustoria in cultures of *S. apiculatum* M. Yamada, Endoh and Degawa. The formation of haustorial structures in cultural conditions suggests the mycoparasitic nature of *Sirobasidium*.

2.1.3.1.7.1.2. Distribution

ASIA: India (Kundalkar and Patil 1986), Japan (Yamada *et al.* 2022). EUROPE: Austria (Damon and Hausknecht 2002), France (Maire 1945), Germany (Rodel *et al.* 2017). AUSTRALIA: Australia (Martin 1936). NORTH AMERICA: Costa Rica (Kisimova-Horovitz *et al.* 2000), U.S.A. (Damon and Hausknecht 2002). SOUTH AMERICA: Brazil (Damon and Hausknecht 2002), Ecuador (Bandoni *et al.* 2011).

2.1.3.1.8. Family Tremellaceae Fries

The family Tremellaceae was erected by Fries (1821) to incorporate fungi that produce basidiocarp with jelly nature. Later, Patouillard (1990) restricted this family for fungi with tremelloid basidia. Bandoni (1984, 1995), and Wells

and Bandoni (2001) later revised this family by adding more genera like *Bulleromyces*, *Holtermannia*, *Sirotrema* Bandoni, *Tremella*, *Trimorphomyces* Bandoni and Oberw. and *Xenolachne* D.P. Rogers. Liu *et al.* (2015b) re-defined the family Tremellaceae for the *Tremella sensu stricto* clade, by considering ten *Tremella* species previously included in *mesenterica* and *fuciformis* groups by Chen (1998), and *Cryptococcus yokohamensis* (Liu *et al.* 2015b).

2.1.3.1.8.1. Genus *Tremella* Persoon

The genus *Tremella* Pers. is considered as the most diverse and polyphyletic group in the family Tremellaceae (Liu *et al.* 2015b, Chen 1998). *Tremella* species are dimorphic in nature and contain both diploid filamentous and haploid yeast stages where yeasts develop from the haploid basidiospores either by budding or by repetition. *Tremella* grows on or in association with other groups of fungi and lichens. The fungal hosts can be species of Corticiales, Dacrymycetales, Diaporthales, Pleosporales, Polyporales, Rhytismatales, Russulales, Trechisporales and Xylariales (Diederich 1996, Chen 1998, Liu *et al.* 2015a, Malysheva *et al.* 2015, Zhao *et al.* 2019).

The genus name *Tremella* was first used by Dillenius (1741) for seven taxa that were later found to be members of algae, lichen, *Gymnosporangium*, *Auricularia* and *Exidia*. Persoon (1801) validated the genus based on the form of basidiocarp, and excluded algae. Patouillard (1887, 1990) divided the genus into four sub genera Foliacees, Cerebrinees, Crustacees, and Tuberculiformes based on basidiocarp morphology. In 1888, Brefeld separated *Craterocolla* and *Ulocolla* from the genus *Tremella*. He included only species with spherical spores. Bandoni (1957) listed and discussed all of the valid names and synonyms of *Tremella* known thus far. Lowy (1971) published a monograph of neotropical Tremellales where he introduced many new *Tremella* species. By describing 40 new species, Diederich (1996) set a strong base to the studies of lichenicolous *Tremella*. In 1998, Chen published his monograph "Morphological

and molecular studies in the genus *Tremella*", showing phylogenetic relationships within the genus. Chen (1998) proposed eleven new *Tremella* species, and divided the genus into five groups (*aurantia* group, *foliaceae* group, *fuciformis* group, *indecorata* group, and *mesenterica* group).

According to Chen (1998), *aurantia* group is characterized by basidiocaps mixed with host hyphae up to subhymenium. Species like *T. aurantia*, *T. australiensis*, *T. encephala*, *T. microspora* and *T. giraffa* are placed under the *aurantia* group, and have capitate to pyriform basidia, loose subhymenial structures, and abundant haustoria. The *foliaceae* group is characterised by foliose and brown basidiocarps. Species like *T. fuscusuccinea*, *T. griseobrunnea* Chee J. Chen, *T. neofoliacea* Chee J. Chen, *T. mycophaga*, *T. simplex* and *T. vasifera* Chee J. Chen are placed under *foliaceae* group, and have mostly oval basidia, subhymenium with abundant anastomoses, terminally swollen cells in the interior regions and rare presence of haustoria. The *fuciformis* group members have an association with *Hypoxylon* ascocarps. Species like *T. flava* Chee J. Chen, *T. fuciformis*, *T. resupinata* Chee J. Chen are included in the *fuciformis* group, and have firm subhymenial structures, numerous anastomoses and branched haustorial hyphae, oval basidia, swollen cells in the inner part of basidiocarp. The *indecorata* group members are always associated with pyrenomycetaceous fungi. Species like *T. albida* Huds., *T. moriformis*, *T. nivalis* Chee J. Chen are in the *indecorata* group and have loose hymenial structures, and rarely anastomosing hyphae, and spores broader than long. The *mesenterica* group is characterized by whitish yellow to orange yellow basidiocarps mostly larger than 1 cm, loose hymenial and subhymenial structure, presence of hyphidia in the hymenium, production of conidia and lack of terminally swollen cells in the inner part of basidiocarp. Species like *T. mesenterica*, *T. taiwanensis* Chee J. Chen, *T. tropica* Chee J. Chen belong to this group (Chen 1998).

Based on phylogenetic analyses, Liu *et al.* (2015b) restricted the genus *Tremella* to include only two subclades, *mesenterica* and *fuciformis*, which are morphologically distinguishable. The species in *indecorata* group, *foliacea* group and *aurantia* group were considered under *Pseudotremella* X.Z. Liu *et al.*, *Phaeotremella* and *Naematelia*, respectively.

2.1.3.1.8.1.1. Ecological and economic importance

Polysaccharides of *Tremella fuciformis* have a potential role in the treatment of constipation. *Tremella fuciformis* has high water retention capacity, which improves constipation rate in a study conducted in rats (Chen 2018). *Tremella* polysaccharides can control type II diabetes, cardiovascular disease, obesity, metabolic syndrome, inflammation and aging (Ma *et al.* 2021). *Tremella* species are known for its anti-apoptosis property. Study conducted by Wu *et al.* (2019) observed that polysaccharides of *Tremella* suppressed apoptosis caused by oxidative damage in cardiomyocytes. In the cosmetic industry, polysaccharide from *Tremella* has application as moisturizer and anti-wrinkle agent, which is a cheaper alternative to other moisturising agents (Ma *et al.* 2021).

2.1.3.1.8.1.2. Distribution

AFRICA: Cameroon (Roberts 2001b, 2003a). ASIA: China (Bandoni and Zang 1990, Zhao *et al.* 2019, Fan *et al.* 2021b, Fan *et al.* 2021c), India (Verma *et al.* 2019), Japan (Bandoni and Boekhout 2011), Philipines (Bandoni and Boekhout 2011), Russia (Malysheva *et al.* 2015), Taiwan (Chen 1998, Chen 2018), Ukraine (Malysheva and Akulov 2011). EUROPE: England (Roberts 1995, 1999, 2001a), Finland (Pippola and Kotiranta 2008, Zamora *et al.* 2018), Norway (Zamora *et al.* 2018), Spain (Kout *et al.* 2015, Zamora *et al.* 2017, Zamora *et al.* 2018, Diederich 2020), Sweden (Zamora *et al.* 2018), United Kingdom (Diederich 2020). NORTH AMERICA: Canada (Bandoni and Boekhout 2011, Lindgren *et al.*

2015), Costa Rica (Bandoni *et al.* 1996), Mexico (Lowy 1971), USA (Bandoni and Boekhout 2011, Zamora *et al.* 2018, Diederich 2020). SOUTH AMERICA: Argentina (Bandoni and Boekhout 2011), Brazil (Lowy 1971), Colombia (Lowy 1971).

MATERIALS AND METHODS

3.1. Study area- Kerala State

Physiography of Kerala State

Kerala State is situated on the extreme southern tip of India bordered by the Arabian Sea at the west, Karnataka State at the north, and Tamil Nadu State at the eastern and south sides (Sasidharan 2004). Kerala State lies between north latitude of 8°.17'.30" N and 12°. 47'.40" N and east longitude of 74°.27'.47" E and 77°.37'.12" E (Mohanani 2011). Kerala has an average height of 900 m (Latha and Manimohan 2017). Western Ghat is a UNESCO World Heritage Site and is one of the eight hot-spots in the world (<https://whc.unesco.org/en/list/1342>).

Geographically, Kerala State is divided into three zones: the eastern highlands, the central midlands, and the western lowlands. The highlands (600–1800 m in height) contain the mountain ranges of the Western Ghats and numerous peaks with dense forest areas. The midlands (300–600 m in height) are in between the mountains and the coastal belt, which represents around 40% of the total land area. The midland covers hills and valleys (Thomas 2000). The lowlands (1–300 m in height) include lagoons, river deltas, backwaters, and the coast of the Arabian Sea (Sasidharan 2004, Latha and Manimohan 2017, Vinjusha and Kumar 2022).

Climatic condition

Kerala State has a humid tropical wet climate. The average annual temperature ranges from 25.4°C to 31°C (Sasidharan 2004). The maximum day temperature may increase to 40°C in some places in the summer and the minimum night temperature may decline to 0°C in some parts of the highlands

in the winter (Aravindakshan and Manimohan 2015). Kerala has a maritime tropical climate with two principal rainy seasons (south-west and north-east) in a year (Kumar *et al.* 2019). The south-west monsoon starts in early June and lasts up to September and offers around 60% of the total annual rainfall. The north-east monsoon occurs between October and December and provides much less rainfall than the south-west monsoon (Sasidharan 2004, Latha and Manimohan 2017).

Biodiversity

Various geographical features like tropical climate, monsoon seasons, high rainfall and Western Ghat have contributed to the peculiar vegetation and supported the diverse ecosystems in Kerala (Sasidharan 2004). The presence of the Western Ghats is the major reason for the formation of tropical rainforests along its sides (Sasidharan 2004, Latha and Manimohan 2017).

The types of forests in Kerala include evergreen forests, deciduous forests, shola forests, mangrove forests, grasslands and subtypes such as dry teak forests, littoral forests, lateritic semi-evergreen forests, Nilgiri subtropical hill forests, myristica swamps, south Indian subtropical hill, savannah, southern moist mixed deciduous forests, southern secondary moist mixed deciduous forests, and moist teak forests (Aravindakshan and Manimohan 2015).

Till the middle of the nineteenth century, 70% of Kerala State was under dense forest cover. By the 20th century, it declined to 50%. At present, forest areas and wildlife are under strict protection by the Kerala Forest and Wildlife Department. As per the information from the website of the Kerala Forest and Wildlife Department, the State covers a forest area of 9400.00km² (https://forest.kerala.gov.in/index.php?option=com_contentandview=articleandid=205andItemid=162 accessed on 14-12-2023). Kerala contains

protected forested areas in the form of national parks, wildlife sanctuaries and biosphere reserves to conserve biodiversity. It includes five national parks, 18 wildlife sanctuaries and one community reserve (https://forest.kerala.gov.in/index.php?option=com_contentandview=articleandid=205andItemid=162 accessed on 14-12-2023). The national parks in Kerala are Aanamudi Shola National Park, Eravikulam National Park, Silent Valley National Park, Mathikettan Shola National Park and Pampadum Shola National Park. Wildlife Sanctuaries are Aralam Wildlife Sanctuary, Choolannur Pea Fowl Sanctuary, Chimmony Wildlife Sanctuary, Chinnar Wildlife Sanctuary, Idukki Wildlife Sanctuary, Karimpuzha Wildlife Sanctuary, Kottiyoor Wildlife Sanctuary, Kurinjimala Sanctuary, Malabar Sanctuary, Mangalvanam Bird Sanctuary, Neyyar Wildlife Sanctuary, Peechi-Vaazhaani Wildlife Sanctuary, Peppara Wildlife Sanctuary, Shendurney Wildlife Sanctuary, Thattekkaad Bird Sanctuary and Wayanad Wildlife Sanctuary. Additionally, there are two Tiger Reserves maintained in the State, namely the Parambikulam Wildlife Sanctuary (Tiger Reserve) and Periyar Wildlife Sanctuary (Tiger Reserve). The community reserve is Kadalundi-Vallikunnu Community Reserve (https://forest.kerala.gov.in/index.php?option=com_contentandview=articleandid=205andItemid=162 accessed on 12-12-2023).

In addition to the officially declared biodiversity protecting areas, Kerala has around two thousand small and large sacred groves spanning around 500 hectares of land area (Khan *et al.* 2008). Sacred groves are small forest patches traditionally conserved as part of religious or cultural heritage (Oviedo *et al.* 2005). In Kerala State, Thiruvananthapuram, Kottayam, Thrissur districts contain more number of sacred groves than other districts (http://www.kerenvis.nic.in/Database/Sacred_groves_2204.aspx).



Figure 1: Map of Keral State, India showing major collection localities

3.2 Field study and specimen collection

Specimens used in the study were collected from different localities of Kerala State (Figure 1). Collection sites include agricultural lands, plantations, sacred groves, college campuses and natural forests. Different protected areas like wildlife sanctuaries, national parks, and biosphere reserves were also visited as part of specimen collection trips. More field trips and extensive collections were conducted during the monsoon seasons; south-west monsoon (June to September) and north-east monsoon (October to December). Major collection localities of the study are shown in Figure 1. All the collections described in the treatise except *Sebacina species*, were collected from twigs, decaying wood or barks. *Sebacina species* were collected from soil and from the base of a living plant (formed ectomycorhyzal association).

3.3. Morphological characterisation

Field photographs and macroscopic photographs of the basidiocarps were taken from the field using the Sony cybershot DSE-HX400V camera. Macroscopic data including measurements, shape, colour, texture, substratum, host, habitat etc. were noted. Specimens for DNA isolation was collected separately in appropriate vials. Each collection was carefully wrapped in paper and brought to the laboratory. Small polythene sheet pieces were used sometimes within the paper wrap, to avoid the gluing of gelatinous basidiocarps with the paper. Spore prints of the most collections were collected on microslides by creating artificial humid condition using Petri plates and wet tissue paper.

Appropriate drying options (hot air oven/refrigeration) were used based on the nature of basidiocarp. For heavier specimens, the hot air oven method was preferred over refrigeration since the latter took more time. Hot air oven set at 50°C was used. Most of the specimens were dried using refrigeration method. After proper drying, specimens were transferred to labelled paper bags, and kept in cardboard boxes. Silica crystals were used within the cardboard boxes to avoid moisture contents.

Microscopic analysis was conducted mostly using dried basidiocarps. Hand sectioning with fresh specimens were difficult because of their gelatinous nature. Thin free hand sections were taken from different parts of the specimens. These sections were stained with one drop of 1% aqueous solutions of Congo red or a mix of 1% aqueous solutions of both phloxine and Congo red. 5% aqueous KOH were used to remove the excess stain from section and as mounting medium. The specimens were also mounted in tap water to note the natural pigmentation. Microphotographs of the collections were taken using AMSCOPE digital microscopic camera fitted to the LABOMED Lx400 compound microscope, Magnus MX21iLED compound microscope, and Leica DM 2000 LED microscope with Leica DMC 2900 camera were used to process the microscopic images. Photographic plates were prepared using the ADOBE PHOTOSHOP 2021.

The microscopic structures like basidia, hyphidia, marginal hairs, basidiospores, conidia, conidiophores and tramal hyphae were noted and their shape, colour, measurements were recorded. Colour and pigmentation of the structures were noted with the section mounted in water. Important taxonomic characters, specific for the taxa are noted and studied separately. For obtaining the dimensions of basidiospores, random measurements of 20 mature basidiospores of each specimen were made. The ratio of basidiospore length to its width (Q) was calculated for each of the 20 basidiospores and the average of these values was calculated and given as Qm.

After microscopic examinations, the paper packets containing basidiocarps were vacuum sealed within polypropylene covers, using the modified method of Pradhan *et al.* (2015). Vacuum sealed packets of all the collections have been deposited at the Zamorin's Guruvayurappan College herbarium (ZGC), Kozhikode.

3.4. Terminology followed

Index Fungorum (www.indexfungorum.org) was followed for the latest information on taxonomic and systematic positions.

Systematic study of the genus *Auricularia* was done by following the terminology and methodology of Lowy (1951) and Looney *et al.* (2013). Taxonomic key provided by Wu *et al.* (2021) was mainly followed for identification.

The methods and techniques to study Dacrymycetes follow by Kennedy (1958), Reid (1974), McNaab (1965a, 1965b, 1965c, 1965d, 1965e, 1966, 1969, 1973), Shirouzu *et al.* (2013a), Oberwinkler (2014) and Zamora and Ekman (2020). In Dacrymycetes, the term basidia was used for the basal probasidium (upto the bifurcating point), and epibasidia were used for apical portion of basidia (from the bifurcating point to tip). Sterile hyphal elements in the hymenium are referred as hyphidia. We consistently used the term hyphidia instead of the traditional term 'dikaryophyses' following Savchenko *et al.* (2021). For Tremellomycetes, Chen (1998), Zhao *et al.* (2019), Millanes *et al.* (2021) were referred for the terminologies and methodologies.

Our concepts of structures like inflated cells, swollen cells and vesicles are as follows (Figures 2, 3)

Inflated cells

Inflated cells are exceptionally large cells with less stained protoplasm, thin-walled, easily collapsing, shrinking and losing rigidity. Inflated cells may be present throughout the basidiocap, and can be present in the hymenium, subhymenium or within tramal hyphae depending on the species. Inflated cells may be terminal or sub terminal, may be single or can form chains of cells (Figure 2: A, B; Figure 3: A, B).

Swollen cells

Swollen cells will have a definite size and form and are ellipsoid, fusiform to broadly fusiform, may be thin-walled or thick-walled. Swollen cells

densely stain with phloxine. Present throughout the basidiocarp (Figure 2: D; Figure 3: D).

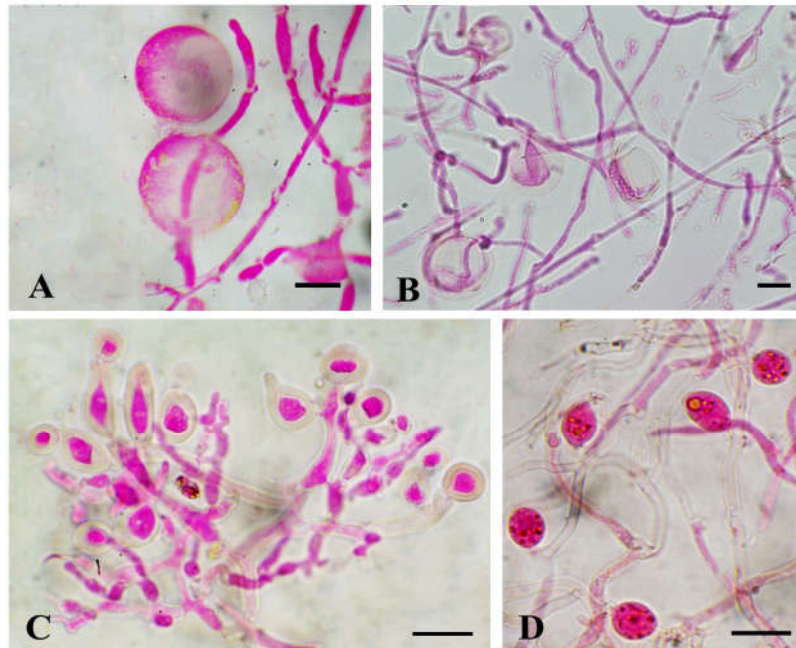


Figure 2: Cell types in Tremellales- **A.** Inflated cells in *Tremella mesenterica*; **B.** Inflated cells in *T. laurisilvae*; **C.** Vesicles in *T. fuciformis*; **D.** Swollen cells in *Tremella* species 2. Scale bars: A-D=10 μ m.

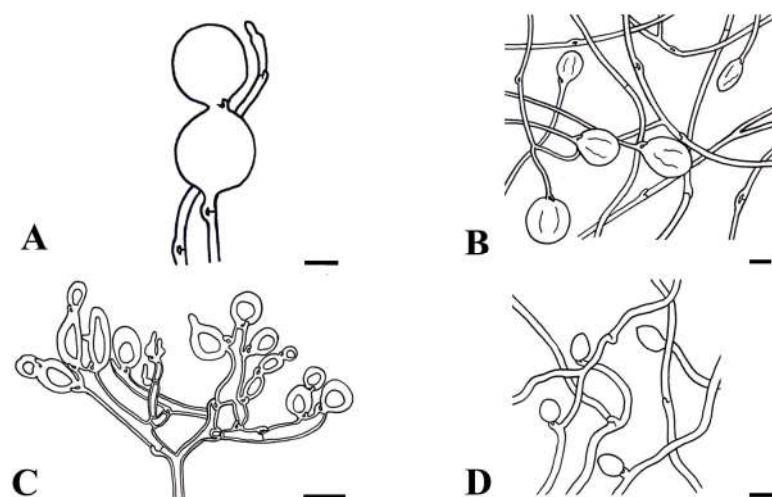


Figure 3: Cell types in Tremellales- **A.** Inflated cells in *Tremella mesenterica*; **B.** Inflated cells in *T. laurisilvae*; **C.** Vesicles in *T. fuciformis*; **D.** Swollen cells in *Tremella* species 2. Scale bars: A-D=10 μ m.

Vesicles

Vesicles are thick-walled cells present throughout the basidiocarp with shape varying from globose, ellipsoid, cylindrical, or clavate (Figure 2: C; Figure 3: C).

3.5. Pure culture establishment

Live cultures were generated in Potato Dextrose Agar (PDA) and Malt Yeast Peptone Agar (MYPA) medium with the help of spore deposits, and live tissues. Tap Water Agar (TWA) and PDA media were used for primary inoculation. Different methods were adopted for generating cultures. Culturing with the help of spore deposits was observed as the most successful way of establishment. Freshly collected basidiocarps were placed on top of a microslide and incubated in a Petri plate lined with moist sterile tissue paper to get spore print. Basidiocarps were removed after overnight incubation, and the spore print obtained on the microslide was taken out. Spore deposit collected in the microslide was scraped into the medium using sterile needles.

Live specimens attached to the upper lid of the Petri plate were allowed to discharge spores into the lower lid on which low nutrient medium (TWA) were poured. After a day, the basidiocarp was removed from the upper lid and the spore prints were kept as such for growing. Live tissues of the basidiocarp, preferably from the interior of basidiocarp or the hymenial surface were inoculated. Since most of the specimens were too small, entire basidiocarps after thorough washing with sterile water were also used. Sometimes basidiocarps vortexed in sterile water for thorough washing. Cultures primarily generated were subcultured into another nutrient medium (PDA or MYPA) and the subculturing continued till the pure culture was established. After the successful establishment of pure culture, they were maintained in small vials or test tubes with nutrient medium.

3.6. Molecular characterisation

Molecular characterisation was done by the isolation of genomic DNA, PCR amplification, and sequencing.

Genomic DNA was isolated by using REExtract-N-Amp kit (Sigma-Aldrich), NucleoSpin Plant II kit (Macherey- Nagel 2014, Germany) following the manufacture's protocol. For some basidiocarps, genomic DNA was extracted using the protocol proposed by Izumitsu *et al.* (2012). In the Izumitsu *et al.* (2012), small pieces of dried/fresh basidiocarp or piece of hyphal mat from the culture were taken using sterile blades and needles. Specimens were then transferred to a 1.5 ml sterile microcentrifuge tube containing 100 µl sterile TE buffer or sterile water. Samples were then homogenised using sterile micropestles. The microcentrifuge tube containing the homogenised mixture was then microwaved (600 W) for 1 minute and then allowed to cool at room temperature for 30 seconds. Directly after cooling, the tube was again microwaved for another 1 minute and then kept at -20 °C for 10 minutes. The tube was then kept at room temperature until the contents liquefied and then was then centrifuged at 10000 rpm for 5 minutes. The supernatant containing genomic DNA of the selected specimen was then transferred to another sterile microcentrifuge tube and this was used as the template DNA for PCR amplification.

PCR amplification of nuclear ribosomal internal transcribed spacer (ITS: ITS1, 5.8S rRNA gene, ITS2) and large subunit ribosomal RNA (nLSU) was done for the study. The PCR reactions were performed with the primers ITS1F and ITS4 for the ITS region (White *et al.* 1990), and LROR and LR7 for nLSU (Vilgalys and Hester 1990) region. PCR mastermix was prepared with 15 µl of Takara Emerald AMP®GT PCR Master Mix followed by 6 µl PCR grade water, 3 µl of primers and 3 µl of template DNA. The PCR amplification cycle of the ITS and LSU regions consisted of 30 sec at 98°C; 40 cycles of 5 sec at 98°C, 10 sec at

58°C, 15 sec at 72°C, and a final extension step of 60 sec at 72°C. Amplification was done in BR BIOCHEM Mini PCR Thermal Cycler. Agarose gel electrophoresis using 1% agarose solution was done with the PCR products and visualised using Gel Documentation System (Biotech). Samples with proper bands were used for sequencing. Purification and sequencing of amplified PCR products were done using commercial facilities like Rajiv Gandhi Centre for Biotechnology (RGCB-Trivandrum, India), Chromous (Bangalore, India), AgriGenome (Cochin, India), Enfys (Trivandrum, India) and Barcode Biosciences (Bangalore, India). In some cases, tissue/culture samples were directly sent to commercial facilities like AgriGenome (Cochin, India), Barcode Biosciences (Bangalore, India) and generated the DNA sequences.

All the sequences generated as part of the study were subjected to Basic Local Alignment Search Tool (BLASTn), an online tool available at the NCBI GenBank DNA database (www.ncbi.nlm.nih.gov), and noted the close hits and the statistical significance of the matches.

3.7. Phylogenetic analyses

The newly generated sequences with good quality were deposited in GenBank (www.ncbi.nlm.nih.gov) database with accession numbers (Table: 7). Sequences selected for the phylogenetic analysis were downloaded from the GenBank and combined dataset of ITS and LSU were prepared with the help of MEGA- X software. Alignment was done with MAFFT version 7 (<https://mafft.cbrc.jp/alignment/server/>). MAFFT aligned datamatrix then manually aligned using MEGAX64 (Kumar *et al.* 2018). Maximum Likelihood (ML) analysis was conducted with IQTREE (IQTREE Web Server: Fast and accurate phylogenetic trees under maximum likelihood (univie.ac.at)) (Nguyen *et al.* 2015). In IQTREE, parameters like auto detecting substitution model, 1000 bootstrap in ultrafast analysis, and SH-like approximate likelihood ratio test (Nguyen *et al.* 2015, Hoang *et al.* 2018). FigTree v1.2.3 was used to display and process the phylogenetic tree (Rambaut 2014).

3.7. 1. Phylogenetic analysis of Auriculariales

The final aligned data matrix included all the major lineages in Auriculariales as ingroups and *Sistotrema brinkmannii* (Bres.) J. Erikss. as the outgroup. *Sistotrema brinkmannii* is set as the out group, by referring Li *et al.* (2022a). The dataset consisted of 310 accessions belonging to 106 species (Table 2). Maximum Likelihood (ML) analysis was conducted with IQTREE (IQTREE Web Server: Fast and accurate phylogenetic trees under maximum likelihood (univie.ac.at)) (Nguyen *et al.* 2015) with TIM2+F+I+G4 model (Kalyaanamoorthy *et al.* 2017).

Table 2: List of species used in the phylogenetic analysis of Auriculariales. GenBank accession number of sequences (ITS and LSU), voucher /strain /isolate, and locality are provided. Name and accessions of sequences generated in the present study are indicated in bold.

| Sl. No | Taxon | ITS | LSU | Voucher /strain /isolate | Country |
|--------|-------------------------------------|----------|----------|--------------------------|----------------|
| 1. | <i>Adustochaete interrupta</i> | MK391518 | MK391527 | LR23435 | Mexico |
| 2. | <i>Adustochaete rava</i> | MK391517 | MK391526 | KHL15526 | Brazil |
| 3. | <i>Alloexidiopsis australiensis</i> | OM801933 | OM801918 | LWZ 20180513-22 | Australia |
| 4. | <i>Alloexidiopsis australiensis</i> | OM801934 | OM801919 | LWZ 20180514-18 | Australia |
| 5. | <i>Alloexidiopsis calcea</i> | AF291280 | AF291326 | MW 331 | Germany |
| 6. | <i>Alloexidiopsis calcea</i> | OM801935 | OM801920 | LWZ20180904-14 | China |
| 7. | <i>Alloexidiopsis calcea</i> | OM104980 | - | PRA-JV19329 | Czech Republic |
| 8. | <i>Alloexidiopsis calcea</i> | OM104979 | - | PRA-JV19330 | Czech Republic |
| 9. | <i>Alloexidiopsis nivea</i> | MZ352947 | - | CLZhao 11204 | China |
| 10. | <i>Alloexidiopsis nivea</i> | MZ352948 | MZ352939 | CLZhao 11210 | China |
| 11. | <i>Alloexidiopsis nivea</i> | MZ352940 | MZ352932 | CLZhao 16260 | China |
| 12. | <i>Alloexidiopsis nivea</i> | MZ352941 | MZ352933 | CLZhao 16280 | China |
| 13. | <i>Alloexidiopsis yunnanensis</i> | MT215568 | MT215564 | CLZhao 4023 | China |

Materials and Methods

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| 14. | <i>Alloexidiopsis yunnanensis</i> | MT215569 | MT215565 | CLZhao 8106 | China |
| 15. | <i>Alloexidiopsis yunnanensis</i> | MT215570 | MT215566 | CLZhao 9132 | China |
| 16. | <i>Amphistereum leveilleanum</i> | KX262119 | KX262168 | FP-106715 | USA |
| 17. | <i>Amphistereum schrenkii</i> | KX262130 | KX262178 | HHB 8476 | USA |
| 18. | <i>Aporpium canescens</i> | JX044152 | - | Otto Miettinen 13352,2 (H) | Norway |
| 19. | <i>Aporpium caryae</i> | AB871751 | AB871730 | WD2207 | Japan |
| 20. | <i>Aporpium caryae</i> | JX044145 | - | Otto Miettinen 14774 (H) | USA |
| 21. | <i>Aporpium hexagonoides</i> | AB871754 | AB871735 | ML297 | Malaysia |
| 22. | <i>Auricularia africana</i> | MH213349 | MZ669897 | Ryvarden 44929 | Uganda |
| 23. | <i>Auricularia africana</i> | MH213350 | MZ669918 | T 3 | Kenya |
| 24. | <i>Auricularia americana</i> | KM396763 | MZ669919 | Dai 13461 | China |
| 25. | <i>Auricularia americana</i> | KM396766 | KM396824 | Dai 13476 | China |
| 26. | <i>Auricularia angiospermarum</i> | KT152096 | KT152112 | TJV-93-12-SP | USA |
| 27. | <i>Auricularia asiatica</i> | KX022009 | KX022040 | Dai_15285 | China |
| 28. | <i>Auricularia auricula-judae</i> | KM396769 | KM396824 | Dai_13210 | France |
| 29. | <i>Auricularia cornea</i> | KX022014 | KX022045 | Dai_15336 | China |
| 30. | <i>Auricularia cornea</i> | MH213354 | MH213398 | Wu_07 | China |
| 31. | <i>Auricularia cornea</i> | PP380396 | - | ZGCAT227 | India |
| 32. | <i>Auricularia delicata</i> | MH213364 | MZ669933 | P 14 | Cameroon |
| 33. | <i>Auricularia fibrillifera</i> | KP765615 | KP765629 | Dai_13598A | China |
| 34. | <i>Auricularia heimuer</i> | KM396789 | MH021028 | Dai 13503 | China |
| 35. | <i>Auricularia heimuer</i> | KM396785 | MH021016 | Dai 2291 | China |
| 36. | <i>Auricularia mesenterica</i> | AB915192 | AB915191 | TUFC12805 | Japan |
| 37. | <i>Auricularia mesenterica</i> | KM396801 | KM396849 | LYBR_5353 | France |

Materials and Methods

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| 38. | <i>Auricularia mesenterica</i> | KP729279 | KP729297 | BRNM_648573 | Czech Republic |
| 39. | <i>Auricularia mesenterica</i> | AF291271 | AF291292 | FO25132 | Germany |
| 40. | <i>Auricularia minutissima</i> | KT152104 | KT152120 | Dai_14881 | China |
| 41. | <i>Auricularia minutissima</i> | KX022030 | KX022061 | Dai_15455 | China |
| 42. | <i>Auricularia nigricans</i> | AB871752 | AB871733 | TUFC12920 | Japan |
| 43. | <i>Auricularia orientalis</i> | KP729270 | KP729288 | Dai_14875 | China |
| 44. | <i>Auricularia sinodelicata</i> | MH213376 | MH213415 | Cui_8596 | China |
| 45. | <i>Auricularia srilankensis</i> | MZ647501 | MZ669912 | Dai_19522 | Sri Lanka |
| 46. | <i>Auricularia srilankensis</i> | PP380394 | - | ZGCAT155 | India |
| 47. | <i>Auricularia submesenterica</i> | KX022037 | KX022068 | Dai_792 | China |
| 48. | <i>Auricularia submesenterica</i> | KX022038 | KX022069 | Dai_14773 | China |
| 49. | <i>Auricularia thailandica</i> | KP765621 | KP765635 | Dai_13759 | China |
| 50. | <i>Auriculariales</i> sp. | - | MH178280 | He5206 | Viet Nam |
| 51. | <i>Auriculariales</i> sp. | MH178257 | MH178281 | He4610 | China |
| 52. | <i>Auriculariales</i> sp. | - | MN475888 | RLMA-2019a | Brazil |
| 53. | Auriculariaceae taxon | PP380637 | - | ZGCAT242 | India |
| 54. | Auriculariaceae taxon | - | PP818916 | ZGCAT106 | India |
| 55. | <i>Basidiodendron eyrei</i> | MT040880 | MT040854 | VS 12003 | Russia |
| 56. | <i>Basidiodendron globisporum</i> | MT040884 | MT040864 | VS 12929 | Russia |
| 57. | <i>Basidiodendron luteogriseum</i> | MT040881 | MT040861 | KHL 16022 | Brazil |
| 58. | <i>Bourdotia galzinii</i> | MG757511 | - | Otto Miettinen X3067 | Spain |
| 59. | <i>Ductifera pululahuana</i> | - | AF291315 | KW 1733 | USA |
| 60. | <i>Ductifera sucina</i> | AY509551 | AY509551 | KW3886 | - |
| 61. | <i>Eichleriella alliciens</i> | KX262120 | KX262169 | HHB 7194 | USA |

Materials and Methods

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| 62. | <i>Eichleriella bactriana</i> | KX262123 | KX26217 | TAAM 96698 | Tajikistan |
| 63. | <i>Eichleriella crocata</i> | KX262100 | KX262147 | TAAM 101077 | Russia |
| 64. | <i>Eichleriella desertorum</i> | KX262142 | KX262190 | LR 49350 | Namibia |
| 65. | <i>Eichleriella flavida</i> | KX262137 | KX262185 | LR 49412 | United Kingdom |
| 66. | <i>Eichleriella leucophaea</i> | KX262111 | KX262161 | LE 303261 | Russia |
| 67. | <i>Eichleriella leucophaea</i> | KX262115 | KX262164 | KHL 15277 | Spain |
| 68. | <i>Eichleriella shearii</i> | AF291284 | AF291335 | USJ 54609 | Costa Rica |
| 69. | <i>Eichleriella tenuicula</i> | KX262141 | KX262189 | LR 17599 | Thailand |
| 70. | <i>Elmerina cladophora</i> | MG757509 | MG757509 | OM X1902 | Indonesia |
| 71. | <i>Elmerina sclerodontia</i> | MG757512 | MG757512 | OM X3269 | Malaysia |
| 72. | <i>Endoperplexa dartmorica</i> | MT235621 | MT235602 | VS 11781 | Norway |
| 73. | <i>Exidia candida</i> | KY801867 | KY801892 | VS 3921 | Russia |
| 74. | <i>Exidia candida</i> | KY801870 | KY801895 | VS 8588 | USA |
| 75. | <i>Exidia candida</i> | KY801868 | KY801893 | LE 313211 | Russia |
| 76. | <i>Exidia candida</i> | KY801871 | KY801896 | LE 38198 | Russia |
| 77. | <i>Exidia candida</i> | KY801872 | KY801897 | O F160269 | - |
| 78. | <i>Exidia candida</i> | KY801875 | KY801900 | VS 8450 | - |
| 79. | <i>Exidia candida</i> | KY801874 | KY801899 | Spirin 10,021 | - |
| 80. | <i>Exidia crenata</i> | MT663359 | MT664778 | Dai 19464 | Canada |
| 81. | <i>Exidia crenata</i> | MT663361 | MT664780 | Wu 26 | Canada |
| 82. | <i>Exidia glandulosa</i> | MH213394 | MH213426 | Dai 18,024 | China |
| 83. | <i>Exidia glandulosa</i> | MH213393 | MH213425 | Dai 17,633 | China |
| 84. | <i>Exidia glandulosa</i> | AF291273 | AF291319 | MW 355 | Germany |
| 85. | <i>Exidia glandulosa</i> | AB871761 | AB871742 | TUFC34008 | Japan |
| 86. | <i>Exidia pithya</i> | AF291275 | AF291321 | MW 313 | Germany |
| 87. | <i>Exidia qinghaiensis</i> | MW353409 | MW353409 | HMAS 156328 | China |
| 88. | <i>Exidia qinghaiensis</i> | MW353408 | MW353408 | HMAS 156376 | China |
| 89. | <i>Exidia recisa</i> | AF291276 | AF291322 | MW 315 | Germany |
| 90. | <i>Exidia recisa</i> | MT663365 | MT664783 | SL 180317 | Finland |
| 91. | <i>Exidia repanda</i> | MT663367 | MT664784 | LY BR 7046 | France |
| 92. | <i>Exidia saccharina</i> | AF291277 | AF291323 | RoKi 88 | Germany |
| 93. | <i>Exidia saccharina</i> | OP605366 | OP605350 | Dai 15848 | China |

Materials and Methods

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| 94. | <i>Exidia saccharina</i> | OP605367 | OP605351 | Dai 15890 | China |
| 95. | <i>Exidia subsaccharina</i> | OP605370 | OP605354 | Dai 22195 | France |
| 96. | <i>Exidia subsaccharina</i> | OP605371 | OP605355 | Dai 22187 | France |
| 97. | <i>Exidia thuretiana</i> | KY801878 | KY801905 | Spirin 9999 | Finland |
| 98. | <i>Exidia thuretiana</i> | AF291278 | AF291324 | MW 373 | Germany |
| 99. | <i>Exidia thuretiana</i> | KY801889 | KY801914 | Spirin 11,185 | Norway |
| 100. | <i>Exidia truncata</i> | AF291279 | AF291325 | MW 365 | Germany |
| 101. | <i>Exidia truncata</i> | MT663369 | MT664785 | Dai 21231 | Finland |
| 102. | <i>Exidia yadongensis</i> | MT663370 | MT664786 | Dai 17209 | China |
| 103. | <i>Exidia yadongensis</i> | MT663373 | MT664789 | Dai 17212 | China |
| 104. | <i>Exidia yadongensis</i> | MT663375 | MT664791 | Dai 17268 | China |
| 105. | <i>Exidiopsis effusa</i> | KX262145 | KX262193 | Miettinen 19136 | Finland |
| 106. | <i>Exidiopsis effusa</i> | MZ159758 | - | K(M):257342 | United Kingdom |
| 107. | <i>Exidiopsis grisea</i> | AB871765 | AB871746 | TUFC100049 | Japan |
| 108. | <i>Exidiopsis grisea</i> | AF291281 | AF291328 | RoKi 162 | Germany |
| 109. | <i>Exidiopsis mucedinea</i> | MW740308 | - | HHB-19402 | New Zealand |
| 110. | <i>Exidiopsis mucedinea</i> | MW740309 | - | HHB-19135 | New Zealand |
| 111. | <i>Exidiopsis plumbescens</i> | AF395309 | AF395309 | RJB 13036 | - |
| 112. | <i>Exidiopsis species</i> | AB871764 | AB871745 | TUFC34333 | Japan |
| 113. | <i>Exidiopsis species</i> | ON897989 | ON885451 | LWZ 20201011-32 | China |
| 114. | <i>Exidiopsis species</i> | AF291282 | AF291329 | FO 46291 | Germany |
| 115. | <i>Exidiopsis species</i> | OP809643 | OP809644 | CWU(Myc)AB694 | Ukraine |
| 116. | <i>Gelacantha pura</i> | MK098882 | MK098930 | LE 254018 | Russia |
| 117. | <i>Grammatis semis</i> | KX262146 | KX262194 | OM 10618 | China |
| 118. | <i>Heteroradulum adnatum</i> | KX262116 | KX262165 | LR 23453 | Mexico |
| 119. | <i>Heteroradulum australiense</i> | MZ325254 | MZ310424 | 20180512-20 | - |
| 120. | <i>Heteroradulum australiense</i> | MZ325255 | MZ310425 | 20180512-25 | - |
| 121. | <i>Heteroradulum deglubens</i> | AF291272 | AF291318 | FO 12006 | Germany |
| 122. | <i>Heteroradulum deglubens</i> | KX262112 | KX262162 | LE 38182 | Sweden |

Materials and Methods

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| 123. | <i>Heteroradulum kmetii</i> | KX262135 | KX262183 | DAOM 145605 | Canada |
| 124. | <i>Heteroradulum kmetii</i> | KX262124 | KX262173 | - | Slovakia |
| 125. | <i>Heteroradulum labyrinthinum</i> | KM379137 | KM379138 | SHY-2014 | - |
| 126. | <i>Hirneolina hirneoloides</i> | AF291283 | AF291334 | USJ 55480 | Costa Rica |
| 127. | <i>Hydrophana sphaerospora</i> | MK098883 | MK098931 | VS 11133 | Norway |
| 128. | <i>Hydrophana sphaerospora</i> | MK098884 | MK098932 | VS 11622 | Norway |
| 129. | <i>Metulochaete sanctae-catharinae</i> | MK484065 | MK480575 | AM 0678 | Brazil |
| 130. | <i>Mycostilla vermiformis</i> | MG735417 | MG735425 | VS 11330 | Russia |
| 131. | <i>Mycostilla vermiformis</i> | MG857093 | MG857098 | VS 11621 | Norway |
| 132. | <i>Myxariellum concinnum</i> | MK098885 | MK098933 | VS 8393c | USA |
| 133. | <i>Myxariellum tenerum</i> | MK098886 | MK098934 | VS 8685 | USA |
| 134. | <i>Myxarium cinnamomescens</i> | KY801882 | KY801909 | O F160494 | - |
| 135. | <i>Myxarium populinum</i> | KY801883 | KY801910 | Haikonen 24623 | - |
| 136. | <i>Ofella glaira</i> | MK098920 | MK098964 | VS 11809 | Norway |
| 137. | <i>Protoacia delicata</i> | MK098923 | MK098967 | VS 4615 | Russia |
| 138. | <i>Protoacia delicata</i> | MK098922 | MK098966 | VS 7824 | Russia |
| 139. | <i>Protodaedalea foliacea</i> | JQ764666 | JQ764644 | Yuan 5691 | - |
| 140. | <i>Protodaedalea hispida</i> | AB871767 | AB871748 | E701 | Japan |
| 141. | <i>Protodaedalea hispida</i> | AB871768 | AB871749 | WD 548 | Japan |
| 142. | <i>Protodontia subgelatinosa</i> | MG735412 | MK098970 | 11079 (O) | Norway |
| 143. | <i>Protodontia subgelatinosa</i> | MK098926 | MK098969 | VS 11038 | Norway |
| 144. | <i>Protohydnum cartilagineum</i> | MG735419 | MG735426 | SP467240 | Brazil |

Materials and Methods

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|------|-------------------------------------|----------|----------|------------|-----------|
| 145. | <i>Protomerulius substuppeus</i> | JX134482 | JQ764649 | O 19171 | - |
| 146. | <i>Protomerulius subreflexus</i> | MG757508 | MG757508 | OM 14402 | Indonesia |
| 147. | <i>Pseudohydnum gelatinosum</i> | AF384861 | - | F14063 | - |
| 148. | <i>Pseudohydnum gelatinosum</i> | DQ520094 | - | MW 298 | - |
| 149. | <i>Sclerotrema griseobrunneum</i> | KX262144 | KX262192 | TN 2722 | Canada |
| 150. | <i>Sclerotrema griseobrunneum</i> | KX262140 | KX262188 | VS 7674 | Russia |
| 151. | <i>Sistotrema brinkmannii</i> | JX535169 | JX535170 | 236 | Russia |
| 152. | <i>Stypella papillata</i> | EU118672 | - | KHL 11751 | Finland |
| 153. | <i>Stypellopsis farlowii</i> | MG857095 | MG857099 | 12337 | USA |
| 154. | <i>Stypellopsis hyperborea</i> | MG857096 | MG857102 | 11066 | Norway |
| 155. | <i>Tremellochaete atlantica</i> | MG594382 | MG594384 | URM 90198 | Brazil |
| 156. | <i>Tremellochaete atlantica</i> | MG594381 | MG594383 | URM 90199 | Brazil |
| 157. | <i>Tremellochaete atlantica</i> | OP605374 | OP605358 | Dai 22363 | China |
| 158. | <i>Tremellochaete atlantica</i> | OP605375 | OP605359 | Dai 22375 | China |
| 159. | <i>Tremellochaete australiensis</i> | OP605376 | OP605360 | Dai 18601A | Australia |
| 160. | <i>Tremellochaete australiensis</i> | OP605377 | OP605361 | Dai 18664 | Australia |
| 161. | <i>Tremellochaete cerradensis</i> | MK391524 | MK391530 | URM 90200 | Brazil |
| 162. | <i>Tremellochaete ciliata</i> | MK391523 | MK391529 | SP 467241 | Brazil |
| 163. | <i>Tremellochaete japonica</i> | AF291274 | AF291320 | TAA 42689 | Russia |
| 164. | <i>Tremellochaete japonica</i> | KX262110 | KX262160 | LE 303446 | Russia |

3.7. 2. Phylogenetic analysis of Sebaciales

The final aligned data matrix included all the major lineages in Sebaciales as ingroups and *Eichleriella xinpingensis* C.L. Zhao as outgroup. The dataset consisted of 117 accessions belong to 108 species (Table 3). Maximum Likelihood (ML) analysis was conducted with IQTREE (IQTREE Web Server: Fast and accurate phylogenetic trees under maximum likelihood (univie.ac.at)) (Nguyen *et al.* 2015).

Table 3: List of species used in the phylogenetic analysis of Sebaciales. GenBank accession number of sequences (ITS and LSU), voucher /strain /isolate, and locality are provided. Name and accessions of sequences generated in the present study are indicated in bold.

| Sl. No | Taxon | ITS | LSU | Voucher /strain /isolate | Country |
|--------|--------------------------------------|----------|-----------|--------------------------|--------------|
| 1. | <i>Chaetospermum artocarpi</i> | - | EF589735 | BCC18581 | - |
| 2. | <i>Chaetospermum artocarpi</i> | KF516968 | KF516974 | MFLUCC12-0536 | Thailand |
| 3. | <i>Chaetospermum camelliae</i> | - | KY304487 | R. Kirschner 4308 | Taiwan |
| 4. | <i>Chaetospermum camelliae</i> | MT223786 | MT223881 | CPC:34736 | South Africa |
| 5. | <i>Chaetospermum camelliae</i> | KF516969 | KF516975 | MFLUCC12-0537 | Thailand |
| 6. | <i>Ditangium cerasi</i> | DQ520103 | AY505542 | V. Kummer 02.12.2001 | - |
| 7. | <i>Ditangium cerasi</i> | KF061265 | - | TUB 020203 | Germany |
| 8. | <i>Efibulobasidium albescens</i> | AF384860 | - | RJB 12952 | - |
| 9. | <i>Efibulobasidium albescens</i> | KF307622 | - | 13RBGC6 | - |
| 10. | <i>Eichleriella xinpingensis</i> | NR164605 | NG 068882 | SWFC 812 | China |
| 11. | <i>Globulisebacina rolleyi</i> | - | AF291317 | RJB 6889 | Canada |
| 12. | <i>Globulisebacina rolleyi</i> | AY509550 | - | RJB794 | - |
| 13. | <i>Helvellosebacina conrescens</i> | JQ665516 | - | TUB 019706 | Germany |
| 14. | <i>Helvellosebacina conrescens</i> | MG844991 | - | 27.2 | Russia |
| 15. | <i>Helvellosebacina conrescens</i> | MG844992 | - | 27.3 | Russia |
| 16. | <i>Helvellosebacina helvelloides</i> | KF000415 | - | TUB 019983 | - |
| 17. | <i>Helvellosebacina helvelloides</i> | KJ546097 | - | TUB:019681 | Austria |
| 18. | <i>Helvellosebacina helvelloides</i> | KF000459 | - | TUB 020031 | Germany |
| 19. | <i>Helvellosebacina helvelloides</i> | KF000461 | - | TUB 020033 | Germany |

Materials and Methods

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|-----|--|-----------|----------|----------------|---------|
| 20. | <i>Helvellosebacina helvelloides</i> | JQ665515 | - | TUB 019707 | Germany |
| 21. | <i>Helvellosebacina</i> species | KF000449 | - | TUB 020021 | Germany |
| 22. | <i>Paulisebacina allantoidea</i> | KF061266 | | RoKi 179 | - |
| 23. | <i>Paulisebacina allantoidea</i> | AF490396 | - | RoKi 179 | - |
| 24. | <i>Sebacina</i> aff. <i>epigaea</i> | - | AF291363 | MW 526 | Germany |
| 25. | <i>Sebacina</i> aff. <i>incrustans</i> | AJ966755 | - | TAA185327 | Estonia |
| 26. | <i>Sebacina</i> aff. <i>incrustans</i> | DQ917652 | DQ521406 | PBM 2709 (CUW) | USA |
| 27. | <i>Sebacina</i> cf. <i>epigaea</i> | - | AY505559 | Y91A | Austria |
| 28. | <i>Sebacina concrescens</i> | KF307625 | - | K(M)132289 | - |
| 29. | <i>Sebacina cystidiata</i> | KF000453 | - | TUB 020025 | Germany |
| 30. | <i>Sebacina cystidiata</i> | JQ665511 | - | TUB 019704 | Germany |
| 31. | <i>Sebacina cystidiata</i> | JQ665512 | - | TUB 019705 | Germany |
| 32. | <i>Sebacina cystidiata</i> | NR 154609 | - | TUB 020024 | Germany |
| 33. | <i>Sebacina cystidiata</i> | KF000454 | | TUB 020026 | Germany |
| 34. | <i>Sebacina cystidiata</i> | KF000455 | - | TUB 020027 | Germany |
| 35. | <i>Sebacina dimitica</i> | KF061271 | | TUB 019987 | Austria |
| 36. | <i>Sebacina dimitica</i> | KF061274 | - | TAA169135 | Estonia |
| 37. | <i>Sebacina dimitica</i> | OQ430783 | - | >628-18 | - |
| 38. | <i>Sebacina dimitica</i> | KF061268 | - | TUB 020205 | - |
| 39. | <i>Sebacina epigaea</i> | JQ665505 | | TUB 019680 | Germany |
| 40. | <i>Sebacina epigaea</i> | JQ665503 | - | TUB 019678 | Germany |
| 41. | <i>Sebacina epigaea</i> | JQ665510 | - | TUB 019687 | Germany |
| 42. | <i>Sebacina epigaea</i> | JQ665509 | - | TUB 019686 | Germany |
| 43. | <i>Sebacina epigaea</i> | JQ665479 | - | TUB 019702 | Germany |
| 44. | <i>Sebacina epigaea</i> | JQ665481 | - | TUB 019652 | Germany |
| 45. | <i>Sebacina epigaea</i> | JQ665484 | - | TUB 019654 | Germany |
| 46. | <i>Sebacina epigaea</i> | JQ665483 | - | TUB 019651 | Germany |
| 47. | <i>Sebacina epigaea</i> | JQ665485 | - | TUB 019675 | Germany |
| 48. | <i>Sebacina epigaea</i> | KF000411 | - | TUB 019979 | Austria |
| 49. | <i>Sebacina epigaea</i> | JQ665487 | - | TUB 019674 | Germany |
| 50. | <i>Sebacina epigaea</i> | JQ665486 | - | TUB 019671 | Germany |
| 51. | <i>Sebacina epigaea</i> | JQ665488 | - | TUB 019673 | Germany |
| 52. | <i>Sebacina epigaea</i> | JQ665491 | - | TUB 019676 | Germany |
| 53. | <i>Sebacina epigaea</i> | JQ665489 | - | TUB 019672 | Germany |
| 54. | <i>Sebacina epigaea</i> | JQ665490 | - | TUB 019670 | Germany |
| 55. | <i>Sebacina epigaea</i> | AJ966754 | - | L995 | Estonia |

Materials and Methods

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|-----|--------------------------------|----------|----------|--------------------------|-----------|
| 56. | <i>Sebacina epigaea</i> | JQ665492 | - | TUB 019677 | Germany |
| 57. | <i>Sebacina epigaea</i> | JQ665515 | - | TUB 019707 | Germany |
| 58. | <i>Sebacina flagelliformis</i> | JQ665501 | - | TUB 019656 | Germany |
| 59. | <i>Sebacina flagelliformis</i> | KF000463 | - | TUB 020035 | Germany |
| 60. | <i>Sebacina flagelliformis</i> | KF000464 | - | TUB 020036 | Germany |
| 61. | <i>Sebacina guayanensis</i> | KF773778 | - | 5MM2 | Venezuela |
| 62. | <i>Sebacina incrustans</i> | EU819442 | - | JMP0084 | |
| 63. | <i>Sebacina incrustans</i> | JQ665518 | - | TUB 019617 | Germany |
| 64. | <i>Sebacina incrustans</i> | JQ665517 | | TUB 019620 | Germany |
| 65. | <i>Sebacina incrustans</i> | JQ665523 | - | TUB 019603 | Germany |
| 66. | <i>Sebacina incrustans</i> | JQ665534 | - | TUB 019604 | Germany |
| 67. | <i>Sebacina incrustans</i> | JQ665533 | - | TUB 019606 | Germany |
| 68. | <i>Sebacina incrustans</i> | JQ665532 | - | TUB 019605 | Germany |
| 69. | <i>Sebacina incrustans</i> | - | FJ644513 | LKH Obj-97-2 | |
| 70. | <i>Sebacina incrustans</i> | AF490395 | AF291365 | MW 524 | Germany |
| 71. | <i>Sebacina incrustans</i> | JQ665536 | - | TUB 019630 | Germany |
| 72. | <i>Sebacina incrustans</i> | JQ665535 | - | TUB 019629 | Germany |
| 73. | <i>Sebacina incrustans</i> | JQ665539 | - | TUB 019628 | Germany |
| 74. | <i>Sebacina incrustans</i> | JQ665540 | - | TUB 019631 | Germany |
| 75. | <i>Sebacina incrustans</i> | JQ665541 | - | TUB 019632 | Germany |
| 76. | <i>Sebacina incrustans</i> | JQ665543 | - | TUB 019625 | Germany |
| 77. | <i>Sebacina incrustans</i> | JQ665542 | - | TUB 019622 | Germany |
| 78. | <i>Sebacina incrustans</i> | JQ665546 | - | TUB 019623 | Germany |
| 79. | <i>Sebacina incrustans</i> | JQ665545 | - | TUB 019624 | Germany |
| 80. | <i>Sebacina incrustans</i> | JQ665555 | | TUB 019636 | Germany |
| 81. | <i>Sebacina incrustans</i> | JQ665548 | - | TUB 019637 | Germany |
| 82. | <i>Sebacina incrustans</i> | JQ665556 | - | TUB 019644 | Germany |
| 83. | <i>Sebacina incrustans</i> | JQ665558 | - | TUB 019643 | Germany |
| 84. | <i>Sebacina incrustans</i> | - | AY505545 | RoKi 946 | Yunnan |
| 85. | <i>Sebacina pallida</i> | JQ665564 | - | TUB 019649 | Germany |
| 86. | <i>Sebacina pallida</i> | KF061276 | - | TUB 020209 | - |
| 87. | <i>Sebacina pallida</i> | JQ665560 | - | TUB 019648 | Germany |
| 88. | <i>Sebacina pileata</i> | KF307630 | - | K(M)133631 | - |
| 89. | <i>Sebacina species</i> | MT302587 | MT302588 | KATO F. 4080 | Turkey |
| 90. | <i>Sebacina species</i> | - | DQ521412 | F1143128 (F) Illinois | - |

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|------|-------------------------------------|-----------------|-----------------|------------------|-------------|
| 91. | <i>Sebacina</i> species | - | AY505544 | FO 41103 | USA |
| 92. | <i>Sebacina</i> species | AF465191 | - | F6 | France |
| 93. | <i>Sebacina</i> species | OQ918288 | OQ918308 | ZGCAT302 | India |
| 94. | <i>Sebacina</i> species | PP388210 | - | ZGCAT301 | India |
| 95. | <i>Sebacina tomentosa</i> | KF773782 | - | 10PDM3 | Venezuela |
| 96. | <i>Serendipita indica</i> | DQ411527 | - | AFTOL-ID 612 | - |
| 97. | <i>Serendipita indica</i> | AF019636 | - | taxon:65672 | - |
| 98. | <i>Serendipita vermifera</i> | AF202728 | - | CBS 572.83 | - |
| 99. | <i>Serendipita vermifera</i> | JQ711842 | - | FFP328 | Canada |
| 100. | <i>Tremellodendron pallidum</i> | EU819445 | - | JMP0087 | - |
| 101. | <i>Tremellodendron schweinitzii</i> | KF307633 | - | 13RBGF7 | - |
| 102. | <i>Tremelloscypha dichroa</i> | KF061280 | - | VB4210 | Mexico |
| 103. | <i>Tremelloscypha dichroa</i> | KF061279 | - | LM4353 | Mexico |
| 104. | <i>Tremelloscypha dichroa</i> | KF061283 | - | Ryvardeen 45376 | Puerto Rico |
| 105. | <i>Tremelloscypha gelatinosa</i> | JQ012947 | - | VB4212 | Mexico |
| 106. | Uncultured fungus | KM247668 | - | OTU74 | France |
| 107. | Uncultured <i>Sebacina</i> | KF000600 | - | 12123_B_vivipara | Germany |
| 108. | Uncultured <i>Sebacina</i> | HQ154314 | - | TUB 019406 | - |

3.7. 3. Phylogenetic analysis of Dacrymycetes

The final aligned data matrix included all the major lineages in Dacrymycetales as ingroups. *Coprinus comatus* (O.F. Müll.) Pers. and *Suillus pictus* (Peck) Kuntze are set as outgroup by referring Shirouzu *et al.* (2017). The dataset consisted of 203 accessions belong to 74 species (Table 4). Maximum Likelihood (ML) analysis was conducted with IQTREE (IQTREE Web Server: Fast and accurate phylogenetic trees under maximum likelihood (univie.ac.at)) (Nguyen *et al.* 2015).

Table 4: List of species used in the phylogenetic analysis of Dacrymycetes. GenBank accession number of sequences (ITS and LSU), voucher /strain /isolate, and country are provided. Name and accessions of sequences generated in the present study are indicated in bold.

| Sl. No | Taxon | ITS | LSU | Voucher /strain /isolate | Country |
|--------|----------------------------------|----------|----------|--------------------------|-------------|
| 1. | <i>Calocera cf. guepinioides</i> | LC131407 | LC131366 | PDD:105005 | New Zealand |
| 2. | <i>Calocera cf. guepinioides</i> | LC131410 | LC131369 | PDD 107929 | New Zealand |
| 3. | <i>Calocera cf. guepinioides</i> | LC131408 | LC131367 | PDD 105033 | New Zealand |
| 4. | <i>Calocera cf. guepinioides</i> | LC131411 | LC131370 | PDD 107969 | New Zealand |
| 5. | <i>Calocera cf. guepinioides</i> | LC131412 | LC131371 | PDD 107981 | New Zealand |
| 6. | <i>Calocera cf. guepinioides</i> | LC131409 | LC131368 | PDD 107874 | New Zealand |
| 7. | <i>Calocera cornea</i> | LC131404 | - | PDD 107847 | New Zealand |
| 8. | <i>Calocera cornea</i> | LC131403 | LC131362 | PDD 104991 | New Zealand |
| 9. | <i>Calocera cornea</i> | - | MH867839 | CBS:151.48 | France |
| 10. | <i>Calocera cornea</i> | OP225573 | - | NAMPA2218-22 | USA |
| 11. | <i>Calocera cornea</i> | OP225572 | - | NAMPA2219-22 | USA |
| 12. | <i>Calocera cornea</i> | OM522297 | - | iNAT:17639535 | USA |
| 13. | <i>Calocera cornea</i> | AB712437 | AB472738 | CBS 124.84 | Canada |
| 14. | <i>Calocera cornea</i> | - | AF291302 | MW 55 | Germany |
| 15. | <i>Calocera cornea</i> | - | AB299077 | 376 | Japan |
| 16. | <i>Calocera cornea</i> | - | AB299068 | 267 | Japan |
| 17. | <i>Calocera cornea</i> | - | AB472722 | 452 | Japan |
| 18. | <i>Calocera cornea</i> | - | AB299076 | 358 | Japan |
| 19. | <i>Calocera furcata</i> | MW191958 | MW159087 | TU135016 | Estonia |
| 20. | <i>Calocera fusca</i> | LC131405 | LC131364 | PDD:107930 | New Zealand |
| 21. | <i>Calocera fusca</i> | LC131406 | LC131365 | PDD:107972 | New Zealand |

Materials and Methods

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| 22. | <i>Calocera lutea</i> | LC131414 | LC131373 | PDD 107842 | New Zealand |
| 23. | <i>Calocera lutea</i> | LC131413 | LC131372 | PDD 107841 | New Zealand |
| 24. | <i>Calocera lutea</i> | AB712438 | AB712379 | CBS 291.82 | Australia |
| 25. | <i>Calocera pedicellata</i> | LC131416 | LC131375 | PDD 107925 | New Zealand |
| 26. | <i>Calocera pedicellata</i> | LC131415 | LC131374 | PDD 107830 | New Zealand |
| 27. | <i>Calocera</i> species | FJ195751 | - | Wu9910-12 | Taiwan |
| 28. | <i>Calocera</i> species | FJ195754 | - | Wu 0703-6 | Taiwan |
| 29. | <i>Calocera</i> species | FJ195755 | - | JCH070726 | Taiwan |
| 30. | <i>Calocera viscosa</i> | AB712439 | - | TUFC12873 | Japan |
| 31. | <i>Cerinomyces albosporus</i> | AB712440 | - | TNS-F-15706 | Japan |
| 32. | <i>Cerinomyces canadensis</i> | AB712441 | AB472696 | TNS-F-21034 | Japan |
| 33. | <i>Cerinomyces ceraceus</i> | AB712442 | - | HHB-8969 | USA |
| 34. | <i>Cerinomyces crustulinus</i> | AB712443 | AB712423 | TUFC 30545 | Canada |
| 35. | <i>Cerinomyces grandinioides</i> | AB712444 | - | HHB-6908 | USA |
| 36. | <i>Cerinomyces lagerheimii</i> | AB712445 | - | RLG-13487 | USA |
| 37. | <i>Cerinomyces pallidus</i> | AB712446 | AB712426 | FP150848 | Belize |
| 38. | <i>Coprinus comatus</i> | AY854066 | AY635772 | AFTOL-ID 626 | USA |
| 39. | <i>Dacrymyces adpressus</i> | AB712447 | AB472707 | TNS-F-21045 | Japan |
| 40. | <i>Dacrymyces ancyleus</i> | AB712448 | NG_059060 | MAFF 241177 | Japan |
| 41. | <i>Dacrymyces aureosporus</i> | AB712449 | AB299057 | TUFC12833 | Japan |
| 42. | <i>Dacrymyces aureosporus</i> | KJ713985 | - | KUC11082 | South Korea |
| 43. | <i>Dacrymyces aureosporus</i> | MF445221 | - | SFC20150618-05 | South Korea |
| 44. | <i>Dacrymyces capitatus</i> | AB712450 | AB472741 | CBS 293.82 | Canada |
| 45. | <i>Dacrymyces capitatus</i> | OL587808 | OL546776 | Dai20023 | China |
| 46. | <i>Dacrymyces cerebriformis</i> | OM955201 | OM955196 | Dai 19826 | China |
| 47. | <i>Dacrymyces</i> cf. <i>microsporus</i> | - | LC131388 | PDD 104992 | New Zealand |
| 48. | <i>Dacrymyces</i> cf. <i>microsporus</i> | - | LC131389 | PDD 104993 | New Zealand |
| 49. | <i>Dacrymyces</i> cf. <i>tortus</i> | MN595620 | - | UPS F-940777 | Sweden |

Materials and Methods

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| 50. | <i>Dacrymyces chiangraiensis</i> | KY498587 | - | MFLU:16-0572 | - |
| 51. | <i>Dacrymyces chrysocomus</i> | AB712451 | AB712427 | CBS 280.84 | UK |
| 52. | <i>Dacrymyces chrysospermus</i> | AB712452 | AB299073 | TNS-F-15712 | Japan |
| 53. | <i>Dacrymyces citrinus</i> | LC131417 | LC131376 | PDD 107915 | New Zealand |
| 54. | <i>Dacrymyces citrinus</i> | LC131418 | LC131377 | PDD 107979 | New Zealand |
| 55. | <i>Dacrymyces corticioides</i> | LC222844 | LC222843 | TNS:F-54019 | Japan |
| 56. | <i>Dacrymyces cylindricus</i> | LC131420 | LC131379 | PDD 107989 | New Zealand |
| 57. | <i>Dacrymyces cylindricus</i> | LC131419 | LC131378 | PDD 105052 | New Zealand |
| 58. | <i>Dacrymyces cyrtosporus</i> | LC131422 | LC131381 | PDD 107980 | New Zealand |
| 59. | <i>Dacrymyces cyrtosporus</i> | LC131421 | LC131380 | PDD 107952 | New Zealand |
| 60. | <i>Dacrymyces dendrocalami</i> | AB712453 | AB712428 | TNS-F-38903 | Japan |
| 61. | <i>Dacrymyces dictyosporus</i> | AB712454 | AB712429 | HHB-8618 | USA |
| 62. | <i>Dacrymyces estonicus</i> | MN595632 | - | UPS F-940137 | Sweden |
| 63. | <i>Dacrymyces flabelliformis</i> | AB712455 | AB712430 | PDD 76696 | New Zealand |
| 64. | <i>Dacrymyces flabelliformis</i> | LC131423 | LC131382 | PDD 107863 | New Zealand |
| 65. | <i>Dacrymyces intermedius</i> | - | MH870480 | CBS:411.66 | Argentina |
| 66. | <i>Dacrymyces lacrymalis</i> | AB712456 | AB299069 | TNS-F-15719 | Japan |
| 67. | <i>Dacrymyces longistipitatus</i> | LC131425 | LC131386 | PDD 107996 | New Zealand |
| 68. | <i>Dacrymyces longistipitatus</i> | LC131426 | LC131387 | PDD 107997 | New Zealand |
| 69. | <i>Dacrymyces macnabbii</i> | MN595650 | - | UPS F-940949 | Sweden |
| 70. | <i>Dacrymyces microsporus</i> | OL587811 | - | Wu561 | China |
| 71. | <i>Dacrymyces microsporus</i> | - | AB472716 | 390 | Japan |
| 72. | <i>Dacrymyces microsporus</i> | - | AB472711 | TNS-F-21049 | Japan |
| 73. | <i>Dacrymyces microsporus</i> | PP760154 | - | ZGCAT336 | India |

Materials and Methods

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|-----|---|-----------------|-----------------|--------------|-------------|
| 74. | <i>Dacrymyces microsporus</i> | AB712457 | AB472712 | TNS-F-21050 | Japan |
| 75. | <i>Dacrymyces minor</i> | AB712458 | AB299063 | TNS-F-15721 | Japan |
| 76. | <i>Dacrymyces minutus</i> | AB712459 | AB472733 | TNS-F-21073 | Japan |
| 77. | <i>Dacrymyces novae-zelandiae</i> | LC131427 | LC131390 | PDD 107892 | New Zealand |
| 78. | <i>Dacrymyces novae-zelandiae</i> | LC131428 | LC131391 | PDD 107953 | New Zealand |
| 79. | <i>Dacrymyces novae-zelandiae</i> | AB712460 | AB472700 | TNS-F-21038 | Japan |
| 80. | <i>Dacrymyces ovisporus</i> | MN595635 | - | UPS F-940139 | Sweden |
| 81. | <i>Dacrymyces pachysporus</i> | LC131430 | LC131393 | PDD 107916 | New Zealand |
| 82. | <i>Dacrymyces pachysporus</i> | LC131429 | LC131392 | PDD 105004 | New Zealand |
| 83. | <i>Dacrymyces paratenosporus</i> | LC131431 | LC131394 | PDD 104960 | New Zealand |
| 84. | <i>Dacrymyces paratenosporus</i> | LC131432 | LC131395 | PDD 104963 | New Zealand |
| 85. | <i>Dacrymyces pezizoides</i> | LC386890 | LC386894 | TNS:F-54909 | Japan |
| 86. | <i>Dacrymyces pinacearum</i> | AB712461 | AB472718 | TNS-F-21056 | Japan |
| 87. | <i>Dacrymyces san-augustinii</i> | PP760155 | - | ZGCAT266 | India |
| 88. | <i>Dacrymyces san-augustinii</i> | AB712463 | AB299081 | TNS-F-15726 | Japan |
| 89. | <i>Dacrymyces sinostenosporus</i> | MW540888 | MW540890 | Dai20003 | China |
| 90. | <i>Dacrymyces sinostenosporus</i> | MW540889 | MW540891 | Dai20008 | China |
| 91. | <i>Dacrymyces species 1</i> | PQ014733 | - | ZGCAT134 | India |
| 92. | <i>Dacrymyces species 1</i> | PQ014734 | PQ012568 | ZGCAT226 | India |
| 93. | <i>Dacrymyces species 2</i> | PP758320 | - | ZGCAT232 | India |
| 94. | <i>Dacrymyces species 2</i> | PP758322 | - | ZGCAT208 | India |
| 95. | <i>Dacrymyces stenosporus</i> | LC131434 | LC131397 | PDD 107970 | New Zealand |
| 96. | <i>Dacrymyces stenosporus</i> | LC131433 | LC131396 | PDD 105018 | New Zealand |
| 97. | <i>Dacrymyces stillatus</i> | AB712464 | AB299061 | TNS-F-15727 | Japan |
| 98. | <i>Dacrymyces subalpinus</i> | AB712465 | AB299060 | TNS-F-15730 | Japan |

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|------|--|-----------------|----------|--------------|-------------|
| 99. | <i>Dacrymyces subantarcticensis</i> | AB712466 | AB712431 | PDD 76679 | New Zealand |
| 100. | <i>Dacrymyces subantarcticensis</i> | LC131436 | - | PDD 107988 | New Zealand |
| 101. | <i>Dacrymyces subarcticus</i> | AB712467 | AB472727 | TNS-F-21067 | Japan |
| 102. | <i>Dacrymyces variisporus</i> | AB712470 | AB299067 | TNS-F-15732 | Japan |
| 103. | <i>Dacryonaema macrosporum</i> | MN595664 | - | UPS F-941000 | Finland |
| 104. | <i>Dacryonaema rufum</i> | MN595680 | - | UPS F-941011 | Sweden |
| 105. | <i>Dacryopinax elegans</i> | AB712471 | AB712433 | HHB-18731 | USA |
| 106. | <i>Dacryopinax primogenitus</i> | PP758341 | - | ZGCAT92 | India |
| 107. | <i>Dacryopinax primogenitus</i> | PP758342 | - | ZGCAT89 | India |
| 108. | <i>Dacryopinax primogenitus</i> | KT251038 | KT251039 | MIN:862738 | Costa Rica |
| 109. | <i>Dacryopinax spathularia</i> | AB712473 | AB472710 | TNS-F-21048 | Japan |
| 110. | <i>Dacryopinax sphenocarpa</i> | AB712474 | AB472708 | TNS-F-21046 | Japan |
| 111. | <i>Dendrodacrys brasiliense</i> | AB744230 | AB723514 | INPA:241458 | Brazil |
| 112. | <i>Dendrodacrys rigoratum</i> | AB712447 | AB472707 | TNS-F-21045 | Japan |
| 113. | <i>Ditiola radicata</i> | MN595641 | - | UPS F-939957 | Sweden |
| 114. | <i>Femsjonina peziziformis</i> | AB712476 | AB299080 | TNS-F-15737 | Japan |
| 115. | <i>Guepiniopsis buccina</i> | DQ206986 | AY745711 | AFTOL-ID 888 | USA |
| 116. | <i>Guepiniopsis buccina</i> | AB712477 | AB299085 | TNS-F-15738 | Japan |
| 117. | <i>Heterotextus miltinus</i> | AB712478 | AB712436 | ICMP 16702 | New Zealand |
| 118. | <i>Heterotextus miltinus</i> | LC131437 | LC131401 | PDD 104962 | New Zealand |
| 119. | <i>Heterotextus miltinus</i> | LC131438 | LC131402 | PDD 107924 | New Zealand |
| 120. | <i>Suillus pictus</i> | AY854069 | AY684154 | AFTOL-ID 717 | USA |
| 121. | <i>Unilacryma bispora</i> | MN595670 | - | UPS F-941254 | Sweden |
| 122. | <i>Unilacryma unispora</i> | AB712468 | AB299074 | TNS-F-15731 | Japan |
| 123. | <i>Unilacryma unispora</i> | AB712469 | AB712432 | TNS-F-38904 | Japan |

3.7. 4. Phylogenetic analysis of Tremellomycetes

The final aligned data matrix included all the major lineages in Tremellales as ingroups and *Auriculoscypha anacardiicola* D.A. Reid and Manim.

as outgroup. The dataset consisted of 359 accessions belong to 149 species (Table 5). Maximum Likelihood (ML) analysis was conducted with IQTREE (IQTREE Web Server: Fast and accurate phylogenetic trees under maximum likelihood (univie.ac.at)) (Nguyen *et al.* 2015). ITS and LSU sequences of *T. boninensis* (Kobayasi) S. Ito and S. Imai were obtained from the website (https://www.gene.affrc.go.jp/databases-micro_search_detail_en.php?maff=243761 (ITS) https://www.gene.affrc.go.jp/databases-micro_search_detail_en.php?maff=244276 (LSU), which were absent in GenBank. Hence not listed within Table 5.

Table 5: List of species used in the phylogenetic analysis of Tremellomycetes. GenBank accession number of sequences (ITS and LSU), voucher /strain /isolate, and locality are provided. Name and accessions of sequences generated in the present study are indicated in bold.

| Sl. No | Taxon | ITS | LSU | Voucher /strain /isolate | Country |
|--------|---------------------------------------|-----------------|-----------------|--------------------------|-----------|
| 1 | <i>Auriculibuller fuscus</i> | - | AB727064 | RP083 | - |
| 2 | <i>Auriculoscypha anacardiicola</i> | NR119581 | NG068724 | MIN AK 274 | - |
| 3 | <i>Bandonia marina</i> | NR_144778 | NG_058617 | CBS 5235 | - |
| 4 | <i>Bandonia marina</i> | MH595437 | MH595192 | UCDFST:12-134 | Australia |
| 5 | <i>Bandoniozoma tunnelae</i> | KJ095620 | KJ095636 | SD2S3Y2 | - |
| 6 | <i>Bulleribasidium oberjochense</i> | KY101804 | KY106253 | CBS:9108 | - |
| 7 | <i>Bulleribasidium wuzhishanensis</i> | GQ438830 | - | AS 2.4163 | - |
| 8 | <i>Carlosrosaea foliicola</i> | MK050282 | - | CGMCC2.3447 | - |
| 9 | <i>Carlosrosaea hohenbergiae</i> | NR_159754 | NG_064407 | CBS 14563 | Brazil |
| 10 | <i>Carlosrosaea simaoensis</i> | MK050283 | - | CGMCC2.3580 | - |
| 11 | <i>Carlosrosaea vrieseae</i> | KP691956 | KP691955 | BRO199 | Brazil |
| 12 | Cryptococcaceae Taxon | - | PP188486 | ZGCAT323 | India |
| 13 | Cryptococcaceae Taxon | PP188483 | PP188481 | ZGCAT324 | India |

Materials and Methods

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|----|-------------------------------------|-----------|-----------|--------------|----------------|
| 14 | <i>Cryptococcus amyloletus</i> | KY102605 | - | CBS:6039 | South Africa |
| 15 | <i>Cryptococcus decagattii</i> | KU642657 | - | CBS:11687 | Spain |
| 16 | <i>Cryptococcus gattii</i> | JN939485 | - | CBS 6955 | |
| 17 | <i>Cryptococcus neoformans</i> | NR_171785 | - | ATCC 32045 | - |
| 18 | <i>Cryptococcus tetragattii</i> | KY102963 | - | CBS:11718 | - |
| 19 | <i>Cryptococcus wingfieldii</i> | KY105769 | KY109979 | CBS:7118 | South Africa |
| 20 | <i>Cryptotrichosporon anacardii</i> | AY549984 | AY550000 | CBS 9550 | Nigeria |
| 21 | <i>Dimennazyma cistialbidi</i> | KY103339 | KY107630 | CBS:10049 | |
| 22 | <i>Dioszegia aurantiaca</i> | KY103346 | KY107635 | CBS:6980 | Canada |
| 23 | <i>Dioszegia butyracea</i> | KY103348 | KY107637 | CBS:10122 | |
| 24 | <i>Dioszegia catarinonii</i> | KY103349 | KY107638 | CBS:10051 | |
| 25 | <i>Dioszegia changbaiensis</i> | NR_136964 | NG_059069 | CGMCC 2.2309 | China |
| 26 | <i>Dioszegia crocea</i> | KY558368 | - | KT212A | Czech Republic |
| 27 | <i>Dioszegia cryoxerica</i> | FJ640565 | - | ANT 03-071 | - |
| 28 | <i>Dioszegia fristingensis</i> | KY103352 | NG_070549 | CBS:10052 | - |
| 29 | <i>Dioszegia heilongjiangensis</i> | MK050293 | - | CGMCC2.5672 | - |
| 30 | <i>Dioszegia kandeliae</i> | MK050296 | - | CGMCC2.5658 | |
| 31 | <i>Dioszegia maotaiensis</i> | MK050295 | - | CGMCC2.4537 | |
| 32 | <i>Dioszegia xingshanensis</i> | KY103359 | KY107649 | CBS:10120 | China |
| 33 | <i>Fibulobasidium inconspicuum</i> | OQ694461 | - | UCDFST 89-39 | - |
| 34 | <i>Filobasidium magnum</i> | NR_130655 | NG_069409 | CBS 140 | - |
| 35 | <i>Filobasidium magnum</i> | KY103433 | KY107722 | CBS:140 | - |
| 36 | <i>Filobasidium oeirense</i> | KY103438 | KY107723 | CBS:8681 | - |
| 37 | <i>Fonsecazyma mujuensis</i> | KY103451 | KY107735 | CBS:10308 | - |
| 38 | <i>Genolevuria amylolyticus</i> | KF036585 | KY107744 | CBS: 10048 | - |
| 39 | <i>Genolevuria paynescottiae</i> | NR_185656 | OK626336 | BRIP 45079a | - |
| 40 | <i>Genolevuria tibetensis</i> | NR_159814 | - | CBS 10456 | - |

Materials and Methods

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|----|-----------------------------------|-----------|-----------|----------------|-------------|
| 41 | <i>Hannaella kunmingensis</i> | JQ825256 | JQ825254 | ATT265 | - |
| 42 | <i>Hannaella sinensis</i> | OR088115 | OR088138 | KLG-121 | - |
| 43 | <i>Hannaella surugaensis</i> | MN861547 | - | CHF-3NN | - |
| 44 | <i>Hannaella zaeae</i> | KY103515 | NG_058304 | CBS:10801 | Austria |
| 45 | <i>Holtermannia corniformis</i> | KY103592 | KY107868 | CBS:7675 | - |
| 46 | <i>Holtermannia saccardoii</i> | MK050338 | - | CGMCC2.3462 | - |
| 47 | <i>Kwoniella bestiolae</i> | KY103928 | KY108196 | CBS:10118 | Viet Nam |
| 48 | <i>Kwoniella botswanensis</i> | HF545756 | HF545769 | CBS 12716 | - |
| 49 | <i>Kwoniella dejecticola</i> | KY103929 | KY108197 | CBS:10117 | Viet Nam |
| 50 | <i>Kwoniella dendrophila</i> | KY103932 | KY108198 | CBS:6074 | - |
| 51 | <i>Kwoniella endophytica</i> | MH237945 | - | CBS:15359 | - |
| 52 | <i>Kwoniella europaea</i> | HE984341 | HE996972 | CBS 7868 | Switzerland |
| 53 | <i>Kwoniella fici</i> | MK070336 | - | DBVPG:10122 | Italy |
| 54 | <i>Kwoniella heveanensis</i> | MK973005 | - | DSM:109546 | - |
| 55 | <i>Kwoniella mangrovensis</i> | KY103934 | KY108202 | CBS:8507 | - |
| 56 | <i>Kwoniella newhampshirensis</i> | KM384101 | KM408127 | yHKS256 | - |
| 57 | <i>Kwoniella ovata</i> | MK050289 | - | CGMCC2.3439 | CHINA |
| 58 | <i>Kwoniella pini</i> | KY103936 | KY108203 | CBS:10737 | Russia |
| 59 | <i>Kwoniella shandongensis</i> | MW710831 | - | XZY66-5 | - |
| 60 | <i>Kwoniella shandongensis</i> | MW534891 | MW534919 | Y2-2-411 | - |
| 61 | <i>Kwoniella shandongensis</i> | NR_156242 | - | CBS 12478 | - |
| 62 | <i>Kwoniella shivajii</i> | KY103937 | KY108204 | CBS:11374 | |
| 63 | <i>Naematelia aurantia</i> | AF444315 | AF189842 | CBS 6965 | - |
| 64 | <i>Naematelia aurantia</i> | NR155873 | NG057657 | CBS 6965 | - |
| 65 | <i>Naematelia aurantia</i> | KP986510 | KP986543 | LE<RUS>:253851 | Russia |
| 66 | <i>Naematelia aurantia</i> | MT229987 | - | WA0000072740 | Poland |
| 67 | <i>Naematelia aurantialba</i> | DQ404321 | EF010939 | Strain 9102 | |
| 68 | <i>Naematelia aurantialba</i> | DQ400104 | EF010937 | Strain 9901 | China |
| 69 | <i>Naematelia aurantialba</i> | OQ629799 | - | NX-20 | - |
| 70 | <i>Naematelia aurantialba</i> | OL614834 | OL616185 | Dai 23432 | China |

Materials and Methods

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| 71 | <i>Naematelia encephala</i> | OL739376 | OL739376 | UCDFST 68-887.2 | - |
| 72 | <i>Naematelia encephala</i> | EU673082 | - | FBCC1144 | Northern Finland |
| 73 | <i>Naematelia encephala</i> | EU673083 | - | FBCC1145 | Northern Finland |
| 74 | <i>Naematelia encephala</i> | KY104315 | - | CBS 8220 | - |
| 75 | <i>Naematelia encephala</i> | OK051297 | - | yHKS553 | USA |
| 76 | <i>Naematelia encephala</i> | KU680964 | - | S_F169949 | - |
| 77 | <i>Naematelia encephala</i> | OQ422967 | - | CBS 6976 | Canada |
| 78 | <i>Naematelia encephala</i> | KP986506 | KP986540 | LE<RUS>:253857 | Russia |
| 79 | <i>Naematelia encephala</i> | MZ314474 | - | KBP:Y-6478 | Russia |
| 80 | <i>Naematelia encephala</i> | AF042402 | AF042220 | CCJ897 | Taiwan |
| 81 | <i>Naematelia encephala</i> | AF410474 | AF189867 | CBS 6968 | - |
| 82 | <i>Naematelia encephaloidea</i> | OQ621795 | OQ621978 | ZGCAT326 | India |
| 83 | <i>Naematelia encephaloidea</i> | OQ621748 | - | ZGCAT327 | India |
| 84 | <i>Naematelia encephaloidea</i> | OQ621803 | - | ZGCAT325 | India |
| 85 | <i>Naematelia encephaloidea</i> | OQ621704 | OR068134 | ZGCAT329 | India |
| 86 | <i>Naematelia microspora</i> | AF042435 | AF042253 | BPI702328 | South Africa |
| 87 | <i>Nielozyma formosana</i> | KY104385 | KY108665 | CBS:10306 | SP23 |
| 88 | <i>Papiliotrema bandonii</i> | KY104458 | KY108730 | CBS:9107 | SP23 |
| 89 | <i>Papiliotrema pseudoalba</i> | KY101798 | KY106246 | CBS:7344 | Japan |
| 90 | <i>Papiliotrema siamense</i> | AB915387 | AB909023 | DMKU-SP85 | Thailand |
| 91 | <i>Phaeotremella foliacea</i> | NR155680 | NG058368 | CBS 6969 | Canada |
| 92 | <i>Phaeotremella mycetophiloides</i> | MF580587 | LN870265 | DSM5728 | Germany |
| 93 | <i>Phaeotremella simplex</i> | LT904697 | AF042246 | FO31782 | Germany |
| 94 | <i>Phaeotremella skinneri</i> | NR073211 | NG068966 | CBS 5029 | North America |
| 95 | <i>Pseudotremella lacticolor</i> | NR158875 | NG060058 | CBS 10915 | Japan |
| 96 | <i>Pseudotremella moriformis</i> | NR155685 | NG058379 | CBS 7810 | Canada |
| 97 | <i>Rhynchogastrema coronatum</i> | LN870267 | - | DSM 28188 | - |

Materials and Methods

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|-----|---|-----------------|-----------------|---------------------|-------------|
| 98 | <i>Rhynchogastrema glucofermentans</i> | NR_119978 | NG_042404 | BG 02-7-15-015A-1-1 | - |
| 99 | <i>Saitozyma flava</i> | MK182935 | MK182934 | ON6 | South Korea |
| 100 | <i>Saitozyma paraflava</i> | KY105298 | KY109525 | CBS:10100 | - |
| 101 | <i>Saitozyma podzolicus</i> | LC155937 | LC155938 | ND-1 | - |
| 102 | <i>Saitozyma pseudoflava</i> | MK050284 | - | XZ200A1 | - |
| 103 | <i>Sirobasidium apiculatum</i> | LC203428 | LC203429 | MY62-4 | Japan |
| 104 | <i>Sirobasidium brefeldianum</i> | - | ON930081 | AM257 | - |
| 105 | <i>Sirobasidium brefeldianum</i> | JN053472 | JN043578 | AM71 | - |
| 106 | <i>Sirobasidium brefeldianum</i> | PP976611 | PP976613 | ZGCAT189 | India |
| 107 | <i>Sirobasidium intermediae</i> | OQ694452 | - | CBS 7805 | - |
| 108 | <i>Sirobasidium japonicum</i> | LC203420 | LC016573 | MY111-05 | Japan |
| 109 | <i>Sirobasidium japonicum</i> | LC203422 | LC203423 | MY111-09 | Japan |
| 110 | <i>Sirobasidium japonicum</i> | PP179383 | - | ZGCAT167 | India |
| 111 | <i>Sirobasidium magnum</i> | - | PP179309 | ZGCAT26 | India |
| 112 | <i>Sirobasidium magnum</i> | KY105423 | KY109656 | CBS:8485 | Taiwan |
| 113 | <i>Sirobasidium magnum</i> | KY105426 | KY109655 | CBS:8482 | Taiwan |
| 114 | <i>Sirobasidium magnum</i> | KY105421 | KY109658 | CBS:6964 | |
| 115 | <i>Takashimella koratensis</i> | Y101790 | KY106240 | CBS:10484 | - |
| 116 | <i>Teunia betulae</i> | KM384106 | KM408129 | yHKS303 | - |
| 117 | <i>Teunia cuniculi</i> | KY102622 | KY106982 | CBS:10309 | South Korea |
| 118 | <i>Teunia globosa</i> | MK050288 | - | CGMCC2.5648 | China |
| 119 | <i>Teunia helanensis</i> | MK050287 | - | CBS 12498 | - |
| 120 | <i>Teunia korlaensis</i> | MK050286 | - | CGMCC2.3835 | China |
| 121 | <i>Tremella australe</i> | MT445847 | - | Dai 11539 | Taiwan |
| 122 | <i>Tremella australe</i> | MT445848 | MT425188 | Wu 154 | China |
| 123 | <i>Tremella basidiomaticola</i> | MH712820 | MH712784 | CGMCC2.5724 | China |
| 124 | <i>Tremella basidiomaticola</i> | MH712821 | MH712785 | CGMCC2.5725 | China |

Materials and Methods

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|-----|----------------------------------|-----------------|----------|-----------------------|------------|
| 125 | <i>Tremella caloplacae</i> | JN053468 | JN043573 | Kukwa 4385a (S) | Greenland |
| 126 | <i>Tremella candelariellae</i> | JN053470 | JN043575 | Diederich 12808 (S) | Luxembourg |
| 127 | <i>Tremella cerebriformis</i> | MH712823 | MH712787 | ZRL 20170101 | China |
| 128 | <i>Tremella cerebriformis</i> | MH712824 | MH712788 | ZRL 20170269 | China |
| 129 | <i>Tremella cheejenii</i> | MH712825 | MH712789 | GX 20172598 | China |
| 130 | <i>Tremella cheejenii</i> | MH712826 | MH712790 | GX 20172640 | China |
| 131 | <i>Tremella cinnabarina</i> | AF444430 | AF189866 | CBS 8234 | - |
| 132 | <i>Tremella cladoniae</i> | JN053477 | JN043583 | Suija 872 (TU) | Estonia |
| 133 | <i>Tremella coalescens</i> | KY105678 | AF189865 | CBS 6967 | USA |
| 134 | <i>Tremella coalescens</i> | NR155934 | NG069418 | CBS 6967 | USA |
| 135 | <i>Tremella coppinsii</i> | JN053495 | JN043601 | Diederich 15628 (S) | UK |
| 136 | <i>Tremella dendrographae</i> | JN053471 | JN043576 | Tehler 7068 (S) | USA |
| 137 | <i>Tremella dysenterica</i> | KP986509 | KP986542 | LE 303447 | Russia |
| 138 | <i>Tremella dysenterica</i> | KP986531 | - | VLA M 18599 | Russia |
| 139 | <i>Tremella erythrina</i> | MH712827 | MH712791 | HMAS 255317 | China |
| 140 | <i>Tremella erythrina</i> | MH712828 | MH712792 | HMAS 279591 | China |
| 141 | <i>Tremella erythrina</i> | OR457653 | - | ZGCAT305 | India |
| 142 | <i>Tremella erythrina</i> | OR453169 | - | ZGCAT314 | India |
| 143 | <i>Tremella everniae</i> | JN053493 | JN043599 | Kneiper s.n. (S) | USA |
| 144 | <i>Tremella fibulifera</i> | MT445850 | MT425190 | SP 211759 | Brazil |
| 145 | <i>Tremella fibulifera</i> | MT445851 | MT425191 | Alvarenga 471 | Brazil |
| 146 | <i>Tremella flava</i> | KY105681 | - | CBS 8471 | Taiwan |
| 147 | <i>Tremella flava</i> | AF042403 | AF042221 | CCJ 907 | Taiwan |
| 148 | <i>Tremella flava</i> | MH712846 | MH712810 | YN180 | - |
| 149 | <i>Tremella flava</i> | AF042407 | AF042225 | CCJ1023 | Taiwan |
| 150 | <i>Tremella flava</i> | AF042405 | AF042223 | CCJ928 | Taiwan |
| 151 | <i>Tremella flava</i> | AF042411 | AF042229 | CCJ1098 | Taiwan |
| 152 | <i>Tremella fuciformis</i> | KY105683 | AF075476 | CBS 6970 | Taiwan |
| 153 | <i>Tremella fuciformis</i> | AF042410 | AF042228 | CCJ1080 | - |
| 154 | <i>Tremella globispora</i> | AF042425 | AF042243 | UBC 586 | Canada |
| 155 | <i>Tremella globispora</i> | AF444432 | AF189869 | CBS 6972 | Canada |
| 156 | <i>Tremella guangxiensis</i> | MT445843 | MT425186 | Wu 3 | China |
| 157 | <i>Tremella huuskonenii</i> | KR857031 | KR857095 | Goward 11-50 (UBC) | Canada |
| 158 | <i>Tremella latispora</i> | MT445852 | MT425192 | Dai 17574 | China |

| | | | | | |
|-----|-------------------------------------|-----------------|-----------------|-----------------------------|----------|
| 159 | <i>Tremella latispora</i> | MT445853 | MT425193 | Dai 17568 | China |
| 160 | <i>Tremella laurisilvae</i> | JN053467 | JN043572 | S-F 102408(AM4) | Portugal |
| 161 | <i>Tremella laurisilvae</i> | - | OR461202 | ZGCAT271 | India |
| 162 | <i>Tremella laurisilvae</i> | OR478036 | OR478037 | ZGCAT276 | India |
| 163 | <i>Tremella leptogii</i> | JN053476 | JN043582 | Vital and Buck 19510 (S) | Brazil |
| 164 | <i>Tremella lloydiae-candidae</i> | KP986536 | KP986559 | VLA M 11702 | Russia |
| 165 | <i>Tremella lloydiae-candidae</i> | KP986537 | - | VLA M 11703 | Russia |
| 166 | <i>Tremella lobariacearum</i> | JN053473 | JN043579 | Diederich 4935 (S) | Madeira |
| 167 | <i>Tremella mesenterica</i> | AF444433 | - | CBS 6973 | Canada |
| 168 | <i>Tremella mesenterica</i> | - | AF042265 | FO 24610 | Germany |
| 169 | <i>Tremella mesenterica</i> | NR155937 | NG069419 | CBS 6973 | Canada |
| 170 | <i>Tremella mesenterica</i> | - | PP179305 | ZGCAT139 | India |
| 171 | <i>Tremella neofibulifera</i> | MT445844 | MT425187 | Wu 248 | China |
| 172 | <i>Tremella nephromatis</i> | JN053475 | JN043581 | Zhurbenko 97213 (LE) | Russia |
| 173 | <i>Tremella pertusariae</i> | JN053494 | JN043600 | Diederich 16331(S) | France |
| 174 | <i>Tremella poilkavensis</i> | OL616066 | OL616061 | ZGCAT243 | India |
| 175 | <i>Tremella poilkavensis</i> | OQ096659 | - | ZGCAT14 | India |
| 176 | <i>Tremella resupinata</i> | AF042421 | AF042239 | CBS 8488 | Taiwan |
| 177 | <i>Tremella saccharicola</i> | AB915386 | AB909022 | DMKU-SP40 | Thailand |
| 178 | <i>Tremella saccharicola</i> | AB915385 | AB909021 | DMKU- SP23 | Thailand |
| 179 | <i>Tremella sairandhrana</i> | ON668075 | ON668076 | ZGCAT89 | India |
| 180 | <i>Tremella salmonea</i> | MH712851 | MH712815 | GX 20172637 | China |
| 181 | <i>Tremella samoensis</i> | KP986508 | KP986541 | LE 303465 | Russia |
| 182 | <i>Tremella samoensis</i> | KP986532 | KP986555 | VLA M 18603 | Russia |
| 183 | <i>Tremella seclusa</i> | MZ868642 | MZ868641 | LIP GG-210221-001 | France |
| 184 | <i>Tremella seclusa</i> | OR452983 | OR452985 | ZGCAT183 | India |
| 185 | <i>Tremella shuangheensis</i> | MK050285 | MK050285 | CBS 15561 | China |
| 186 | <i>Tremella species 1</i> | OR452937 | OR452957 | ZGCAT52 | India |
| 187 | <i>Tremella species 1</i> | OR452981 | OR457652 | ZGCAT108 | India |
| 188 | <i>Tremella species 3</i> | PP179218 | OR452984 | ZGCAT195 | India |
| 189 | <i>Tremella species 3</i> | PP179217 | - | ZGCAT32 | India |
| 190 | <i>Tremella subfibulifera</i> | MT445849 | MT425189 | Alvarenga 334 | Brazil |

Materials and Methods

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|-----|-------------------------------------|-----------------|-----------------|----------------------------|-----------------|
| 191 | <i>Tremella taiwanensis</i> | AF042412 | AF042230 | CBS 8479 | Taiwan |
| 192 | <i>Tremella taiwanensis</i> | MH712854 | MH712818 | GX 20170625 | China |
| 193 | <i>Tremella taiwanensis</i> | OR453171 | - | ZGCAT316 | India |
| 194 | <i>Tremella tropica</i> | KY105697 | KY109908 | CBS 8483 | Taiwan |
| 195 | <i>Tremella tropica</i> | KY105696 | KY109909 | CBS 8486 | Taiwan |
| 196 | <i>Tremella wirthii</i> | JN053492 | JN043598 | Herk s.n (herb. Diederich) | The Netherlands |
| 197 | <i>Tremella yokohamensis</i> | HM222926 | HM222927 | JCM 16989 | Japan |
| 198 | <i>Tremella yokohamensis</i> | KY105698 | KY109910 | CBS 11776 | Japan |
| 199 | <i>Tremella zhejiangensis</i> | MW626837 | MW624328 | Wu 391 | China |
| 200 | <i>Tremella zhejiangensis</i> | MW626836 | W624327 | Wu 346 | China |
| 201 | <i>Trimorphomyces papilionaceus</i> | AF444483 | - | CBS 443.92 | - |
| 202 | <i>Trimorphomyces sakaeratica</i> | AY211544 | - | TISTR 5803 | - |
| 203 | <i>Trimorphomyces sakaeratica</i> | NR077088 | - | JCM 11900 | - |
| 204 | <i>Vishniacozyma carnescens</i> | PP576307 | - | isolate NIMM80564 | - |
| 205 | <i>Vishniacozyma dimennae</i> | MW791874 | - | Y321H | Spain |
| 206 | <i>Vishniacozyma heimaeyensis</i> | HQ875391 | - | CBS 8933 | - |
| 207 | <i>Vishniacozyma nebularis</i> | - | EU266921 | taxon:499827 | Taiwan |
| 208 | <i>Vishniacozyma peneaus</i> | NR_165987 | NG_058433 | CBS 2409 | USA |
| 209 | <i>Vishniacozyma species</i> | - | PP724435 | ZGCAT354 | India |
| 210 | <i>Vishniacozyma species</i> | - | PP724719 | ZGCAT359 | India |
| 211 | <i>Vishniacozyma tephrensensis</i> | LC515100 | - | GR6-1-20-4 | Canada |
| 212 | <i>Vishniacozyma victoriae</i> | OQ415428 | OQ415498 | isolate K34 | South Korea |
| 213 | <i>Vishniacozyma victoriae</i> | HG994864 | - | CV_80 | - |
| 214 | <i>Vishniacozyma victoriae</i> | - | OQ415498 | isolate K34 | South Korea |

RESULTS AND DISCUSSION

Basidiocarps of heterobasidiomycetes were collected from different localities of Kerala State during a five year period (August 2018– August 2023). All the collected specimens were studied with relevant taxonomic characters. The specimens collected during the study belong to four orders, Auriculariales, Sebaciales, Dacrymycetales and Tremellales. Forty seven species belongs to 10 families and 12 genera were documented in the study.

Order Auriculariales is represented by 8 species of the family Auriculariaceae. This includes 7 species of the genus *Auricularia*, and a taxon that could not be identified to genus level (described here as Auriculariaceae taxon). Order Sebaciales represented by one species (belong to Sebaciaceae), which is to be proposed as new to science. Order Dacrymycetales is represented by 20 species belonging to five genera *Calocera*, *Dacrymyces*, *Dacryopinax*, *Dendrodacrys*, and *Guepiniopsis* (all coming under Dacrymycetaceae). In the family Dacrymycetaceae, the highest number of species belongs to the genus *Dacrymyces* (13 species). Among the 20 species of Dacrymycetaceae, 2 are unidentified to species level (*Dacrymyces* species 1, *Dacrymyces* species 2) and may represent species new to science. Order Tremellales is represented by 18 taxa, distributed in 6 families. Among the species of Tremellales, one taxon is identified up to family level only (Cryptococcaceae taxon). Remaining 17 species belong to *Naematelia* (Naemateliaceae), *Phaeotremella* (Phaeotremellaceae), *Sirobasidium* (Sirobasidiaceae), *Tremella* (Tremellaceae), and *Vishniacozyma* (Bulleribasidiaceae). Within the Tremellales, genus *Tremella* contains the largest number of species (12 species). Within Tremellales, *Naematelia encephaloidea*, *Tremella poilkavensis*, *Tremella sairandhriana* are formally proposed as new to science (Thomas and Kumar 2023, 2024; Liu *et al.* 2024). Four species (*Tremella*

species 1, *Tremella* species 2, *Tremella* species 3 and *Vishniacozyma* species) are identified only up to genus level only. These unidentified taxa may represent species new to science.

Following species have been documented in the study.

Family - Auriculariaceae

1. *Auricularia cornea*
2. *Auricularia fibrillifera*
3. *Auricularia heimuer*
4. *Auricularia sinodelicata*
5. *Auricularia srilankensis*
6. *Auricularia subglabra*

Family- Bulleribasidiaceae

7. *Vishniacozyma* species

Family- Dacrymyceataceae

8. *Calocera cornea*
9. *Dacrymyces* species 1
10. *Dacrymyces* species 2
11. *Dacrymyces capitatus*
12. *Dacrymyces "cerebriformis"*
13. *Dacrymyces cupularis*
14. *Dacrymyces dacryomitriiformis*
15. *Dacrymyces falcatus*
16. *Dacrymyces lacrymalis*
17. *Dacrymyces microsporus*
18. *Dacrymyces novae-zelandiae*
19. *Dacrymyces san-augustinii*

20. *Dacrymyces sinostenosporus*
21. *Dacrymyces spathularia*
22. *Dacryopinax indacocheae*
23. *Dacryopinax petaliformis*
24. *Dacryopinax primogenitus*
25. *Dacryopinax yungensis*
26. *Dendrodacrys paraphysatum*
27. *Guepiniopsis buccina*

Family- Naemateliaceae

28. *Naematelia encephaloidea*

Family- Phaeotremellaceae

29. *Phaeotremella yunnanensis*

Family Sebacinaceae

30. *Sebacina* species

Family- Sirobasidiaceae

31. *Sirobasidium brefeldianum*
32. *Sirobasidium japonicum*
33. *Sirobasidium magnum*

Family- Tremellaceae

34. *Tremella armeniaca*
35. *Tremella erythrina*
36. *Tremella fuciformis*
37. *Tremella laurisilvae*
38. *Tremella mesenterica*
39. *Tremella poilkavensis*
40. *Tremella sairandhriana*

- 41. *Tremella seclusa*
- 42. *Tremella* species 1
- 43. *Tremella* species 2
- 44. *Tremella* species 3
- 45. *Tremella taiwanensis*

Unidentified taxa

- 46. Cryptococcaceae taxon
- 47. Auriculariaceae taxon

4.1. Taxonomy

4.1.1. TAXONOMIC KEY TO THE HETEROBASIDIOMYCETES IN KERALA

Key to the classes

- 1a. Mycoparasitic, haustoria present, dolipore-type septa surrounded by sacculate parenthesomes..... Tremellomycetes
- 1b. Saprobic or mycorrhizal, haustoria absent, dolipore-type septa surrounded by cap-like parenthesomes2
- 2a. Basidia bifurcating, basidiospore not capable of producing secondary ballistospores Dacrymycetes
- 2b. Basidia not bifurcating, basidiospores capable of producing secondary ballistospores Agaricomycetes

Key to the taxa of Tremellomycetes (Tremellales)

- 1a. Clamp-connection absent *Vishniacozyma* species
- 1b. Clamp-connections present2
- 2a. Basidia catenulate, globose to ellipsoid. *Sirobasidium*
- 2b. Basidia single, globose to ellipsoid3
- 3a. Mycoparasites of basidiomycetous fungi, basidiocarp heterogenous, inner region partially filled with host hyphae, host hyphae macroscopically distinguishable..... *Naematelia encephaloidae*

- 3b. Mycoparasites of ascomycetous and basidiomycetous fungi, basidiocarp homogenous, host hyphae may present in trama, host hyphae macroscopically indistinguishable *Tremella sensu lato*

Key to the species of *Sirobasidium*

- 1a. Basidiocarp foliose, brown to reddish brown, basidiospores $6-8 \times 6.7-8.6 \mu\text{m}$ *S. magnum*
- 1b. Basidiocarp cerebriform, resupinate, yellow or white..... 2
- 2a. Basidiocarp yellowish; basidia cylindrical, phaseoliform, ellipsoid, two to four segmented, basidiospores $4-5.5 \times 5-6 \mu\text{m}$
..... *S. japonicum*
- 2b. Basidiocarp white; basidia ellipsoid to fusiform, two segmented, basidiospores $8-9.5 \times 9-10 \mu\text{m}$ *S. brefeldianum*

Key to the species of *Tremella sensu lato*

- 1a. Hyphidia absent.....2
- 1b. Hyphidia present. 6
- 2a. Basidia globose to ellipsoid with out stalk3
- 2b. Basidia capitate stalked, basidiospores $6-9.8 \times 4-6.2 \mu\text{m}$
..... *T. poilkavensis*
- 3a. Basidiocarp white, basidiospores $4.7-8.0 \times 4.3-6 \mu\text{m}$ *T. fuciformis*
- 3b. Basidiocarp yellow or brown4
- 4a. Swollen cells present in the trama..... 5
- 4b. Swollen cells absent in the trama, basidiospores $5-8 \times 5-6.5 \mu\text{m}$
.....*Tremella* species 1
- 5a. Basidiocarp brown..... 6
- 5b. Basidiocarp yellowish orange, basidiospores $9.2-11 \times 9.3-10.8 \mu\text{m}$
Tremella species 2
- 6a. Inflated cells present, basidiospores $7-10.5 \times 5.5-8 \mu\text{m}$ *T. laurisilvae*
- 6b. Inflated cells absent, basidiospores $6-10 \times 5.5-9 \mu\text{m}$
..... *Phaeotremella yunanensis*
- 6a. Basidiocarp blackish brown, basidiospores $11-15.5 \times 11-15 \mu\text{m}$... *T. seclusa*

- 6b. Basidiocarp white, yellow, orange, red.....7
- 7a. Phialide like conidiophore present, basidiospores $5.7-7.1 \times 4.1-5.1 \mu\text{m}$
.....*T. armeniaca*
- 7b. Phialide like conidiophores absent..... 8
- 8a. Basidiocarp white, resupinate, basidiospores $16-19 \times 17-20 \mu\text{m}$
.....*T. sairandhriana*
- 8b. Basidiocarp cerebriform to foliose, white, whitish yellow, yellow.....9
- 9a. Inflated cells abundantly present in the hymenium, basidiospores $7.4-11 \times 7.5-10.5 \mu\text{m}$ *T. mesenterica*
- 9b. Inflated cells absent in hymenium.....10
- 10a. Hyphidia septate.....11
- 10b. Hyphidia non-septate, basidiospores $6.34-7.95 \times 5.33-7.81 \mu\text{m}$
..... *T. erythina*
- 11a. Basidiocarp white to whitish yellow, basidiospores $12-19.3 \times 12-18 \mu\text{m}$
..... *T. taiwanensis*
- 11b. Basidiocarp yellow to yellowish orange, basidiospores $14-18$
 $14-19 \mu\text{m}$ *Tremella* species 3

Key to the taxa of Dacrymycetes (Dacrymycetales)

- 1a. Zonation is present in transverse section..... *Calocera*
- 1b. Zonation is absent in transverse section2
- 2a. Basidiocarp with cupulate or obliquely cupulate pileus; and inflated,
sometimes catenulate marginal hair..... *Guepiniopsis buccina*
- 2b. Basidiocarp pustulate, cerebriform, spathulate, cylindrical, capitate, with
or without marginal hairs. 3
- 3a. Hymenium always unilateral; basidiocarp mostly spathulate.
..... *Dacryopinax*
- 3b. Hymenium amphigenous or unilateral, limited to the upper part of
basidiocarp; basidiocarp pustulate, cerebriform, spathulate, cylindrical or
capitate4
- 4a. Basidiocarp with dendrohyphidia; 0-3 septate basidiospores.....
..... *Dendrodacrys paraphysatum*

- 4b. Basidiocarp with or without hyphidia; 0–3, 0–7 or 0–15, septate basidiospores..... *Dacrymyces*

Key to the species of *Dacryopinax*

- 1a. Basidiospores 0–1 septate..... 2
- 1b. Basidiospores 0–3 septate3
- 2a. Marginal hairs thick-walled, inflated, occasionally catenulate, 4–13 µm wide; thin-walled inflated cells absent in the subcortical zone; basidiospores 8.5–11 × 3.5–4.5 µm..... *D. indacocheae*
- 2b. Marginal hairs thin- to slightly thick-walled, cylindrical, entwining and tuft forming, 2.5–3 µm wide; thin-walled inflated cells abundant in the subcortical zone; basidiospores 7–9.5 × 3–4.5 µm.....*D. primogenitus*
- 3a. Inflated vesicle-like cells (within hyphae) present near abhymenial and cortical marginal hairs; basidiospores 10.5–13 × 4.5–5.5 µm*D. yungensis*
- 3b. Inflated vesicle-like cells (within hyphae) absent near abhyenial and cortical marginal hairs; basidiospores 10–15 × 3–5 µm*D. petaliformis*

Key to the species of *Dacrymyces*

- 1a. Basidiocarp stipitate, pileate. 2
- 1b. Basidiocarp sessile to substipitate, pulvinate.....5
- 2a. Hymenium unilateral; basidiospores 0-1 septate; basidiospores 7.5–9 × 4–5 µm*D. spathularia*
- 2b. Hymenium amphigenous on the head/ pileus surface; basidiospores 0–3 or 0–1 septate3
- 3a. Basidiospore 0–3 septate; basidiospores 10.2–14.5 × 3.1–5.3 µm.
.....*D. dacryomitiformis*
- 3b. Basidiospores 0–1 septate.....4
- 4a. Basidiocarp capitate with globose or semiglobose head; marginal hair cylindrical to subclavate; basidiospores 9–11 × 4–5 µm..... *D. microsporus*
- 4b. Basidiocarp cylindrical, lobed; marginal hair flexouse and irregularly shaped; basidiospores 6–9 × 3–4 µm*D. species 1*
- 5a. Basidiospores with up to 3 septate. 6
- 5b. Basidiospores with more than 3 septate. 8

- 6a. Basidiocarp substipitate or stipitate.....7
- 6b. Basidiocarp pustulate or pulvinate; basidiospores $10-15 \times 4.5-5 \mu\text{m}$
..... *D. lacrymalis*
- 7a. Basidiocarp not coalescing, individual basidiocarps up to 8mm;
basidiospores $10-14 \times 5-7 \mu\text{m}$ *D. cupularis*
- 7b. Basidiocarp coalescing and extending up to 21mm; basidiospores $9-13 \times$
 $4-6 \mu\text{m}$ *D. capitatus*
- 8a. Basidiospores more than 7 septate up to 15; basidiospores $19-26 \times 5.8-$
 $7.5 \mu\text{m}$ *D. falcatus*
- 8b. Basidiospores 0-7 septate..... 9
- 9a. Basidiocarp extending up to 60 mm; basidiospores $16-19.5 \times 4.4-6.5 \mu\text{m}$...
..... *D. novae-zelandiae*
- 9b. Basidiocarp not extending more than 10 mm.....9
- 10a. Hyphidia branched, basidiospores $15-22 \times 5-6.5 \mu\text{m}$ *D. san-augustinii*
- 10b. Hyphidia unbranched..... 11
- 11a. Basidiocarp pustulate to substipitate; basidiospores $14-19 \times 3.5-5.5 \mu\text{m}$. ..
..... *D. species 2*
- 11b. Basidiocarp cerebriform, discoid and applanate. 12
- 12a. Basidiospores $18-21 \times 5-7 \mu\text{m}$, narrower, Q value = $3.14-3.28 \mu\text{m}$
..... *D. "cerebriformis"*
- 12b. Basidiospores $17-21 \times 6.5-8 \mu\text{m}$, broader,.....Q value = $2.63-2.77 \mu\text{m}$
..... *D. sinostenosporus*

Key to the taxa of Agaricomycetes

- 1a. Tramal hyphae with clamp-connections; basidia longitudinally or
transversely septate, saprobicAuriculariales
- 1b. Tramal hyphae without clamp-connections; basidia always longitudinally
septate, mostly mycorrhizal or endophytic.....*Sebacina* species

Key to the genera of Auriculariales (Auriculariaceae)

- 1a. Basidia cylindrical to clavate with transverse septa..... *Auricularia*
- 1b. Basidia with globose to broadly ellipsoid with longitudinal septa.
..... Auriculariaceae taxon

Key to the species of *Auricularia*

- 1a. Basidiocarp resupinate to effused reflexed, abhymenium villose to hispid with blakish brown concentric zones, basidiospores $8-13.5 \times 5-8 \mu\text{m}$
.....*A. srilankensis*
- 1b. Basidiocarp sessile or substipitate, auriculiform-petaloid, abhymenium pilose to tomentose without concentric zones2
- 2a. Hymenial surface reticulate..... 3
- 2b. Hymenial surface smooth with folds.....4
- 3a. Schizomedulla absent, Basidiospores $10-13.5 \times 4.5-5 \mu\text{m}$ *A. sinodelicata*
- 3b. Schizomedulla present, Basidiospores $8-11 \times 4-6 \mu\text{m}$ *A. subglabra*
- 4a. Abhymenial hairs tomentose/densly pilose $>150 \mu\text{m}$, basidiospores $9-13.5 \times 4-5 \mu\text{m}$ *A. cornea*
- 4b. Abhymenial hairs glabrous to pilose $< 150 \mu\text{m}$ 5
- 5a. Basidiocarp gray to pale pink, abhymenium scarsly pilose, Basidiospores $9-13.5 \times 4-5 \mu\text{m}$*A. fibrillifera*
- 5b. Basidiocarp greyish brown to reddish brown, abhymenium pilose, Basidiospores $11-15 \times 4.5-5.5 \mu\text{m}$ *A. heimuer*

4.2. TAXONOMIC DESCRIPTIONS

4.2.1. Taxonomic descriptions of Tremellales

Vishniacozyma X.Z. Liu, F.Y. Bai, M. Groenew. and Boekhout

Basidiocarp pustulate, gelatinous, mycoparasitic. Basidia subglobose to ellipsoid, capitate or clavate, two to four celled, longitudinally or obliquely septate. Basidiospores ellipsoid. Hyphae thin-walled with or without clamp-connections. Haustoria not known. Zygoconidia (H shaped conidia may be present or absent). Sexual reproduction and hyphae formation not observed in culture. Budding cells and ballistoconidia present.

***Vishniacozyma* species**

Figure 4

Basidiocarp 3–8 × 2–3 mm, soft gelatinous, pustular, discrete, occasionally coalescing, translucent, off white to white when fresh turning to thin film adhered on the substratum when dry. Host is unidentified ascocarp. Spore print whitish.

Hymenium limited to the upper surface. **Hyphidia** absent. **Basidia** 20–34 × 17–19 µm, globose, spheropedunculate, two to four celled, longitudinally or obliquely septate, thin-walled, guttulate, hyaline. **Basidiospores** 8–12 × 8–12 µm (Q = 0.88–1.04 µm, Qm = 0.97 µm), subglobose to globose, hyaline, thin-walled, smooth, guttulate, apiculate. Secondary spore production from basidiospores observed. **Zygoconidia** not observed. **Tramal hyphae** 3–9 µm wide, thick-walled towards base, branched, smooth, hyaline, frequently anastomosing, gelatinous, without clamp-connections. **Haustoria** not observed.

Specimens examined: INDIA. Kerala State, Kozhikode District, Kakkad, 13 December 2023, Anjitha Thomas, ZGCAT354; INDIA. Kerala State, Kozhikode District, Kakkad, 13 December 2023, Anjitha Thomas, ZGCAT359.

Habitat: On dead wood.

Comments: Morphological characters like the presence of gelatinous pustular basidiocarp, association with a host fungus; longitudinally septate, globose, spheropedunculate basidia; subglobose to globose basidiospores, and secondary spore formation from basidiospores indicate a tremellaceous identity. Clamp-connection and haustoria have not been observed in this taxon.

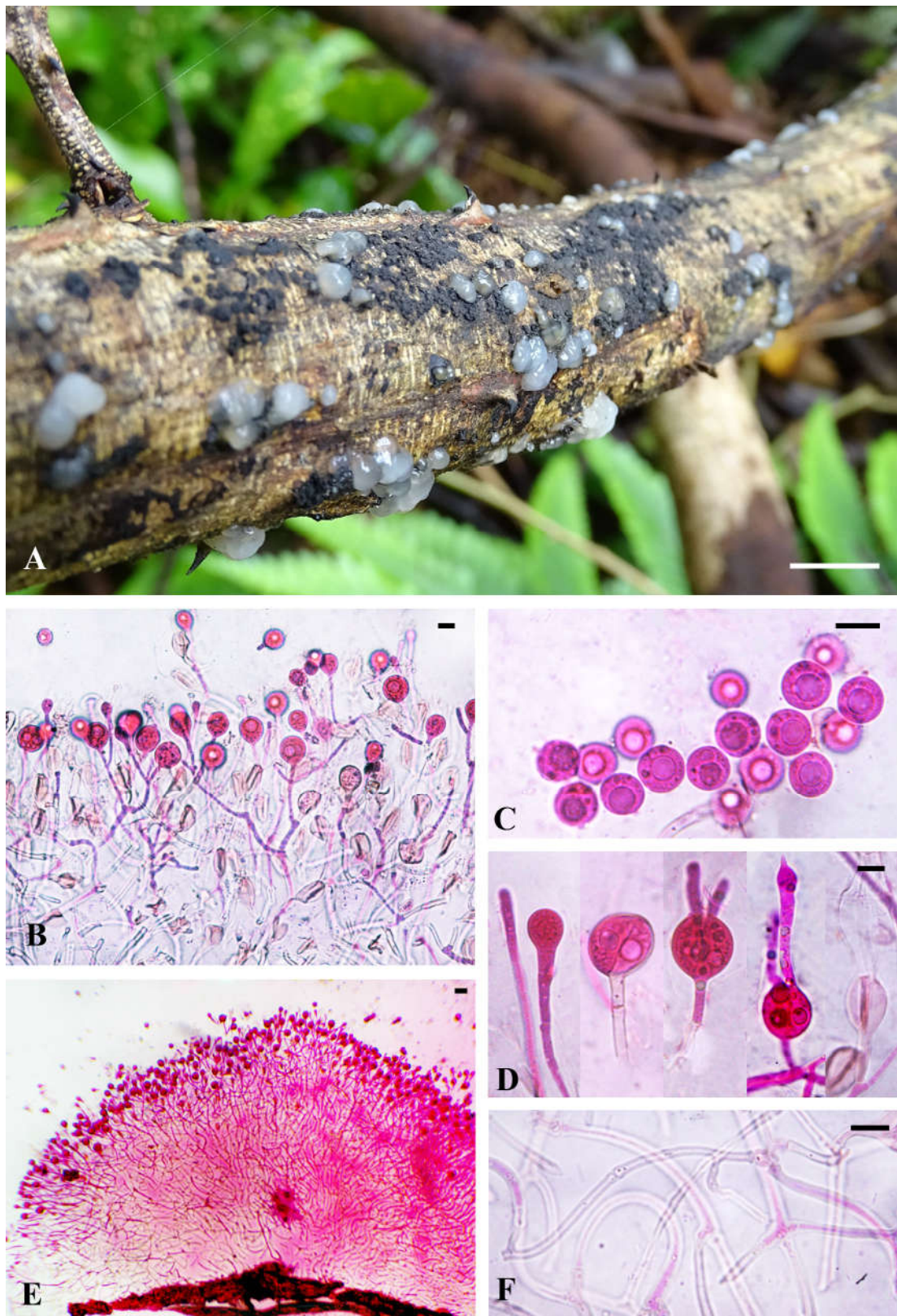


Figure 4: *Vishniacozyma* species- **A.** Basidiocarp; **B.** Hymenium; **C.** Basidiospores; **D.** Basidia of different developmental stages; **E.** Cross section of basidiocarp; **F.** Tramal hyphae without clamp-connections. Scale bars: A=10mm, B-F=10 μ m.

In the molecular phylogenetic analysis (Figure 54), the Kerala collections clustered along with *Vishniacozyma* clade members, which settled as a sister clade to *Tremella*. Our collections showed distinction from all *Vishniacozyma* members by the complete absence of clamp-connections. From the morphological and molecular information, it seems that the collections from Kerala represent a so far undescribed *Vishniacozyma* species. This is the first report of *Vishniacozyma* species with the absence of clamp-connection. There are no reports of this genus from India so far.

Sirobasidium Lagerh. and Pat.

Basidiocarp gelatinous, pulvinate, foliose, lobed. Clamp-connections present. Hymenium amphigenous, basidia arranged in simple or branched chains. Basidial cells maturing basipetaly. Shape varies from spherical, fusiform. Septation may longitudinal or transverse, 1-3 septate. Epibasidia fusiform. Producing short sterigma. Basidiospore apiculate, germinating by repetition and production of budding cells.

Sirobasidium magnum Boedijn, Bulletin du Jardin botanique de Buitenzorg, 3 Sér. 13: 266 (1934)

Figure 5

Basidiocarp 4–55 × 7–22 mm, gelatinous, foliose to lobate, hollow, brown to reddish brown when fresh becoming darker when dry. Basidiocarp growing on unidentified Ascomycete host found on dead and decaying wood.

Hymenium pale yellow in water, amphigenous. **Hyphidia** absent. **Basidia** in chains, 14.6–19.5 × 8.5–10 µm, oblong to broadly fusiform, two segmented, 2-spored, obliquely septate, thin-walled, hyaline, guttulate with basal septa and basal clamp-connection. A neck-like portion connects two basidia. Basidia are formed basipetally. Up to 8 basidia are observed in a basidial chain (including the collapsed mature basidia). **Epibasidia** 16–20.5 × 4–

5.3 μm , fusiform, hyaline, thin-walled, smooth, guttulate, sterigma formed on epibasidia produce basidiospores. **Basidiospores** 6–8 \times 6.7–8.6 μm (Q = 0.84–0.97 μm , Qm = 0.91 μm), subglobose, broader than long, guttulate, thin-walled, hyaline, smooth, with apiculum. **Tramal hyphae** 2–4 μm , smooth, thin-walled, septate, hyaline, with clamp-connections. Vesicles absent. Swollen cells absent. **Haustoria** not observed. **Conidia** absent.

Specimens examined: INDIA. Kerala State, Kozhikode District, Kakkad, 15 June 2021, Anjitha Thomas, ZGCAT230; Vallikkattu Kavu, 29 August 2018, Anjitha Thomas, ZGCAT26; Thurayil kotta, 1 August 2018, Anjitha Thomas, ZGCAT28; Kannur District, Aralam Wildlife Sanctuary, 26 June 2019, Anjitha Thomas, ZGCAT62; ZGCAT63; 28 June 2019, Anjitha Thomas, ZGCAT64; ZGCAT65; ZGCAT66; Kozhikode District, Thurayil Kotta, 2 July 2019, Anjitha Thomas, ZGCAT78; Palakkad District Silent Valley National Park, 5 July 2019, Anjitha Thomas, ZGCAT94; ZGCAT95; ZGCAT97; Waynad District, Thollayiram Kandi, 12 July 2019, Anjitha Thomas, ZGCAT105; Kollam District, Thenmala, 22 September 2019, Manju, ZGCAT138; 23 September 2019, Anjitha Thomas, ZGCAT147; ZGCAT148; Malappuram District, New Amarambalam, 4 September 2021, Anjitha Thomas, ZGCAT265; ZGCAT278; Thiruvananthapuram District, Palode, 1 October 2021, Anjitha Thomas, ZGCAT282; Palakkad District, Silent Valley National Park, 24 June 2022, Anjitha Thomas, ZGCAT321; ZGCAT322.

Habitat: On dead wood.

Comments: *Sirobasidium* members are easily distinguishable from other tremellaceous members by the presence of catenulate basidia. *Sirobasidium magnum* is characterised by its association with Ascomycete species, brownish basidiocarp with catenulate basidia, fusiform epibasidia and globose basidiospores. *Sirobasidium magnum* is a common species in Kerala. *Sirobasidium magnum* differs from *S. albidum*, *S. brefeldianum* and *S. sandwicense* Gilb. and Adask. by the colour of basidiocarp, where *S. magnum*

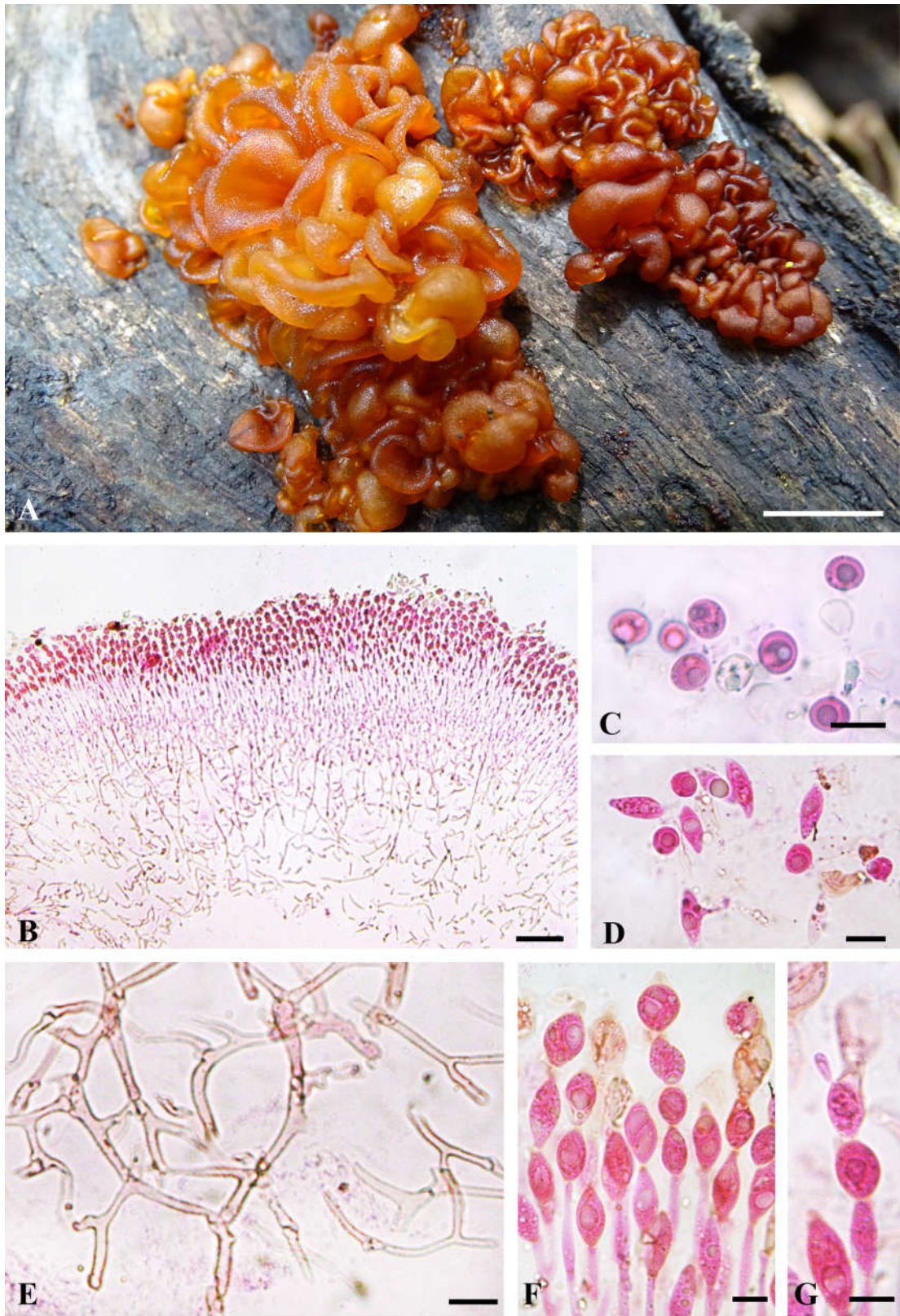


Figure 5: *Sirobasidium magnum*- **A.** Basidiocarp; **B.** Cross section of basidiocarp; **C.** Basidiospores; **D.** Epibasidia with basidiospores; **E.** Tramal hyphae; **F.** Basidial chains; **G.** Basidia with epibasidia. Scale bars: A=10mm, B=100µm, C-G=10µm.

has reddish brown colour and others have hyaline or white colour (Chen 1998). *Sirobasidium sanguineum* have reddish brown basidiocarp similar to *S. magnum*, but they differ by the size of the basidiocarp, and in number of basidia in a basidial chain. *Sirobasidium sanguineum* has 4–20 mm wide basidiocarp and 2–4 basidia in a basidia chain (Dämon and Hausknecht 2002), whereas *S. magnum* have 4–55 mm wide basidiocarps with 2–8 basidia in a basidial chain.

Our phylogenetic analysis (Figure 54) agrees with that of Millanes *et al.* (2011), Liu *et al.* (2015b), Kachalkin *et al.* (2019) and Yamada *et al.* (2022) that the *Sirobasidium* is polyphyletic. However, circumscription of the true *Sirobasidium* species is difficult due the non-availability of molecular characters from the type specimen. LSU sequence of *S. magnum* generated in the present study (GenBank accession: PP179309) clustered with other available *S. magnum* sequences with 100% bootstrap support value (Figure 54). There are no reports of this species from India so far.

Sirobasidium japonicum Kobayasi, Transactions of Mycological Society of Japan 4: 29 (1962)

Figure 6

Basidiocarps 7–17 × 7–16 mm wide, gelatinous, emerging as pustules, coalescing to form cerebriform, resupinate basidiocarps, whitish, pale yellow to orangish yellow when fresh, becoming brownish orange when dry. Growing on black ascomycetous host, from which basidiocarp can be easily peeled off.

Hymenium hyaline. **Hyphidia** absent. **Basidia** in chains, 17–38 × 4–8 µm, cylindrical, phaseoliform, ellipsoid, two to four segmented, obliquely or transversely septate, thin-walled, hyaline, guttulate with basal septa. Neck-like portion connects two basidia and basal clamp-connection are absent between basidia in the basidial chain. Clamp-connection is present at the base of basidial chain. Collapsed basidia are present above the contented cyanophilic basidia. Up to 5 basidia are observed in a basidial chain. **Epibasidia** 10–12 × 4–

5 µm, fusiform, hyaline, thin-walled, smooth, guttulate, germinating by repetition. **Basidiospores** 4–5.5 × 5–6 µm (Q = 0.72–0.91 µm, Qm = 0.87 µm), subglobose, broader than long, thin-walled, hyaline, smooth, guttulate, with apiculum. **Tramal hyphae** 2–4 µm, smooth, thick-walled in tramal region and thin-walled in subhymenium and hymenial region, septate, hyaline, with clamp-connections. **Vesicles** absent. Swollen cells absent. **Haustoria** not observed.

Specimens examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 24 October 2019, Anjitha Thomas, ZGCAT167; INDIA. Kerala State, Palakkad District, Silent Valley National Park, 25 October 2019, Anjitha Thomas, ZGCAT177.

Habitat: On dead wood.

Comments: *Sirobasidium japonicum* is characterised by white to yellow, applanate to cerebriform basidiocarp, cylindrical to ellipsoid, thin-walled, basidia and dorsy-ventrally depressed thin-walled globose basidiospores. This specimen differs from *S. rubrofusum* (Berk.) P. Roberts and *S. sanguineum* by their brownish red to reddish basidiocarp. *Sirobasidium minutum* Kisim.-Hor., Oberw. and L.D. Gómez has ashy white basidiocarp and long neck in between basidia in the basidial chain, which is a different character from *S. japonicum*.

In the key provided by Chen (1998) for *Sirobasidium* members, *S. japonicum* is listed under basidiocarps not developing on Ascomycetes hosts, but current specimen is associated with unidentified Ascomycetes host (asci were observed in our host collections). Report of *S. japonicum* from Japan (Yamada *et al.* 2022) also supports the association of the species with *Biscogniauxia capnodes* (Berk.) Y.M. Ju and J.D. Rogers. In the phylogenetic tree, sequence derived from the present specimen (ZGCAT167: ITS= PP179383) clusters with other *S. japonicum* sequences with 100% bootstrap support value (Figure 54). *Sirobasidium japonicum* has only been reported from China and Japan (Kobayasi 1962, Peng *et al.* 1992) so far. This is the first report of this species from India.

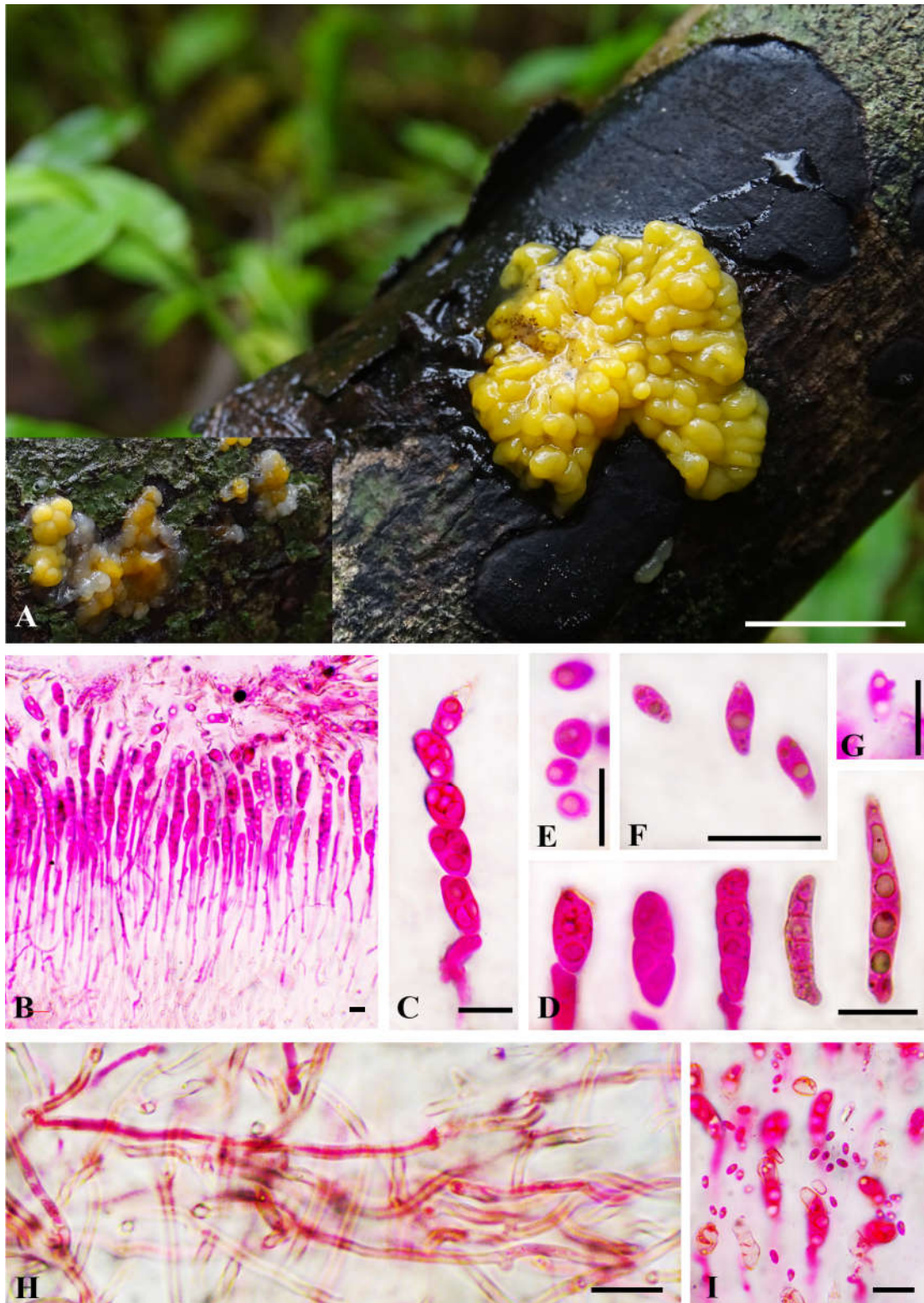


Figure 6: *Sirobasidium japonicum*- **A.** Basidiocarp, initial stage in insight; **B.** Hymenium with basidial chain; **C.** Basidial chain; **D.** Different shapes of basidia; **E.** Basidiospores; **F.** Epibasidia; **G.** Sterigmatal initial from epibasidia; **H.** Tramal hyphae; **I.** Conidia budding off from basidia. Scale bars: A=10mm, B-I=10µm.

Sirobasidium brefeldianum Möller, Bot. Mitt. Trop. 8: 165 (1895)

Synonyms

Sirobasidium brefeldianum f. *microsporum* Maire, Bull. Soc. Hist. nat. Afr. N. 36(3): 38 (1945)

Sirobasidium intermediae Kund. and M.S. Patil, Indian Phytopath. 39(3): 357 (1987) [1986]

Figure 7

Basidiocarps 5–13 × 5–8 mm in diameter, gelatinous, slimy, resupinate, emerging as pustules that coalesce later, with less than 1 mm height. Pure white when fresh, turning to almost invisible when dry.

Hymenium hyaline. **Hyphidia** absent. **Basidia** in chains, 20–34 × 8–13 µm, ellipsoid to fusiform, two segmented, two spored, obliquely or transversely septate, thin-walled, hyaline, guttulate with basal septa and basal clamp-connection. Up to 6 basidia are observed in a basidial chain (including the collapsed ones). **Epibasidia** 17–23 × 6–8 µm, fusiform, hyaline, thin-walled, smooth, guttulate, germinating by repetition. **Basidiospores** 8–9.5 × 9–10 (Q = 0.84–0.95 µm, Qm = 0.9 µm) µm, subglobose, broader than long, thin-walled, hyaline, smooth, guttulate, with apiculum. **Tramal hyphae** 2–4 µm, smooth, thin-walled, septate, hyaline, with clamp-connections. **Vesicles** 11–15 × 6–15 µm wide, globose to ellipsoid, thick-walled. **Swollen cells** absent. **Haustoria** not observed. **Conidia** not observed.

Specimens examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 24 October 2019, Anjitha Thomas, ZGCAT189.

Habitat: On dead wood.

Comments: *Sirobasidium brefeldianum* is characterised by the hyaline to white basidiocarps with ellipsoid to fusiform basidia. Number of basidia varies from 8–13 in a basidial chain (Rödel *et al.* 2017). Among the four whitish members in *Sirobasidium*, the present specimen differs from *S. apiculatum* by the lack of two

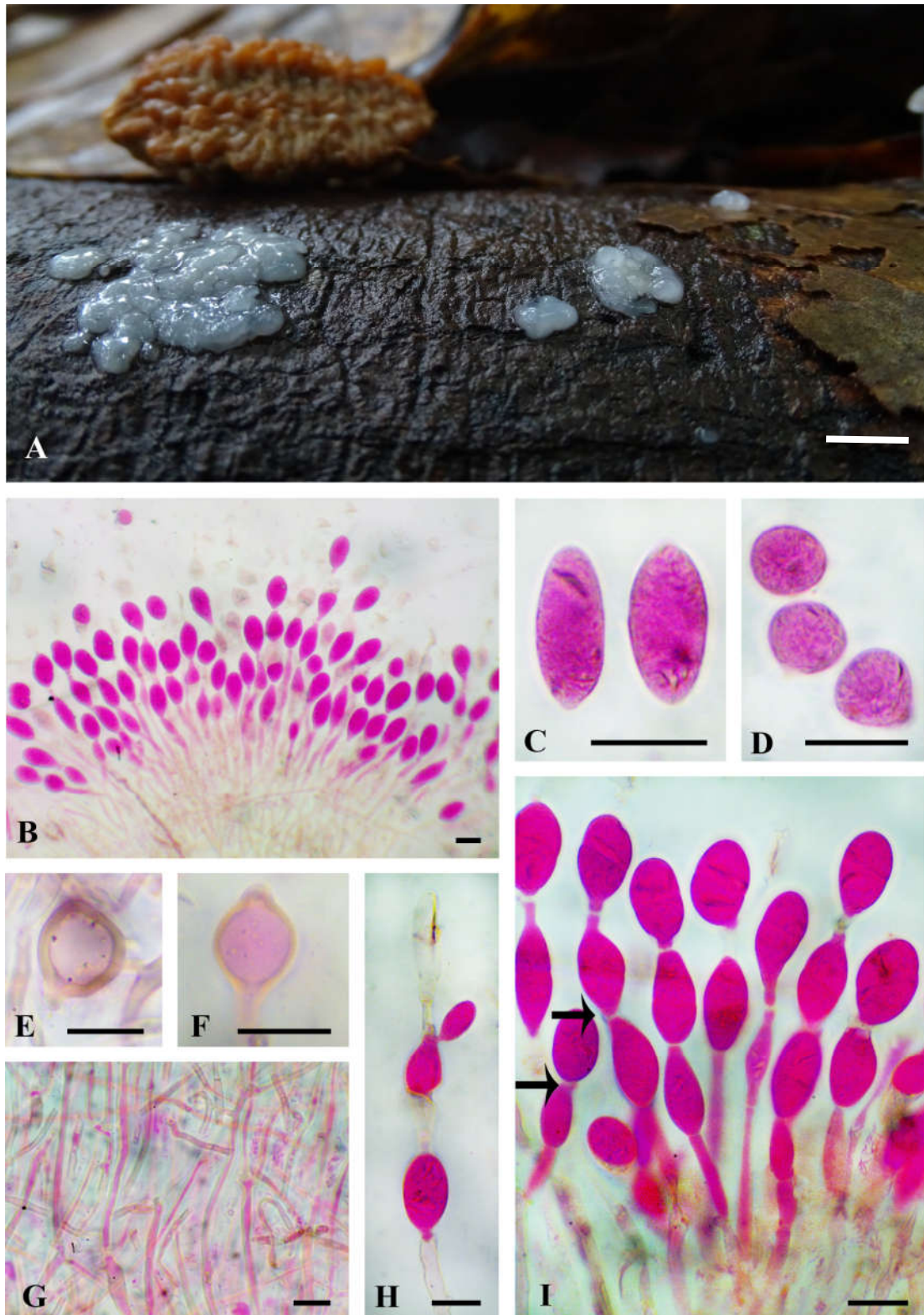


Figure 7: *Sirobasidium brefeldianum*- **A.** Basidiocarp; **B.** Hymenium with basidial chains; **C.** Epibasidia; **D.** Basidiospores; **E&F.** Vesicles; **G.** Tramal hyphae; **H.** Basidia with attached epibasidia; **I.** Basidial chains, arrows showing clamp-connections between basidia. Scale bars: A=10mm, B-I=10µm.

celled basidia with longitudinal septum and apiculate epibasidia (Rödel *et al.* 2017). *Sirobasidium albidum* has subglobose to globose basidia (Chen 1998) which contrast with the ellipsoid to fusiform nature of basidia of the Kerala collection. *Sirobasidium minutum* has a short section of hyphae (6–12 µm long) that separate each basidium in the basidial chain, and smaller basidiospores (5–5.4 µm) (Kisimova-Horovitz *et al.* 2000). *Sirobasidium sandwicense* has smaller basidiocarp (1–2 mm diameter) and is parasitic on *Diatrypella favacea* (Fr.) Ces. and De Not. (Chen 1998).

The morphological character of our collection agrees well with the description of *S. brefeldianum* (Rödel *et al.* 2017). Phylogenetic analysis using ITS and LSU regions of Kerala collections was done with all the available sequences of *Sirobasidium*. Sequence of the Kerala collection clustered in the *Sirobasidium* clade which contained *S. apiculatum*, *S. japonicum* and *S. magnum* (Figure 54). A sequence of *S. brefeldianum* (isolate AM71) available in GenBank however did not settled in the *Sirobasidium* clade. That sequence and a sequence of *S. intermediae* Kund. and M.S. Patil settled as a distinct clade. Since the identity of the *Sirobasidium* species that settled away from the main *Sirobasidium* clade could not be ascertained due to the lack of sequences from the holotype, its placement is debatable. Kundalkar and Patil (1986) have reported *S. brefeldianum* from India. From Kerala, this species has no previous reports.

***Naematelia* Fr.**

The basidiocarp is characterised by caespitose, cerebriform, tuberculate or spherical to thick foliaceous or crumpled. The colour varies from yellow to orange and red. Basidia subglobose to globose, ovoid, two-four celled, both vertical and transverse septa may seen. Tramal hyphae with clamp-connections and haustorial branches. Budding cells present. Ballistoconidia sometimes present.

Naematelia encephaloidea A. Thomas and T.K.A. Kumar, Phytotaxa 646: 61 (2024)

Figure 8

Basidiocarp 5–53 × 4–40 mm, firm gelatinous, cartilaginous, cerebriform, lobed, sessile, cream to yellowish brown, becoming paler with maturity, darkening on drying. Inner region partially composed of whitish host hyphae. Parasitic on an unidentified *Stereum* species.

Hymenium pale yellowish in water. **Hyphidia** not observed. **Basidia** 11–16 × 10–13 µm, subglobose to broadly ellipsoid, two to four-celled, longitudinally or obliquely septate, thin- to thick-walled, guttulate, hyaline. **Epibasidia** 19–108 × 2–3 µm, slightly thick-walled, up to 5 µm towards tip. **Basidiospores** 6.2–9 × 5–7 µm (Q = 1.1–1.4 µm, Qm = 1.16 µm), subglobose to globose, broadly ellipsoid, obovoid, hyaline, thin- to thick-walled, smooth, apiculate, guttulate. Direct germination and secondary spore formation observed. **Tramal hyphae** mixed with host hyphae, 2–5.5 µm wide, frequently inflated, slightly thick- to thick-walled, branched, smooth, guttulate, hyaline with clamp-connections. **Haustoria** abundantly present throughout the trama, frequently branched, up to 5 haustorial hyphae from a haustorial cell, with basal clamp-connection. **Swollen cells** are of two types. Type 1; 4–10 × 4–6 µm, subglobose, globose, ellipsoid, cylindrical, narrowly utriform, thick-walled, prominently guttulate, non germinating, with basal clamp-connections, borne on hyphae. Type 1 swollen cells were abundant in the basidiocarp developing on the host (*Stereum*) basidiocarp and not observed in basidiocarp developing on the bark. Type 2; 4–12 × 3–5 µm, ellipsoid, lemoniform, oblong and clavate, sometimes with 3–8 µm long apical protuberances, thin-walled, guttulate, rarely germinating, commonly terminal. Type 2 swollen cells were rare in basidiocarp developing on the host (*Stereum*) basidiocarp and abundant in basidiocarp developing on the bark. **Inflated cells** 12–16 × 6–5 µm, versiform, thin-walled. **Conidia** 3–5 × 3–5 µm, globose, abundant, thick-walled, guttulate.

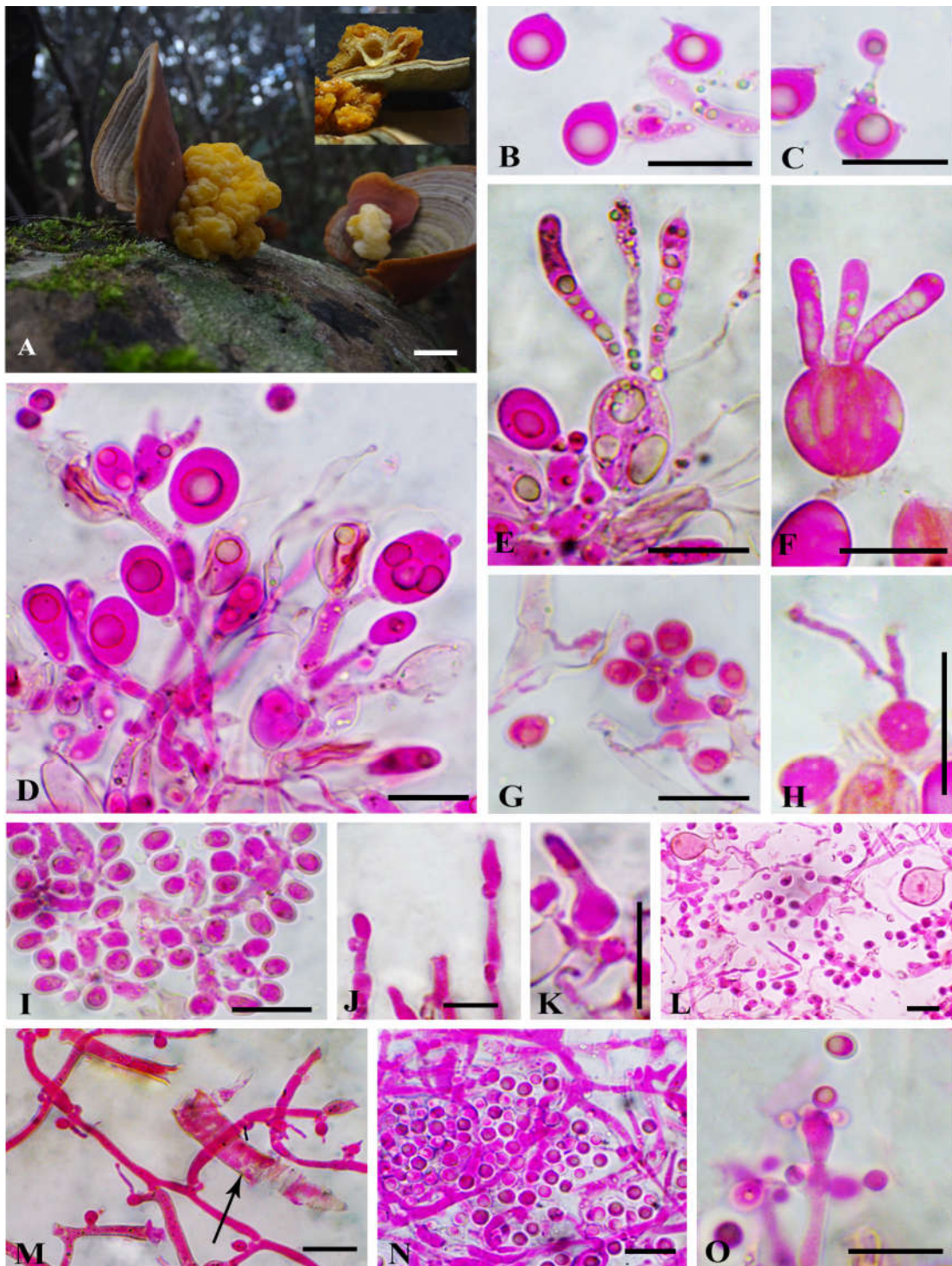


Figure 8: *Naematelia encephaloidea*- **A.** Basidiocarp (dried specimen showing interior is given as inset); **B&C.** Basidiospores; **D.** Hymenium; **E&F.** Basidia; **G&H.** Swollen cells and haustoria with haustorial hyphae; **I.** Thick-walled swollen cells; **J.** Thin-walled swollen cell; **K.** Germinating thin-walled swollen cell; **L.** Trama with abundant thick-walled swollen cells and two inflated cells; **M.** Tramal hyphae with haustoria and host hyphae (arrow); **N.** Tramal hyphae with conidiospores; **O.** Conidiophore with conidiospores. Scale bars: A=10mm, B-O=10µm.

Specimen examined: INDIA, Kerala State, Palakkad District, Silent Valley National Park, 24 June 2022, Anjitha Thomas, ZGCAT325; ZGCAT326; ZGCAT327; ZGCAT329.

Habitat: On *Stereum* species.

Comments: *Naematelia encephaloidea* is characterised by the presence of whitish host hyphae partially in the inner region of basidiocarp; two types of swollen cells, thick-walled, non germinating swollen cells, and thin-walled, germinating swollen cells; thick-walled, globose, conidia formation from tramal hyphae; inflated cells in the trama; lack of hyphidia, and parasitic nature on *Stereum* species.

In the phylogenetic tree generated using ITS and LSU sequences (Figure 54), *N. encephaloidea* clusters in between *N. aurantialba* and *N. encephala*. When comparing with *N. aurantialba*, *N. encephaloidea* has small sized (5–53 × 4–40 mm) basidiocarps, smaller basidiospores (6.5–9 × 5–7 µm) and basidia (11–16 × 10–13 µm). Whereas, *N. aurantialba* has larger basidiocarp (60–170 × 35–110 mm), larger basidiospores (10–14 × 9–12.5 µm) and basidia (16–32 × 10–20 µm) (Bandoni and Zang 1990). *Naematelia encephala* has solid, non-gelatinous, whitish mass of host hyphae in the inner core of basidiocarp (Chen 1998), whereas *N. encephaloidea* have a partially hollow inner core of basidiocarp. *Naematelia encephala* is associated with the host *Stereum sanguinolentum* (Alb. and Schwein.) Fr. (Bandoni 1961, Roberts 1999, Hawksworth *et al.* 2016). Whereas, *N. encephaloidea* has a different host species (GenBank accession number of host organism of *N. encephaloidea*: ITS=OR083274. For more details of *N. encephaloidea*, refer: Thomas and Kumar (2024).

Tremella Pers.

Tremella sensu stricto is characterized by minute to large (0.3–10 cm), pustular, cerebriform to foliose or lobed, cream, yellow, yellowish orange, brown or reddish black basidiocarps. Dikaryotic hyphae are with haustorial

branches and clamp-connections. Basidia are subglobose, globose, ellipsoid, oval or pyriform, two to four celled, with longitudinal, transverse or oblique septa. Basidiospores are subglobose to globose, oblong or ellipsoid, apiculate and guttulate. Budding cells, conidia, terminal cells, swollen cells, hyphidia and vesicles may be present or absent. Fermentation is absent.

Tremella poilkavensis A. Thomas and T.K.A. Kumar, Phytotaxa 600: 38 (2023)

Figure 9

Basidiocarp 55–75 × 7–26 mm, gelatinous to cartilaginous, cerebriform, hollow, sessile, broadly attached to the substratum, amber brown to blackish brown when fresh, turning more blackish when dry. Basidiocarp developing on ascomata of a *Biscogniauxia* species. Spore print pale yellow.

Hymenium pale yellow to brownish yellow in water, hyphidia absent.

Basidia 19–31 × 9–13.3 µm (including stalk), pyriform to capitate, four-celled, oblique or longitudinally septate, cruciate, thick-walled, guttulate, pale yellow to brownish yellow, with basal clamp-connections. Stalk of basidia 5–21 × 2.5–4.5 µm. **Epibasidia** 21–38 × 2–3 µm. Basidia budding off subglobose to ellipsoid conidiospores. **Basidiospores** 6–9.8 × 4–6.2 µm (Q = 1.06–1.8 µm, Qm = 1.43 µm), ellipsoid, subcylindrical, subglobose or amygdaliform, hyaline, thin-walled, smooth, apiculate, guttulate. Direct germination, secondary spore production and yeast formation observed. **Yeasts** 2–3 × 1.5–2 µm, subglobose to ellipsoid. Terminal swollen cells present within the trama, 7.7–13.3 × 4–7.6 µm, broadly fusiform, ellipsoid, lemoniform, oblong, capitate or clavate in shape, sometimes with 1–3 × 1–1.53 µm apical protuberances. **Tramal hyphae** mixed with host hyphae, 2–4 µm wide, thick-walled, branched, smooth, guttulate, with clamp-connections. **Haustoria** abundantly present throughout the trama, frequently branched, with basal clamp-connection, often attached to the host hyphae.

Specimens examined:—INDIA. Kerala State, Kozhikode District, Poilkave sacred grove, 29 August 2018, Anjitha Thomas ZGCAT14; 14 July 2021, Anjitha Thomas, ZGCAT243.

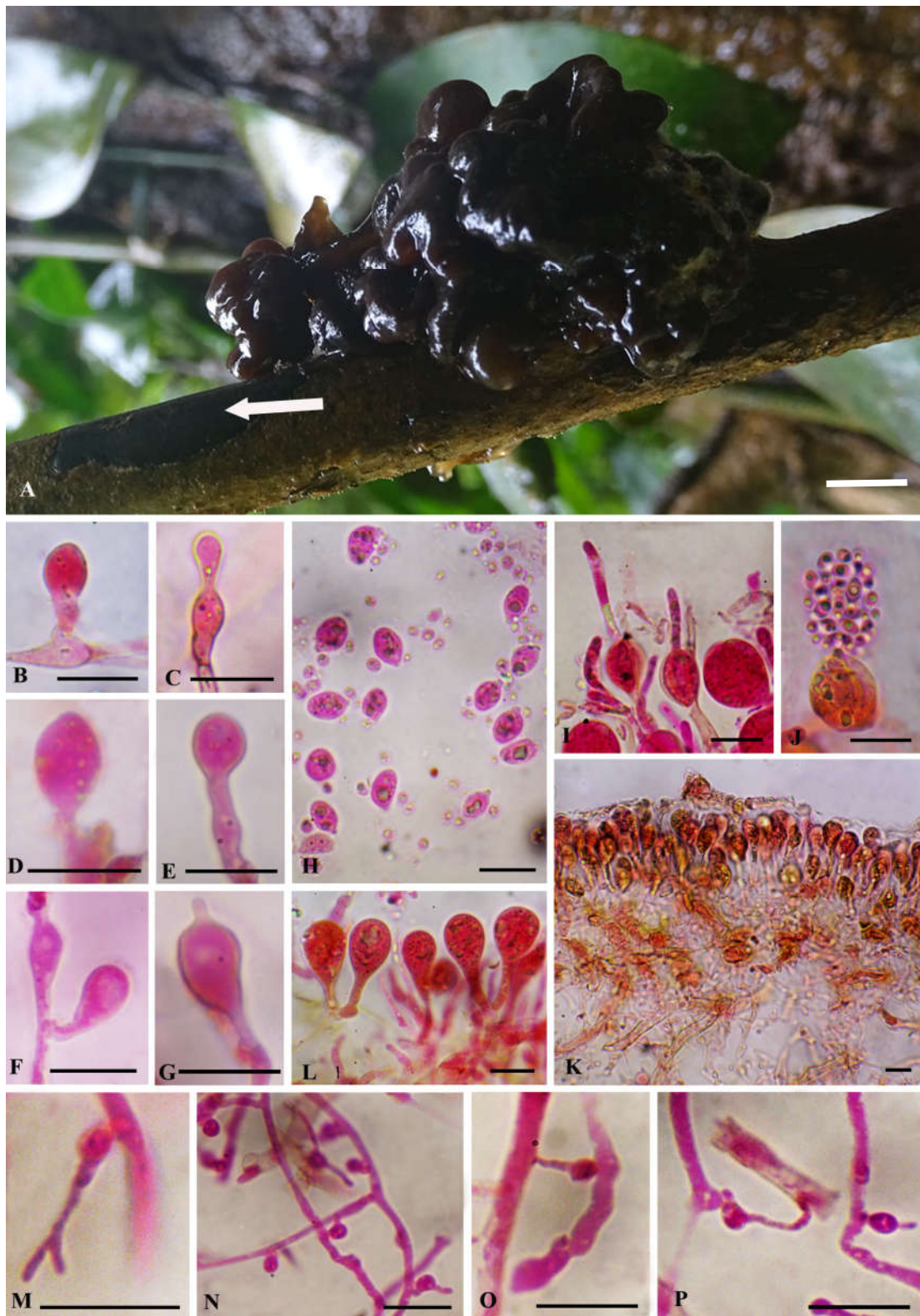


Figure 9: *Tremella poilkavensis*- **A.** Basidiocarp growing on host (host in white arrow); **B-G.** Swollen cells; **H.** Basidiospores with yeast cells; **I&L.** Basidia; **K.** Cross section showing hymenium, trama; **J.** Conidiophores from basidia; **M-N.** Branched haustoria; **O-P.** Haustoria attached to the host hyphae. Scale bars: A=10mm, B-P=10µm.

Habitat: On dead wood.

Comments: *Tremella poilkavensis* was originally described by Thomas and Kumar (2023) from Kerala. *Tremella poilkavensis* is characterised by its amber brown to blackish brown basidiocarp, capitate to pyriform stalked basidia and basidia capable of budding conidiospores. Morphologically *T. poilkavensis* is related to *T. globispora*, which possesses capitate basidia and conidiospores budding off from basidia. But *T. globispora* is distinct from *T. poilkavensis* by its basidiocarp morphology and shape of basidiospores. Basidiocarp of *T. globispora* is hyaline, 2–5 mm in size, and basidiospores are dorsi-ventrally depressed (Chen 1998). *Tremella steidleri* (Bres.) Bourdot and Galzin shows resemblance with *T. poilkavensis* by the size of basidiocarp, shape and size of basidia and basidiospores. But *T. steidleri* differs from *T. poilkavensis* by the colour of the basidiocarp (dull brown to date brown with whitish matt pruina), and by being parasitic on *Stereum* species (Robberts 1999). All the collections of *T. poilkavensis* obtained so far were found to be associated with ascomata of *Biscogniauxia* species. *Tremella poilkavensis* is closely related to two undescribed *Tremella* specimen [Dai 21969 and Dai 21970] based on molecular data. However, these specimens have not been formally described which makes it impossible to compare morphological characteristics between them.

Tremella fuciformis Berk., Hooker's journal of botany and Kew Garden miscellany 8: 277 (1856)

Synonyms:

Nakaiomyces nipponicus Kobayasi, Sci. Rep. Tokyo Bunrika Daig., Sect. B 4: 4 (1939)
Tremella fuciformis f. *corniculata* Kobayasi, Sci. Rep. Tokyo Bunrika Daig., Sect. B 4: 25 (1939)

Tremella nipponica (Kobayasi) Wojewoda, Mała Flora Grzybów, 2 Basidiomycetes (Podstawczaki) Tremellales (Trzesakowe) Auriculariales (Uszakowe) (Warszawa): 142 (1981)

Figure 10

Basidiocarp 10–75 × 5–30 mm, firm gelatinous, foliose, caespitose, lobed, margins crenate, crisped, undulate or entire, sessile, white when fresh

and yellowish white when dry. Growing on the ascocarp of an unidentified fungus. Spore print not obtained.

Hymenium hyaline in water. **Hyphidia** absent. **Basidia** 10–18 × 8–9 µm, subglobose to broadly ellipsoid, two to four celled, longitudinally or obliquely septate, thin-walled, guttulate, hyaline, with basal clamp-connection. **Epibasidia** 21–36 × 2–3 µm. **Basidiospores** 5–8.0 × 4–6 µm (Q = 1.0–1.33 µm, Qm = 1.16 µm), broadly ellipsoid to ellipsoid, hyaline, thin-walled, smooth, guttulate, apiculate. Germination by germ tube and secondary spore formation. **Vesicles** 7.5–18 × 5.5–7.5 µm, globose to ellipsoid or clavate, in catenulate chains, thick-walled, gelatinised. **Inflated cells** 12–39 × 9–20 µm, , versiform, thin- to slightly thick-walled, with clamp-connections, inflated cells are frequent towards the base of the basidiocarp. **Tramal hyphae** 2–4 µm wide, slightly thick- to thick-walled, branched, smooth, hyaline, gelatinous, with clamp-connections. **Haustoria** abundant towards the base, often branched, more than one hyphae arise from one haustorial cell, with basal clamp-connections.

Specimens examined: INDIA, Kerala State, Malappuram District, University of Calicut campus, 9 July 2018, Anjitha Thomas, ZGCAT5; Palakkad District, Pattambi, 30 september 2018, Anjitha Thomas, ZGCAT30; Kozhikode District, Kuttiady, 31 October 2018, Salna N., ZGCAT31; Kannur District, Aralam Wildlife Sanctuary, 28 June 2019, Anjitha Thomas, ZGCAT67; Palakkad District, Silent Valley National Park, 4 July 2019, Anjitha Thomas, ZGCAT87; Palakkad District, Silent Valley National Park, on 4 July 2019, Anjitha Thomas, ZGCAT88; Kozhikode District, Thottilpalam, 5 August 2019, Salna N., ZGCAT123; Palakkad District, Silent Valley National Park, 22 October 2019, Anjitha Thomas, ZGCAT169; Kozhikode District, Engapuzha, 9 August 2020, Anjitha Thomas, ZGCAT213; Malappuram District, Valluvassery, 13 January 2021, Anjitha Thomas,

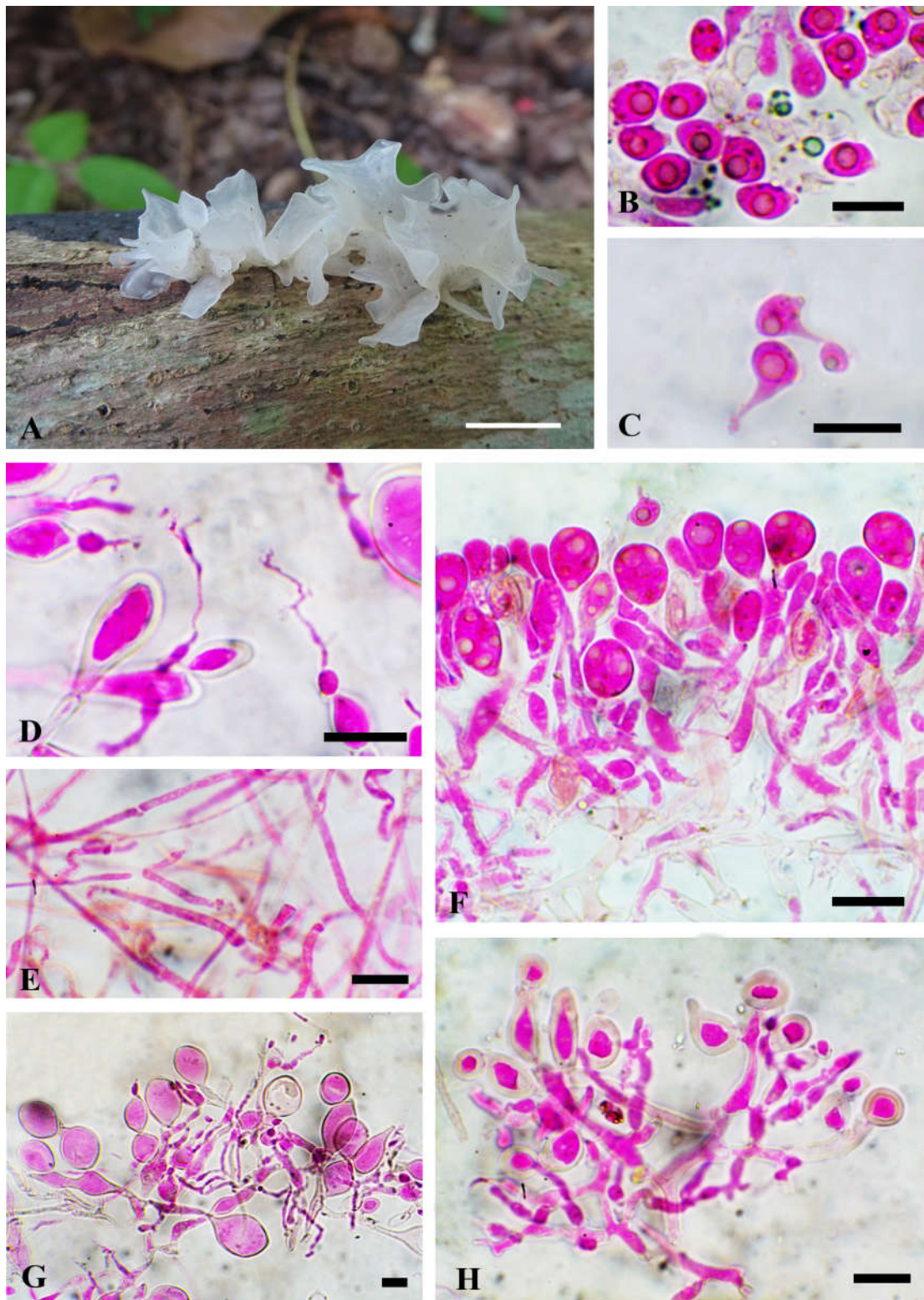


Figure 10: *Tremella fuciformis*- **A.** Basidiocarp; **B.** Basidiospores; **C.** Basidiospores with secondary ballistosporic production; **D.** Vesicles with haustoria; **E.** Tramal hyphae; **F.** Hymenium with basidia and basidiospores; **G.** Swollen cells; **H.** Vesicles. Scale bars: A=10mm, B-H=10µm.

ZGCAT224; Kozhikode District, The Zamorins Guruvayurappan College campus, 19 June 2021, Anjitha Thomas, ZGCAT239; Kannur District, Aralam Wildlife Sanctuary, 6 August 2021, Anjitha Thomas, ZGCAT260; Pathanamthitta District, Ranni, 12 April 2022, Salna N., ZGCAT308; Kozhikode District, The Zamorins Guruvayurappan College Campus, 16 June 2022, Anjitha Thomas, ZGCAT315; Kannur District, Kannavam, 15 October 2022, Vaishnavi M., ZGCAT339.

Habitat: On dead wood.

Comments: Present collection agrees with the taxonomic descriptions of *T. fuciformis* by Chen (1998). Chen (1998), however, did not observe vesicles in his study but mentions that Olive (1947) had earlier observed vesicles in the hymenium of *T. fuciformis*. Kerala specimens have both vesicles and inflated cells.

***Tremella* species 1**

Figure 11

Basidiocarp 5–31 × 6–17 mm, gelatinous, foliose to cornute, lobed, hollow, sessile, yellow when fresh and dry. Associated with ascocarp of unidentified ascomycete. Spore print not obtained.

Hymenium pale yellowish in water. **Hyphidia** absent. **Basidia** 9–14 × 7–14 µm, globose, subglobose, obovoid, ellipsoid, four-celled, oblique or longitudinally septate, thin-to slightly thick-walled, guttulate. **Epibasidia** up to 25 µm long. **Basidiospores** 5–8 × 5–6.5 µm (Q = 1.1–1.6 µm, Qm = 1.39 µm), globose, subglobose to broadly ellipsoid, hyaline, thin-walled, smooth, apiculate, guttulate. Direct germination, repetitive spore formation and budding yeast cells are observed. **Yeast cells** 2–3 × 1.5–2.5 µm, subglobose, broadly ellipsoid to ellipsoid, thin-walled, guttulate. Vesicles 6–12 × 6–7 µm, present in hymenium, subglobose, ellipsoid to cylindrical, broadly clavate, thick-walled. Swollen cells 5–10 × 3–10 µm, present in subhymenium and trama,

subglobose to oval, clavate, urniform, thin-walled, guttulate with basal clamp-connection. **Tramal hyphae** 2–7 μm wide, thin-to thick-walled, gelatinous, smooth, guttulate with clamp-connections. **Haustoria** present, rare, haustorial hyphae unbranched, one to two haustorial hyphae from a cell.

Additional specimens examined: INDIA. Kerala State, Kozhikode District, Poilkave sacred grove, 20 June 2019, Anjitha Thomas, ZGCAT52; Ernakulam District, Iringole kavu, 17 July 2019, Anjitha Thomas, ZGCAT107; ZGCAT108; Kozhikode District, Poilkave sacred grove, 19 September 2019, Anjitha Thomas, ZGCAT136; 14 July 2021, Anjitha Thomas, ZGCAT244; Malappuram District, University of Calicut campus, 16 June 2022, Anjitha Thomas, ZGCAT318; 24 September 2022, Anjitha Thomas, ZGCAT335.

Habitat: On dead wood.

Comments: Morphologically, this species has similarities with *T. flava* and *T. boninensis* (Kobayasi) S. Ito and S. Imai. Basidiocarp of *T. flava* has foliose, hollow nature, and lack of hyphidia similar to *T. species 1*. But, *T. species 1* has shorter basidia (*T. species 1*: 9–14 \times 7–14 μm ; *T. flava*: 14–17 \times 11–13 μm) and thick-walled vesicles in the hymenial region, which is absent in *T. flava* (Chen 1998, Bandoni and Boekhout 2011). In addition, *T. species 1* has unbranched haustorial hyphae and rare occurrence of haustoria, whereas, *T. flava* has abundant haustoria with frequently branched haustorial hyphae (Chen 1998). *Tremella boninensis* also has yellowish basidiocarp, lack of hyphidia and association with ascomycetous fungi, similar to *T. species 1*. But the former has longer basidia (*T. boninensis*, 15.5–17.5 \times 10.5–14 μm ; *T. species 1*, 9–14 \times 7–14 μm), and non-hollow basidiocarps (Chen 1998). The present species has shorter basidia, and foliose to cornute basidiocarp with hollow lobes. *Tremella cinnabarina* (Bull.) has a larger basidiocarp (50–100 mm high) and is phylogenetically distinct (Bandoni and Boekhout 2011). Basidiocarp of *T. species 1* is smaller (5–31 \times 6–17 mm) compared to *T. cinnabarina*. *Tremella fuciformis* and *T. yokohamensis* are phylogenetically related to *T. species 1* (Figure 54), but both of them have whitish basidiocarps (Malysheva *et al.* 2015).

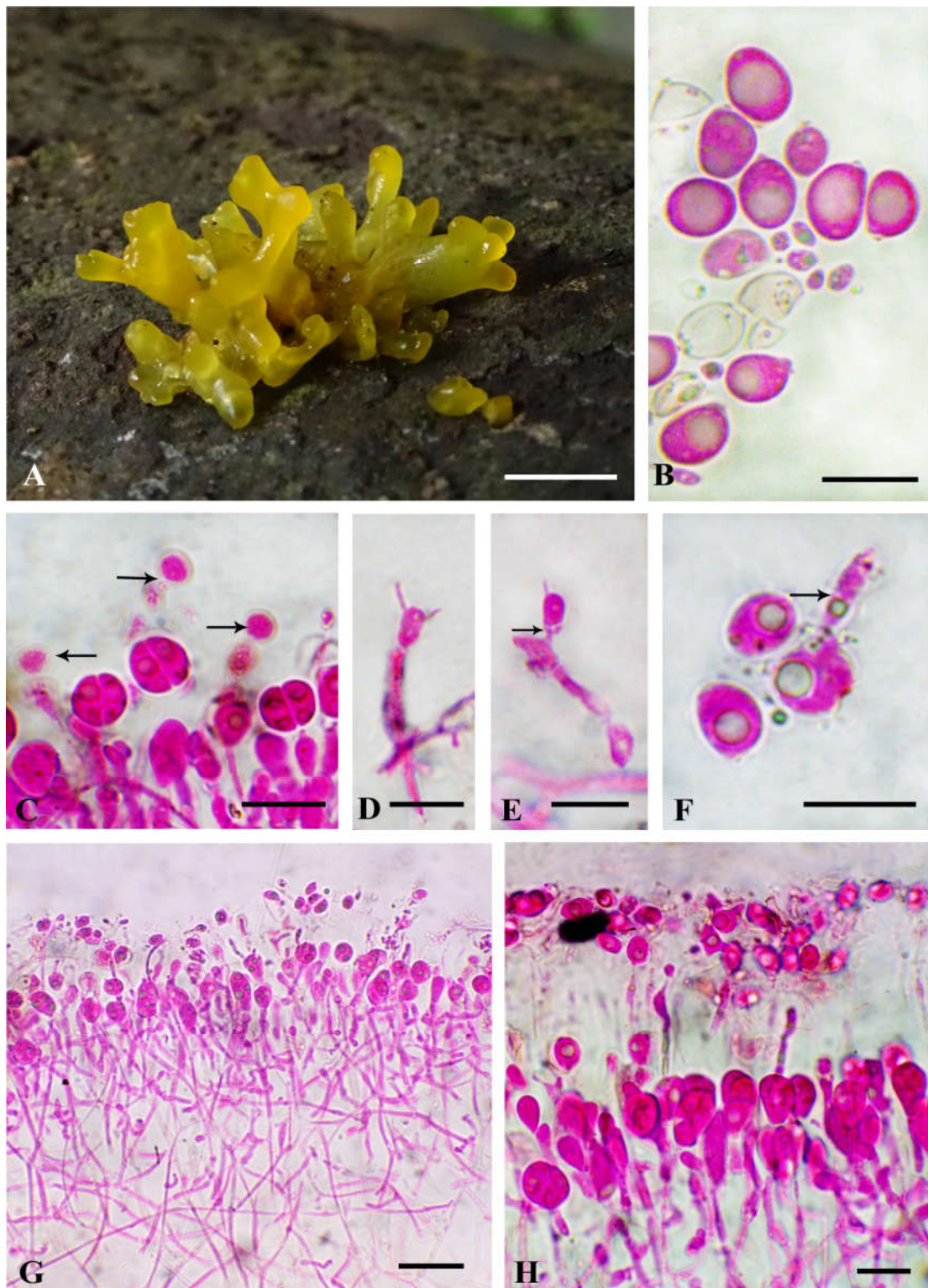


Figure 11: *Tremella* species 1- **A.** Basidiocarp; **B.** Basidiospores budding yeast cells; **C.** Basidia with thick-walled vesicles (arrow) in the hymenium; **D&E.** Haustoria with basal clamp-connection (arrow) and haustorial hyphae; **F.** Basidiospores, germ tube (arrow); **G&H.** Hymenium with tramal hyphae, basidia and basidiospores. Scale bars: A=10 mm, B-H=10 μ m.

In the phylogenetic tree (Figure 54) prepared using combined ITS and LSU sequences, *T. species 1* clustered with other *fuciformis* group members. According to Chen, *fuciformis* group is characterised by foliose white, yellowish or reddish basidiocarp, association with Ascomycete (Xylariaceae) species and lack of hyphidia, which morphologically support the placement of *T. species 1*. Phylogenetically, *T. species 1* is clustered separately from *T. basidiomaticola* Xin Zhan Liu and F.Y. Bai, *T. boninensis*, *T. flava*, *T. cinnabarina*, *T. yokohamensis*, and *T. fuciformis* with 100% bootstrap support value.

Tremella species 2

Figure 12

Basidiocarp 7–19 × 6–14 mm, firm gelatinous, adpressed, resupinate, solid, yellowish orange when fresh and becoming paler when dry. Spore print not obtained.

Hymenium hyaline in water. **Hyphidia** absent. **Basidia** 18–24 × 22–24 µm, subglobose to globose, two to four celled, longitudinally septate, thin-walled, guttulate, hyaline. **Epibasidia** 99–134 × 4–5 µm, guttulate, thin-walled. **Basidiospores** 9–11 × 9–11 µm (Q = 0.9–1.16 µm, Qm = 1.01 µm), subglobose to globose, hyaline, smooth, guttulate, apiculate. Germinating by direct germ tube formation and budding blastospores. Thin-walled and thick-walled basidiospores present. **Swollen cells** 6.5–24 × 5.8–9.3 µm, subglobose, globose, ovoid, conical to cylindrical, thin-walled, some swollen cells germinating to form new hyphae, present throughout the basidiocarp, with clamp-connections. **Tramal hyphae** 2–4 µm wide, thin-to slightly thick-walled, branched, smooth, hyaline, gelatinous, with clamp-connections. **Haustoria** not observed.

Specimen examined: INDIA. Kerala State, Idukki District, Munnar, 07 August 2021, Salna N., ZGCAT262.

Habitat: On dead wood.

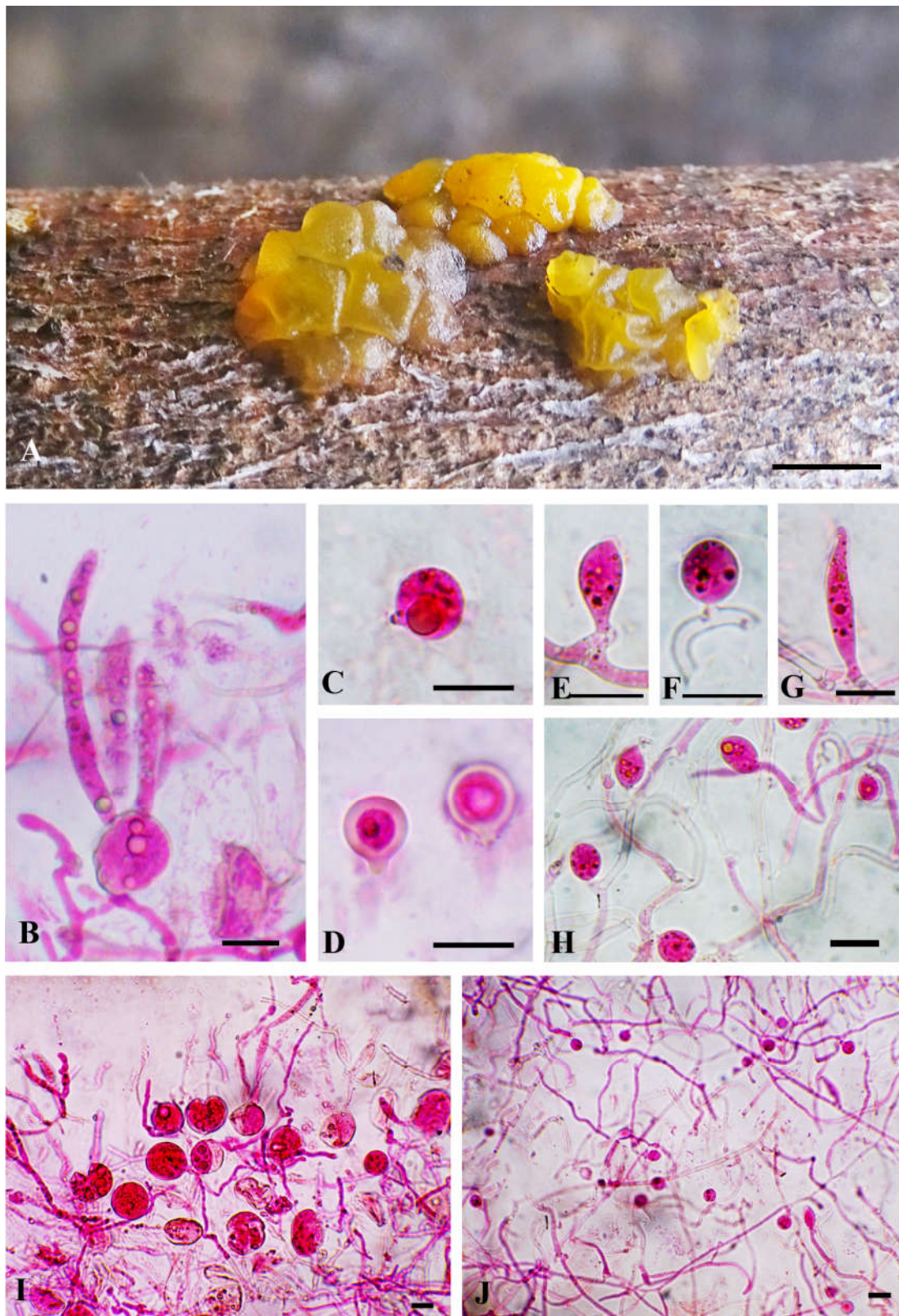


Figure 12: *Tremella* species 2- **A.** Basidiocarp; **B.** Basidia; **C&D.** Basidiospores; **E-H.** Terminal swollen cells; **I.** Hymenium; **J.** Tramal hyphae with swollen cells. Scale bars: A=10mm, B-J=10µm.

Comments: Absence of hyphidia, 18–24 × 22–24 µm wide basidia, 9.2–11 × 9.3–10.8 µm wide basidiospores and presence of swollen cells throughout the basidiocarp are the characteristic features of this *Tremella* species 2. Combination of morphological characters of this species do not match with those of the other described *Tremella* species.

The collection from Kerala (ZGCAT262), is morphologically similar to *T. mesenterica* and *T. mesenterella* Bandoni and Ginns with yellowish orange, gyrose basidiocarp and presence of swollen cells in trama, but differ by the absence of hyphidia. *Tremella armeniaca* Bandoni and J. Carranza and *T. dysenterica* Möller have yellowish orange basidiocarp without hyphidia in hymenium, but *T. armeniaca* have basidiocarp with hollow lobes, and compactly arranged phialide like conidiogenous cells, which is absent in this *Tremella* species 2 (Bandoni *et al.* 1996). *Tremella dysenterica* differs from ZGCAT262 in having irregularly lobed basidiocarp, smaller basidia and basidiospores (Basidia 11 × 7.5 µm; basidiospores 5–7 × 4–5 µm, from description by Roberts 2001) and by the absence of swollen cells.

Tremella laurisilvae Kout, in Kout, Quijada and Beltrán-Tejera, Phytotaxa 226: 77 (2015)

Figure 13

Basidiocarp 4–36 × 4–22 mm, gelatinous, foliose, lobed, hollow, caespitose, sessile, yellowish brown to amber brown when fresh, turning blackish brown when dry. More brownish towards base. Basidiocarp developing on ascocarp of unidentified fungus. Spore print white.

Hymenium pale yellow in water. **Hyphidia** absent. **Basidia** 12–16 × 9.5–11.5 µm, subglobose to globose, four celled, longitudinally septate, thin-walled, guttulate, pale yellow, with basal clamp-connections. **Epibasidia** 19–45 × 2–3 µm. **Basidiospores** 7–10.5 × 5.5–8 µm (Q = 1.15–1.45 µm, Qm = 1.27 µm),

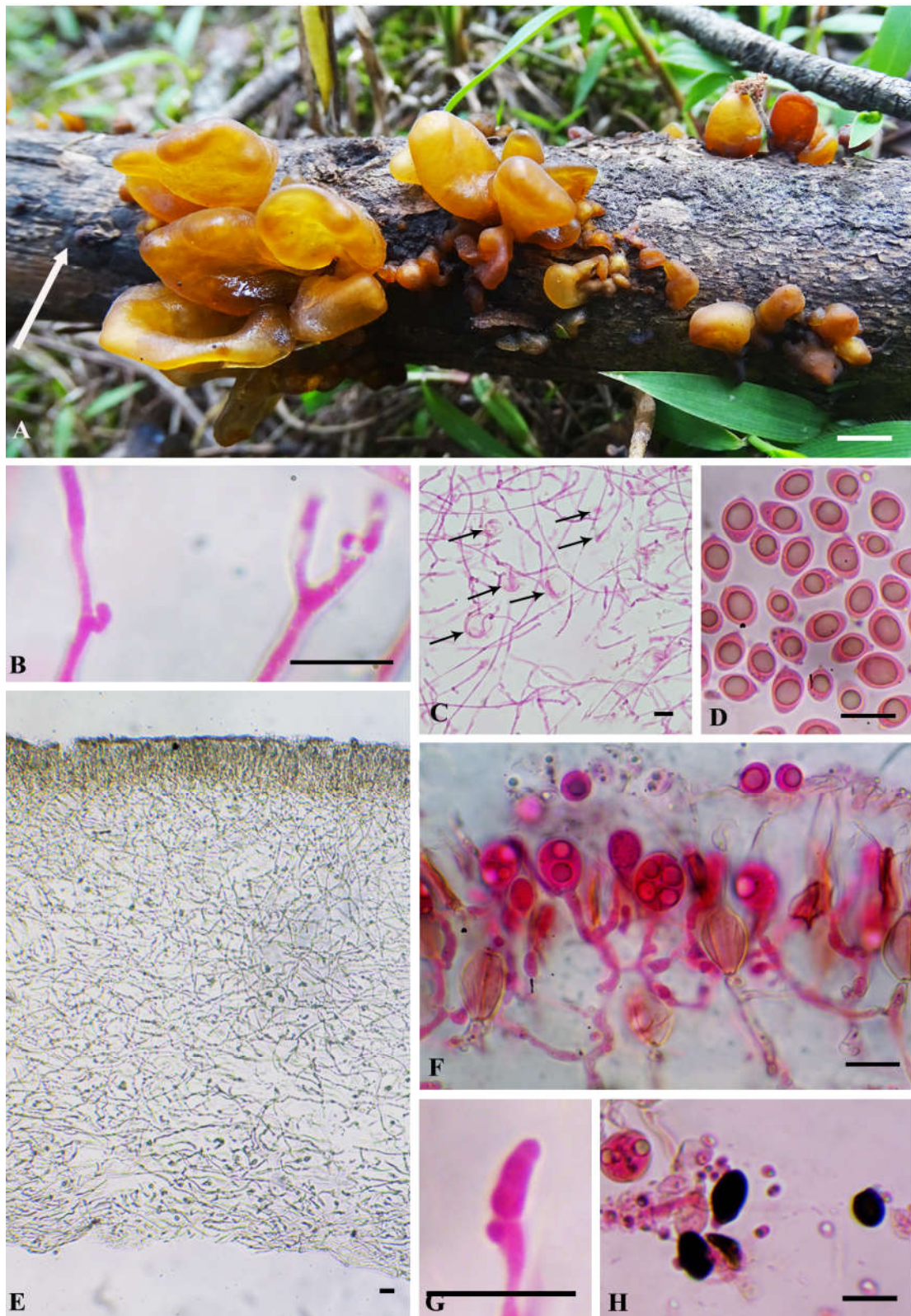


Figure 13: *Tremella laurisilvae*- **A.** Basidiocarp; **B.** Hyphae with clamp-connections; **C.** Inflated cells (arrow); **D.** Basidiospores; **E.** Cross section; **F.** Hymenium; **G.** Terminal swollen cell; **H.** Ascomycetous host spore. Scale bars: A=10mm, B-H=10µm.

subglobose, broadly ellipsoid to ovoid, hyaline, thin-walled, smooth, guttulate. Germinating by germ tube, repetition and yeast cell formation. Yeast cells 2.6–3 × 2.6–2.9 µm, subglobose to broadly ellipsoid. **Terminal swollen cells** present throughout the trama, 5.7–10 × 2.2–2.6 µm, cylindrical, thin-walled. **Inflated cells** 23–31 × 18–25 µm, thin-walled, subglobose to globose, broadly ellipsoid, present throughout the trama. **Tramal hyphae** thin- to slightly thick-walled, 2–4 µm wide, branched, smooth, guttulate, with normal and loop-like clamp-connections. **Haustoria** not observed.

Specimens examined: INDIA, Kerala State, Idukki District, Anamudi Shola National Park, 09 September 2021, Anjitha Thomas, ZGCAT271; ZGCAT275; ZGCAT276.

Habitat: On dead wood.

Comments: The present specimen fits with the original description of *T. laurisilvae* (Kout *et al.* 2015). Blackish brown colour of basidiocarp, lack of hyphidia in the hymenium, and presence of inflated cells in the trama are the characteristic features of this species. Although the original description has reported the presence of haustorial hyphae, haustoria has not been observed in the present collection. In the phylogenetic analysis, sequences of the Kerala collections (ZGCAT271, ZGCAT276) show similarity with the holotype sequences (Figure 54). This species is not reported from India till date.

Phaeotremella Rea

Basidiocarps may present or absent. If present, foliaceous with cespitose lobes, gelatinous, brown, tan, light brown when fresh and dark brownish to black when dry. Hyphae with clamp-connections. Haustoria with branched haustorial hyphae. Basidia subglobose to globose, ovoid or ellipsoid, longitudinally to diagonally or transversely septate, four-celled. Basidiospores subglobose to broadly ellipsoid. Budding cells develop when culturing.

Phaeotremella yunnanensis L.F. Fan, F. Wu and Y.C. Dai, in Yuan *et al.*, Fungal Diversity: 1-7, [245] (2020)

Figure 14

Basidiocarp 12–53 × 8–38 mm, firm gelatinous, cerebriform, hollow, sessile, brownish when fresh. Becoming darker when dry. Growing on the ascocarp of an unidentified fungus. **Spore print** whitish.

Hymenium pale brownish in water. **Hyphidia** absent. **Basidia** 17–23 × 9–15 µm, ovoid, ellipsoid to broadly ellipsoid, four celled, thin-walled, guttulate. **Epibasidia** clavate, up to 44 µm, swollen at tip up to 5 µm, easily detaching from basidia. **Basidiospores** 6–10 × 5.5–9 µm (Q = 1.09–1.42 µm, Qm = 1.19 µm) subglobose to broadly ellipsoid, hyaline, thin-walled, smooth, apiculate, guttulate. Secondary ballistospore formation and budding yeast cells are observed. **Vesicles** not observed. **Terminal swollen cells** present rarely in trama, 8–11 × 3–5 µm, cylindrical to clavate, thin-walled. **Tramal hyphae** 2–6.5 µm wide, slightly thick-walled, gelatinous, smooth, guttulate with clamp-connections. **Haustoria** not observed.

Specimens examined: INDIA. Kerala State, Kozhikode District, Poilkave sacred grove, 01 August 2018, Anjitha Thomas, ZGCAT18; INDIA. Kerala State, Kozhikode District, Kakkavayal, 28 August 2018, Anjitha Thomas, ZGCAT24; INDIA. Kerala State, Kozhikode District, Vanaparvam Biopark, 28 May 2019, Anjitha Thomas, ZGCAT49; INDIA. Kerala State, Kannur District, Aralam Wildlife Sanctuary, 29 June 2019, Anjitha Thomas, ZGCAT72; INDIA. Kerala State, Ernakulam District, Iringole Kavu, 17 July 2019, Anjitha Thomas, ZGCAT110; INDIA. Kerala State, Kozhikode District, Thottil Palam, 5 August 2019, Salna N., ZGCAT120; INDIA. Kerala State, Palakkad District, Silent Valley National Park, 24 October 2019, Anjitha Thomas, ZGCAT186; INDIA. Kerala State, Kozhikode District, The Zamorins Guruvayurappan College campus, 10 July 2021, Anjitha Thomas, ZGCAT240; INDIA. Kerala State, Thrissur District, Chimmini Wildlife Sanctuary, 26 July 2021, Salna N., ZGCAT247; INDIA. Kerala State, Kozhikode District, Iringannur, 26 June 2023, Karthika, ZGCAT350.

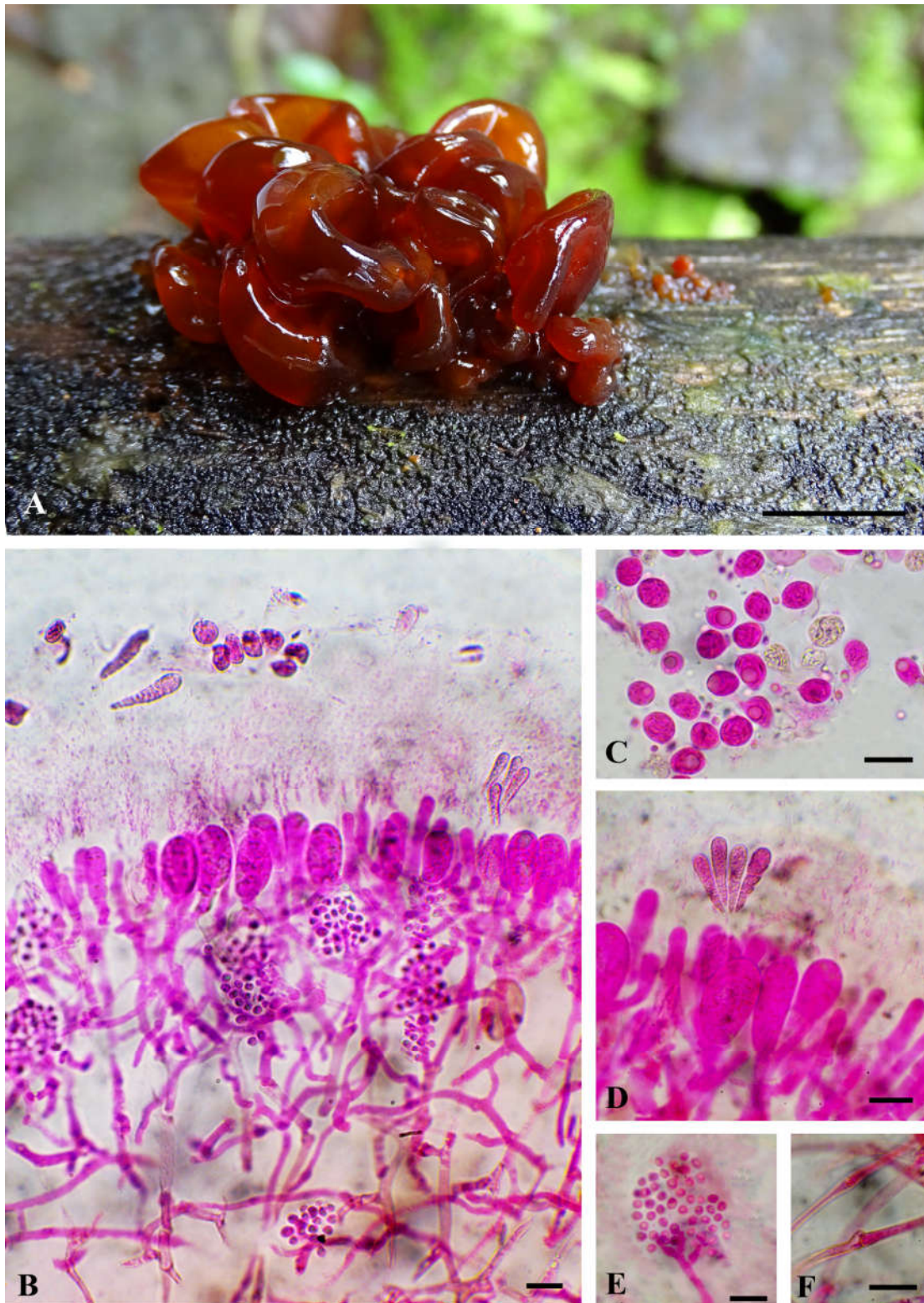


Figure 14: *Phaeotremella yunnanensis*- Basidiocarp; **B.** Hymenium with basidia, epibasidia, basidiospores, tramal hyphae and conidiospores; **C.** Basidiospores; **D.** Basidia with four epibasidia; **E.** Conidiophores and conidia; **F.** Hyphae with clamp-connection. Scale bars: A=10mm, B-E=10 μ m.

Habitat: On dead wood.

Comments: *Phaeotremella yunnanensis* has foliaceous, brownish, sessile, lobed nature with absence of clamp-connection, vesicles and hyphidia. Presence of spherical to ovoid, thick-walled conidia in the hymenial region is a characteristic feature of *P. yunnanensis*. *Phaeotremella yunnanensis* is widely distributed in the Kerala State. Information regarding the identity of host organism is absent in the holotype description (Yuan *et al.* 2020). All the collected specimens in this study are associated with a blackish Ascomycete. This species is not reported from India till date.

Tremella seclusa Cazenave and G. Gruhn, in Gruhn and Cazenave, Bulletin de la Société mycologique de France 138: 37-68 (2022)

Figure 15

Basidiocarp 12–33 × 5–8 mm, gelatinous to cartilaginous, cerebriform, hollow, sessile, broadly attached to the substratum, brownish black when fresh. Black when dry. Host association is not observed. Spore print not obtained.

Hymenium brownish in water. **Hyphidia** 2–4 µm wide, cylindrical, branched, septate, with clamp-connections, gelatinous, frequently agglutinates together and extending beyond basidial level. **Basidia** 23–36 × 28–40 µm, subglobose to globose, four celled, oblique or longitudinally septate, thin-walled, guttulate, brownish, with basal clamp-connections. **Epibasidia** 100–180 × 2–4 µm. **Basidiospores** 11–15.5 × 11–15 µm (Q = 1–1.03 µm, Qm = 1.004 µm) globose, hyaline, thin-walled, smooth, apiculate, guttulate. Direct germination observed. **Terminal swollen cells** present in hymenium, 16–18 × 4.7–7.1 µm, broadly fusiform, oblong, thin- to slightly thick-walled. **Tramal hyphae**, 2–6 µm wide, inflates up to 8 µm, thick-walled, branched, gelatinous, smooth, guttulate with clamp-connections. **Haustoria** present, haustorial hyphae branched, one to four haustorial hyphae from a cell.

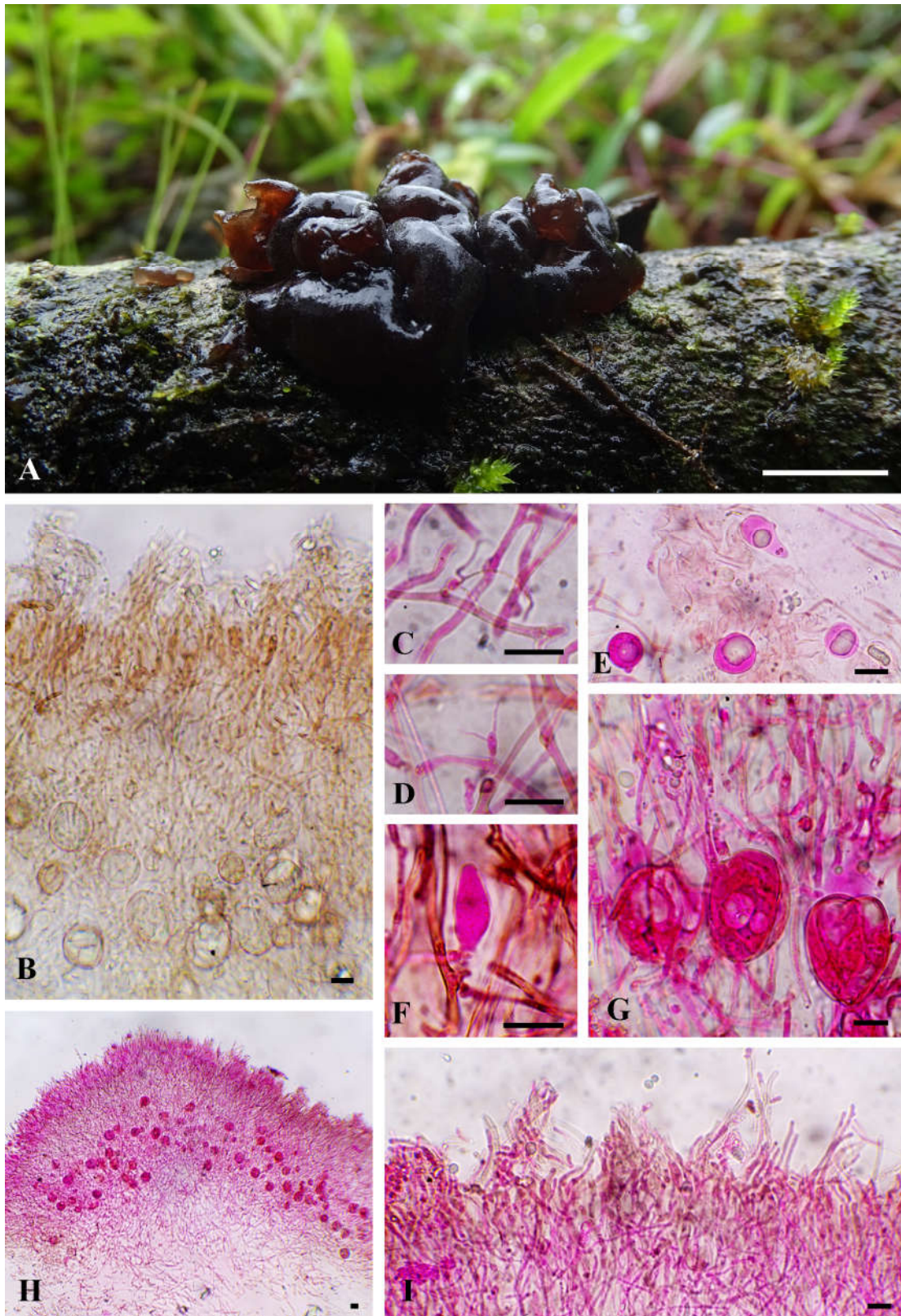


Figure 15: *Tremella seclusa*- **A.** Basidiocarp; **B&H.** Cross section showing basidia and hyphidia; **C&D.** Branched haustoria; **E.** Basidiospores; **F.** Terminal swollen cell in hymenium; **G.** Basidia; **I.** Hyphidia. A=10mm, B-I=10µm.

Specimen examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 24 October 2019, Anjitha Thomas, ZGCAT183.

Habitat: On decaying wood log of *Litsea floribunda* (Bl.) Gamble.

Comments: A wide hyphidial layer (extending up to 180 μm beyond the basia), presence of prominent clamp-connections, and terminal swollen cells in the subhymenium are the characteristic features of the Kerala collections. Interestingly, the presence of hyphidia was not noted in the original description of *T. seclusa* (Gruhn and Cazenave 2022), although hyphidia are noticeable in the photographic plate (Figure. 1 of Gruhn and Cazenave (2022)) available with the original description. Basidia and basidiospores of this specimen are relatively larger than those given in the type description. Type description has 20–26 \times 17–22 μm wide basidia and 9–11.5 \times 8–10 μm wide basidiospores, whereas; the Kerala specimen has 23–36 \times 28–40 μm wide basidia and 11–15.5 \times 11–15 μm wide basidiospores. Although these two specimens have above mentioned morphological differences, similarity in the molecular data (ITS and LSU), confirmed its identity as *T. seclusa*.

Tremella coalescens L.S. Olive is morphologically similar with *T. seclusa* in having blackish brown to cinnamon brown basidiocarp, abundance of hyphidia, globose to ellipsoid basidia (24–40 \times 24–29 μm) and globose to broadly ellipsoid basidiospores (10–18.5 \times 11–16.5 μm) (Chen 1998). But, *T. seclusa* have terminal swollen cells in subhymenium, which is not reported in *T. coalescens* (Olive 1951, Chen 1998, Bandoni and Boekhout 2011), and *T. seclusa* have longer hyphidia (110–125 μm in length), where *T. coalescens* have shorter hyphidia (less than 30 μm in length) (Chen 1998). *Tremella coalescens* have inconspicuous clamp-connections in the tramal hyphae (Olive 1951) whereas, *T. seclusa* have prominent and sometimes looped clamp-connections. *Tremella coffeicola* (Berk.) P. Roberts, *T. indecorata* Sommerf. and *T. laurisilvae* have blackish brown basidiocarp similar to *T. seclusa*. Hyphidia are not described in *T. coffeicola*, *T. indecorata* and *T. laurisilvae* (Roberts and Spooner 2004, Pippola and Kotiranta 2008, Kout *et al.* 2015).

Molecular sequences from the type specimen of *T. seclusa* (ITS-MZ868642, LSU-MZ868641) and sequence from the Kerala collection are phylogenetically similar. This species is originally reported from France (Gruhn and Cazenave 2022) and this is the Asian record of *T. seclusa*.

Tremella armeniaca Bandoni and J. Carranza, in Bandoni, Carranza and Bandoni, *Revista de Biología Tropical* 44: 16 (1997) [1996]

Figure 16

Basidiocarp 31–60 × 10–40 mm, gelatinous to cartilaginous, cerebriform to foliose, sessile, broadly attached to the substratum, shades of white, yellow, orange and red present in the same basidiocarp when fresh. Orangish red when dry. Host is not observed. Spore print not obtained.

Hymenium pale yellow in water. **Hyphidia** 20–38 × 2–4 µm wide, septate, rarely branched, thick-walled, with clamp-connections. **Basidia** 14–22 × 6–8.5 µm, subcylindrical, ellipsoid to obovoid, two to four celled, oblique or longitudinally septate, thin-walled, guttulate. New basidia emerge from the lower basidial branches. **Basidiospores** 5.5–7.0 × 4.0–5.0 µm (Q = 1.2–1.7 µm, Qm = 1.48 µm), subglobose to broadly ellipsoid, thin-walled, smooth, apiculate, guttulate. Yeast cells 1.2–4.5 × 1–2.5 µm, subglobose, broadly ellipsoid to ellipsoid, oblong, thin-walled. **Conidia** 2.0–4.5 × 1.5–3 µm, broadly ellipsoid to ellipsoid, guttulate, thin-walled. Conidiogenous cells lageniform, with multiple spores arising from the tip. **Tramal hyphae** 2.5–5 µm wide, thick-walled, branched, gelatinised, guttulate, with clamp-connections. **Haustoria** not observed.

Specimen examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 23 October 2019, Anjitha Thomas, ZGCAT180.

Habitat: On dead wood.

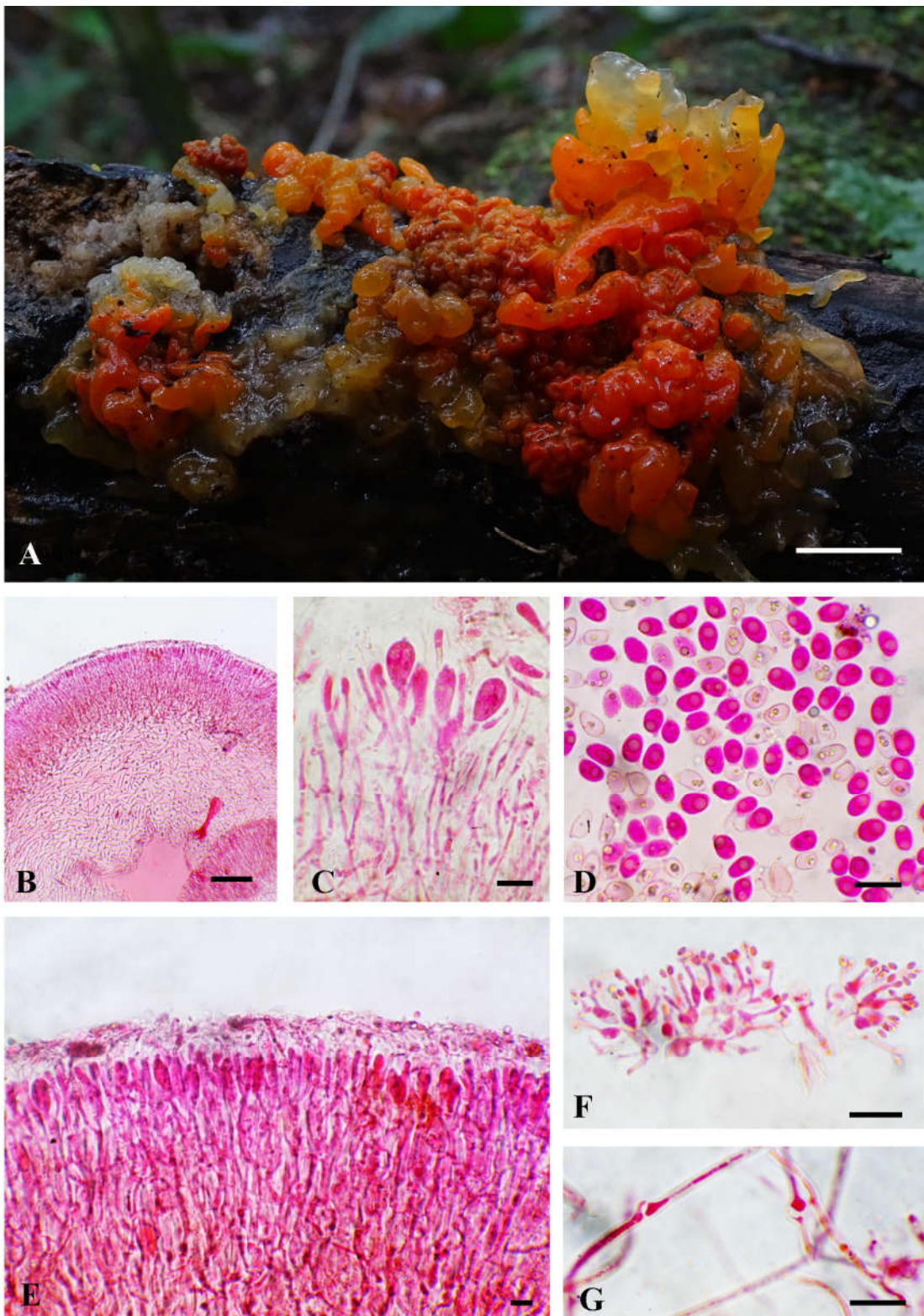


Figure 16: *Tremella armeniaca*- **A.** Basidiocarp; **B.** Cross-section of basidiocarp; **C.** Hymenium with basidia, hyphidia and basidioles; **D.** Basidiospores; **E.** Hymenium; **F.** Conidiophores and conidia; **G.** Tramal hyphae with clamp-connections. Scale bars. A=10mm, B=100µm, C-G=10µm.

Comments: The Kerala collections agree with the characters given in the original description (Bandoni *et al.* 1996) of *T. armeniaca*. However, basidiocarp of the Kerala collection is relatively larger. Presence of hyphidia, and production of multiple spores from the apical processes of lageniform conidiophores are characters that are observed in the Kerala collections, but not mentioned in the original description by Bandoni *et al.* (1996). Kerala collection did not yield molecular sequences even after repeated attempts. There are no records of this species from India till date.

Tremella sairandhriana A. Thomas and T.K.A. Kumar, in Liu *et al.*, Fungal Diversity 124: 196 (2024)

Figure 17

Basidiocarp 10–45 × 1.5–3.5 mm, soft gelatinous, resupinate, cerebriform, sessile, broadly attached, easy to separate from the substratum, margin sometimes wavy, white to pale yellowish white when fresh and pale yellowish brown when dry. Spore print whitish.

Hymenium pale brown in water. **Hyphidia** 3–7 µm, branched, septate, thick-walled, with clamp-connections. **Basidia** 27–35 × 26–27.5 µm, subglobose to globose, two to four celled, longitudinally, transversely (rare), or obliquely septate, thin-walled, guttulate, hyaline, with basal clamp-connections. **Epibasidia** 59–96 × 6.5–9 µm, sometimes with swollen tip (up to 11 µm), septate, branched, occasionally producing conidia. **Conidia** from epibasidia 3–7 × 3–7 µm, globose, hyaline, smooth, thin-walled. **Basidiospores** 16–19 × 17–20 µm (Q = 0.84–1 µm, Qm = 0.956 µm), subglobose to globose, hyaline, thin-walled, smooth, guttulate, apiculate. Secondary spore production, and yeast cell formation from basidiospores observed. **Yeast cells** 3–7 × 3–7 µm, globose, subglobose, broadly ellipsoid. **Vesicles** 10.5–13 × 5.9–7.8 µm, ellipsoid, oval, thick-walled. Swollen cells absent. **Tramal hyphae** 2–5.5 µm wide, slightly thick- to thick-walled, branched, smooth, hyaline, frequently anastomosing, with clamp-connections. **Haustoria** abundant on hyphidia and subhymenium, rarely branched, with basal clamp-connections, sometimes with forked tip.

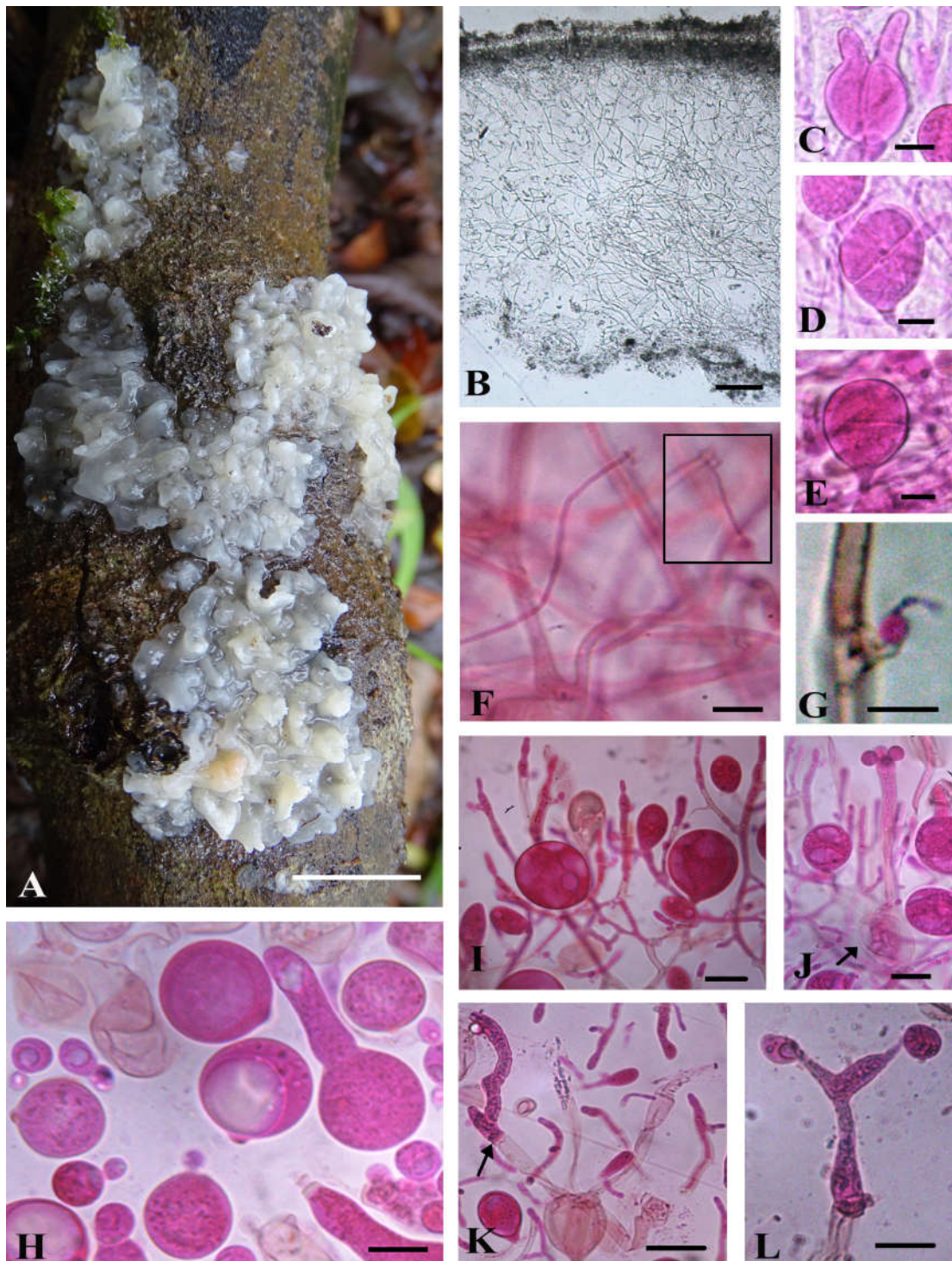


Figure 17: *Tremella sairandhriana*- **A.** Basidiocarp; **B.** Cross section mounted in water; **C-E.** Different septations in mature basidia; **F.** Trametal hyphae; insight showing haustorial cell and its hyphae attached to host hyphae; **G.** Haustoria; **H.** Basidiospores, budding and germination via germ tube; **I.** Hyphidia with basidia of different developmental stages; **J.** Collapsed basidia (arrow) and conidia from its epibasidia; **K.** Septate epibasidia (arrow); **L.** Bifurcating sterigmata bearing basidiospores. Scale bars: A=10mm, B=100µm, C-L=10µm.

Specimens examined: INDIA, State, Palakkad District, Silent Valley National Park, 04 July 2019, Anjitha Thomas, ZGCAT89.

Habitat: On dead wood.

Comments: *Tremella sairandhriana* was originally described by Thomas and Kumar from Kerala (Liu *et al.* 2024). *Tremella sairandhriana* is characterised by whitish, resupinate basidiocarp, presence of hyphidia, subglobose to globose basidia, formation of conidia from epibasidia, and rarely branched haustoria. Among the whitish *Tremella* members, *T. sairandhriana* show close similarity to *T. resupinata* in the resupinate nature of basidiocarp and larger size of basidia and basidiospores. But *T. sairandhriana* differs from *resupinata* in the following characters; relatively large basidiocarp, branched, septate, thick-walled, clamped hyphidia, and conidial formation from epibasidia. *Tremella cheejenii* Xin Zhan Liu and F.Y. Bai has similarity with *T. sairandhriana* in its whitish cerebriform basidiocarp, and formation of conidia from epibasidia. But *T. cheejenii* has smaller basidiospores (5–10 µm) when compared to *T. sairandhriana*. *Tremella latispora* F. Wu, L.F. Fan and Y.C. Dai also have whitish basidiocarp and are similar in morphology with *T. sairandhriana*. *Tremella latispora* differs by their smaller basidia (17.2–24.0 µm, Fan *et al.* 2021b) and basidiospores (10.1–11.8 µm Fan *et al.* 2021b).

In the molecular phylogenetic analysis, *T. sairandhriana* is clustering with *T. resupinata* (Figure 53) together forming a sister clade to the *T. fibulifera* Möller complex of Fan *et al.* (2021b). Members of *T. fibulifera* complex are morphologically characterised by cerebriform whitish basidioma and abundant clamp-connections (Fan *et al.* 2021b). The resupinate nature of basidiocarp, and the larger sized basidia and basidiospores of *T. sairandhriana* and *T. resupinata* segregate them from the *T. fibulifera* complex.

Tremella mesenterica Retz., K. svenska Vetensk-Akad. Handl., ser. 1 30: 249 (1769)

synonym:

Oncomyces mesentericus (Retz.) Klotzsch, [as 'mesenterica'] Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur., Suppl. 1 19: 240 (1843)

Figure 18

Basidiocarp 14–22 × 6–11 mm, firm gelatinous, foliose, yellow when fresh and orangish yellow when dry. Host not observed. Spore print not obtained.

Hymenium pale yellow in water. **Hyphidia** thin- to slightly thick-walled, branched, septate, with clamp-connections. **Basidia** 17–22 × 16–21 µm, subglobose to globose, two to four celled, longitudinally or obliquely septate, thin-walled, guttulate, hyaline. **Epibasidia** 29–99 × 3.7–4.9 µm, sometimes branched, guttulate, thin-walled, conidia formation from epibasidia, sometimes with swollen tip. **Basidiospores** 7.5–11 × 7.5–10.5 µm (Q = 1.0–1.12 µm, Qm = 1.04 µm), subglobose to globose, hyaline, thin-walled, smooth, guttulate, apiculate. Germinating by direct germ tube formation. **Vesicles** 17–20 × 16–20 µm, subglobose to globose, ovoid as catenulate chains, thick-walled, gelatinised. **Inflated cells** 6–25 × 5–24 µm, present throughout the basidiocarp, abundant above basidial level in the hymenium, globose, subglobose, oval, lemoniform to lanceolate, thin-walled, with clamp-connections. **Tramal hyphae** 2–3.5 µm wide, thick-walled, branched, smooth, hyaline, gelatinous, with normal and loop-like clamp-connections. **Haustoria** branched, more than three hyphae from a haustorial cell, present in tramal hyphae and hyphidia.

Specimens examined: INDIA, Kerala State, Kollam District, Thenmala, 19 September 2019, Anjitha Thomas, ZGCAT139; Waynad District, Kuruva islets, 13 October 2021, Salna N., ZGCAT294.

Habitat: On dead wood.

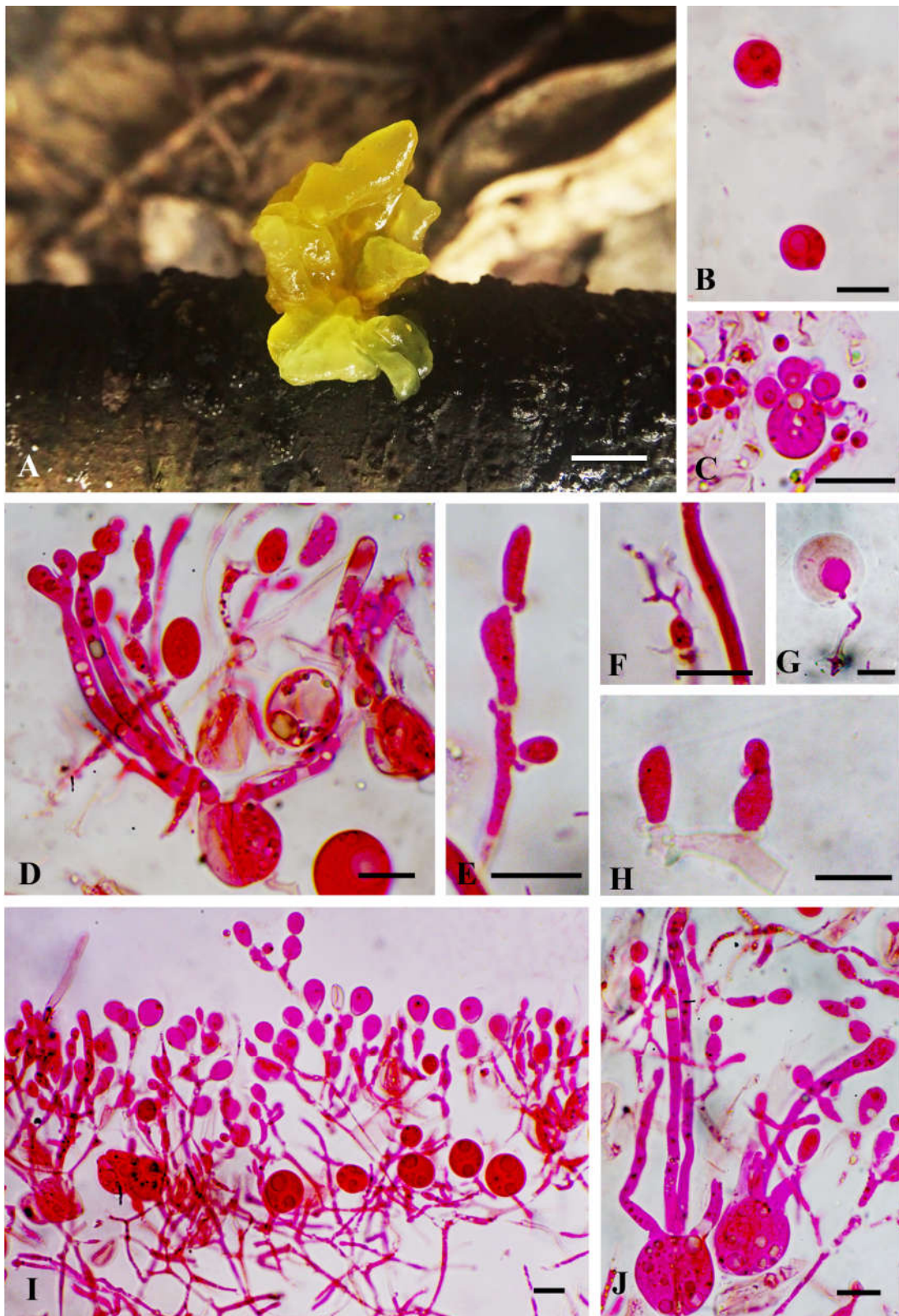


Figure 18: *Tremella mesenterica*- **A.** Basidiocarp; **B.** Basidiospores; **C.** Budding basidiospore; **D&J.** Basidia with sterigma; **E.** Hyphidia; **F.** Haustoria; **G.** Vesicle; **H.** Swollen cells; **I.** Hymenium with inflated cells. Scale bars: A=10mm, B-J=10µm.

Comments: *Tremella mesenterica* is characterised by cerebriform to foliose yellowish basidiocarp, presence of hyphidia, inflated cells in the hymenium, subglobose to globose basidia and basidiospore and presence of thick-walled vesicles (Roberts 1995, Chen 1998, Pippola and Kotiranta 2008).

Kerala collections are morphologically similar to *T. tropica* by the presence of inflated cells along with basidia in the hymenium, but vesicles are not reported in the type description of *T. tropica*. All collections, including the Kerala collections of *T. mesenterica* have vesicles in the hymenium and trama. In the phylogenetic analysis, sequence generated in the study (ZGCAT139=PP179305) cluster with other *T. mesenterca* with 95% support value. Mohanan (2011) has previously reported this species from Kerala State.

Tremella erythrina Xin Zhan Liu and F.Y. Bai, in Zhao, Liu and Bai, MycoKeys 47: 84 (2019)

Figure 19

Basidiocarp 6–27 × 4–6 mm, gelatinous, cerebriform, hollow, sessile, broadly attached to the substratum, yellow, yellowish orange to orange when fresh. Orangish when dry. Host is not observed. Spore print not obtained.

Hymenium pale yellow to brownish yellow in water. **Hyphidia** 2–6 µm wide, septate, branched, slightly thick-walled with clamp-connections. **Basidia** 13–16.5 × 10.5–14 µm, globose, subglobose, broadly ellipsoid to ellipsoid, two to four celled, oblique or longitudinally septate, thin-walled, guttulate, pale yellow, with basal clamp-connection. **Epibasidia** 14–31 × 1.7–3.5 µm. **Basidiospores** 6.5–8 × 5.5–8 µm (Q = 0.90–1.44 µm, Qm = 1.17 µm), subglobose to broadly ellipsoid, pale yellow, thin-walled, smooth, apiculate, guttulate. Secondary spore production and yeast cell formation observed. Yeast cells 2–3 × 1–2 µm, broadly ellipsoid to ellipsoid, thin-walled, guttulate. **Conidia** 2–3 × 1–1.5 µm, broadly ellipsoid to ellipsoid, guttulate, thin-walled. **Tramal hyphae** 2.5–5 µm wide, slightly thick- to thick-walled, branched, smooth and roughened, guttulate, with clamp-connections. **Haustoria** not observed.

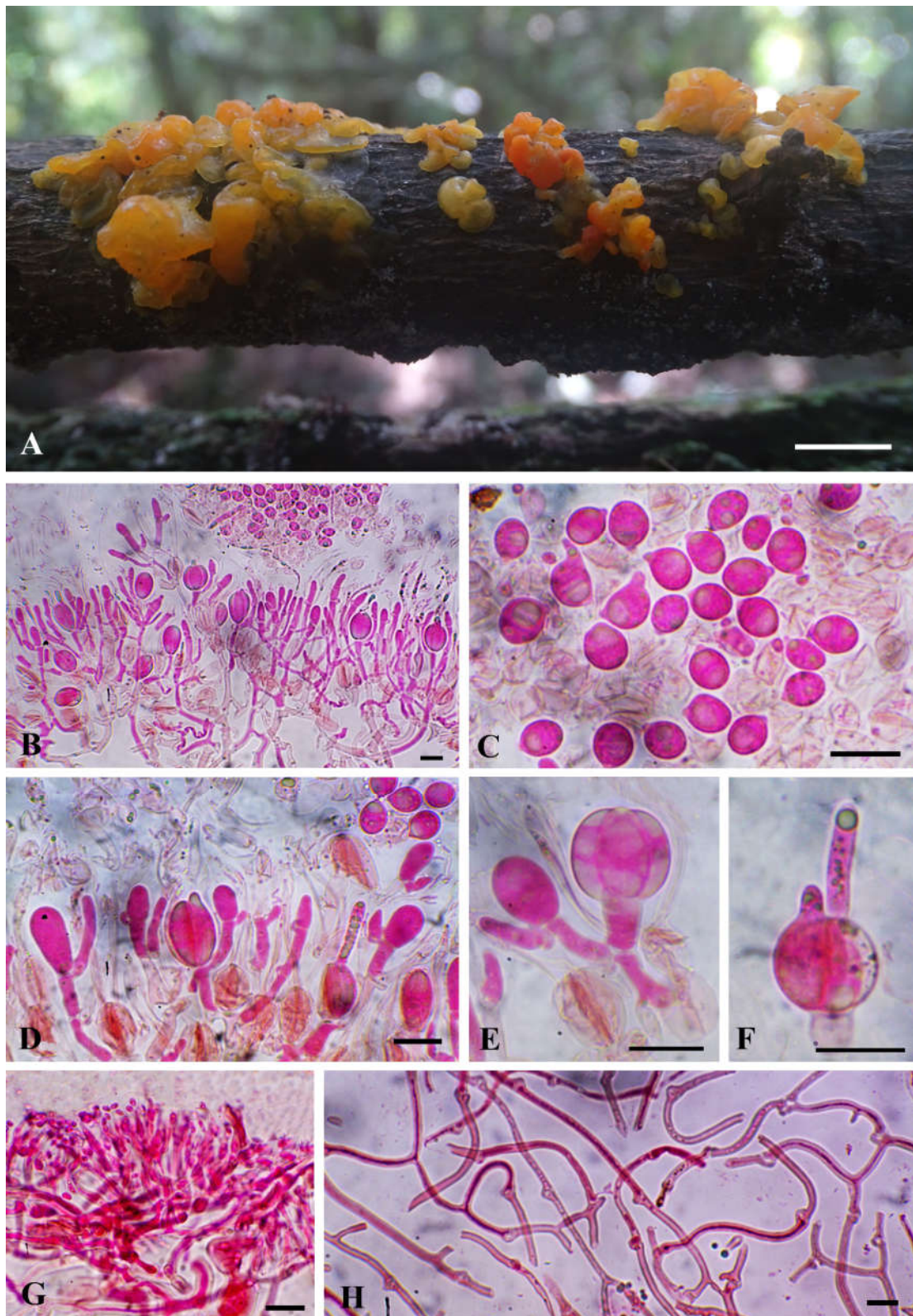


Figure 19: *Tremella erythrina*- **A.** Basidiocarp; **B.** Hymenium with basidia and hyphidia; **C.** Basidiospores; **D.** Basidia with basidioles and hyphidia; **E&F.** Basidia; **G.** Conidiophore with conidiospores; **H.** Tramal Hyphae. Scale bars: A=10mm, B-H=10µm.

Specimens examined: INDIA. Kerala State, Kozhikode District, Poilkave sacred grove, 1 August 2018, Anjitha Thomas, ZGCAT17; 12 April 2022, Anjitha Thomas, ZGCAT305; Palakkad District, Parambikulam Tiger Reserve, 12 June 2022, Anjitha Thomas, ZGCAT314.

Habitat: On dead wood.

Comments: Morphological and morphological data (Figure 54) support the placement of the Kerala collections as *T. erythrina*. The type specimen of *T. erythrina* has slightly larger basidiospores ($7\text{--}10 \times 5\text{--}7 \mu\text{m}$) and wider basidia ($12\text{--}18 \times 13\text{--}19 \mu\text{m}$). Also, conidia and conidiophores were not mentioned in the description by Zhao *et al.* (2019). *Tremella erythrina* differs from the closely related *T. samoensis* by the presence of hyphidia (see description of *T. samoensis* by Chen 1998). There are no records of this species from India till date.

Tremella taiwanensis Chee J. Chen, Bibliotheca Mycologica 174: 44 (1998)

Figure 20

Basidiocarp 5–13 × 6–18 mm, soft gelatinous, substipitate and pileate, cerebriform, caespitose, lobed, translucent, white when fresh becoming whitish when dry. Spore print whitish.

Hymenium hyaline in water. **Hyphidia** abundant, branched, septate, thin-walled, guttulate with clamp-connections. **Basidia** 18–31 × 18–29 μm , subglobose to globose, two to four celled, longitudinally or obliquely septate, thin-walled, guttulate, hyaline. **Epibasidia** 65–80 × 4.5–6.5 μm . **Basidiospores** 12–19 × 12–18 μm (Q = 0.90–1.06 μm , Qm = 0.96 μm), subglobose to globose, mostly dorsy-ventrally depressed, hyaline, thin-walled, smooth, guttulate, apiculate. Secondary spore production, and yeast cell formation from basidiospores observed. Yeast cells 3–7 × 3–7 μm , globose, subglobose, broadly ellipsoid. **Tramal hyphae** 3–7 μm wide, thick-walled, branched, smooth, hyaline, frequently anastomosing, gelatinous, with clamp-connections. **Haustoria** not observed.



Figure 20: *Tremella taiwanensis*- **A.** Basidiomata; **B.** Hymenium with basidia and hyphidia; **C.** Basidiospores with budding and direct germination; **D.** Hyphidia; **E.** Basidia; **F.** Trametal hyphae. Scale bars: A=10mm, B-F=10µm.

Specimen examined: INDIA. Kerala State, Malappuram District, University of Calicut campus, 16 June 2022, Anjitha Thomas, ZGCAT316; Kozhikode District, Kakkad, 13 December 2023, Anjitha Thomas, ZGCAT356.

Habitat: On dead wood.

Comment: Morpho-molecular data identify the Kerala collection as *T. taiwanensis*. According to Chen (1998), monokaryotic conidia were present on the apex of epibasidia, side of epibasidia, and on basidia. However, these were not observed in the Kerala specimen. In addition, Chen (1998) observed hyphidia rarely in his specimen, but Kerala specimen has abundant hyphidia in the hymenium.

In the phylogenetic tree, the ITS sequence of the present collection clustered along other *T. taiwanensis* sequences with 97% bootstrap value (Figure 54). There are no records of this species from India till date.

***Tremella* species 3**

Figure 21

Basidiocarp 10–36 × 6–29 mm, firm gelatinous, gyrose to cerebriform, broadly attached to the substratum, bright orangish when fresh and dull white to dull yellow and when dry. Host not observed. Spore print not obtained.

Hymenium hyaline in water. **Hyphidia** 2–4.5 µm wide, branched, guttulate, abundant, septate, thin-walled with clamp-connections. **Basidia** 29–34 × 26–32 µm, subglobose to globose, two to four celled, longitudinally septate, thin-walled, guttulate, hyaline. **Epibasidia** 70–90 × 6–7 µm. **Basidiospores** 14–18 × 14–19 µm (Q = 0.83–1.13 µm, Qm = 0.95 µm), subglobose to globose, hyaline, thin-walled, smooth, guttulate, apiculate. Germinating by budding yeast cells and repetition. **Yeast cells** 5–8 × 5–8 µm, globose, thin-walled, guttulate. Tramal hyphae 2–5 µm wide, slightly thick- to

thick-walled, smooth, hyaline, gelatinous, with loop-like and normal clamp-connections. **Haustoria** rare, with basal clamp-connection. Haustorial hyphae branched, more than one hyphae from a haustorial cell.

Holotype: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 24 October 2019, Anjitha Thomas, ZGCAT195.

Habitat: On dead wood.

Specimen examined: INDIA, Kerala State, Malappuram District, University of Calicut campus, 16 July 2018, Anjitha Thomas, ZGCAT9; Kozhikode District, Kuttayadi, 14 October 2018, Anjitha Thomas, ZGCAT32.

Comment: *Tremella* species 3 is characterised by gyrose to cerebriform, orangish basidiocarp, thin-walled, branched abundant hyphidia with clamp-connections, and rare occurrence of haustoria with branched haustorial hyphae. *Tremella* species 3 is closely related to *T. cerebriformis*, *T. salmonea* Xin Zhan Liu and F.Y. Bai, *T. zhejiangensis* F. Wu, L.F. Fan and Y.C. Dai and *T. taiwanensis* based on the morphological and molecular data. *Tremella cerebriformis* has larger basidiospores (17–25 × 18–24 µm) compared to *T. species 3* (14–18 × 14–19 µm) (Chen 1998). *Tremella salmonea* has narrow tramal hyphae (2.0–3.5 µm wide), rare occurrence of hyphidia and haustoria with single hyphae (Zhao *et al.* 2019), whereas, the current specimen has wider tramal hyphae (2–5 µm wide), abundant occurrence of hyphidia and have haustoria with branched multiple haustorial hyphae. *Tremella* species 3 differs from *T. zhejiangensis* by the abundance of hyphidia, where *T. zhejiangensis* have occasional presence of non septate hyphidia (Fan *et al.* 2021b). *Tremella taiwanensis* is whitish yellow in colour, and have smaller basidia (21–31 × 20–27 µm) and producing monokaryotic conidia on the apex and sides of epibasidia, basidia and directly from basidia (Chen 1998). *Tremella* species 3 have orangish basidiocarp, larger basidia (29–34 × 26–32 µm) and the production of conidia from epibasidia or basidia have not been observed.

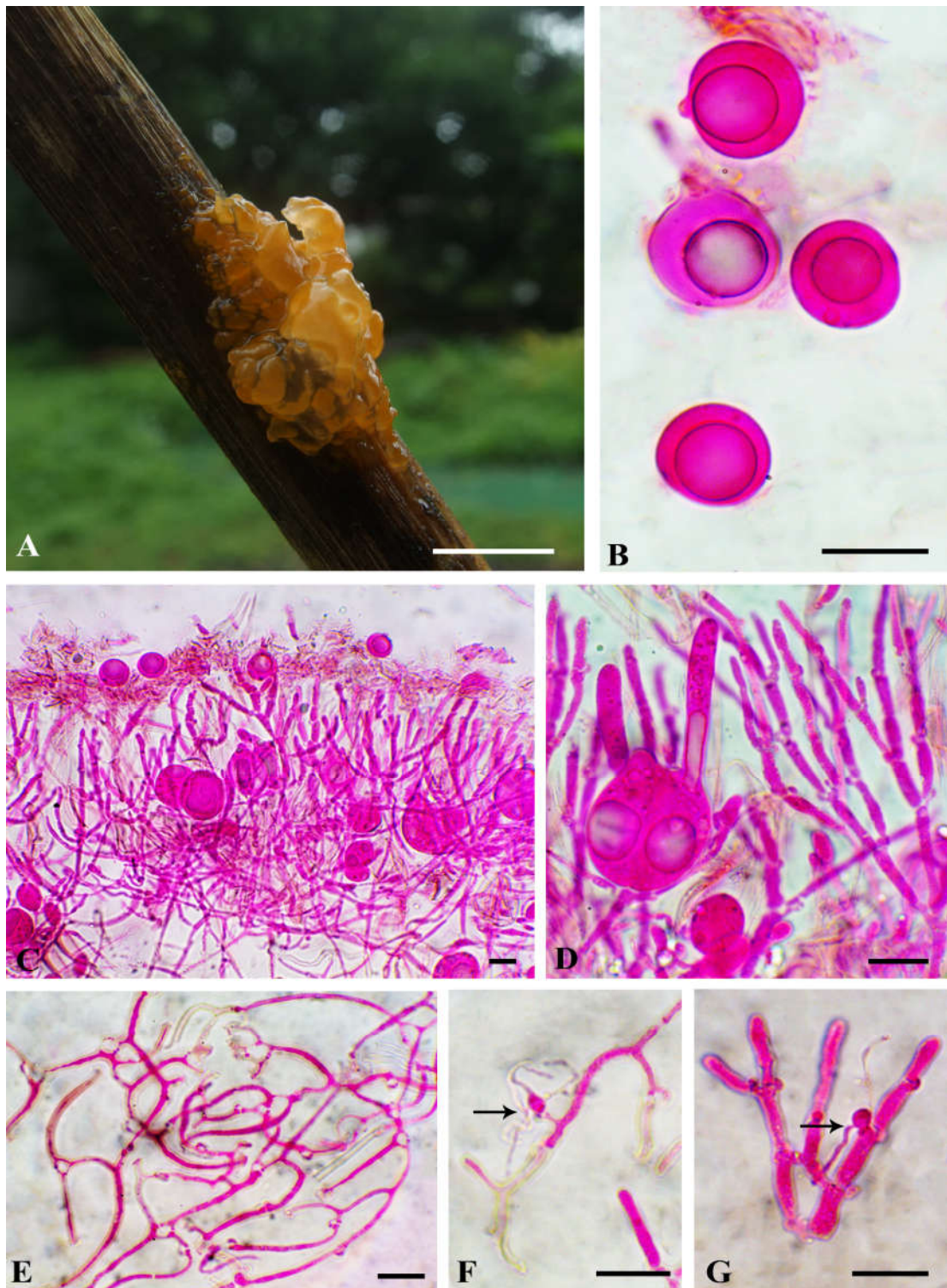


Figure 21: *Tremella* species 3- **A.** Basidiocarp; **B.** Basidiospores; **C.** Hymenium with basidia, hyphidia and basidiospores; **D.** Basidia with hyphidia; **E.** Tramal hyphae with clamp-connections; **F.** Branching, multiple haustorial hyphae from a haustorial cell in trama; **G.** Haustoria in hyphidia. Scale bars: A=10mm, B-G=10 μ m.

Phylogenetic analysis using molecular data also supports the novelty of *Tremella* species 3 (Figure 54). The sequences generated from holotype and additional collection formed a sister clade to *T. zhejiangensis* and *T. cerebriformis* with 98% bootstrap support value. In the phylogenetic tree, *Tremella* species 3 clustered with *mesenterica* group *sensu* Chen. According to Chen (1998), the *mesenterica* group is characterised by whitish yellow to orange, larger (more than 1 cm) basidiocarp, loose hymenial, subhymenial structure and presence of hyphidia in the hymenium. All these characters support the morphological and phylogenetic placement of *Tremella* species 3.

Unidentified taxa under Tremellales:

Cryptococcaceae taxon

Figure 22

Conidiomata 8–59 × 5–9 mm, soft gelatinous, cerebriform, coalescing together to form large masses, resupinate, whitish when fresh to pale brown when dry. Host is an unidentified ascocarp. Spore print not obtained.

Conidia emerging from sides of conidiophore. Conidia 6–9 × 4.5–5.5 μm (Q = 1.09–1.8 μm, Qm = 1.53 μm) subglobose to broadly ellipsoid, guttulate, thin-walled. **Tramal hyphae** 5–9 μm, thick-walled, branched, gelatinous with prominent clamp-connections.

Specimens examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 24 June 2022, Anjitha Thomas, ZGCAT323; ZGCAT324.

Habitat: On dead wood.

Comments: In the phylogenetic analysis, it is clear that the Kerala specimen belongs to Cryptococcaceae family. Cryptococcaceae consists of three genera: *Kwoniella*, *Cryptococcus*, and *Teunia* (Li *et al.* 2020). In *Teunia*, sexual

reproduction is not known and they produce cream to yellow mucoid colonies with budding cells. Ballistoconidia, pseudohyphae and hyphae are not formed in *Teunia* members (Li *et al.* 2020). Conidiomata and hyphae formation are not reported in any species of *Teunia*. The present species is morphologically distinct from other *Teunia* members by the presence of true hyphae and conidiomata. In phylogenetic analysis (Figure 54), *Teunia* members form a distinct clade from Cryptococcaceae taxon with 84% bootstrap value.

Kwoniella are characterised by the absence of basidiocarp, ballistoconidia, ballistospores and presence of different types of basidia, which may globose, ovoid, lageniform or navicular with longitudinal, transverse or oblique septa (Statzell-Tallman *et al.* 2008). *Kwoniella* species are saprobic in nature (Findley *et al.* 2009, Guerreiro *et al.* 2013, Liu *et al.* 2015b, Coelho *et al.* 2023). In the phylogenetic analysis using combined ITS-LSU regions, the present taxon deviates from the major clade of *Kwoniella* (clade of 7 *Kwoniella* species including the type species *Kwoniella mangrovensis* Statzell, Belloch and Fell). Along with Cryptococcaceae taxon, *K. shandongensis* R. Chen, Yuan M. Jiang and S.C. Wei ex M. Groenew. and Q.M. Wang and *K. newhampshirensis* K. Sylvester, Q.M. Wang and Hittinger also deviating from the major clade with 76% support value. Morphologically the present taxon differs from *Kwoniella*.

Basidiocarp formation is not reported in the genus *Cryptococcus*, whereas true hyphae may be present after mating. Cylindrical, spheropedunculate, slender basidia, and four chains of bacilliform to globose or obpyriform basidiospores are the characteristic feature of *Cryptococcus* (Liu *et al.* 2015b). Phylogenetically, the present taxon is distinct from *Cryptococcus*. Cryptococcaceae taxon should be studied further with additional collections and gene regions to confirm its taxonomic identity.

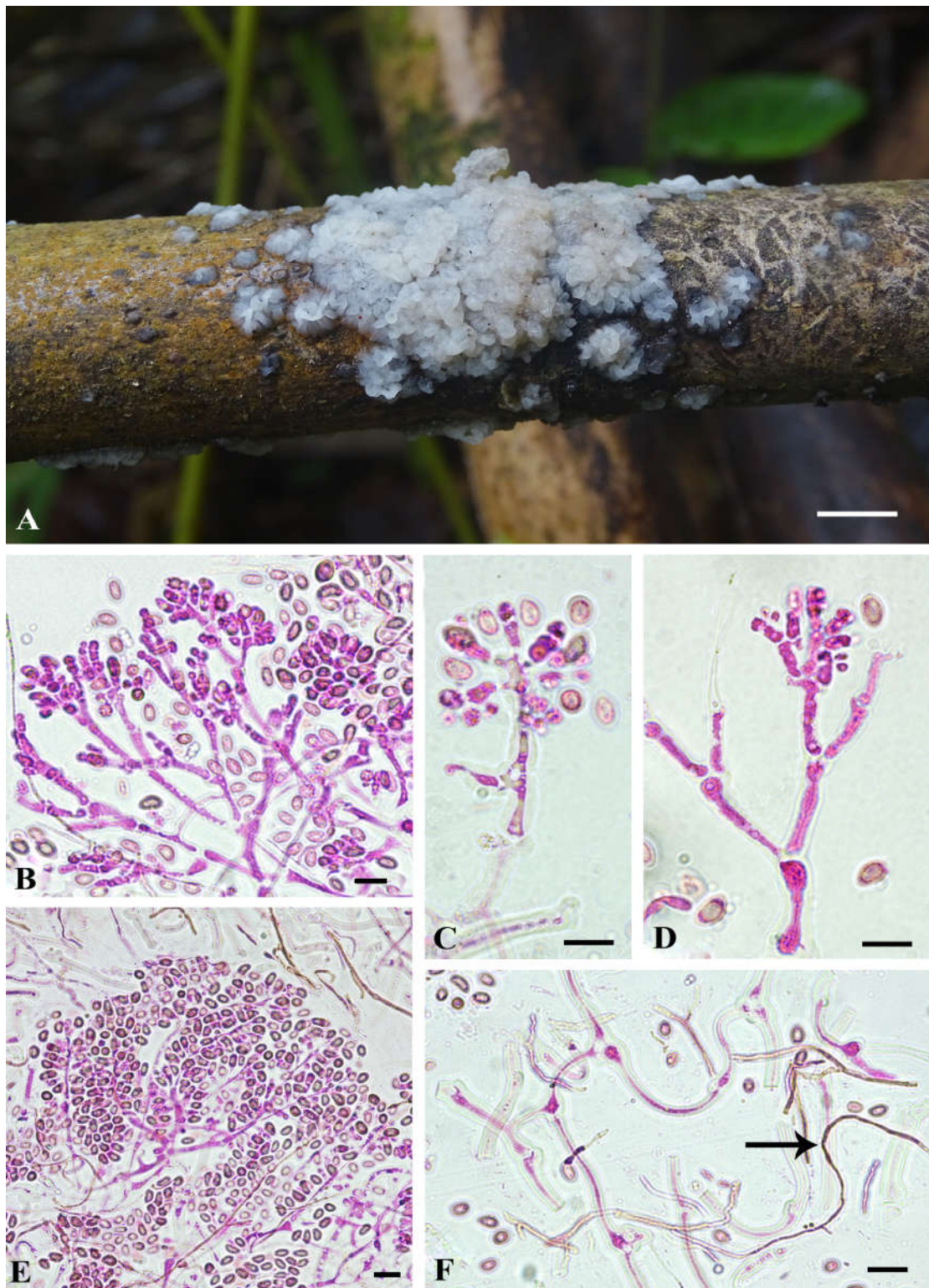


Figure 22: Cryptococcaceae taxon- **A.** Basidiocarp; **B-E.** Conidiophores and conidiospores; **F.** Tramal hyphae, conidiospores and suspecting host hyphae (arrow). Scale bars: A=10mm, B-F=10µm.

4.2.2. Taxonomic descriptions of Dacrymycetales

Calocera Fries

Basidiocarp erect, simple to branched, cylindrical, clavate, fusiform, spatulate. Branched or forked at tip, palmately lobed, with or without a sterile stipe. Firm gelatinous when fresh, drying to hard texture, pale yellow to golden yellow, hymenium amphigenous which covers one third of the total area, smooth or wrinkled. Hyphal composition homogenous, distinctly zonate. Central core zone of compactly packed parallel hyphae surrounded by a zone of loosely arranged hyphae (subhymenium) and outer hymenium consisting of basidia and hyphidia. Hyphidia cylindrical to clavate. Basidia forked and bifurcating, probasidia cylindrical to clavate. Basidiospores curved, cylindrical, elliptic to slightly allantoid, 1–3 septate, either directly germinate by forming a germ tube or forms conidia.

Calocera cornea (Batsch) Fr., Stirp. agri fensio. 5: 67 (1827) [1825-27]

Synonyms:

Calocera aculeiformis (Bull.) Chevall., Fl. gén. env. Paris (Paris) 1: 112 (1826)
Calocera cornea f. *gracilis* Kobayasi, Sci. Rep. Tokyo Bunrika Daig., Sect. B 4: 223 (1939)
Calocera cornea var. *minima* Coker, J. Elisha Mitchell scient. Soc. 35(3): 182 (1920) [1919]
Calocera cornea var. *subsimplex* Bres., in Schulzer, Hedwigia 24(4): 149 (1885)
Calocera cornes (Batsch) Fr., Stirp. agri fensio. 5: 67 (1827) [1825-27]
Calocera palmata (Schumach.) Fr., Epicr. syst. mycol. (Upsaliae): 581 (1838) [1836-1838]
Calocera striata (Hoffm.) Fr., Epicr. syst. mycol. (Upsaliae): 582 (1838) [1836-1838]
Clavaria aculeiformis Bull., Hist. Champ. Fr. (Paris) 1(1): 214 (1791)
Clavaria cincta (Pers.) Secretan, Mycogr. Suisse 3: 252 (1833)
Clavaria cornea Batsch, Elench. fung. (Halle): 139 (1783)
Clavaria cornea var. *aculeiformis* (Bull.) Pers., Syn. meth. fung. (Göttingen) 2: 596 (1801)
Clavaria cornea var. *cincta* Pers., Comm. fung. clav. (Lipsiae): 54 (1797)
Clavaria cornea var. *communis* Alb. and Schwein., Consp. fung. (Leipzig): 288 (1805)
Clavaria cornea var. *major* (O.F. Müll.) Pers., Syn. meth. fung. (Göttingen) 2: 596 (1801)
Clavaria cornea var. *striata* (Hoffm.) Pers., Syn. meth. fung. (Göttingen) 2: 596 (1801)
Clavaria major O.F. Müll., Schr. Ges. naturf. Freunde, Berlin 3: 351 (1777)
Clavaria medullaris Holmsk., Beata Ruris Otia FUNGIS DANICIS 1: 80 (1790)
Clavaria striata Hoffm., Deutschl. Fl., Zweiter Theil (Erlangen): tab. 7, fig. 1 (1796) [1795]
Corynoides cornea (Batsch) Gray, Nat. Arr. Brit. Pl. (London) 1: 654 (1821)
Tremella aculeiformis (Bull.) Pers., Mycol. eur. (Erlanga) 1: 106 (1822)
Tremella palmata Schumach., Enum. pl. (Kjbenhavn) 2: 442 (1803)

Figure 23

Basidiocarp 9–17 × 1–1.5 mm wide, firm gelatinous, stipitate, cylindrical, attenuate, rarely forked, sometimes branched, gregarious, discrete, yellow to orangish yellow when fresh, paler towards base, orangish when dry.

Basidiocarp organised in to three zones in transverse section. **Hymenium** amphigenous except towards the basal area, composed of basidia and hyphidia. **Hyphidia** 20–33 × 1.5–3 µm, cylindrical, unbranched, rarely septate, guttulate, thin- to slightly thick-walled. **Basidia** 14–24 × 3.5–4 µm, cylindrical to clavate, bifurcating, guttulate, thin- to slightly thick-walled. **Basidiospores** 7.5–9 × 3–4 µm (Q = 2–2.8 µm, Qm = 2.3 µm), ellipsoid, guttulate, apiculate, 0–1 septate, centrally constricted in septate spores, thin-walled. **Tramal hyphae** 2–4.5 µm, gelatinised, guttulate, smooth and roughened hyphae, thin- to slightly thick-walled, without clamp-connections. **Marginal hyphae** 120–140 µm wide, present in the sterile basal portion, compactly arranged, intertwined, cylindrical to irregularly shaped, branched, thick-walled, gelatinised, often with inflated tip.

Specimens examined: INDIA. Kerala State, Malappuram District, University of Calicut Campus, 16 July 2018, Anjitha Thomas, ZGCAT12; 30 September 2018, Anjitha Thomas, ZGCAT36; Kozhikode District, The Zamorin's Guruvayurappan College campus, 25 June 2019, Anjitha Thomas, ZGCAT55; ZGCAT56; Kannur District, Aralam, 28 June 2019, Anjitha Thomas, ZGCAT58; 29 June 2019, Anjitha Thomas, ZGCAT69; Kozhikode District, Kakkad, 9 August 2020, Anjitha Thomas, ZGCAT214; Malappuram District, Valluvassery, 13 January 2021, Anjitha Thomas, ZGCAT223; Kozhikode District, The Zamorin's Guruvayurappan College campus, 5 January 2021, Anjitha Thomas, ZGCAT229; Thiruvananthapuram District, Ammayambalam, 2 October 2021, Anjitha Thomas, ZGCAT287.

Habitat: On dead wood.

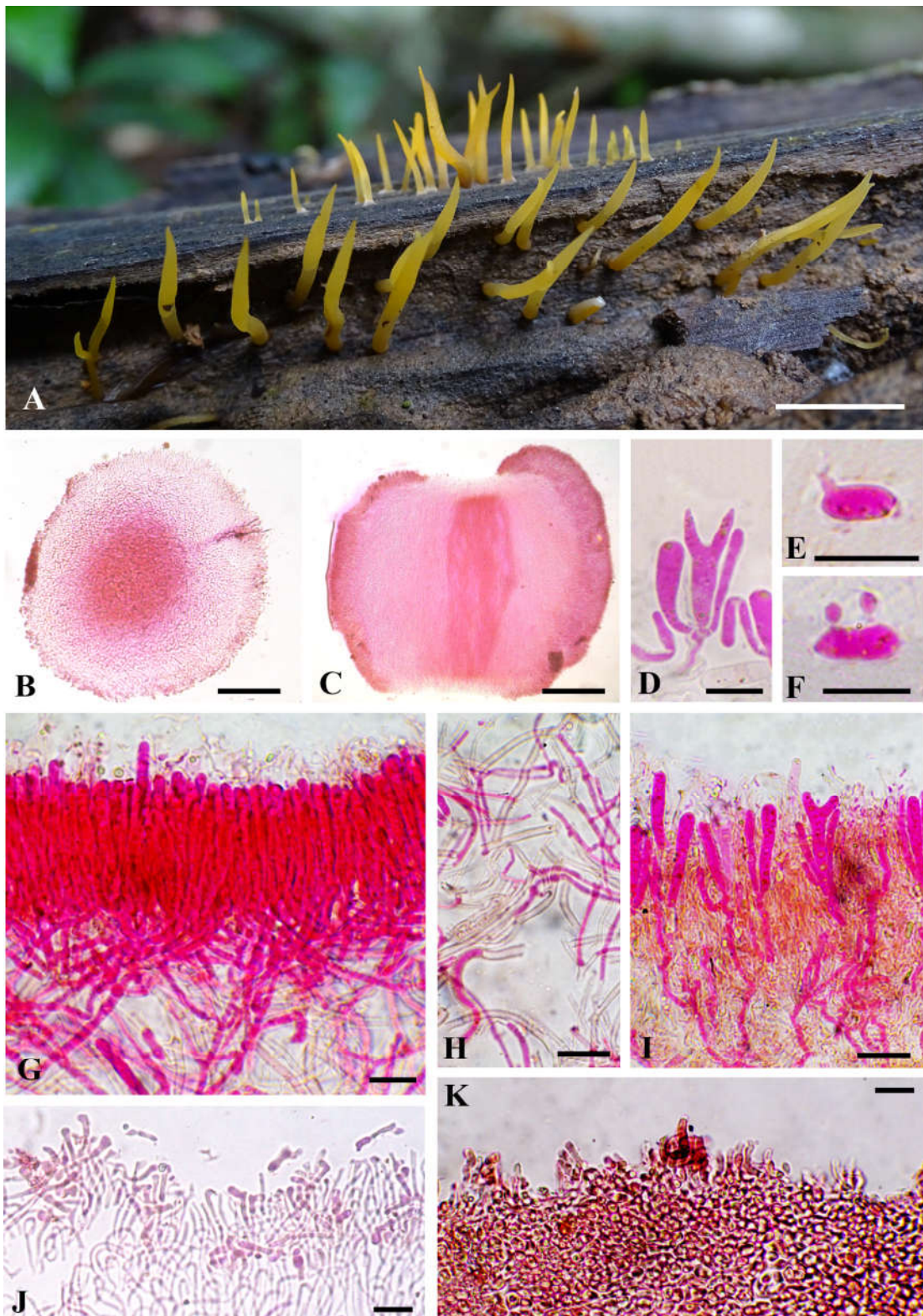


Figure 23: *Calocera cornea*- **A.** Basidiocarp; **B.** Cross-section of basidiocarp; **C.** Longitudinal section of basidiocarp; **D.** Basidia; **E&F.** Basidiospores; **G.** Hymenium; **H.** Tramal hyphae; **I.** Basidia in hymenium; **J&K.** Marginal hairs. Scale bars: A=10mm, B&C=100 μm, D-K=10 μm.

Comments: *Calocera cornea* is commonly distributed in Kerala state. It is characterised by the cylindrical orangish yellow basidiocarp with zonation in the cross section, single septate basidiospores, unbranched hyphidia and tramal hyphae without clamp-connections. Morphologically and phylogenetically, *C. cornea* is closely related *C. viscosa*. Both the species have 0-1 septate basidiospores and lack of clamp-connections. However, *C. cornea* has simple cylindrical basidiocarp and *C. viscosa* has repeatedly dichotomous, large basidiocarp that may be up to 100 mm high (McNabb 1965a). Mohanan (2011) has previously reported this species from Kerala State.

Guepiniopsis Patouillard

Basidiocarp firm gelatinous, sessile, substipitate, stipitate with cupulate or obliquely cupulate pileus. Hyphae thin-walled, with or without clamp-connections. Stipe and sterile surfaces covered with a palisade of cortical hairs/marginal hairs. Each of the cortical hairs may thin or thick-walled, septate, inflates at its end and sometimes appears as catenulate chains. Hymenium limited to the interior of the cupulate pileus, smooth. Basidia cylindrical to subclavate, bifurcating. Basidiospores cylindrical to curved cylindrical, apiculate, 1–3 septate. Germination by germ tube or conidia formation.

Guepiniopsis buccina (Pers.) L.L. Kenn., Mycologia 50: 888 (1959) [1958]

Figure 24

Basidiocarp 3–5 × 3–9 mm, firm gelatinous, gregarious, stipitate and pileate. Stipe central, widening towards pileus. Pileus cupulate or obliquely cupulate, expands and widens on aging, have longitudinal ribs on external surface. Pale yellowish to yellow when fresh, more yellowish towards base. Orangish yellow when dry.

Hymenium limited to the interior of the cup, consists of basidia intertwined with hyphidia. **Basidia** 28–48 × 4–5 µm, thin-walled, cylindrical to narrowly

clavate, apically bifurcating. **Hyphidia** 31–52 × 2.5–3.5 µm, narrow, septate, cylindrical, thin-walled. **Basidiospores** 11–13 × 3.5–6 µm (Q = 2–3 µm, Qm = 2.43 µm), oblong to subcylindrical, 0–3 septate, thin-walled, guttulate, apiculate. Germination by producing conidia or by direct germination with germ tube. **Marginal hyphae** present on abhymenial surface of pileus and stipe, a palisade of thick-walled, septate, gelatinised hyphae with rounded apex. **Tramal hyphae** 2–7 µm wide, thick-walled up to 1.5 µm, smooth and roughened, septate, ring like thickening around septa with bulbous swelling and without clamp-connections.

Specimens examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 23 October 2019, Anjitha Thomas, ZGCAT179.

Habitat: On dead wood.

Comments: *Guepiniopsis buccina* is characterised by stipitate, cupulate basidiocarp with longitudinal striations on the external surface, lack of clamp-connections and thick-walled, septate, heavily gelatinised marginal hyphae. The present specimen perfectly fits with the description of *G. buccina* based on morphological features (McNabb 1965b). According to McNabb (1965b), the species have a world-wide distribution, but not a common species in any country. This is the first report of genus *Guepiniopsis* from India. It is morphologically distinct from other members of the genus like *G. suecica* (McNabb) Jülich, *G. estonica* (Raitv.) M. Dueñas and *G. oresbia* Rangkuti and Rifai by the number of septations in basidiospores. All these three species have more than three septations in basidiospore (Rangkuti and Rifai 1975, Dueñas 2005). This is a new genus and species record from Kerala State.



Figure 24: *Guepiniopsis buccina*- **A.** Basidiocarp; **B.** Basidiospores; **C.** Basidioles and hyphidia; **D&F.** Hymenium with basidia and basidiospore; **E.** Marginal hairs on the hymenium; **G.** Marginal hairs on the stipe. Scale bars: A=10mm, B-G=10 μ m.

Dacryopinax Martin

Basidiocarp is stipitate, with a spatulate, petaloid, flabellate, cupulate, obliquely cupulate, inversely cupulate, or foliose morphology, and may be occasionally lobed, firm gelatinous to cartilaginous, generally homogenous, thin- or thick-walled hyphae. Cortical hairs thin- or thick-walled, cylindrical or inflated, septate. Hymenium unilateral, superior, rarely amphigenous, smooth, folded or papillate. Probasidia cylindrical or subclavate, basidiospores cylindrical to curved-cylindrical, apiculate, 1–3 septate, germination by conidia and/or germ tubes.

Dacryopinax indacocheae Lowy, Mycologia 51: 848 (1961) [1959]

Figure 25

Basidiocarp 9–13 × 7–17 mm, firm gelatinous, stipitate, flabelliform, margin wavy, wrinkled inferior hymenium, discrete. Yellowish orange when fresh, turning to brownish orange to orange when dry.

Hymenium unilateral, composed of basidia intertwined with hyphidia. **Hyphidia** 23–30 × 2–3 µm, cylindrical, unbranched, thin-to slightly thick-walled. **Basidia** 25–40 × 3–6 µm wide, cylindrical to clavate, guttulate, apically furcate, thin-to slightly thick-walled. **Basidiospores** 8.5–11 × 3.5–4.5 µm (Q = 2.25–3.1µm, Qm = 2.5µm), 0–1 septate, guttulate, apiculate, cylindrical, ellipsoid, phaseoliform, with central constriction, thin-to slightly thick-walled. **Tramal hyphae** 2–5.5 µm wide, gelatinous, smooth or roughened inflated up to 15 µm in some areas, thick-walled, without clamp-connections. **Marginal hairs** 10–70 µm wide zone, thick-walled, inflated, unbranched, heavily gelatinised, occasionally catenulate, intertwined. Conidiophores and conidia are abundant within the marginal hairs of stipe. Conidiophore thick-walled, gelatinised, irregularly branched, narrow (2–4.5 µm) compared to tramal hyphae and marginal hair.

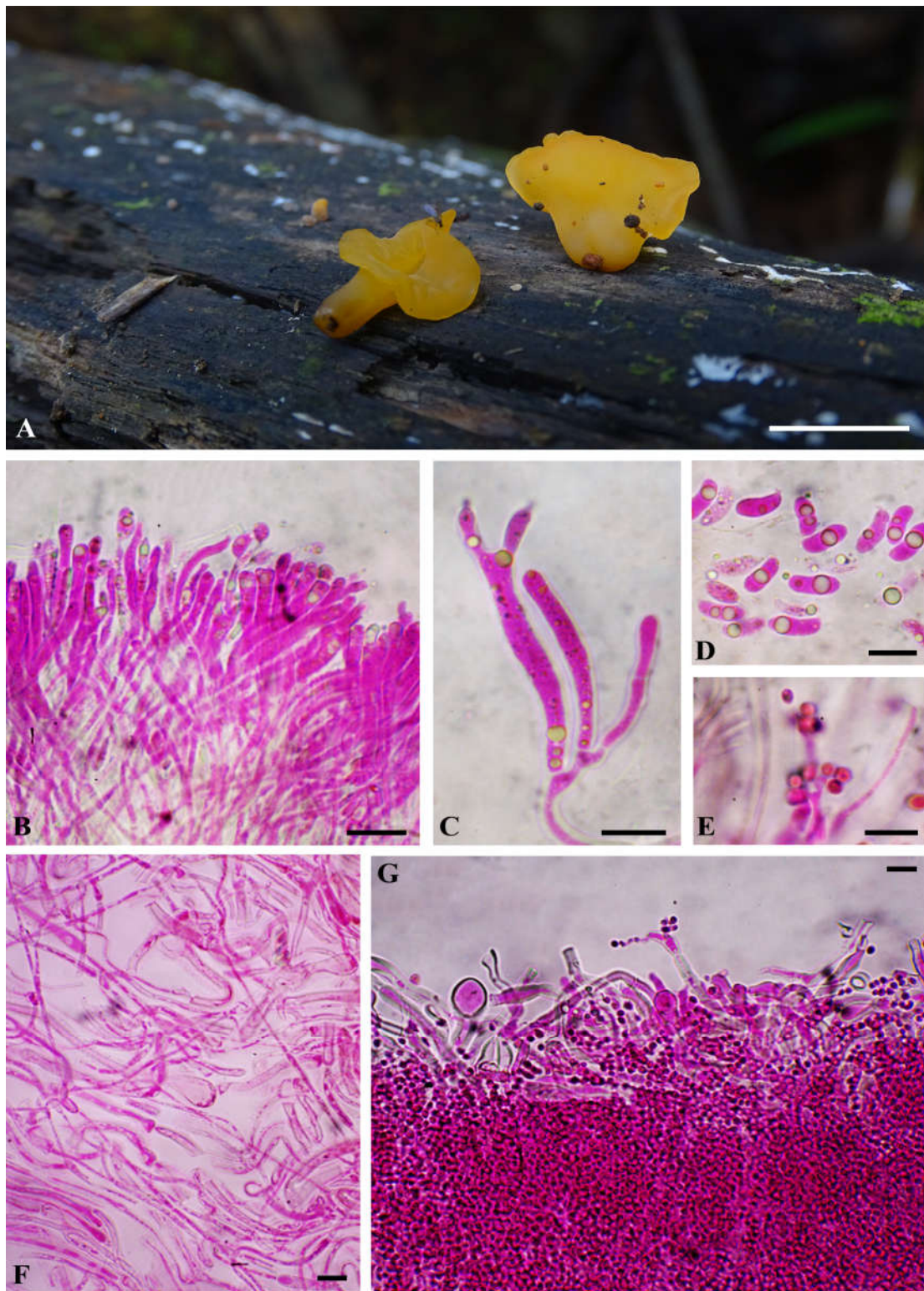


Figure 25: *Dacryopinax indacocheae*- **A.** Basidiocarp; **B.** Hymenium; **C.** Basidia; **D.** Basidiospore; **E.** Conidiogenous cell and conidia; **F.** Tramal hyphae; **G.** Marginal hyphae with conidiogenous cells and conidia. Scale bars: A=10mm, B-G=10µm.

Specimens examined: INDIA. Kerala State, Malappuram District, Vaniyambuzha, 27 October 2020, Anjitha Thomas, ZGCAT222.

Habitat: On dead wood.

Comments: Stipitate-pileate with foliose, lobed basidiocarp having 0–1 septate basidiospores, and thick-walled inflated vesicles in the marginal areas of stipe are the characteristic features of *D. indacocheae*. The type specimen of *D. indacocheae* is tan when fresh, foliose with 20 mm in height and 3 mm in width (Lowy 1959). The current basidiocarp is yellowish orange when fresh, shorter compared to type specimen. Excluding these characters, the current specimen is identical with the basidia, basidiospore and vesicles features (Lowy 1959, McNabb 1965b).

Dacryopinax maxidorii also has flabellate basidiocarps, 0–1 septate basidiospores and cylindrical to slightly inflated unbranched marginal hairs similar to the current specimen. But, *D. maxidorii* larger with 50mm wide, deeply branched pileus and elongated, firmly rooted stalk which is contrasting to the short (17mm wide) pileus and short, broad (5–8 mm long and 4–7 mm wide) stalk of current specimen (Lowy 1981). *Dacryopinax primogenitus* has similarity with the current specimen in basidiocarp shape, colour, basidiospore septation, but *D. primogenitus* has cylindrical, sometimes inflated, entwining and tuft forming, thin-walled cortical hairs (100 × 2.5–3 µm) and spherical to sphaeropedunculate cells of 4–5 µm width (McLaughlin *et al.* 2016). The Kerala specimens have thick-walled, occasionally catenulate, inflated cells up to 13 µm wide, which is the characteristic feature of *D. indacocheae*. There are no records of this species from India till date.

Dacryopinax primogenitus D.J. McLaughlin and E.G. McLaughlin, in McLaughlin, Healy, Kumar, McLaughlin, Shirouzu and Binder, *Mycologia* 108: 460 (2016)

Figure 26

Basidiocarp 25–32 × 16–25 mm, firm gelatinous, caespitose, stipitate, petaloid, flabelliform, deeply lobed and lobes with crenate margin. Pale yellowish orange when fresh becoming paler (dull orange) when dry.

Hymenium unilateral, pale yellowish in water, composed of basidia and hyphidia. **Hyphidia** 40–48 × 2.5–3 µm, narrow, cylindrical, unbranched, thin-walled. **Basidia** 26–35 × 2.5–4.5 µm, cylindrical to narrowly clavate, thin-walled, guttulate, with yellowish guttules, apically furcate. **Basidiospores** 7–9.5 × 3–4.4 µm (Q = 1.86–3.1 µm, Qm = 2.39 µm), ellipsoid to oblong with median constriction, 0–1 septate, thin-walled, hyaline. Conidiophores and conidia are abundant throughout the basidiocarp. Conidiophore thin-walled, gelatinised, branched. Conidia 3–4 × 2.5–3 µm, subglobose to ellipsoid, thin-walled. **Crystalline contents** present in the trama. **Tramal hyphae** 2–5 µm wide, gelatinous, inflated up to 12 µm wide in some areas, septa with bulbous swellings, thin- to slightly thick-walled, without clamp-connections. **Marginal hairs** 30–60 µm long, 2–4 µm wide, thin- to slightly thick-walled, unbranched, gelatinised. **Inflated cells** 6–30 µm wide, thin- to slightly thick-walled, gelatinised, abundant in the subcortical zone.

Specimens examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 04 July 2019, Anjitha Thomas, ZGCAT86; 05 July 2019, Anjitha Thomas ZGCAT91; ZGCAT92; Pathanamthitta District, Ranni, 12 April 2022, Anjitha Thomas, ZGCAT309.

Habitat: On dead wood.

Comments: *Dacryopinax primogenitus* is characterised by flabelliform to spathulate, lobed basidiocarp; inflated cells in the cortex; thin-walled, cylindrical, intertwined marginal hairs; obovate to ellipsoid conidia and, 0–1 septate, thin-walled basidiospores. All these features are present in the

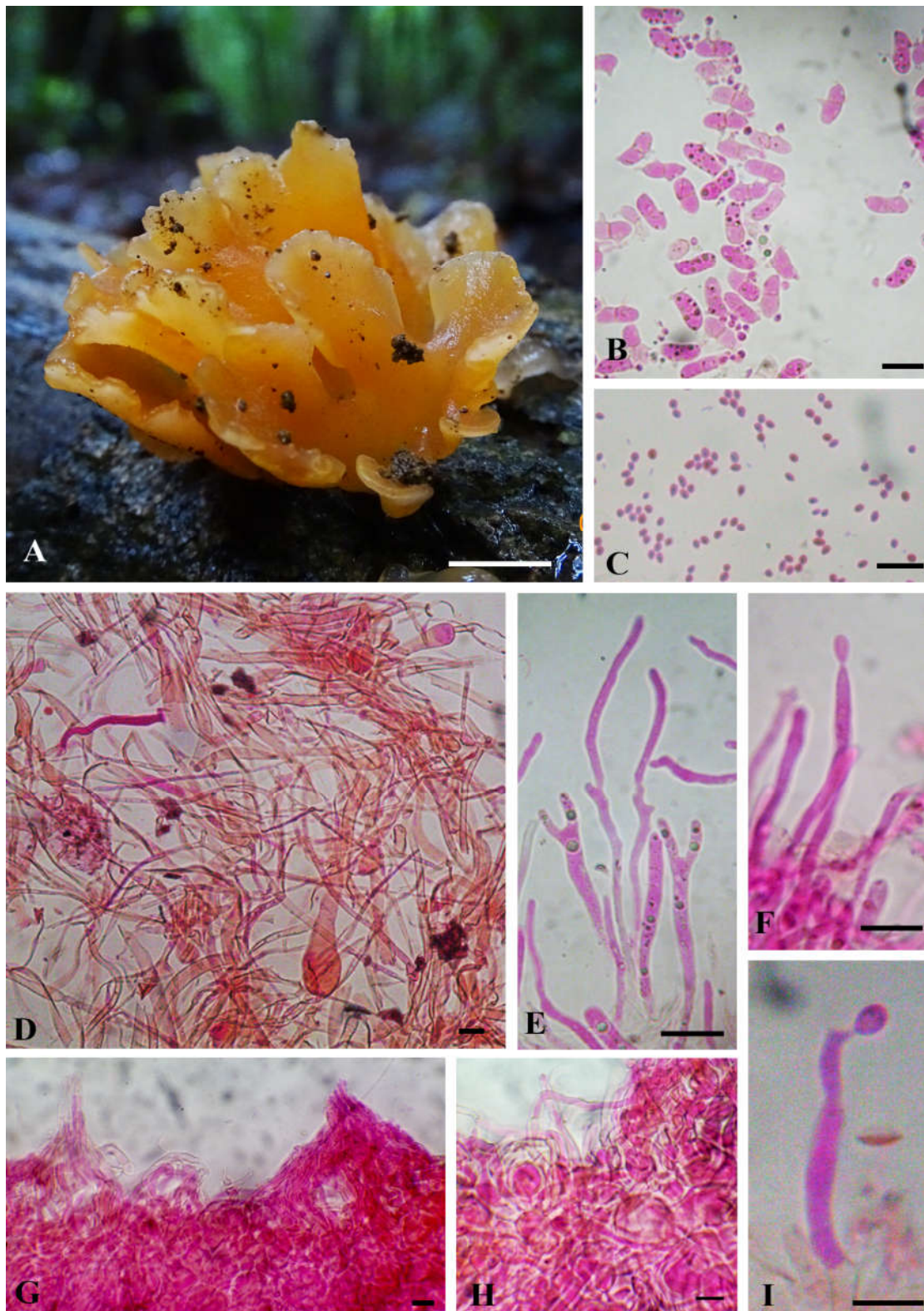


Figure 26: *Dacryopinax primogenitus*- **A.** Basidiocarp; **B.** Basidiospores with microconidia; **C.** Conidia; **D.** Tramal hyphae; **E.** Basidia with conidiophores; **F&I.** Conidiophore and conidia; **G.** Marginal hyphae; **H.** Inflated cells. Scale bars: A=10mm, B-I=10 μ m.

specimens collected during this study. *Dacryopinax primogenitus* is closely related to *D. indacocheae* as evident from morphological and molecular data. But, the latter have thick-walled, inflated, catenulate cells in the marginal areas, where *D. primogenitus* have long intertwined unbranched marginal hairs (McNabb 1965b). In the phylogentic analysis, sequences generated in the present study (ZGCAT89: ITS= PP758342, ZGCAT92: ITS= PP758341) clustered with *D. primogenitus* with 97 % support value (Figure 53). *Dacryopinax primogenitus* is originally reported from Costa Rica in 2016. There are no records of this species from India till date.

Dacryopinax yungensis Lowy, Mycologia 5: 849 (1961) [1959]

Figure 27

Basidiocarp 11–19 × 5–14 mm, firm gelatinous, stipitate and pileate, gregarious, initially emerges as conical, cylindrical, turbinate and later pileus expands to flabellate to spathulate. Margin smooth initially, becoming lobed and wavy on maturity. Pale orange to yellowish orange when fresh, turning to orange when dry. Spore print whitish.

Hymenium unilateral, composed of basidia and hyphidia. **Hyphidia** 35–52 × 2–3 µm, narrow, cylindrical, septate, thin-walled. **Basidia** 33–41 × 4–5 µm, slightly thick-walled, cylindrical to narrowly clavate, with yellowish guttules, apically. **Basidiospores** 10.5–13 × 4.5–5.5 µm (Q = 2–2.6 µm, Qm = 2.3 µm), obovoid to phaseoliform in side view, subcylindrical to obong in frontal view, apiculate, guttulate, 0–3 septate, thin-septate. Germination by microconidia. Conidiophores emerges from the basidiospores, short, cylindrical to conical, 1.5–3.2 µm long. **Microconidia** 1–2.5 × 1–1.5 µm, subglobose to globose, ellipsoid, thin-walled. **Marginal hairs** of stipe is thick-walled, long, cylindrical, septate, up to 80µm long and 5.5 µm wide. Marginal hairs of abhymenium is shorter and cylindrical to clavate compared to the hair in stipe. **Inflated vesicle like cells** present below the marginal hairs in abhymenium and stipe, 10–15 × 7–9 µm, thick-walled, catenulate, branched, subglobose to globose, broadly

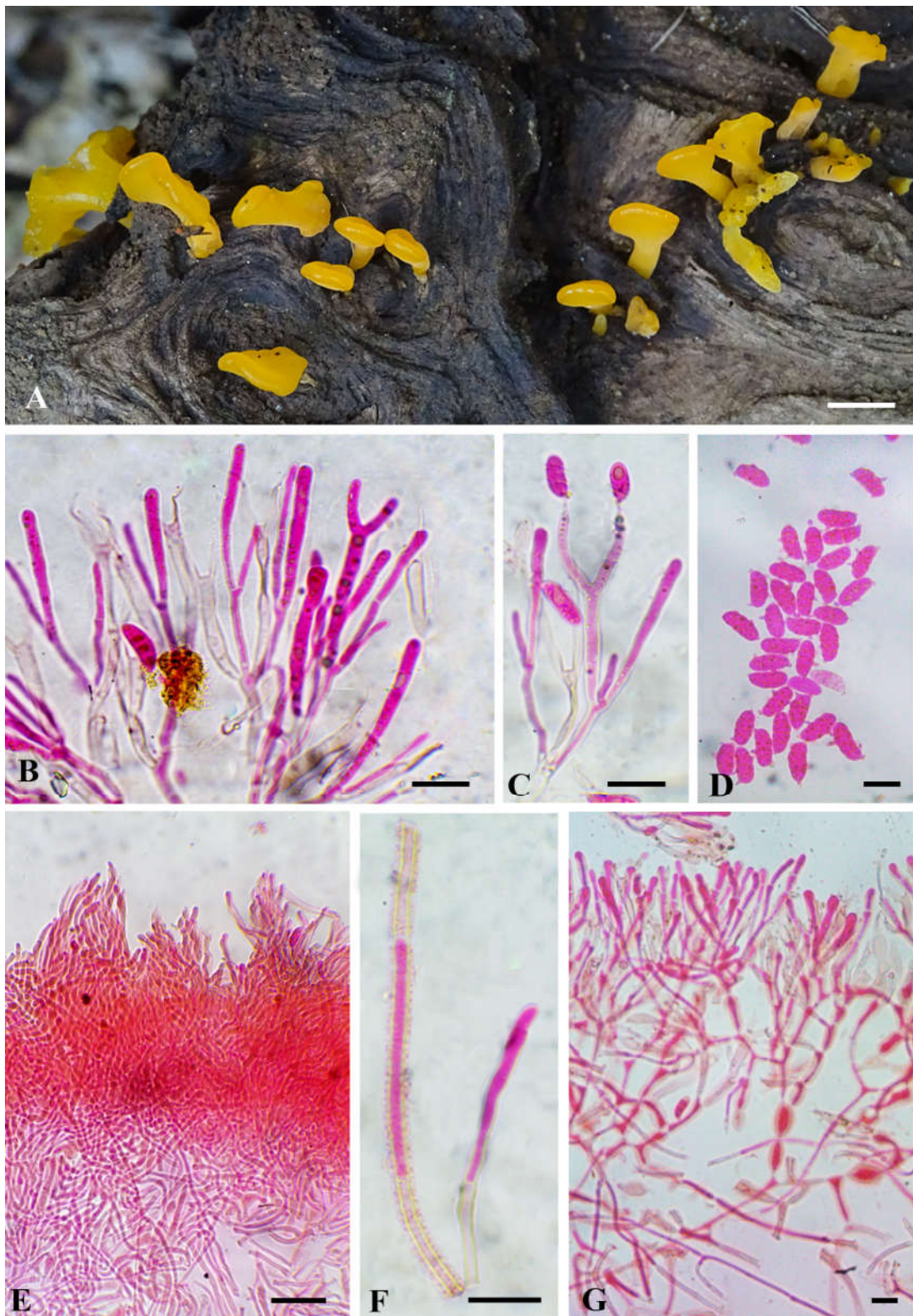


Figure 27: *Dacryopinax yungensis*- **A.** Basidiocarp; **B.** Hymenium; **C.** Basidia; **D.** Basidiospores; **E.** Marginal hairs on stipe; **F.** Smooth and rough tramal hyphae; **G.** Abhymenium. Scale bars: A=10mm, B-G=10 μ m.

fusiform, ellipsoid, shapeless, clavate, prominent in the zone just below the abhymenium, than subcortical zone of stipe. **Tramal hyphae** 2–4.5 μm wide, thick-walled, smooth and roughened, with bulbous septa and without clamp-connections.

Specimens examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 23 October 2019, Anjitha Thomas, ZGCAT182. Kannur District, Kannavam forest, 15 October 2022, Vaishnavi M., ZGCAT338.

Habitat: On dead wood.

Comments: *Dacryopinax yungensis* is characterised by flabellate to spathulate basidiocarp, 0–3 septate basidiospores, cylindrical long intertwined marginal hairs in stipe, cylindrical to clavate short hairs on abhymenium, and inflated vesicle like cells prominent in the abhymenium. *Dacryopinax yungensis* is closely related to *D. dennisii* McNabb and *D. petaliformis* in having 0–3 septate basidiospores, and cylindrical to inflated marginal hairs (McNabb 1965b). But these two species lack vesicle-like cells. There are no records of this species from India so far.

Dacryopinax petaliformis (Berk. and M.A. Curtis) McNabb, New Zealand Journal of Botany 3: 70 (1965)

Synonym:

Guepinia petaliformis Berk. and M.A. Curtis, in Berkeley, Grevillea 2(no. 13): 5 (1873)

Figure 28

Basidiocarp 9–18 \times 2–6 mm, firm gelatinous, caespitose, gregarious, initially conical to cylindrical, pileus becoming spathulate to irregularly lobed, solid, hollow base observed in some large basidiocarps. Yellowish orange, paler towards the base, becoming reddish orange when dry.

Hymenium unilateral, sometimes limited to the tip portion, pale yellowish in water, composed of basidia and hyphidia. **Hyphidia** 20–40 \times 2–4

μm , narrow, cylindrical, unbranched, thin-walled. **Basidia** 25–44 \times 3–6 μm , cylindrical to narrowly clavate, thick-walled, guttulate, apically furcate. **Basidiospores** 10–15 \times 3–5 μm (Q = 2.3–3.2 μm , Qm = 2.7 μm) cylindrical, 0–3 septate, thin-walled, thin septate, hyaline. **Crystalline contents** present in the trama. **Tramal hyphae** 2–5 μm wide, gelatinous, inflated up to 6 μm in some areas, slightly inflated towards the septum in some hyphae, slightly thick- to thick-walled, smooth and roughened hyphae, without clamp-connections. **Marginal hairs** formed of both inflated cells and cylindrical hyphae. Inflated, catenulate cells, 4–8 μm wide, thick-walled, gelatinised are common in the abhymenium. In the cortical zone of stipe, 4–6 μm wide occasionally branched, gelatinous, thick-walled, intertwining hyphae are present.

Specimens examined: INDIA. Kerala State, Kozhikode District, Kakkayam, 26 October 2018, Anjitha Thomas, ZGCAT37; Palakkad District, Silent Valley National Park, 24 October 2019, Anjitha Thomas, ZGCAT188; Wayanad District, Kuruva islets, 20 April 2022, Salna N., ZGCAT310; Palakkad District, Parambikulam, 12 June 2022, Anjitha Thomas, ZGCAT313; Thrissur District, Sholayar, 20 October 2022, Jeena Rose Pious, ZGCAT340; ZGCAT341.

Habitat: On dead wood.

Comments: Red brown basidiocarp, presence of simple or occasionally branched, thick-walled, septate, often inflated marginal hairs, 0–3 septate basidiospores are the characteristic features of *D. petaliformis*. *Dacryopinax petaliformis* is similar to *D. primogenitus* by the orangish red basidiocarp and inflated thick-walled marginal hairs. However, the former has 3-septate basidiospores, whereas the latter has 1-septate basidiospores. When compared to *D. yungensis*, *D. petaliformis* lack inflated cells in the subhymenial region of basidiocarp (McNabb 1965b).

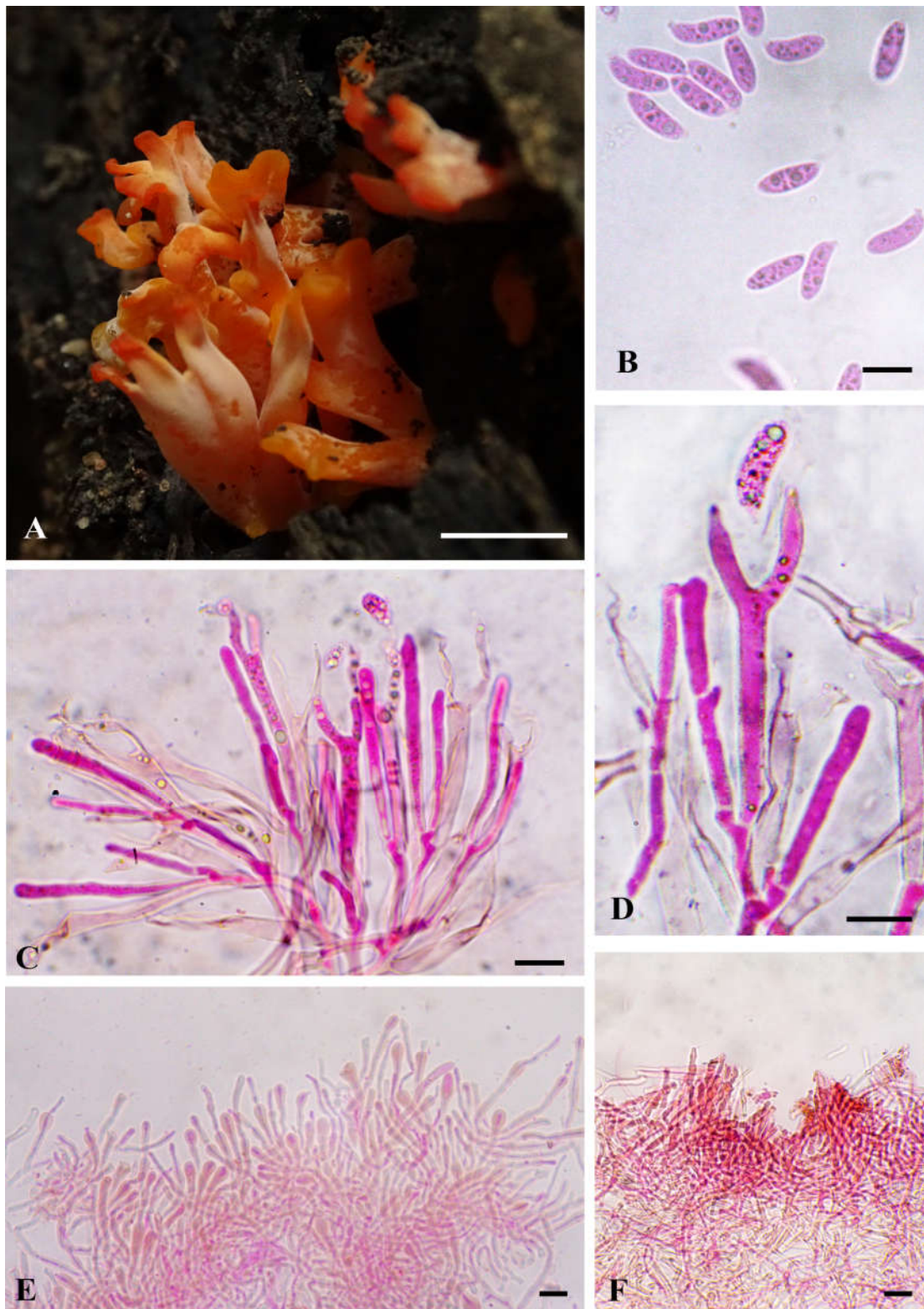


Figure 28: *Dacryopinax petaliformis*- **A.** Basidiocarp; **B.** Basidiospores; **C.** Hymenium; **D.** Basidia and basidiospore; **E&F.** Marginal hairs. Scale bars: A=10mm, B-F=10µm.

Out of six collections, four of them were infected by an unidentified tremellaceous member. The infected basidiocarps looked perfect externally without any colour or shape variation. But in microscopic preparations, parasitic hyphae with clamp-connections, conidiophores and haustoria were observed intertwined with host hyphae. Due to the presence of haustoria, we suspect that the parasite is a tremellaceous member. There are no records of this species from India till date.

Dendrodacrys J.C. Zamora, A. Savchenko, Gonz.-Cruz, Prieto-García, Olariaga and Ekman

Basidiocarps firm to soft gelatinous when fresh, sessile or stipitate, rooting base may be present or absent, pulvinate to depressed, spatulate to foliose, yellow, orange to brown. Hymenium may be amphigenous or limited to the upper part of the basidiocarp. Clamp-connection may be present or absent. Terminal cells of marginal/cortical hyphae, cylindrical to narrowly clavate, and thin- to thick-walled. Tramal hyphae mostly thin-walled. Basidia bisterigmate, bispored, cylindrical to clavate, rarely \pm urniform. Hyphidia branched. Branched hyphidia may extend beyond the level of basidia. Basidiospores 0–3 septate, hyaline, thin- to thick-walled, subglobose to cylindrical-allantoid. Spore print cream to orange. Microconidia not common, ellipsoid to cylindrical. Cell cytoplasm with guttules and with carotenoides.

Dendrodacrys paraphysatum (L.S. Olive) J.C. Zamora and A. Savchenko, in Zamora, Savchenko, González-Cruz, Prieto-García, Olariaga and Ekman, *Fungal Systematics and Evolution* 9: 41 (2022)

Synonym:

Dacrymyces paraphysatus L.S. Olive, *Bull. Torrey bot. Club* 85: 106 (1958)

Figure 29

Basidiocarps 10–45 × 1–2 mm, gelatinous, sessile, emerging as pustules, later coalesces to form appanate, cerebriform masses. Orangish

yellow when young becoming amber brown to dark grey with age and on drying.

Hymenium limited to the upper surface of basidiocarp. Basidia intermixed with hyphidia. **Hyphidia** 28–49 × 1.5–3 µm, long, narrow, hyaline, profusely branched, septate, guttulate, with clamp-connections, hyphidia surpassing the level of young basidia. **Basidia** 30–59 × 3–6 µm hyaline, slightly thick- to thick-walled, guttulate, cylindrical to narrowly clavate, apically furcate, basal clamp-connection present. **Basidiospores** 12.5–17 × 5–8 µm (Q = 2–2.6 µm, Qm = 2.37 µm), 0–3 septate, with guttules, apiculate, ellipsoid to phaseoliform, thick-walled and thick septate. **Germination** not observed. **Marginal hairs** 15–24 × 2–2.5 µm, cylindrical, slightly thick- to thick-walled, with clamp-connections. **Tramal hyphae** 2–5 µm wide, slightly thick- to thick-walled, gelatinous, smooth or roughened, with clamp-connections, swollen up to 11 µm towards septa.

Specimens examined: India. Kerala State, Malappuram District, University of Calicut campus, 10 July 2018, Anjitha Thomas, ZGCAT7; Palakkad District, Silent Valley National Park, 24 October 2019, Anjitha Thomas, ZGCAT196; Malappuram District, Vanniyambuzha, 27 October 2020, Anjitha Thomas, ZGCAT219; Kozhikode District, Kakkad, 13 December 2023, Anjitha Thomas, ZGCAT358.

Habitat: On dead wood.

Comments: Basidiocarp pustulate to applanate, cerebriform, easily coalescing, profusely branched hyphidia, 0–3 septate, thick-walled and thick septate basidiospores, and presence of clamp-connections are the characteristic features of *D. paraphysatum*. Characters of the collections fit with the description of the species by Savchenko *et al.* (2022).

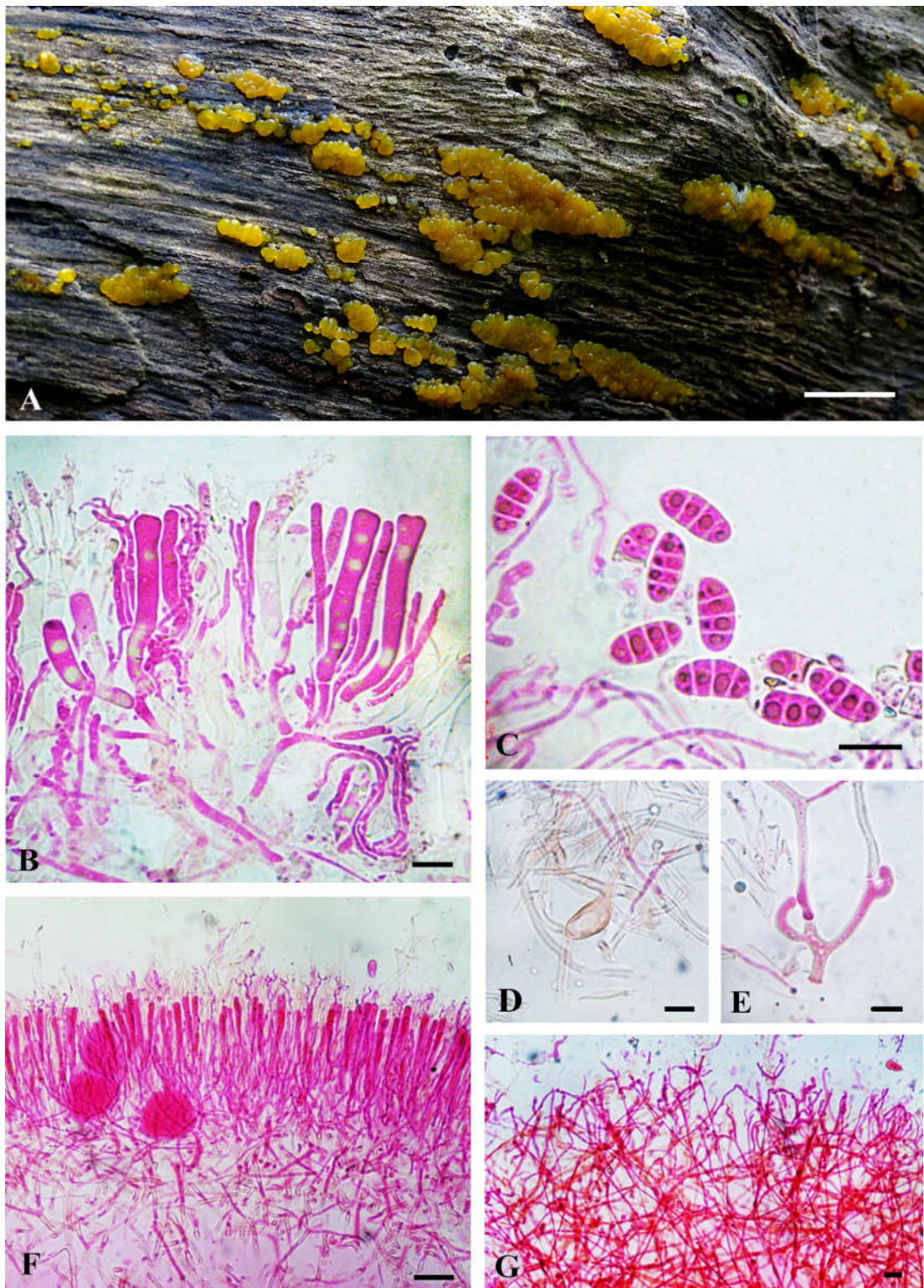


Figure 29: *Dendrodacrys paraphysatum*- **A.** Basidiocarp; **B.** Hymenium with basidia, basidioles and hyphidia; **C.** Basidiospores; **D.** Hyphae swollen towards septa; **E.** Clamp-connections; **F.** Hymenium; **G.** Marginal hairs. Scale bars: A=10mm, B-G=10 μ m.

Dendrodacrys paraphysatum is closely related to *D. conrescens*, *D. ciprense*, *D. laetum*, *D. pezizoideum* and *D. rigoratum* in having cylindrical to allantoid, slightly curved, 0-3 septate basidiospores with abundant clamp-connections and dendrohyphidia. *Dendrodacrys pezizoideum* has white hirsute stalk or margin, which is absent in *D. paraphysatum*. *Dendrodacrys laetum* differs from *D. paraphysatum* in having basidiocarps that retain yellowish colour even after drying, whereas, basidiocarps of *D. paraphysatum* become amber brown on drying. *Dendrodacrys conrescens* has fused pustulate basidiocarps that are relatively light coloured when dry when compared with that of *D. paraphysatum*, and normal clamp-connections in the tramal hyphae *D. paraphysatum* has slightly cerebriform basidiocarp that becomes dark brown on drying, and with both swollen and normal the clamp-connections in the tramal hyphae. *Dendrodacrys ciprense* and *D. rigoratum* have basidiocarps which remain often as solitary (Savchenko *et al.* 2022, Zamora *et al.* 2022), whereas, the basidiocarps of *D. paraphysatum* easily coalesce and form resupinate masses. This is a new genus record from India.

***Dacrymyces* Nees**

Basidiocarps sessile or stipitate, may be pustulate, pulvinate, discoid, turbinate, pezizoid, spathulate, flabellate, lobed or cerebriform, discrete or coalescing, attached to the woody substrate on a point or with rooting base, tramal hyphae may be gelatinous, with or without clamp-connections. Colour varies from off white, yellow, orange to dark brown. Except for the marginal hairs, tramal composition is homogenous. Marginal region may be composed of a palisade of thin- or thick-walled terminal cells/hairs that are cylindrical, subclavate, or ovate. Hymenium amphigenous, unilateral, or confined to the superior surface of stipitate species. Hyphidia may be present or absent, probasidia cylindrical to subclavate, obpyriform or urniform, metabasidia bifurcating. Basidiospores cylindrical, allantoid, ovate or subglobose, apiculate,

septate at maturity. Germination by conidia and/or by the formation of germ tubes.

Dacrymyces spathularia (Schwein.) Alvarenga [as 'spathularius'], in Mendes-Alvarenga and Gibertoni, Mycological Progress 21: 6 (2022)

Figure 30

Synonyms:

Cantharellus spathularia (Schwein.) Schwein., Trans. Am. phil. Soc., New Series 4(2): 153 (1832) [1834]

Dacryopinax spathularia (Schwein.) G.W. Martin, Lloydia 11: 116 (1948)

Dacryopinax spathularia f. *agariciformis* (Lloyd) D.A. Reid, Jl S. Afr. Bot. 39(2): 178 (1973)

Guepinia agariciformis Lloyd, Ann. Univ. Stellenbosch, Reeks A 1(1): 4 (1923)

Guepinia spathularia (Schwein.) Fr., Elench. fung. (Greifswald) 2: 32 (1828)

Guepinia spathularia f. *alba* G.W. Martin, Proc. Iowa Acad. Sci. 50: 165 (1944)

Guepiniopsis spathularia (Schwein.) Pat., Essai Tax. Hyménomyc. (Lons-le-Saunier):30 (1900)

Masseola spathulata (Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 2: 859 (1891)

Merulius spathularia Schwein., Schr. naturf. Ges. Leipzig 1: 92 [66 of repr.] (1822)

Basidiocarp 9–19 × 2–8 mm, firm gelatinous, stipitate, spathulate, flabelliform, gregarious, discrete. Yellowish orange when fresh, turning to orange when dry.

Hymenium unilateral, composed of basidia intermixed with hyphidia.

Hyphidia 10–22 × 2–3, cylindrical, septate, unbranched, thin-walled. **Basidia** 18.5–29 × 2.7–4.5 µm wide, cylindrical to clavate, guttulate, apically furcate, thin-walled. **Basidiospores** 7.5–9 × 4–5 µm (Q = 1.7–2.2 µm, Qm = 1.9 µm), 0–1 septate, guttulate, apiculate, cylindrical, ellipsoid, phaseoliform, obovate, with central constriction, thin-walled and with thin-walled septa. Germination by microconidia. **Microconidia** 1–2 × 1–2 µm, subglobose to globose, guttulate, thin-walled. **Tramal hyphae** 2–5.5 µm wide, gelatinous, smooth or roughened, inflated up to 14 µm wide in some areas, slightly thick-walled. **Marginal surface** 35–60 × 1.5–4 µm long, thick-walled, cylindrical, flexuose, sometimes tufted, intertwined hairs.

Specimens examined: INDIA. Kerala State, Malappuram District, University of Calicut campus, 05 June 2018, Anjitha Thomas, ZGCAT3; 09 July 2018, Anjitha Thomas, ZGCAT4; 16 July 2018, Anjitha Thomas, ZGCAT11; Kozhikode District, Thottil palam, 22 May 2019, Anjitha Thomas, ZGCAT48; University of Calicut campus, 26 June 2019, Anjitha Thomas, ZGCAT57; Kannur District, Aralam, 28 June 2019, Anjitha Thomas, ZGCAT59; Kozhikode District, Thottil palam, 25 June 2019, Anjitha Thomas, ZGCAT74; Kollam District, Thenmala, 23 September 2019, Anjitha Thomas, ZGCAT144; Palakkad District, Silent Valley National Park, 24 October 2019, Anjitha Thomas, ZGCAT197; Kozhikode District, Engapuzha, 16 May 2020, Anjitha Thomas, ZGCAT205; Kootalida, 06 July 2020, Anjitha Thomas, ZGCAT210; Malappuram District, Vanniyambuzha, 27 October 2020, Anjitha Thomas, ZGCAT221; New Amarambalam, 04 September 2021, Anjitha Thomas, ZGCAT279; ZGCAT280; Kollam District, Thenmala, 2 October 2020, Anjitha Thomas, ZGCAT286; Kozhikode District, The Zamorin's Guruvayurappan College campus, 06 June 2022, Anjitha Thomas, ZGCAT333; Pokunnu, 12 November 2022, Anjitha Thomas, ZGCAT348.

Habitat: On dead wood.

Comments: *Dacrymyces spathularia* is characterised by stipitate, spathulate, flabelliform basidiocarp with unilateral hymenium, 0–1 septate basidiospores, and long, cylindrical marginal hairs. Unilateral hymenium was widely accepted as the characteristic feature of genus *Dacryopinax*, and *D. spathularia* was treated under *Dacryopinax* until recently. Alvarenga and Gibertoni (2022) proposed a new combination and transferred *D. spathularia* to the genus *Dacrymyces* based on the molecular similarity with *Dacrymyces sensu stricto* members. *Dacrymyces spathularia* is morphologically similar to *Dacryopinax aurantiaca* (Fr.) McNabb and *Dacryopinax indacocheae* in having unilateral hymenium and 0–1 septate basidiospores. But *D. spathularia* has cylindrical long marginal hyphae without inflated cells in subortical zone, where *D. aurantiaca* and *D. indacocheae* have inflated cells in the cortical zone (McNabb 1965b). *Dacrymyces spathularia* has previously reported from Kerala State by Mohanan (2011) as *Dacryopinax spathularia*.

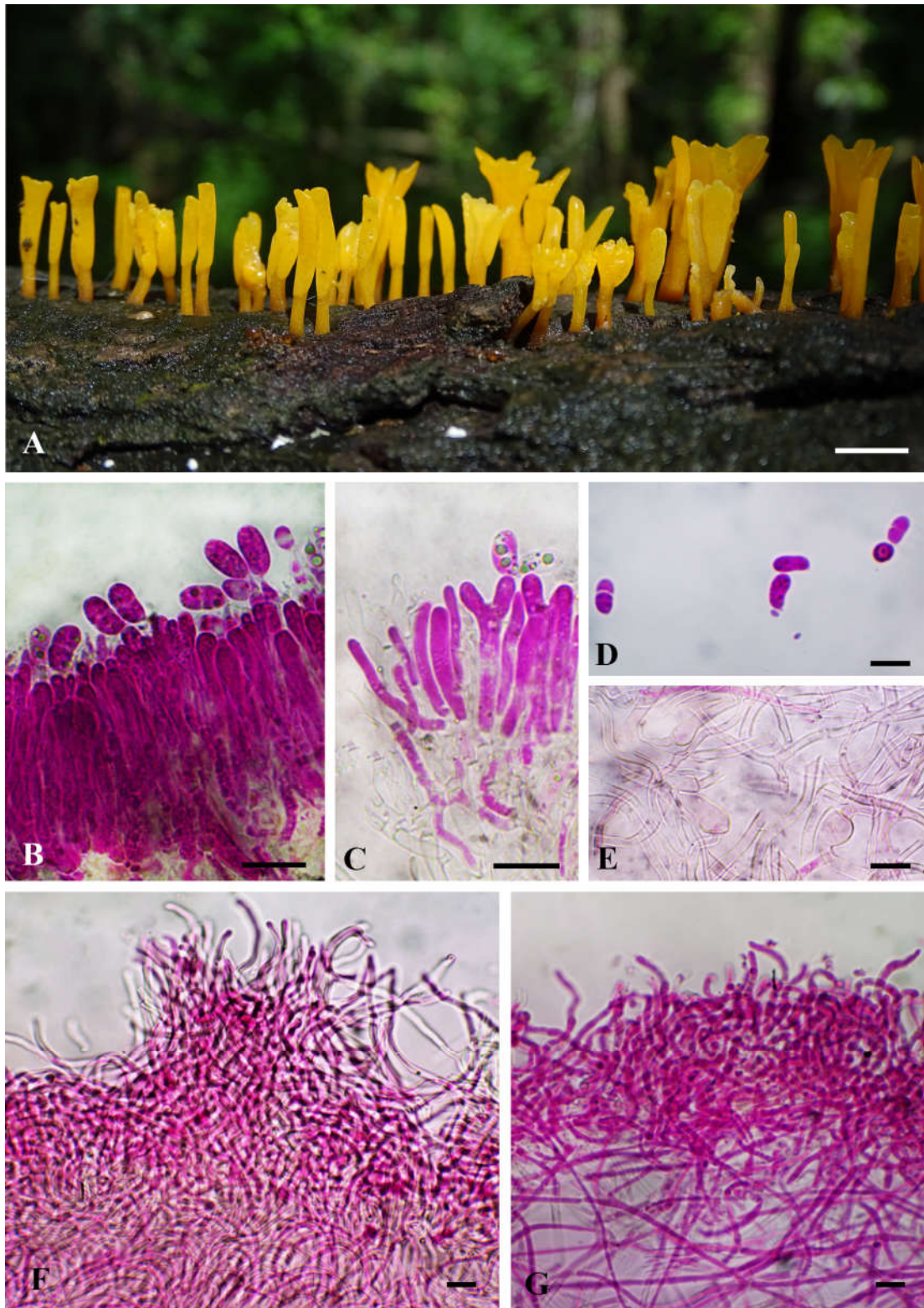


Figure 30: *Dacrymyces spathularia*- **A.** Basidiocarp; **B&C.** Basidia and basidiopores; **D.** Basidiopores; **E.** Tramal hyphae; **F&G.** Marginal hairs. Scale bars: A=10mm, B-G=10µm.

Dacrymyces dacryomitriiformis McNabb, New Zealand Journal of Botany 11: 480 (1973)

Figure 31

Basidiocarp 4–19 × 4–23 mm, soft gelatinous, sessile to stipitate, initially pustulate, becoming cerebriform, and irregularly discoid, gregarious, discrete. Yellowish orange when fresh, turning to amber brown when dry.

Hymenium amphigenous, composed of basidia intermixed with hyphidia.

Hyphidia cylindrical, septate, rarely *branched*, thin-walled. **Basidia** 20–48 × 3–4 µm wide, cylindrical to clavate, guttulate, apically furcate, thin-walled.

Basidiospores 10.2–14.5 × 3.1–5.3 µm (Q = 2.30–3.84 µm, Q_m = 2.95 µm), 0–3 septate, guttulate, apiculate, ellipsoid to oblong, lacrymoid, thick-walled and thick-septate. Germinating directly, or by producing microconidia.

Microconidia 1.5–2.5 × 1–2 µm, subglobose to ellipsoid, guttulate, thin-walled.

Tramal hyphae 2–5 µm wide, gelatinous, smooth or roughened, inflated up to 8.5 µm wide in some areas, slightly thick to thick-walled. **Marginal surface** lack specialised hairs.

Specimens examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 04 July 2019, Anjitha Thomas, ZGCAT83.

Habitat: On dead wood.

Comments: *Dacrymyces dacryomitriiformis* is characterised by the large-sized (4–19 mm high and 4–23 mm wide), sessile to stipitate, pustulate to irregularly pezizoid basidiocarp, having 0–3 septate basidiospores with thick septa, and hyphae without clamp-connections.

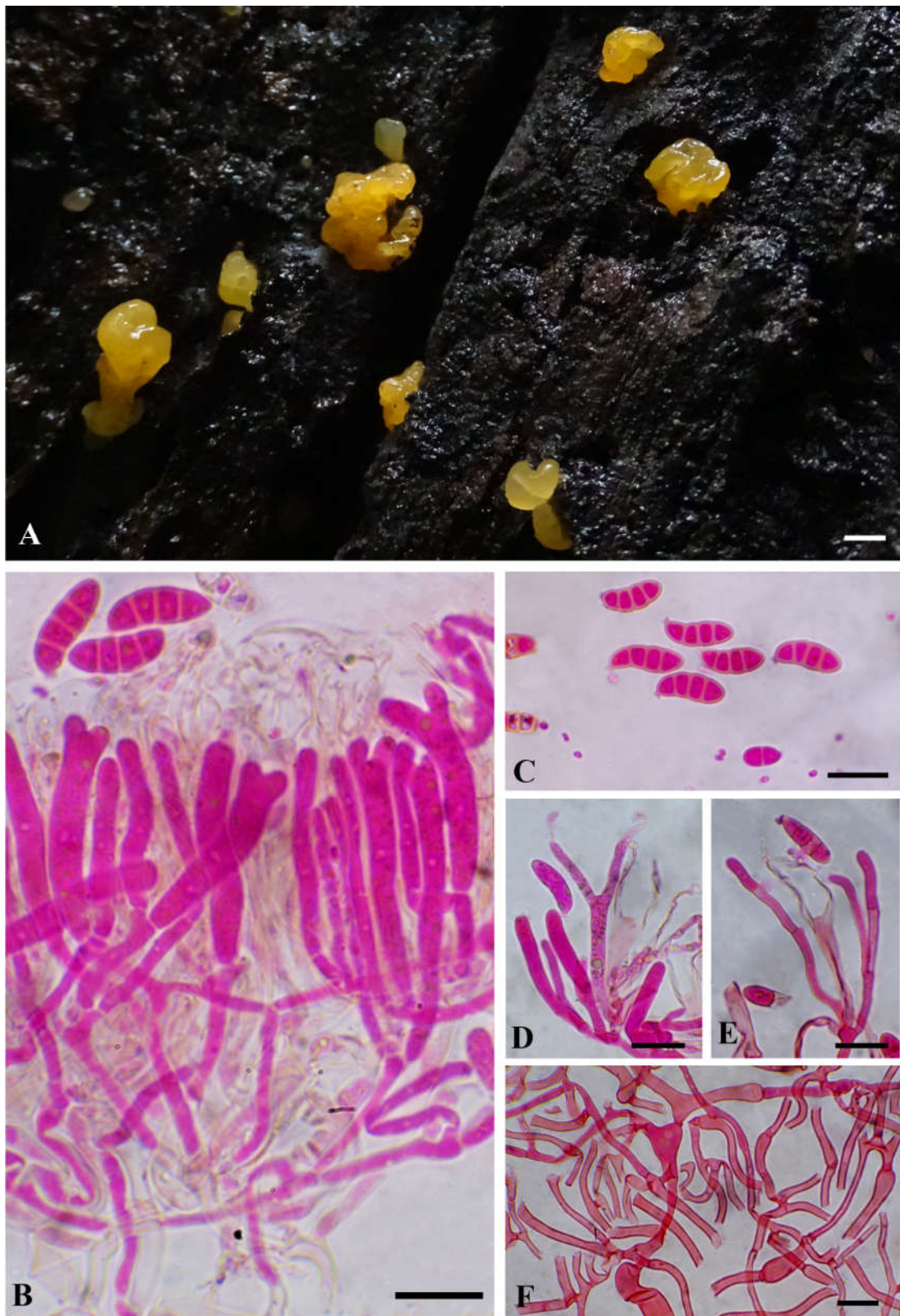


Figure 31: *Dacrymyces dacryomitiformis*- **A.** Basidiocarp; **B.** Hymenium with basidia and basidiospores; **C.** Basidiospores; **D&E.** Basidia of different stages, hyphidia and basidiospore; **F.** Tramal hyphae. Scale bars: A=10mm, B-F=10 μ m.

Dacrymyces capitatus, *D. cupularis*, *D. intermedius* L.S. Olive, *D. lacrymalis*, *D. minor* and *D. stillatus* have similarity with *D. dacryomitiformis* in having 3-septate basidiospores, and hyphae without clamp-connections (McNabb 1973), but differ from *D. dacryomitiformis* in having smaller sized basidiocarps. This is the first record of this species from India.

Dacrymyces microsporus P. Karst., Bidrag till Kännedom av Finlands Natur och Folk 48: 459 (1889)

Figure 32

Basidiocarp 1.5–7 × 0.5–4.5 mm, firm gelatinous, stipitate and pileate, capitate, head portion is globose and later expands to cerebriform, gregarious, discrete. Dull white, yellow to yellowish orange when fresh, turning to orange when dry, paler towards the base.

Hymenium limited to the upper pileal portion of the basidiocarp, which is composed of basidia intermixed with hyphidia. **Hyphidia** 17–36 × 2–3 µm, cylindrical and septate, unbranched, thin-walled. **Basidia** 18–36 × 4–5.5 µm, hyaline, guttulate, cylindrical to narrowly clavate, apically furcate, thin-walled. **Basidiospores** 9–11 × 4–5 µm (Q = 1.8–2.5 µm, Qm = 2.06 µm), 0–1 septate, guttulate, apiculate, ellipsoid, broadly ellipsoid, obovoid, constricted at the septum, thin-walled. **Tramal hyphae** 2–3.5 µm wide, gelatinous, thin-walled, without clamp-connections. Normal and bulged septa present. **Marginal hyphae** 25–42 × 2–3 µm, septate, cylindrical to subclavate, branched and thin-walled.

Specimens examined: INDIA. Kerala State, Kozhikode District, Thusharagiri, 11 July 2019, Anjitha Thomas, ZGCAT102; Kollam District, Thenmala, 22 September 2019, Anjitha Thomas, ZGCAT140; Malappuram District, Vanniyambuzha, 27 October 2020, Anjitha Thomas, ZGCAT218; Wayanad District, Kuruva islets, 14 October 2022, Anjitha Thomas, ZGCAT336.

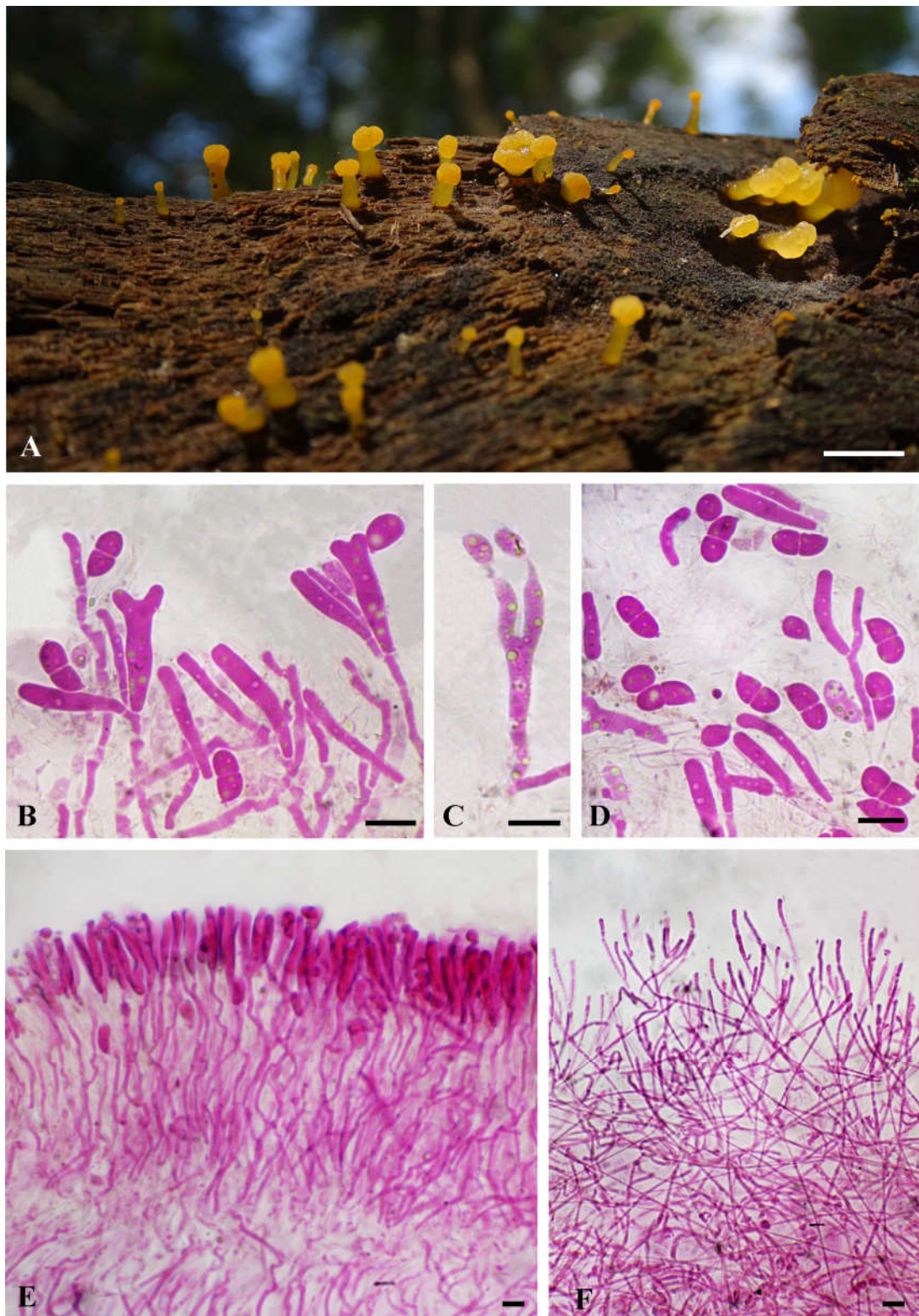


Figure 32: *Dacrymyces microsporus*- **A.** Basidiocarp; **B.** Hymenium with basidia, hyphidia and basidiospores; **C.** Mature basidia; **D.** Single septate basidiospores; **E.** Hymenium; **F.** Marginal hyphae. Scale bars: A=10mm, B-F=10µm.

Habitat: On dead wood.

Comments: *Dacrymyces microsporus* is characterised by stipitate-pileate, capitate basidiocarps with globose, cerebriform pileal portion; cylindrical, septate, unbranched hyphidia; 0–1 septate basidiospores; cylindrical to subclavate, branched marginal hairs and absence of clamp-connections. Different collections of *D. microsporus* from Kerala had significant colour variations from dull white to bright orange. Entire basidiocarps of ZGCAT102 and ZGCAT140 were white to dull white in colour, and ZGCAT218 and ZGCAT336 were yellow to orangish. But, all of the collections possessed similar basidiospores, basidia and marginal hairs. Exceptionally, ZGCAT336 showed a specific core zone in the stipe cross section. In the molecular analysis (Figure 53), ITS sequence generated from ZGCAT336 clustered with *D. microsporus* (Wu561 (China), TUF13032 (Japan)). This species has no previous record from India.

***Dacrymyces* species 1**

Figure 33

Basidiocarp 5–7.5 × 1.5–2 mm, firm gelatinous, emerging as pustules that later become cylindrical, branched and lobed, yellowish, becoming paler with maturity. Spore print pale yellowish orange.

Hymenium distributed on the upper part of the basidiocarp, composed of hyphidia and basidia. **Hyphidia** 13–30 × 2–3 μm, cylindrical, unbranched. **Basidia** 15–29 × 3–4 μm, cylindrical to clavate, apically furcate, hyaline to pale yellow, guttulate, thin-walled. **Basidiospores** 6–10 × 3–5 μm (Q = 1.6–2.8 μm, Qm = 2.14 μm), ellipsoid, ellipsoid with median constriction, obovoid, thin-walled, guttulate with prominent apiculum, 0–1 septate, pale yellow to hyaline, germinating by microconidia. **Microconidia** 1.5–2 × 1.5–2 μm, globose, guttulate. **Tramal hyphae** 2–5 μm, slightly thick-walled, septate, smooth and roughened hyphae without clamp-connections. **Marginal hyphae** present towards the base of basidiocarp, slightly thick-walled, branched, flexuose and irregularly shaped hyphae.

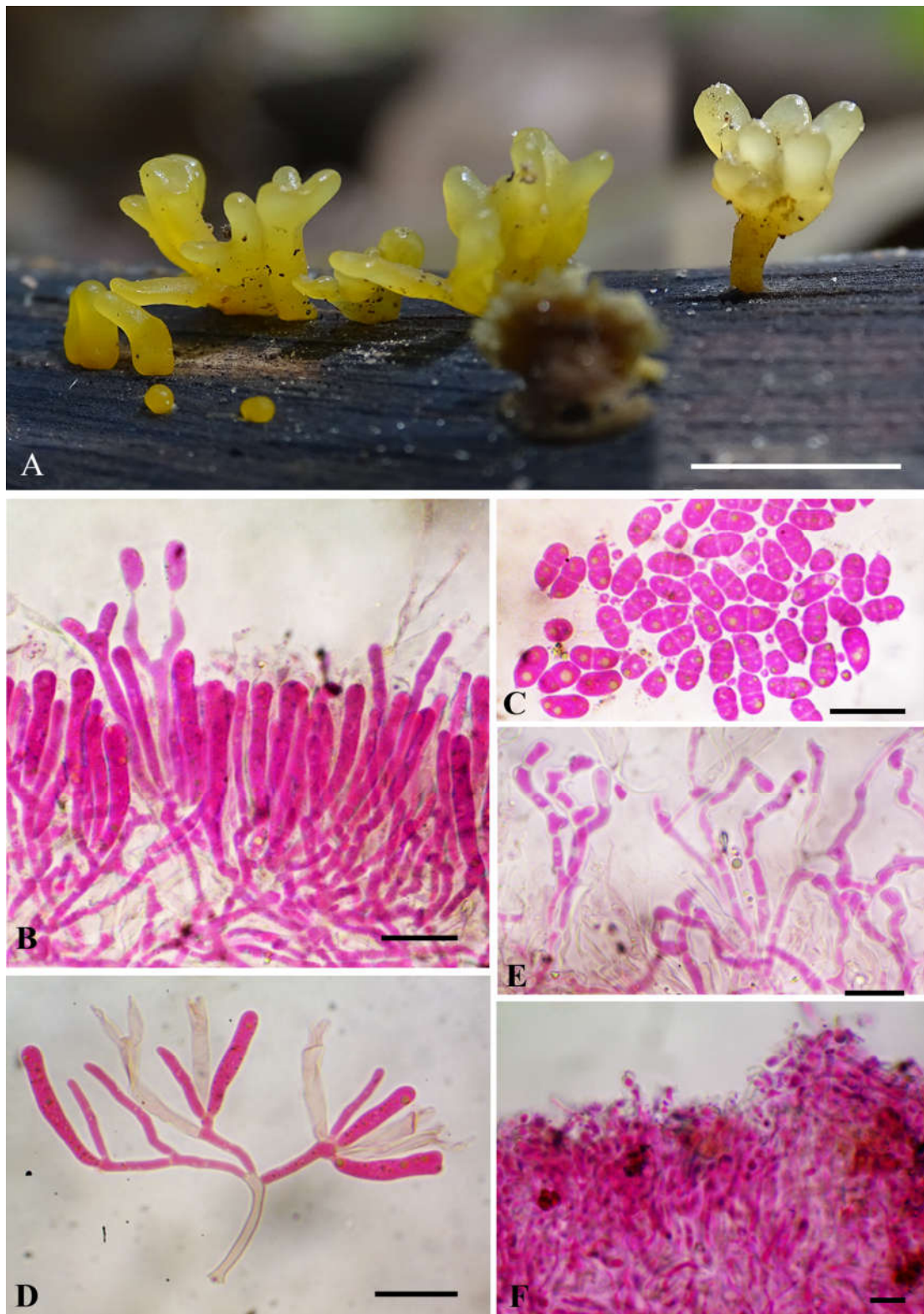


Figure 33: *Dacrymyces* species 1- **A.** Basidicarp; **B.** Hymenium with mature basidia and attached basidiospores; **C.** Basidiospores, septation and microconidia formation can be seen; **D.** Basidia of different stages and hyphidia; **E-F.** Marginal hyphae. Scale bars: A=10mm, B-F=10µm.

Specimens examined: INDIA. Kozhikode District, The Zamorin's Guruvayurappan College Campus, 4 September 2019, Anjitha Thomas, ZGCAT134; Malappuram District, Valluvassery, 14 January 2021, Anjitha Thomas, ZGCAT226.

Habitat: On dead wood.

Comments: *Dacrymyces* species 1 is characterized by cylindrical, branched, lobed yellowish basidiocarp with unbranched hyphidia; cylindrical to clavate bifurcating basidia; ellipsoid to obovoid, thin-walled, 0–1 septate basidiospores; globose microconidia; flexuose and irregularly shaped marginal hyphae, and tramal hyphae without clamp-connections.

In the phylogenetic tree (Figure 53), *Dacrymyces* species 1 is placed as a distinct clade near to the cylindrical, stipitate-pileate *Dacrymyces longistipitatus* Shirouzu and to the *Calocera* clade containing *C. cornea*, *C. furcata* (Fr.) Fr. and *C. viscosa*.

Morphologically, *Dacrymyces* species 1 has similarity with *Calocera* members by the cylindrical, branched, lobed basidiocarp morphology. But the presence of core zone in the cross section, which is the characteristic feature of genus *Calocera*, is absent in *Dacrymyces* species 1. By considering the morphological and phylogenetic similarities, this species can be considered as a member of the genus *Dacrymyces*.

Dacrymyces species 1 differs from *C. viscosa* in the basidiocarp morphology, whereas *C. viscosa* have repeatedly dichotomous, large basidiocarps that may be up to 10 cm high (McNabb 1965a). Although *Dacrymyces* species 1 is similar to *C. cornea* in other microscopic features, internal organisation into three zones is absent in the former. *Dacrymyces longistipitatus* is morphologically distinct by the presence of three septate basidiospores (Shirouzu *et al.* 2017).

Dacrymyces lacrymalis (Pers.) Nees, Syst. Pilze (Würzburg): 89 (1816) [1816-17]

Synonyms:

Dacrymyces deliquescens var. *lacrymalis* (Pers.) Duby, Bot. Gall., Edn 2 (Paris) 2: 729 (1830)

Dacrymyces stillatus var. *lacrymalis* (Pers.) Chevall., Fl. gén. env. Paris (Paris) 1: 98 (1826)

Dacrymyces tortus var. *lacrymalis* (Pers.) J. Kickx f., in Kickx, Fl. Crypt. Flandres (Paris) 2: 115 (1867)

Gyraria lacrymalis (Pers.) Gray [as 'lachrymalis'], Nat. Arr. Brit. Pl. (London) 1: 595 (1821)

Tremella lacrymalis Pers., Syn. meth. fung. (Göttingen) 2: 628 (1801)

Figure 34

Basidiocarp 2–8 × 2–4 mm, soft gelatinous, sessile, pustulate, appanate, irregularly discoid, gregarious, rarely coalescing. Pale yellow to yellow when fresh, turning brownish yellow when dry.

Hymenium amphigenous, composed of basidia intermixed with hyphidia. **Hyphidia** 17–31 × 2–4 µm, cylindrical, septate, branched, guttulate.

Basidia 26–32 × 5–6 µm hyaline, thin to slightly thick-walled, guttulate, cylindrical to narrowly clavate, apically furcate. **Basidiospores** 10–15 × 4.5–5 µm (Q = 1.9–3.5 µm, Qm = 2.41 µm), 0–3 septate, with guttules, apiculate, lacrymoid in side view, ellipsoid to subcylindrical in frontal view, thin to slightly thick-walled. Germination by producing microconidia. **Microconidia** 1–1.5 × 1–1.5 µm, globose, thin-walled, guttulate. Conidiophores present in the hymenium, 1–2 µm wide, flexuose, narrow, branched, budding spores from side. Conidia 1–2 × 1–1.5 µm, ellipsoid to oblong, thin-walled, guttulate. **Trametal hyphae** 2–5 µm wide, thick-walled, gelatinous, without clamp-connections.

Specimens examined: INDIA. Kerala State, Idukki District, Kanthallor, 27 July 2021, Anjitha Thomas, ZGCAT250.

Habitat: On dead wood.

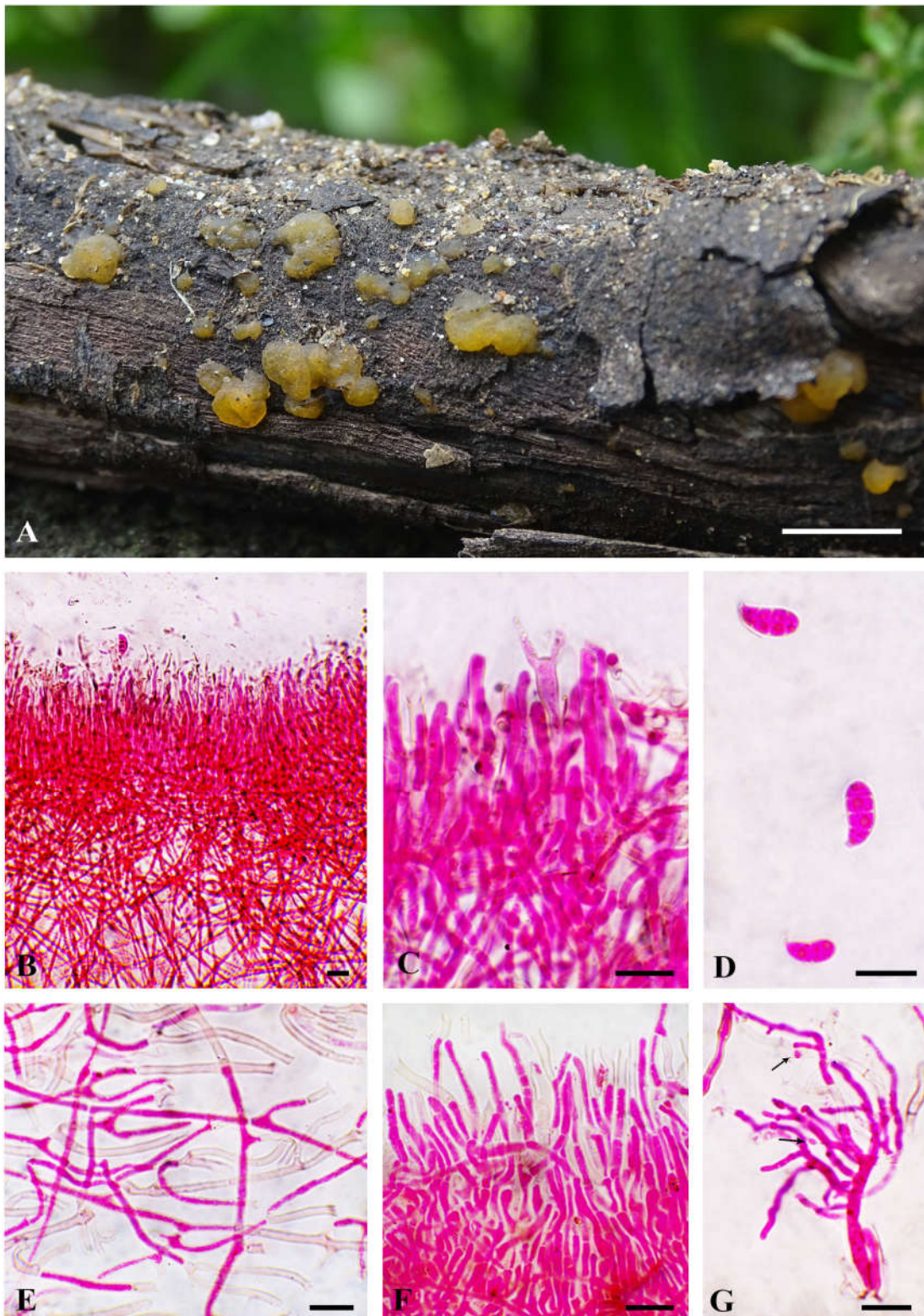


Figure 34: *Dacrymyces lacrymalis*- **A.** Basidiocarp; **B-C.** Hymenium; **D.** Basidiospores; **E.** Tramal hyphae; **F.** Marginal hyphae; **G.** Conidiophore with attached conidia (arrow). Scale bars: A=10mm, B-G=10µm.

Comments: *Dacrymyces lacrymalis* is characterised by pustulate, applanate, irregularly discoid basidiocarp, unbranched and cylindrical hyphidia, 0–3 septate, thin-walled basidiospores and hyphae without clamp-connections. *Dacrymyces lacrymalis* is similar to *D. stillatus* in having same basidiocarp morphology except for the formation of arthrospores in *D. stillatus* (McNabb 1973). Arthrospores were not observed in the Kerala collections and hence the specimen was identified as *D. lacrymalis*. *Dacrymyces lacrymalis* differs from *D. minor* by the size of basidiocarp. *Dacrymyces minor* is small in size with individual basidiocarps of 0.5–2 mm width, whereas the Kerala specimen is larger (2–9 mm wide). This species has no previous record from Kerala State.

Dacrymyces cupularis Lloyd, Mycological Writings (Cincinnati) 7: 1225 (1923)

Synonyms:

Dacrymyces deliquescens f. *stipitatus* Bourdot and Galzin [as 'stipitata'], Bull. Soc. mycol. Fr. 25(1): 33 (1909)

Dacrymyces deliquescens var. *ellisii* (Coker) L.L. Kenn., Mycologia 50(6): 911 (1959) [1958]

Dacrymyces deliquescens var. *stipitatus* (Bourdot and Galzin) Bigeard and H. Guill., Fl. Champ. Supér. France (Chalon-sur-Saône) 2: 508 (1913)

Dacrymyces ellisii Coker, J. Elisha Mitchell scient. Soc. 35(3): 167 (1920) [1919]

Dacrymyces radicans f. *stipitatus* (Bourdot and Galzin) Donk, Mededeelingen van de Nederlandsche mycologische vereeniging 18-20: 121 (1931)

Dacrymyces stipitatus (Bourdot and Galzin) Neuhoff, Ark. Bot. 28A(no. 1): 47 (1936)

Dacryomitra nuda (Berk. and Broome) Pat., Essai Tax. Hyménomyc. (Lons-le-Saunier): 31 (1900)

Dacryopsis nuda (Berk. and Broome) Masee, J. Mycol. 6(4): 182 (1891)

Dacryopsis ulicis (Plowr.) Sacc. and P. Syd., Syll. fung. (Abellini) 16: 223 (1902)

Ditiola nuda Berk. and Broome, Ann. Mag. nat. Hist., Ser. 2 2(no. 10): 267 (1848)

Ditiola ulicis Plowr., Trans. Br. mycol. Soc. 1(2): 55 (1899) [1897-1898]

Figure 35

Basidiocarp 2–5 × 1–5 mm, firm gelatinous, sessile to stipitate with irregularly discoid, subglobose or shallowly depressed pileus, discrete, not coalescing, yellowish to yellowish orange. Pileus becoming darker and stipe turning paler when dry.

Hymenium restricted to the upper surface of basidiocarp, composed of basidia intermixed with hyphidia. **Hyphidia** cylindrical to flexuose, septate, thick-walled and branched. **Basidia** 25–40 × 4.5–6 µm, thin- to thick-walled, cylindrical to narrowly clavate, guttulate, apically furcate. **Basidiospores** 10–14 × 5–7 µm, (Q = 1.6–2.3 µm, Qm = 2.05 µm) ellipsoid, curved cylindrical, phaseoliform, 0–3septate, guttulate, apiculate, thin- to thick-walled. Germination by microconidia. **Microconidia** 1–2 × 0.75–1 µm, subglobose to broadly ellipsoid, thin-walled. Direct germination with germ tube also observed. **Tramal hyphae** 2–4 µm wide, thick-walled, gelatinous, bulbous towards septa, smooth and roughened hyphae, clamp-connections absent. **Marginal hyphae**, thick-walled, with a narrow lumen.

Specimens examined: INDIA. Kerala State, Palakkad District, Parambikulam, 05 December 2019, Chandini, ZGCAT203.

Habitat: On dead wood.

Comments: *Dacrymyces cupularis* is characterised by pustulate, pulvinate basidiocarp with a stipe or stipe like rooting base, basal region often covered with whitish mycelium, 0–3 septate, thin-walled basidiospores and tramal hyphae without clamp-connections. On corticate wood, *D. cupularis* appears as stipitate and on decorticate wood, it appears as sessile and substipitate or short stipitate. *Dacrymyces microsporus* have stipitate basidiocarp with globose to semiglobose pileus. But they differ by the number of spore septations, *D. microsporus* is 0–1 septate and *D. cupularis* is 0–3 septate (McNabb 1973). *Dacrymyces lacrymalis* have 0–3 septate basidiospores and absence of clamp-connections. But *D. cupularis* have sessile, pustulate, applanate basidiocarps (McNabb 1973). This species has no previous record from Kerala State.

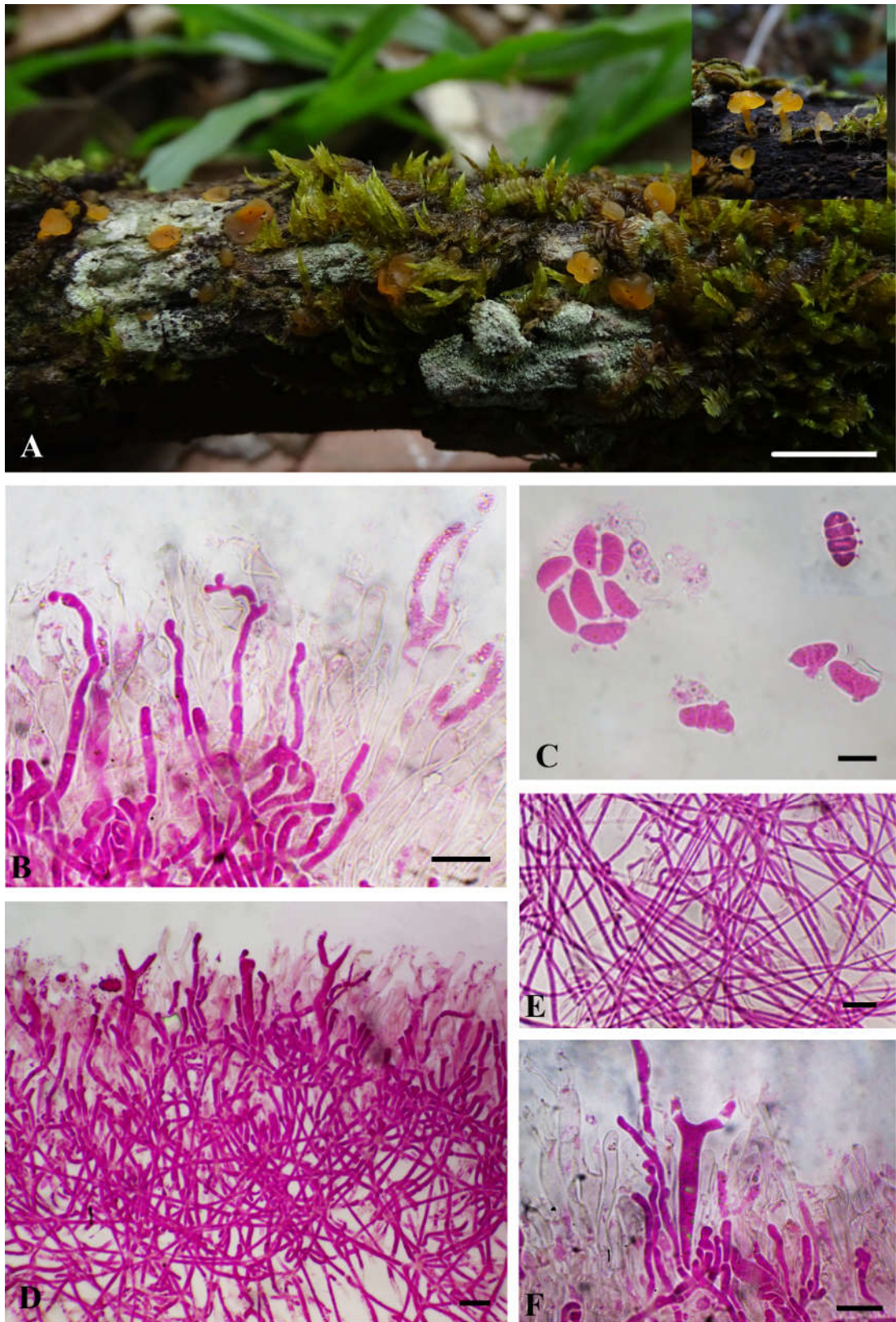


Figure 35: *Dacrymyces cupularis*- **A.** Basidiocarp; **B&D.** Hymenium; **C.** Basidiospores; **E.** Trametal hyphae; **F.** Basidia. Scale bars: A=10mm, B-F=10µm.

Dacrymyces capitatus Schwein., Transactions of American philosophical Society, New Series 4: 186 (1832) [1834]

Figure 36

Basidiocarp 2–21 × 2–7 mm, firm gelatinous, sessile to stipitate, emerging as pustulate to turbinate, capitate, later coalescing to form cerebriform masses. Pale brownish yellow when fresh, turning amber to dark brown when dry.

Hymenium limited to the upper surface of basidiocarp, composed of basidia intermixed with hyphidia. **Hyphidia** 30–45 × 2–3 µm, cylindrical, slightly flexuose, septate, unbranched, guttulate. **Basidia** 34–49 × 4–5 µm, hyaline, thin-walled, guttulate, cylindrical to narrowly clavate, apically furcate. **Basidiospores** 9–13 × 4–6 µm (Q = 1.5–2.6 µm, Qm = 2.13 µm), 0–3 septate, with guttules, apiculate, phaseoliform in side view, oblong, ellipsoid, broadly ellipsoid in frontal view, thin-walled. Germination by budding microconidia. **Microconidia**, subglobose to ellipsoid, thin-walled, guttulate, 1.5–3 × 1–2 µm. **Tramal hyphae** 2–4.5 µm wide, thin-walled, gelatinous, smooth or roughened, without clamp-connections. Conidiophores present within tramal hyphae, 2–3.5 µm wide, highly branched, thin-walled. Conidiospores, subglobose to ellipsoid, 1.5–3 × 1–2 µm, thin-walled, guttulate. **Marginal hyphae** absent.

Specimens examined: INDIA. Kerala State, Malappuram District, Vaniyambuzha, 27 October 2020, Anjitha Thomas, ZGCAT220.

Habitat: On dead wood.

Comments: Frequently coalescing, pustulate, turbinate or capitate basidiocarps, 0–3 septate basidiospores, and absence of clamp-connections are the characteristic features of *D. capitatus*. *Dacrymyces parastenosporus* Shirouzu, *D. pezizoides* Kobayasi and *D. stenosporus* Shirouzu have three septate basidiospores and lack clamp-connections in the tramal hyphae. The basidiospores of *D. capitatus* are smaller and differs from *D. parastenosporus*

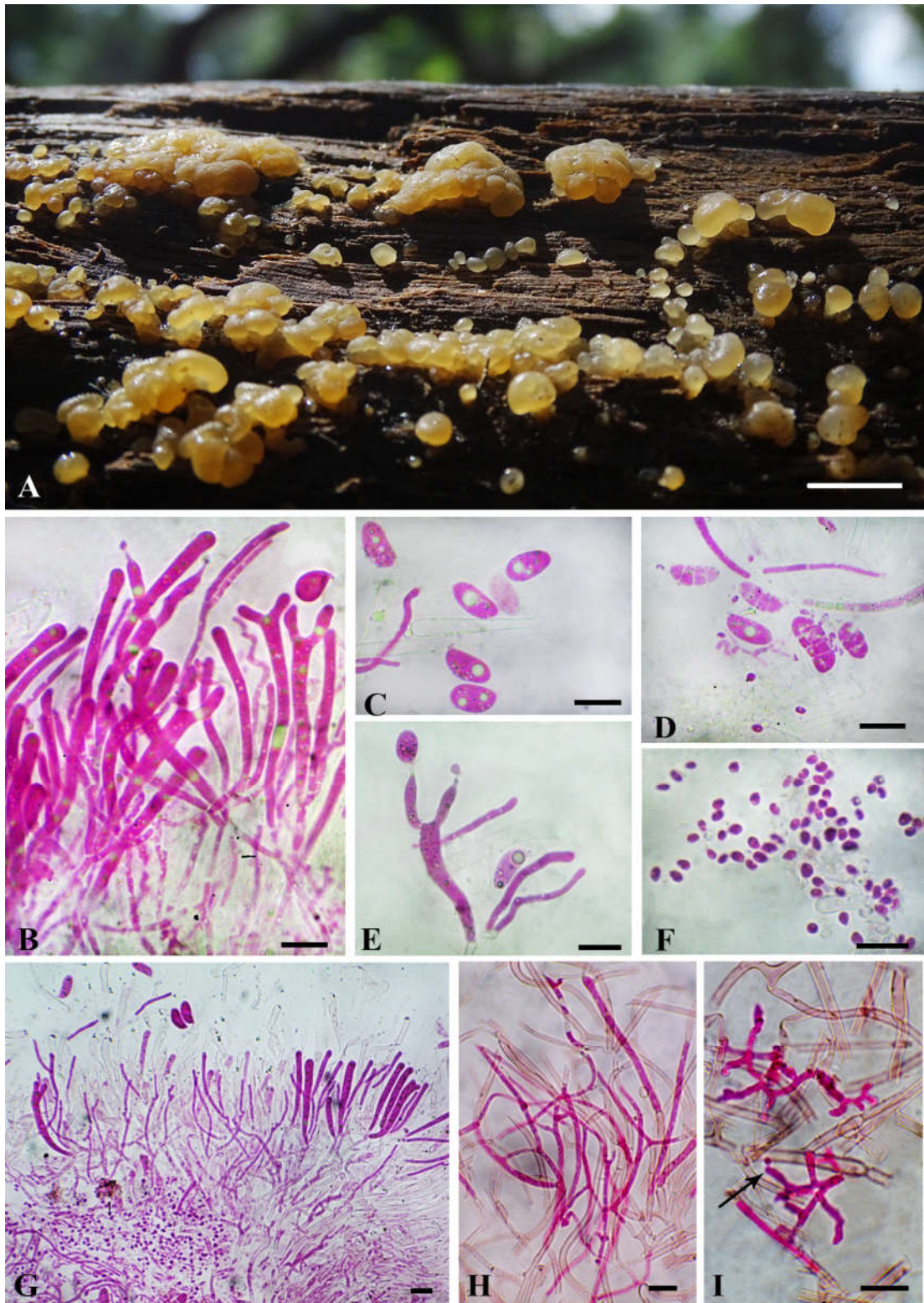


Figure 36: *Dacrymyces capitatus*- **A.** Basidiocarp; **B&E.** Basidia with basidiospores and hyphidia; **C&D.** Basidiospores; **F.** Microconidia; **G.** Hymenium; **H.** Tramal hyphae; **I.** Conidiophore (arrow points towards conidiospore). Scale bars: A=10mm, B-I=10µm.

which has larger basidiospores (14–17 × 4–6 µm, Shirouzu *et al.* 2017). *Dacrymyces stenosporus* has shorter basidia (30–40 × 4 µm) compared to the larger basidia (34–49 × 4–5 µm) of this Kerala collection. *Dacrymyces pezizoides* has straight to flexuose, septate, subglobose to cylindrical thick-walled marginal cells, which is absent in this specimen. This species has no previous record from Kerala.

Dacrymyces falcatus Brasf., Lloydia 1: 154 (1938)

Figure 37

Basidiocarp 2–3 × 1 mm, soft gelatinous, sessile, initially pustulate becoming applanate, irregularly discoid. Orange when fresh, turning to blackish brown when dry.

Hymenium limited to the upper surface of basidiocarp, composed of basidia intermixed with hyphidia. **Hyphidia** 21–34 × 2–4 µm, cylindrical, hyaline, unbranched, septate, guttulate, without clamp-connections. **Basidia** 31–42 × 6.8–7.2 µm, subhyaline, thin-walled, guttulate, cylindrical to clavate, apically furcate. **Basidiospores** 19–26 × 5.8–7.5 µm (Q = 2.9–4 µm, Qm = 3.46 µm), 0–15 septate, guttulate, apiculate, allantoid, subhyaline, thin-walled. **Germination** by microconidia. **Microconidia** 1.5–3 × 1–2 µm, subglobose to ellipsoid, thin-walled, guttulate. **Tramal hyphae** 2–5 µm wide, slightly thick-walled, gelatinous, smooth or roughened, without clamp-connections, swollen up to 8 µm towards septa, ring like bulging present around the septa. Abhymenial surface lack specialised hairs.

Specimens examined: INDIA. Kerala State, Kozhikode District, The Zamorins Guruvayurappan College campus, 11 July 2021, Anjitha Thomas, ZGCAT241.

Habitat: On dead wood.

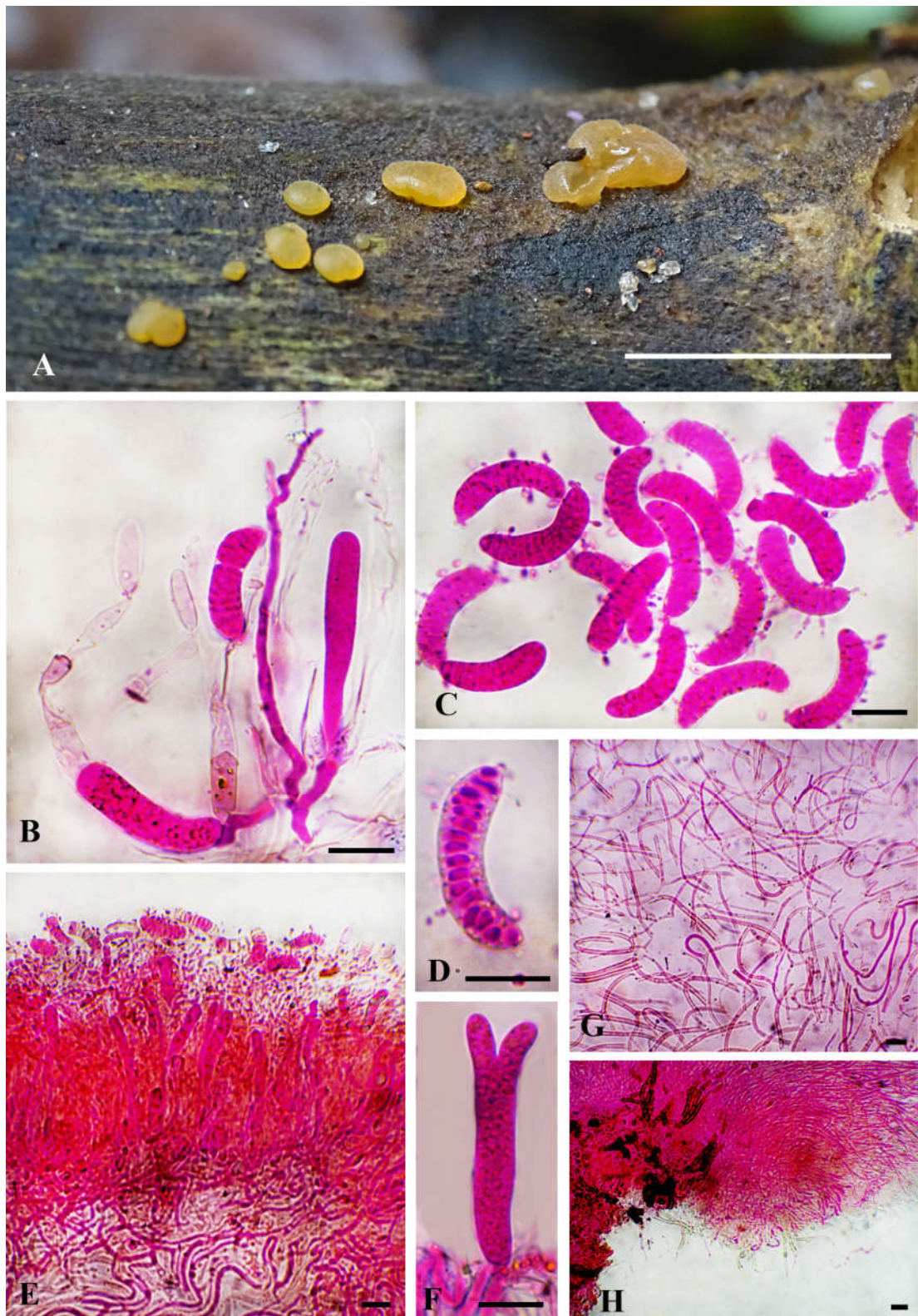


Figure 37: *Dacrymyces falcatus*- **A.** Basidiocarps; **B.** Basidia with hyphidia and basidiospore; **C.** Basidiospores; **D.** Basidiospore with 15 septa; **E.** Hymenium; **F.** Basidia; **G.** Trametal hyphae; **H.** Marginal hyphae. Scale bars: A=10mm, B-H=10µm.

Comments: *Dacrymyces falcatus* is characterised by flattened pustulate to petallate, strongly curved allantoid basidiospores, with 15 or more septations. According to Kennedy (1958), *D. falcatus* has larger basidia (40–60 (–70) × 6–8 µm) whereas, the Kerala specimen has smaller basidia (31–42 × 6.8–7.2 µm). This species has no previous record from India.

Dacrymyces novae-zelandiae McNabb, New Zealand Journal of Botany 11: 493 (1973)

Figure 38

Basidiocarp 6–15 × 5–9 mm, firm gelatinous, sessile, broadly attached to the substratum, applanate to cerebriform, amber brown when fresh, turning blackish brown when dry.

Hymenium limited to the upper surface of basidiocarp, composed of basidia intermixed with hyphidia. **Hyphidia** 40–60 × 2–3 µm, cylindrical, septate, unbranched, thin-walled. **Basidia** 42–53 × 4.5–5.5 µm, subhyaline, thin-walled, guttulate, cylindrical to clavate, apically furcate. **Basidiospores** 16–19.5 × 4.4–6.5 µm (Q = 2.6–4.6 µm, Qm = 3.53 µm), 0–7 septate, guttulate, apiculate, cylindrical to allantoid, thin-walled. Germination by microconidia. **Microconidia** 1.5–2.5 × 1–1.5 µm, ellipsoid to oblong, thin-walled, guttulate. **Tramal hyphae** 2–4.5 µm wide, thick-walled, gelatinous, smooth or roughened, without clamp-connections, hyphae swollen towards septa. **Marginal surface** lacks specialised structures.

Specimens examined: INDIA. Kerala State, Kozhikode District, The Zamorin's Guruvayurappan College campus, 19 June 2021, Anjitha Thomas, ZGCAT238.

Habitat: On dead wood.

Comments: *Dacrymyces novae-zelandiae* is characterised by applanate to cerebriform basidiocarp, simple cylindrical hyphidia, allantoid 0–7 septate basidiospores and hyphae without clamp-connections. The present specimen

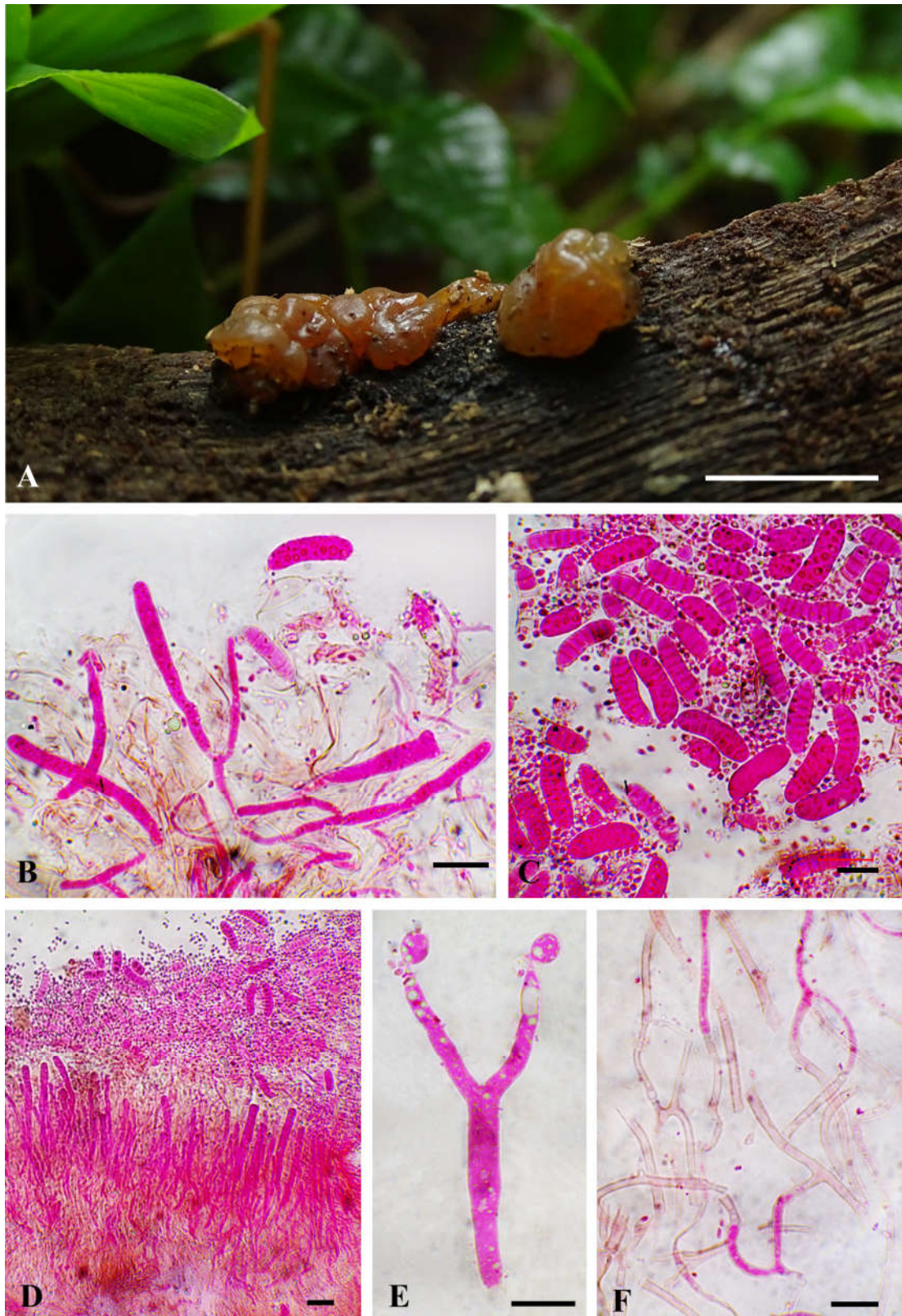


Figure 38: *Dacrymyces novae-zealandiae*- **A.** Basidiocarp; **B.** Basidioles and basidiospores; **C.** Basidiospores; **D.** Hymenium; **E.** Basidia with attached basidiospores; **F.** Tramal hyphae. Scale bars: A=10mm, B-F=10µm.

has thick-walled tramal hyphae, whereas the type specimen has thin-walled tramal hyphae. *Dacrymyces novae-zelandiae* differs from closely related *D. aureosporus* Shirouzu and Tokum. by lacking specialised cells in abhymenial surface. *Dacrymyces aureosporus* has thin-walled marginal hyphae and broader basidiospores ($16\text{--}19.5 \times 4.4\text{--}6.5 \mu\text{m}$ vs $17\text{--}26 \times 6.5\text{--}11 \mu\text{m}$) (Shirouzu *et al.* 2009). *Dacrymyces san-augustinii* has 7 or more septate basidiospores and hyphae without clamp-connections. But *D. san-augustinii* has branched hyphidia which is absent in *D. novae-zelandiae* (McNabb 1973).

Dacrymyces san-augustinii Kobayasi, Science Reports of Tokyo Bunrika Daigaku, Sect. B 4: 122 (1939)

Figure 39

Basidiocarp $3\text{--}11 \times 2\text{--}6$ mm, firm gelatinous, sessile, pustulate to pezizoid, irregularly discoid, cerebriform, discrete, rarely coalescing, yellowish brown to brown when fresh and dark brown when dry.

Hymenium limited to the upper surface of basidiocarp, composed of basidia intermixed with hyphidia. **Hyphidia** $40\text{--}8 \times 2\text{--}4 \mu\text{m}$, branched, septate, thin-walled. **Basidia** $32\text{--}56 \times 5\text{--}6.5 \mu\text{m}$, thin-walled, guttulate, cylindrical to clavate, apically furcate. **Basidiospores** $15\text{--}22 \times 5\text{--}6.5 \mu\text{m}$ ($Q = 2.8\text{--}4 \mu\text{m}$, $Q_m = 3.28 \mu\text{m}$), 0–12 septate, guttulate, apiculate, thin-walled, sub-cylindrical in frontal view, allantoid in side view. Germination by microconidia. **Microconidia** $1.5\text{--}4 \times 1.5\text{--}2 \mu\text{m}$, globose to ellipsoid, thin-walled, guttulate. **Tramal hyphae** $2\text{--}5 \mu\text{m}$ wide, slightly thick-walled, gelatinous, smooth and roughened hyphae, without clamp-connections. **Marginal hyphae** heavily gelatinised and agglutinated, without any specialised structures.

Specimens examined: INDIA. Kerala State, Malappuram District, New Amarambalam, 04 September 2021, ZGCAT266; Kozhikode District, Kakkad, 13 December 2023, ZGCAT355; ZGCAT357.

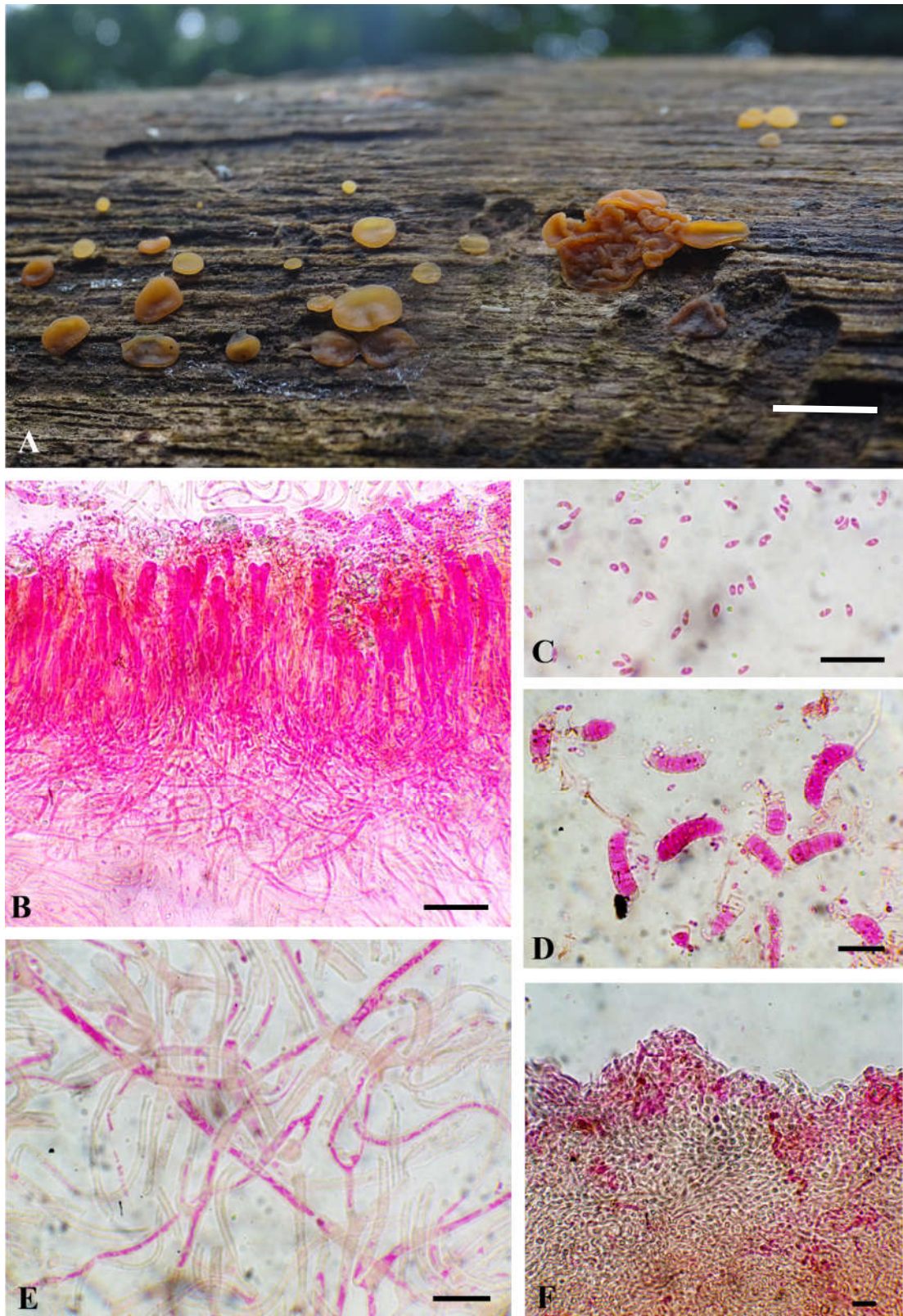


Figure 39: *Dacrymyces san-augustinii*- **A.** Basidiocarp; **B.** Hymenium; **C.** Microconidia; **D.** Basidiospores; **E.** Trametal hyphae; **F.** Marginal hyphae. Scale bars: A=10mm, B-F=10µm.

Habitat: On dead wood.

Comments: *Dacrymyces san-augustinii* is characterised by pustulate to pezizoid, irregularly discoid and cerebriform, with 0–7 septate basidiospores, and hyphae without clamp-connections. Presence of branched hyphidia distinguishes this species from *D. cerebriformis*, *D. sinostenosporus* and *D. novae-zelandiae* (Shirouzu *et al.* 2009, Lian *et al.* 2022).

Molecular sequences generated from ZGCAT226 is clustering with *D. san-augustinii* (TNS-F-15726) with 99% bootstrap support value. This species has no previous record from India.

***Dacrymyces* species 2**

Figure 40

Basidiocarp 2–4 × 2–3 mm, soft gelatinous, sessile to substipitate, pustulate, gregarious, and occasionally coalescing. Whitish, yellow to orangish when fresh, turning paler when dry. Whitish cottony growth observed around the basidiocarp initials.

Hymenium amphigenous, composed of basidia intermixed with hyphidia. **Hyphidia** cylindrical, septate and unbranched. **Basidia** 29–53 × 3.5–5 µm, thin-walled, cylindrical to narrowly clavate, guttulate, apically furcate, false septa frequently present. **Basidiospores** 14–19 × 3.5–5.5 µm (Q = 3.2–4.5 µm, Qm = 3.6 µm), allantoid in side view, cylindrical in frontal view, 0–7 septate, guttulate, apiculate. Germination by microconidia. **Microconidia** 1–2 × 1–1.5 µm, small, subglobose to ellipsoid, thin-walled. **Tramal hyphae** 2–4.5 µm wide, slightly thick-walled, gelatinous, smooth and roughened hyphae, without clamp-connections. **Marginal hyphae** 50–72 × 2–4 µm, thick-walled, cylindrical, septate, branched.

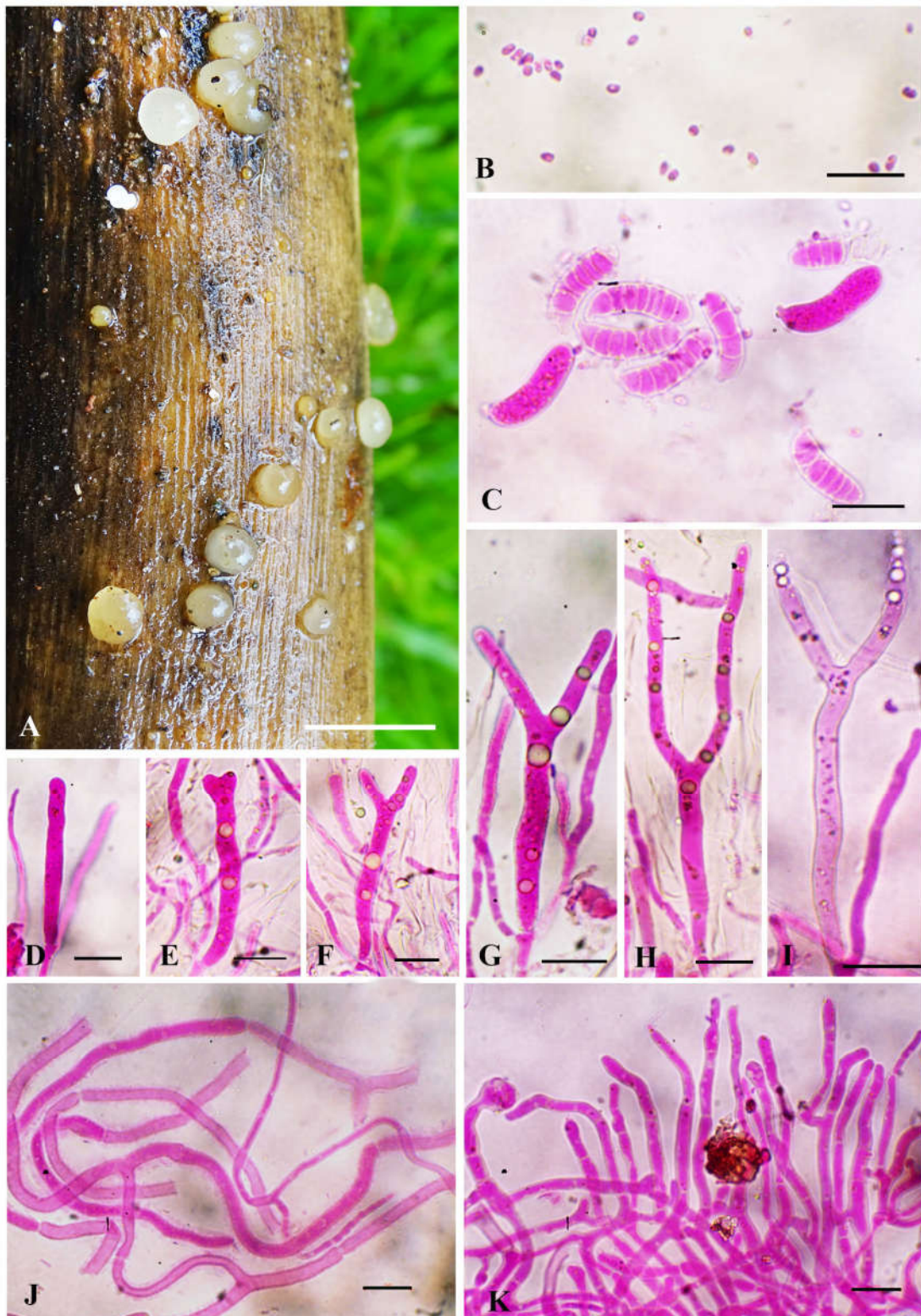


Figure 40: *Dacrymyces* species 2- **A.** Basidiocarp; **B.** Conidiospores; **C.** Basidiospores with conidiospores; **D-I.** Developmental stages of basidia; **J.** Tramal hyphae; **K.** Abhymental hairs. Scale bars: A=10mm, B-K=10µm.

Specimens examined: INDIA. Kerala State, Kozhikode District, Engapuzha, 28 May 2020, Anjitha Thomas, ZGCAT208; Kakkad, 15 June 2021, Anjitha Thomas, ZGCAT232.

Habitat: On dead wood.

Comments: *Dacrymyces* species 2 is characterised by pustulate, sessile or substipitate basidiocarp, absence of clamp-connections on hyphae, and 0–7 septate basidiospores.

Dacrymyces aureosporus, *D. cerebriformis*, *D. chrysospermus* Berk. and M.A. Curtis, *D. novae-zelandiae*, *D. san-augustinii* and *D. sinostenosporus* have 7 septate basidiospores and clamp-connections are absent. *Dacrymyces aureosporus* has turbinate to cerebriform basidiocarp with larger basidia, (46–80 × 5.5–8 µm) and basidiospores (17–26 × 6.5–11 µm). The Kerala specimen has smaller basidia (29–53 × 3.5–5 µm) and smaller basidiospores (14–19 × 3.5–5.5 µm). *Dacrymyces cerebriformis* has larger basidiocarp (up to 3 mm high and 5–10 mm diameter), larger basidiospores (18–23 × 5.4–8 µm), and are phylogenetically distant (Figure 53). *Dacrymyces chrysospermus* has variable basidiocarp morphology ranging from flabellate, stoutly stipitate, spathulate to cupulate forms, which extend up to 6 cm. Whereas, *D. species 2* is pustular and much smaller. *Dacrymyces novae-zelandiae* differs from this specimen in having cerebriform basidiocarp which extends up to 6 cm. *Dacrymyces san-augustinii* differs from *D. species 2* in having branched hyphidia. *Dacrymyces sinostenosporus* differs by its larger basidiospores (17–24 × 5.9–8.4 µm).

In the phylogenetic analysis, *D. species 2* settles in a clade distinct from *D. novae-zelandiae* and *D. san-augustinii* (Figure 53).

Dacrymyces "cerebriformis" F. Wu and Y.P. Lian, in Lian, Tohtirjap and Wu, Diversity 14: 6 (2022)

Figure 41

Basidiocarp 2–15 × 2–6 mm, soft gelatinous, sessile to stipitate, gregarious, caespitose, pustulate to irregularly discoid, cerebriform, lobed, deeply rooted in the bark (substratum). Pure white to orangish yellow when fresh, turning to pale orangish when dry. Spore print pale orange in colour.

Hymenium limited to the upper surface of basidiocarp, composed of basidia intermixed with hyphidia. **Hyphidia** 30–49 × 2–3 µm, cylindrical septate, unbranched and thick-walled. **Basidia** 45–58 × 4–5.5 µm, hyaline, slightly thick-walled, guttulate, cylindrical to narrowly clavate, apically furcate. **Basidiospores** 18–21 × 5–7 µm (Q = 2.5–4 µm, Qm = 3.15 µm), 0–7 septate, with guttules, apiculate, allantoid in side view, ellipsoid in frontal view, thin to slightly thick-walled, thin to slightly thick-septations. Germination by microconidia. **Microconidia** subglobose to ellipsoid, thin-walled, guttulate, 3–5 × 2–3 µm. **Crystalline contents** present throughout basidiocarp. **Marginal hyphae** slightly thick-walled, frequently anastomosing, short, cylindrical to clavate, frequently septate, branched hyphae. **Tramal hyphae** 2–4.5 µm wide, thin to slightly thick-walled, gelatinous, 2–5 µm wide, bulbous towards septa, ring like thickening in septa, inflated in some regions up to 7 µm, without clamp-connections.

Specimens examined: INDIA. Kerala State, Palakkad District, Silent Valley National Park, 22 October 2019, Anjitha Thomas, ZGCAT170; Malappuram District, Vaniyambuzha, 27 October 2020, Anjitha Thomas, ZGCAT216.

Habitat: On dead wood.

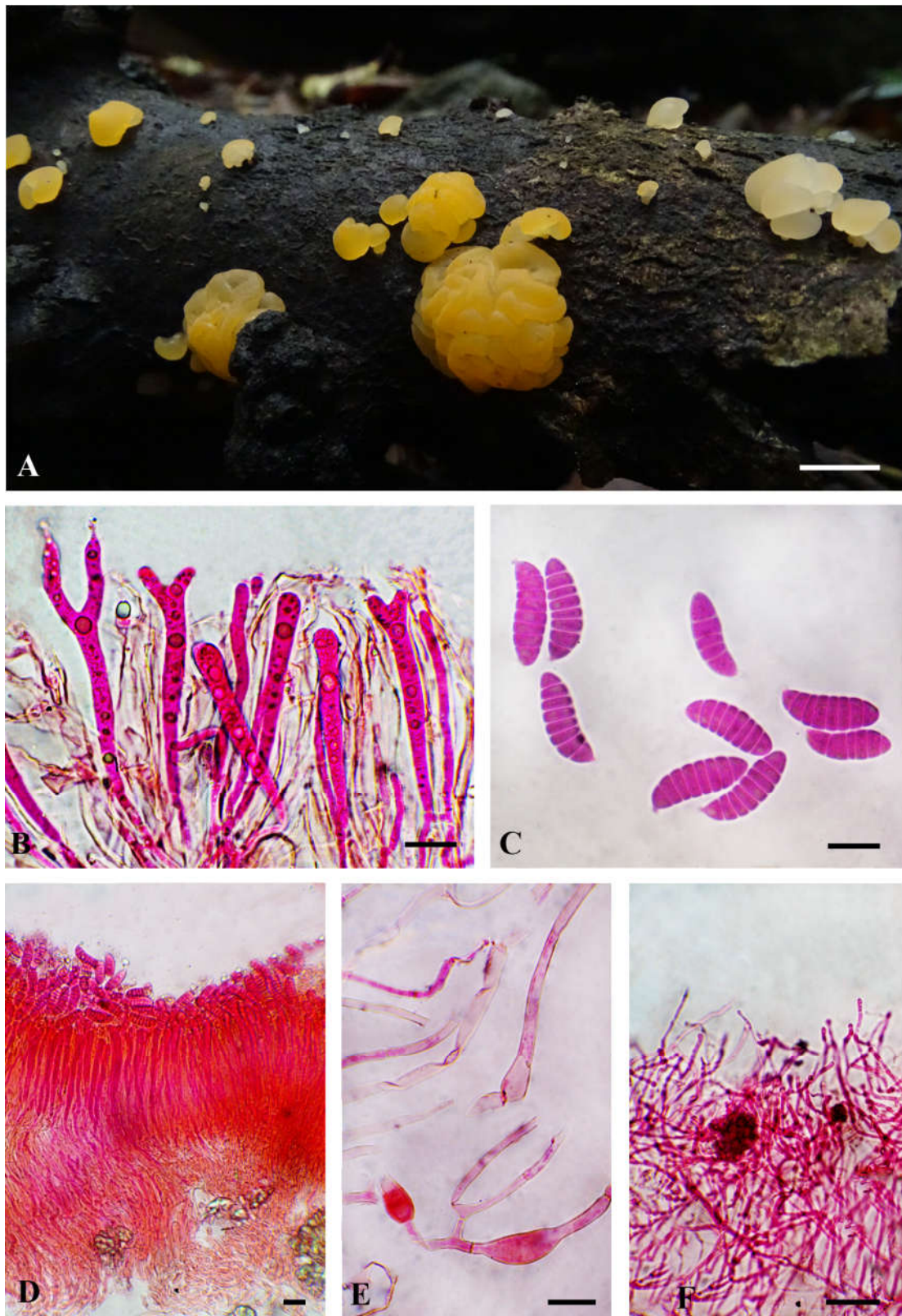


Figure 41: *Dacrymyces "cerebriformis"*- **A.** Basidiocarp; **B.** Basidia and basidioles; **C.** Basidiospores; **D.** Hymenium; **E.** Tramal hyphae; **F.** Marginal hairs. Scale bars: A=10mm, B-F=10µm.

Comments: *Dacrymyces cerebriformis* is characterised by sessile, cerebriform basidiocarp, absence of clamp-connections, and 0–7 septate basidiospores. This specimen is similar to *D. sinostenosporus* by the 0–7 septate basidiospores, and hyphae without clamp-connections. *Dacrymyces sinostenosporus* has broader basidiospores (Q = 2.63–2.77 vs. Q = 3.14–3.28) (Lian *et al.* 2022). *Dacrymyces adpressus* Grognot and *D. sichuanensis* B. Liu and L. Fan have cerebriform basidiocarp similar to *D. cerebriformis*, although both possess 0–3 septate basidiospores (Shirouzu *et al.* 2009, Lian *et al.* 2022). *Dacrymyces aureosporus* has cerebriform basidiocarps with 7 septate basidiospores and lack clamp-connections. But *D. aureosporus* differ from *D. cerebriformis* by having thin-walled marginal hyphae and broader basidiospores (17–26 × 6.5–11 µm vs 18–21 × 5–7 µm) (Shirouzu *et al.* 2009).

Although Lian *et al.* (2022) described the species as *D. "cerebriformis"* (Mycobank number: 843769) from China, another species with the same name existed before the publication of Lian *et al.* (2022). The species name proposed by Lian *et al.* (2022) is hence illegitimate (www.mycobank.org accessed on 13 June 2024). Our collection morphologically agrees with the characters of the species described by Lian *et al.* (2022) as *D. "cerebriformis"*. This species has no previous record from India.

Dacrymyces sinostenosporus F. Wu and Y.P. Lian, in Lian, Tohtirjap and Wu, Diversity 14: 7 (2022)

Figure 42

Basidiocarp 3–11 × 3–8 mm, firm gelatinous, sessile to stipitate, lobed, centrally depressed, cerebriform, discrete, gregarious, pale yellowish to orange when fresh, turning to bright orange when dry, some basidiocarps on the underside of twig (substratum) appeared pale.

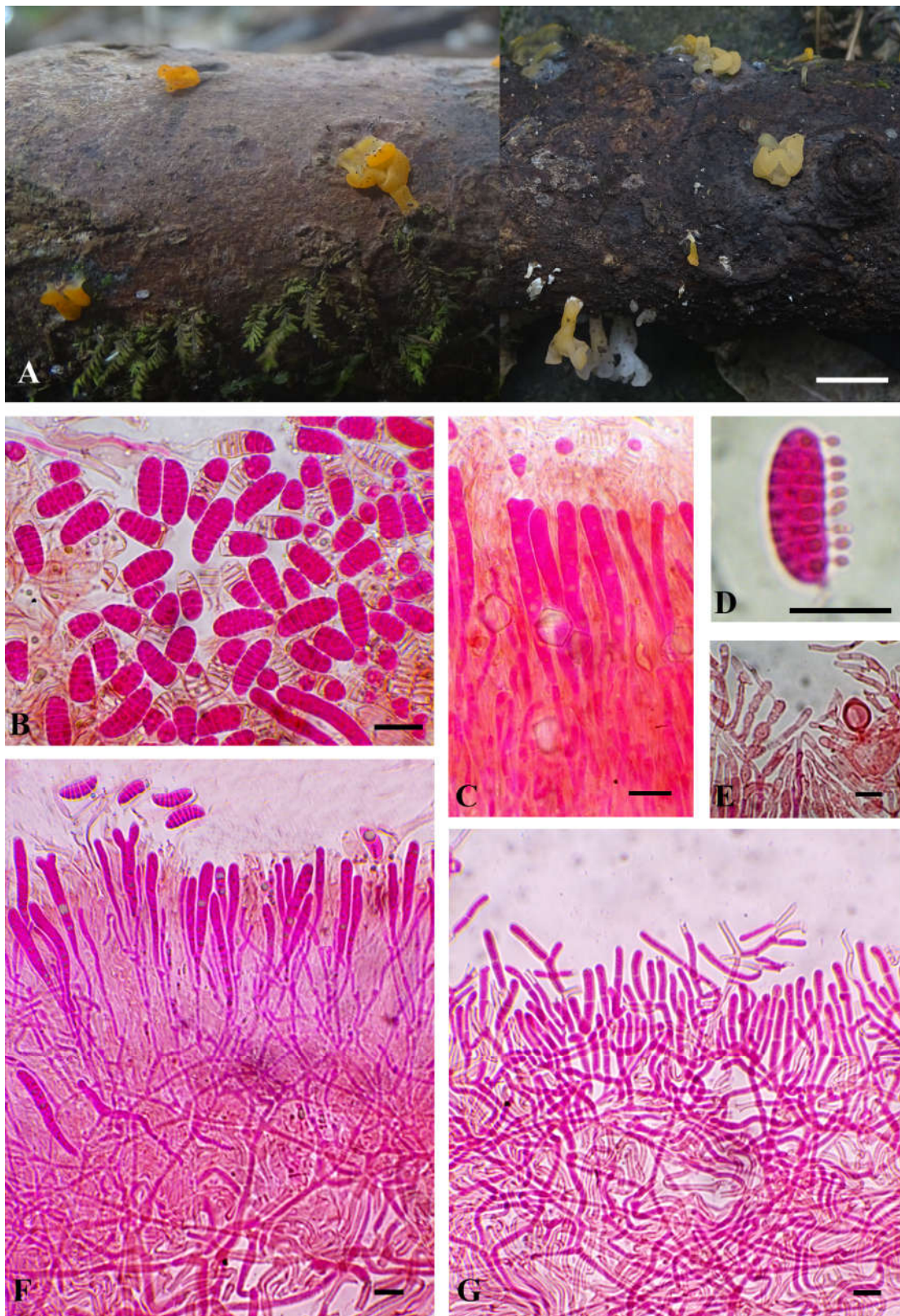


Figure 42: *Dacrymyces sinostenosporus*- **A.** Basidiocarp; **B&D.** Basidiospores; **C&F.** Hymenium with basidia and basidiospores; **E&G.** Marginal hairs. Scale bars: A=10mm, B-G=10µm.

Hymenium limited to the upper surface of basidiocarp, composed of basidia intermixed with hyphidia. **Hyphidia** 15–42 × 2–3 µm, cylindrical and septate, guttulate. **Basidia** 35–66 × 5–6 µm, hyaline, slightly thick-walled, guttulate, cylindrical to narrowly clavate, apically furcate. **Basidiospores** 17–21 × 6.5–8 µm (Q = 2.37–3 µm, Qm = 2.68 µm), 0–7 septate, with guttules, apiculate, allantoid in side view, broadly ellipsoid to subcylindrical in frontal view, thin- to slightly thick-walled. Germination by microconidia. **Microconidia** 1.5–3 × 1–2 µm, subglobose to ellipsoid, thin-walled, guttulate. **Tramal hyphae** 2–4.5 µm wide, slightly thick to thick-walled, gelatinous, without clamp-connections, swollen up to 7 µm towards septa. **Marginal hyphae** cylindrical, thin- to thick-walled, smooth or roughened hairs.

Specimens examined: INDIA. Kerala State, Wayanad District, Kurchyarmala, 26 October 2022, Anjitha Thomas, ZGCAT343; ZGCAT344.

Habitat: On dead wood.

Comments: *Dacrymyces sinostenosporus* is characterised by sessile to stipitate, lobed, cerebriform basidiocarps with simple cylindrical hyphidia, 0–7 septate, thin-walled basidiospores and tramal hyphae without clamp-connections. *Dacrymyces chrysospermus* has micro morphological features similar to *D. sinostenosporus*, but the former coalesces to form masses up to 6 cm in diameter. *Dacrymyces dictyosporus* also have similar basidiocarp, basidial morphology, and absence of clamp-connections. But it differs from *D. sinostenosporus* by the thick-walled basidiospores having both transverse and longitudinal septa. *Dacrymyces novae-zelandiae* differs from the present collection by the coalescent nature of the basidiocarp. *Dacrymyces cerebriformis* is morphologically similar to *D. sinostenosporus*. But the former has narrower basidiospores (Q = 3.14–3.28 µm) compared to *D. sinostenosporus* (Q = 2.37–3 µm). This species has no previous record from India.

4.2.3. Taxonomic descriptions of Auriculariales

Auricularia Bull.

Basidiocarp gelatinous and rubbery when fresh, stipitate or resupinate with free margins, orbiculate, lobed, pileate, cupulate; solitary, gregarious, imbricate or caespitose. When dry, translucent to opaque, thin and brittle. Superior abhymenial surface is hairy, glabrous to velutinous, pubescent, tomentose, villose to hispid, strigose to hirsute. Inferior surface bearing the hymenium; smooth, folded to reticulate. Basidiocarp zonate (*zona pilosa, zona compacta, zona subcompacta superioris, zona laxa superioris, medulla, zona laxa intermedia, zona laxa inferioris, zona subcompacta inferioris*, hymenium). Hymenium with hyphidia. Basidia are transversely three septate, cylindrical to clavate, guttulate and with slender epibasidia. Basidiospores hyaline, inamyloid, cylindrical to allantoid.

Auricularia srilankensis Y.C. Dai and F. Wu, in Wu, Tohtirjap, Fan, Zhou, Alvarenga, Gibertoni and Dai, Journal of Fungi 7: 53 (2021)

Figure 43

Basidiocarp up to 140 mm wide, 1–2.5 mm thick, resupinate to effused reflexed, rosette, coalescing, cartilaginous, lobed. Hymenophore surface smooth with folds, yellowish brown initially changing to blackish brown with maturity. Abhymenial surface villose to hispid with blackish brown concentric zones. Abhymenial hairs whitish when young turning brownish with age.

Abhymenial hairs 900–1700 × 2–3.5 µm, irregular, single to tufted, hyaline when young, yellowish brown on maturity, thick-walled, with narrow lumen, narrower towards the tip, apically acute or obtuse. **Tramal hyphae** 1.5–5.5 µm wide, inflated up to 14.7 µm, thin- to thick-walled, clamp-connections present. **Medulla** absent. **Basidia** 50–73 × 3.5–6 µm, cylindrical, clavate, thin-

walled, transversely 3-septate. **Hyphidia** highly branched, coral like. **Cystidia** not observed. **Basidiospores** 8–13.5 × 5–8 µm (Q = 1.1–2.1 µm, Qm = 1.61 µm) hyaline, subglobose, cylindrical to phaseoliform, thin-walled, guttulate.

Specimens examined: INDIA. Kerala State, Kozhikode District, Janaki forest, 01 October 2018, Anjitha Thomas, ZGCAT29; Palakkad District, Silent Valley National Park, 22 October 2019, Anjitha Thomas, ZGCAT174; Malappuram District, Vanniyambuzha, 27 October 2020, Anjitha Thomas, ZGCAT215; Kannur District, Aralam Wildlife Sanctuary, 06 August 2021, Anjitha Thomas, ZGCAT261; Malappuram District, New Amarambalam, 04 September 2021, Anjitha Thomas, ZGCAT270; Thiruvananthapuram District, Palode, 01 October 2021, Anjitha Thomas, ZGCAT285; Malappuram District, Nilambur, 23 October 2021, Anjitha Thomas, ZGCAT300.

Habitat: On dead wood.

Comments: *Auricularia srilankensis* belongs to the *mesenterica* clade and is characterized by resupinate basidiocarp with concentric zones in the abhymenial surface, lack of medulla zone, cylindrical to clavate basidia (50–73 × 3.5–6 µm), absence of cystidioles, and cylindrical to phaseoliform basidiospores (8–13.5 × 5–8 µm). In the original description of *A. srilankensis* (Wu *et al.* 2021), length of abhymenial hairs range from 400–800 µm, whereas, the Kerala specimens show 900–1700 µm long hairs. *A. srilankensis* is closely related to *A. orientalis* Y.C. Dai and F. Wu, but differs in the presence of have cystidioles (as per the original description by Wu *et al.* 2021) in the latter. In our phylogenetic analysis, *A. srilankensis* form sister clade with *A. asiatica* but differs from *A. asiatica* Bandara and K.D. Hyde in the basidial size (basidia of *A. asiatica*: 40–52 × 3–6 µm). ITS sequence generated from the Kerala collections (ZGCAT155) showed 100% similarity with the type sequence of *A. srilankensis* (Figure 51). *Auricularia srilankensis* is reported from India by Bhagat *et al.* (2024) and this is the first report of this species from Kerala state.

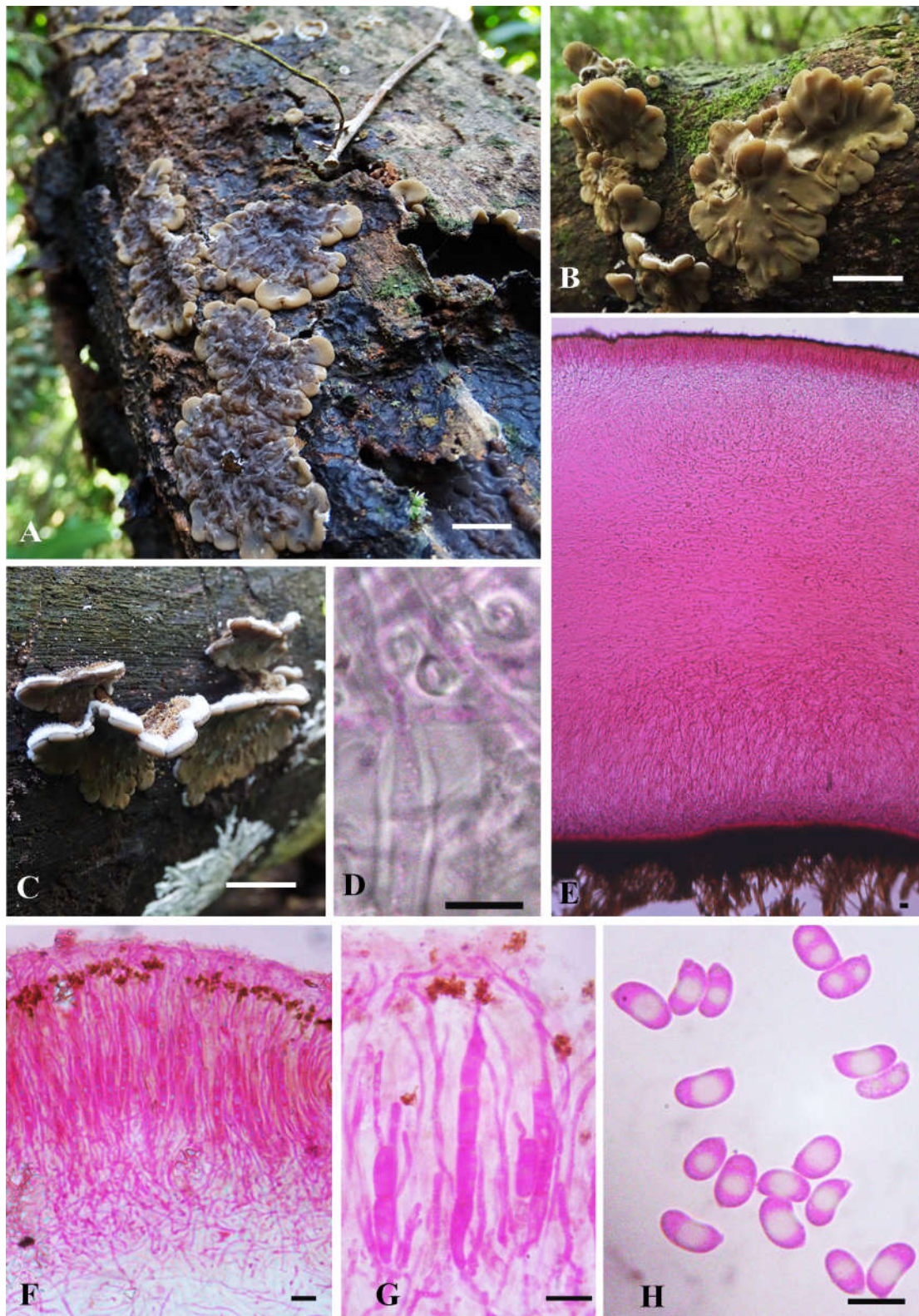


Figure 43: *Auricularia srilankensis*- **A-C.** Basidiocarp; **D.** Inflated hyphae; **E.** Cross-section of basidiocarp; **F.** Hymenium; **G.** Transversely septate basidia with hyphidia; **H.** Basidiospores. Scale bars: A-C=10mm, D-G=10µm.

Auricularia sinodelicata Y.C. Dai and F. Wu, in Wu, Tohtirjap, Fan, Zhou, Alvarenga, Gibertoni and Dai, Journal of Fungi 7: 52 (2021)

Figure 44

Basidiocarp 30–80 mm wide and 1–2 mm thick, sessile, petaliform, solitary, caespitose, cartilaginous. Margin wavy. Hymenophore surface reticulate, yellowish brown to brown, blackish brown at the margin. Abhymenial surface glabrous to slightly pubescent, slightly folded or wrinkled, pale yellow towards the base, and dark brown towards margin.

Abhymenial hairs 35–75 × 6.5–7 µm, single, with slightly swollen base, hyaline to yellowish brown, thick-walled, narrow lumened and narrower towards tip, apically acute or obtuse. **Tramal hyphae** 2– 4.5 µm wide, thin-walled, clamp-connections present. **Medulla** present. **Basidia** 32–45 × 4–5 µm, cylindrical to clavate, thin-walled, transversely 3-septate. **Epibasidia** observed. **Hyphidia** highly branched. **Cystidioles** not observed. **Basidiospores** 10–13.5 × 4.5–5 µm (Q = 2– 2.7 µm, Qm = 2.28 µm) hyaline, cylindrical to oblong in front view and slightly allantoid in side view, thin-walled, guttulate.

Specimens examined: INDIA. Kerala State, Kannur District, Aralam, 29 June 2019, Anjitha Thomas, ZGCAT71; Palakkad District, Silent Valley National Park, 4 Junly 2019, Anjitha Thomas, ZGCAT85; Wayanad District, Kurchyarmala, 26 October 2022, Anjitha Thomas, ZGCAT342; Palakkad District, Parambikulam, 12 June 2022, Anjitha Thomas, ZGCAT312.

Habitat: On dead wood.

Comments: Previously, all *Auricularia* members with reticulate hymenopore were treated as *A. delicata* (Mont. ex Fr.) Henn.. Looney *et al.* (2013) confirmed *A. delicata* as a species complex. By using new morphological features like 'schizomedulla' and phylogenetic analyses, different species like *A. australiana*

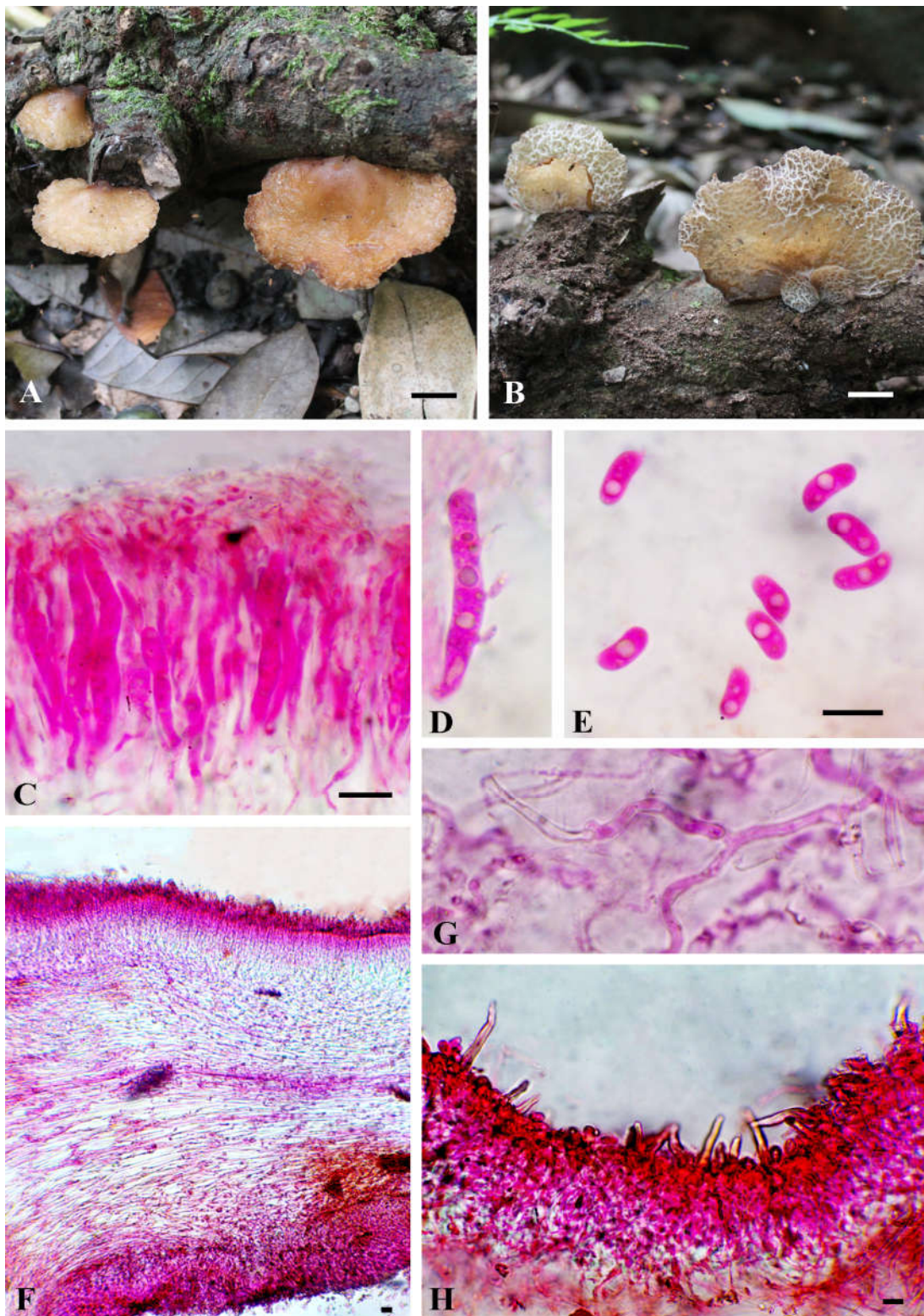


Figure 44: *Auricularia sinodelicata*- **A&B.** Basidiocarps; **C.** Hymenium; **D.** Basidia; **E.** Basidiospores; **F.** Cross section showing tramal zones; **G.** Tramal hyphae with clamp-connections; **H.** Abhymenial hairs. Scale bars: A&B=10mm, C-H=10µm.

Y.C. Dai and F. Wu, *A. conferta* Y.C. Dai and F. Wu, *A. lateralis* Y.C. Dai and F. Wu, *A. pilosa* Y.C. Dai, L.W. Zhou and F. Wu, *A. scissa* Looney, Birkebak and Matheny, *A. sinodelicata* Y.C. Dai and F. Wu, *A. subglabra* and *A. tremellosa* (Fr.) Pat. were described, and resolved as members of *A. delicata* complex members (Looney *et al.* 2013, Wu *et al.* 2021, Rodríguez-Gutiérrez *et al.* 2022). *Auricularia sinodelicata* differs from *A. scissa* and *A. subglabra* in the absence of schizomedulla, where both *A. scissa* and *A. subglabra* have schizomedulla (Looney *et al.* 2013). *Auricularia lateralis* and *A. pilosa* have pilose abhymenial surface with abhymenial hairs more than 100 µm long (Wu *et al.* 2021), whereas, *A. sinodelicata* has abhymenial hairs less than 100 µm long. *Auricularia australiana*, *A. conferta* and *A. delicata* have longer basidia, (more than 45 µm long) compared to *A. sinodelicata*. This is the first report of *A. sinodelicata* from India.

Auricularia subglabra Looney, Birkebak and Matheny, in Schulzer, North American Fungi 8: 17 (2013)

Figure 45

Basidiocarp 20–35 mm wide and 1–2.5 mm thick, solitary or caespitose, petalliform, sessile, gelatinous to rubbery when fresh, rigid and brittle when dry, margin wavy. Hymenophore reticulate, pale yellow. Abhymenial surface glabrous to pubescent, brownish orange with brown margin.

Abhymenial hairs 30–70 × 6–8 µm, irregular, hyaline, apically acute or obtuse, thick-walled, with a narrow lumen. **Tramal hyphae** 1–5 µm wide, with clamp-connections, thin-to slightly thick-walled. **Schizomedulla** present. **Basidia** 35–42 × 4–5 µm, clavate, transversely 3-septate, guttulate. **Epibasidia** rarely observed. **Hyphidia** highly branched. **Cystidioles** not observed. **Basidiospores** 8–11 × 4–6 µm (Q = 1.6–2.75 µm, Qm = 2.03 µm) allantoid, hyaline, thin-walled, smooth, guttulate.

Specimens examined: INDIA, Kerala State, Waynad District, 25 August 2018, Anjitha Thomas, ZGCAT22.

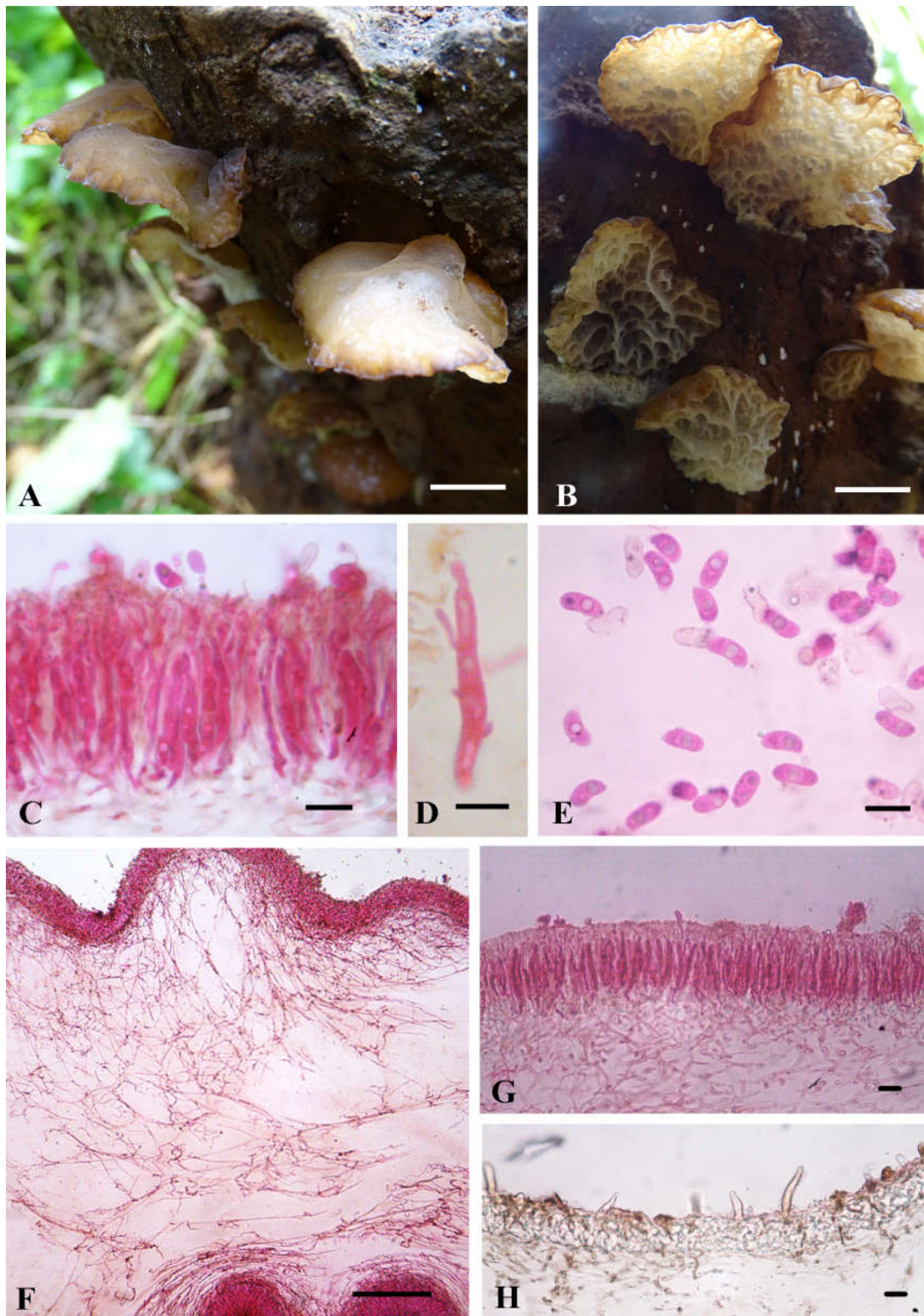


Figure 45: *Auricularia subglabra*- **A&B.** Basidiocarps; **C.** Hymenium with attached basidiospores; **D.** Basidia; **E.** Basidiospores; **F.** Cross-section showing schizomedulla; **G.** Hymenium; **H.** Abhymenium. Scale bars: A&B=10mm, C-E=10 μ m, F=100 μ m, G&H=10 μ m.

Habitat: On dead wood.

Comments: Presence of reticulate hymenium and schizomedulla are the characteristic features of *A. subglabra*. Looney *et al.* (2013) introduced the term schizomedulla to denote medulla that splits apart when sections are mount in KOH. *Auricularia scissa* is closely related to *A. subglabra* with the presence of Schizomedulla. *Auricularia scissa* possesses longer abhymenial hairs 43–148 × 2.3–5.4 µm, whereas *A. subglabra* has shorter (30–70 × 6–8 µm) abhymenial hairs (Looney *et al.* (2013). This is the first report of *A. sinodelicata* from India.

Auricularia cornea Ehrenb., in Nees von Esenbeck (Ed.), Horae Phys. Berol.: 91 (1820)

Synonyms:

Auricula cornea (Ehrenb.) Kuntze, Revis. gen. pl. (Leipzig) 2: 844 (1891)

Exidia cornea (Ehrenb.) Fr., Syst. mycol. (Lundae) 2(1): 222 (1822)

Hirneola cornea (Ehrenb.) Fr., K. svenska Vetensk-Akad. Handl., ser. 3: 147 (1849) [1848]

Figure 46

Basidiocarp 45–69 mm wide and 1–2 mm thick, solitary, discoid, sessile, gelatinous rubbery when fresh. Hymenophore smooth to folded, grayish. Abhymenial surface tomentose, brownish, without any zonations. Margin incurved, undulate. Spore print white.

Abhymenial hairs 70–250 × 5–9 µm, hyaline, tufted, swollen at base, apically acute or obtuse, thick-walled with narrow lumen. **Tramal hyphae** 2–4 µm wide, inflated up to 7 µm in KOH, thin-walled with clamp-connections. **Medulla** present. **Crystalline contents** present. **Basidia** 30–45 × 4–5.5 µm, clavate, transversely 3-septate, guttulate, thin-walled. **Epibasidia** observed. **Hyphidia** highly branched with brownish structure at the tip. **Cystidioles** not observed. **Basidiospores** 11–13.5 × 4–5 µm (Q = 1.5–2.9 µm, Qm = 2.45 µm) ellipsoid, lacrymoid, some with suprahilar depression, hyaline, thin-walled, smooth, guttulate.

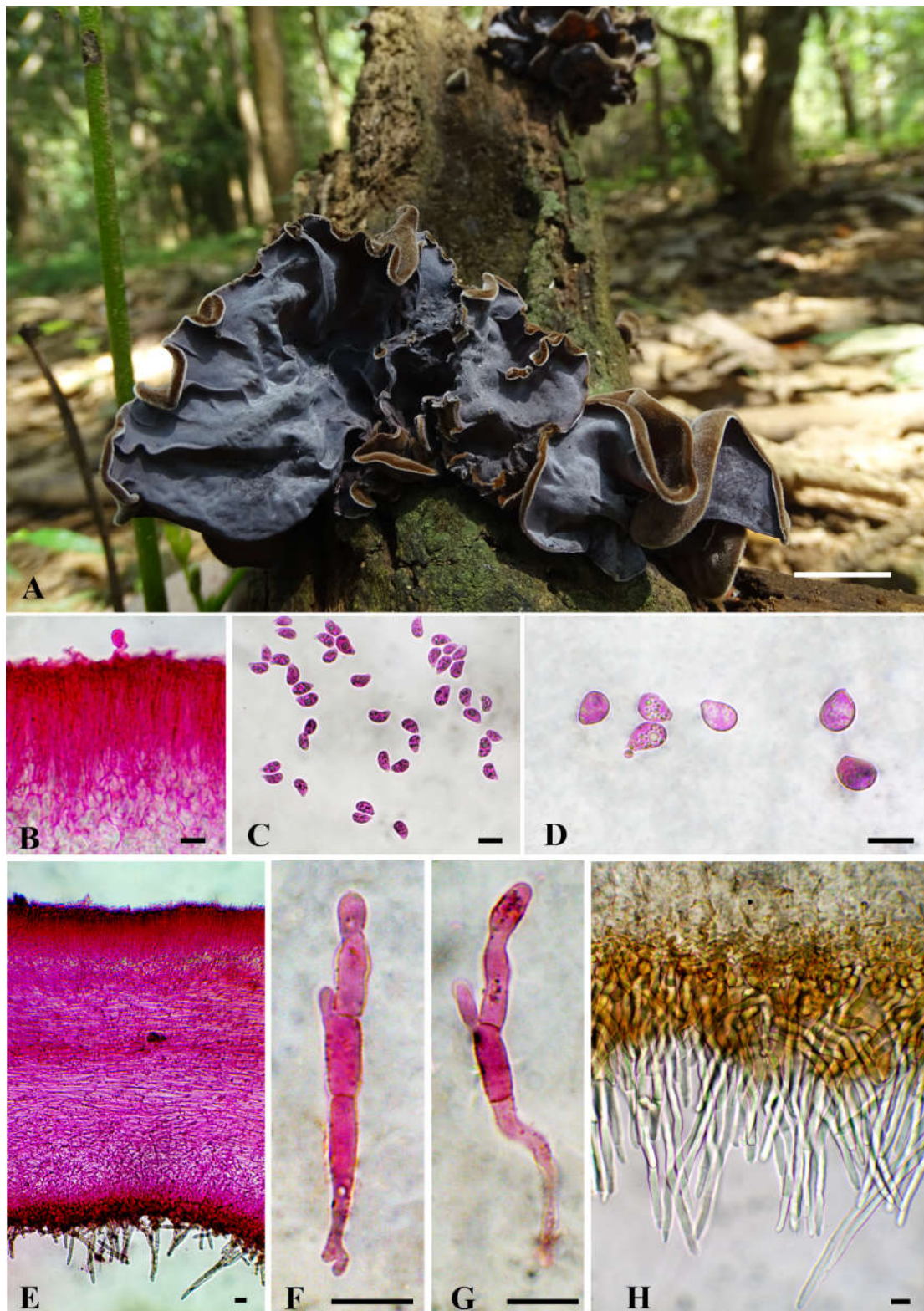


Figure 46: *Auricularia cornea*- **A.** Basidiocarp; **B.** Hymenium with attached basidiospore; **C&D.** Basidiospores; **E.** Cross section showing tramal zones; **F&G.** Transversely septate basidia; **H.** Abhymenial hairs. Scale bars: A=10mm, B-H=10µm.

Specimens examined: INDIA, Kerala State, Kozhikode District, Kootalida, 15 October 2018, Anju John, ZGCAT33; The Zamorin's Guruvayurappan College campus, 22 October 2018, Anjitha Thomas, ZGCAT34; Vallikkattu kaav, 19 December 2018, Anjitha Thomas ZGCAT45; Wayanad District, Kakkavayal, 24 August 2019, Anjitha Thomas, ZGCAT132; Kakkad, 5 January 2021, Anjitha Thomas, ZGCAT226; Malappuram district, Valluvassery, 18 January 2021, Anjitha Thomas, ZGCAT227; New Amarambalam, 4 September 2021, Anjitha Thomas, ZGCAT281.

Habitat: On dead wood.

Comments: *Auricularia cornea* is characterized by the sessile, discoid to foliose basidiocarp; smooth, folded hymenial surface; dense hair on abhymenial surface, and by the presence of a medullary region.

Auricularia cornea has a world-wide distribution (Wu *et al.* 2021) and is common in Kerala State. *Auricularia cornea* is similar to *A. novozealandica* Y.C. Dai and F. Wu, *A. eburnea* L.J. Li and B. Liu and *A. nigricans* (Sw.) Birkebak, Looney and Sánchez-García in having abhymenial hair in 150–1000 μm range. *Auricularia cornea* differs from *A. novozealandica* in having shorter basidia (<70 μm) and a world-wide distribution, where *A. novozealandica* have larger basidia (>70 μm) and has a distribution limited to New Zealand. Compared to *A. cornea*, *A. nigricans* has longer hispid abhymenial hair (300–600 \times 7–9 μm), and *A. cornea* has densely pilose abhymenial hairs (70–250 \times 5–9 μm). *Auricularia eburnean* differs from *A. cornea* by the colour of basidiocarp where, *A. eburnean* has cream to honey-yellow colour and *A. cornea* has brownish colour (Wu *et al.* 2021). One of our collections (ZGCAT227) had exceptionally smaller spores. Molecular sequence generated from ZGCAT227 is clustered with other sequences of *A. cornea* with 100% bootstrap support value.

Auricularia fibrillifera Kobayasi, Bulletin of the National Museum of Nature and Science, Tokyo 16(4): 645 (1973)

Figure 47

Basidiocarp 20–60 mm wide, solitary, orbicular, sessile, gelatinous when fresh. Hymenophore with folds, gray to pale pink. Abhymenial surface glabrous, pale yellowish pink, darkening towards margin. Margin entire.

Abhymenial hairs 25–72 × 4–9 μm, scanty, hyaline, apically acute or obtuse, thick-walled, with lumen that is infrequently septate. **Tramal hyphae** 2–4 μm wide, with clamp-connections, thin-to slightly thick-walled. **Medulla** indistinguishable. **Basidia** 30–51 × 3.5–5.5 μm, clavate, transversely 3-septate, guttulate. **Epibasidia** observed. **Hyphidia** highly branched. **Cystidioles** not observed. **Basidiospores** 9–13.5 × 4–5 μm (Q = 2–3 μm, Qm = 2.45 μm) allantoid, hyaline, thin-walled, smooth, guttulate, 1–3 septate, and producing 'C' shaped microconidia.

Specimens examined: INDIA, Kerala State, Kozhikode District, Poilkave, 20 June 2019, Anjitha Thomas, ZGCAT51; Thurayil kotta, 02 July 2019, Anjitha Thomas, ZGCAT77.

Habitat: On dead wood.

Comments: *Auricularia fibrillifera* is characterized by the gray to pale pink basidiocarp, hymenial surface with folds, glabrous abhymenial surface, indistinct medulla, 30–51 × 3.5–5.5 μm wide basidia, and 9–13.5 × 4–5 μm wide basidiospores. *Auricularia fibrillifera* is closely related to *A. thailandica* both morphologically and geneticaly (Wu *et al.* 2021). But *A. thailandica* lack folding in the hymenial surface. In addition, *A. thailandica* possesses medulla near abhymenium whereas *A. fibrillifera* has indistinct medullary region. This is the first report *A. fibrillifera* from Kerala State.

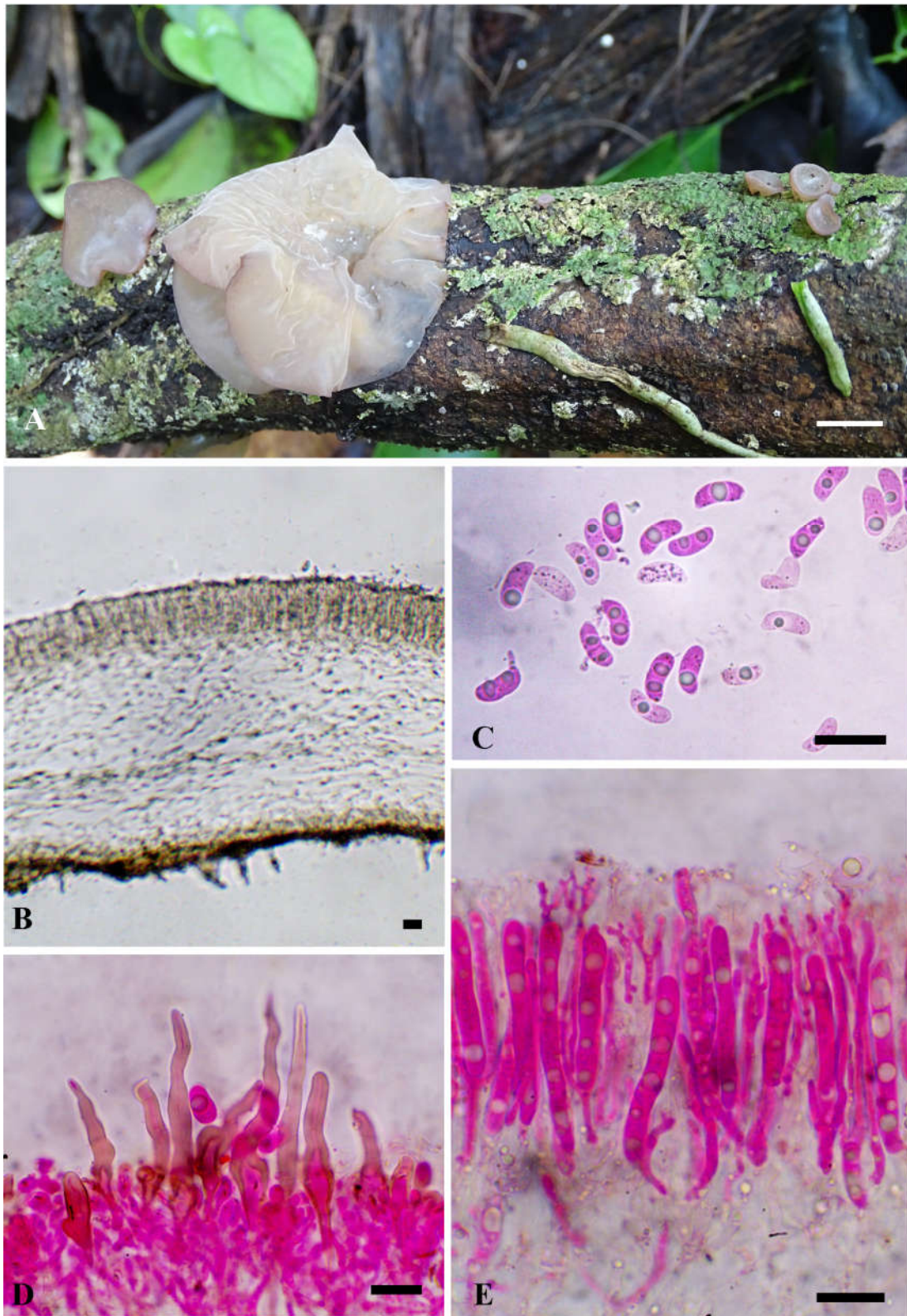


Figure 47: *Auricularia fibrillifera*- **A.** Basidiocarps; **B.** Cross section showing tramal zones; **C.** Basidiospores; **D.** Abhymenial hairs; **E.** Hymenium showing branched hyphidia and basidia. Scale bars: A=10mm, B-E=10µm.

Auricularia heimuer F. Wu, B.K. Cui, Y.C. Dai, in Wu, Yuan, Malysheva, Du and Dai, *Phytotaxa* 186: 248 (2014) Figure 48

Basidiocarp 40–95 mm wide and 1–2.5 mm thick when fresh, auriculiform-petaloid, sessile to substipitate solitary or caespitose, gelatinous to rubbery when fresh, rigid and brittle when dry. Hymenophore surface smooth, folded, glabrous to pruinose, greyish brown when young, changing to reddish brown with age. Abhymenial surface pubescent to tomentose. Margin uniform when fresh, undulate when mature.

Abhymenial hairs 90–150 × 4–6 µm, irregular, hyaline, apically acute or obtuse, thick-walled, with a narrow lumen, tufted. **Tramal hyphae** 1–5 µm wide, thin- to slightly thick-walled with clamp-connections. **Medulla** present. **Basidia** 45–71 × 3–5.5 µm, clavate, transversely 3-septate, epibasidia rarely observed, guttulate. **Crystalline contents** absent. **Hyphidia** highly branched. **Cystidioles** not observed. **Basidiospores** 11–15 × 4.5–5.5 µm (Q = 2.1–2.9 µm, Qm = 2.57 µm) cylindrical to ellipsoid, hyaline, thin-walled, smooth, guttulate.

Specimens examined: INDIA, Kerala State, Malappuram District, 13 July 2018, Anjitha Thomas, ZGCAT8.

Habitat: On dead wood.

Comments: *Auricularia heimuer* is characterized by 90–150 µm long abhymenial hairs, presence of medulla, 45–71 × 3–5.5 µm long basidia, absence of crystalline contents in the cross-section, and 11–15 × 5–6 µm sized basidiospores. *Auricularia auricula-judae*, *A. americana* Parmasto and I. Parmasto ex Audet, Boulet and Sirard and *A. villosula* are closely related to *A. heimuer* both morphologically and phylogenetically (Wu *et al.* 2014). Compared with *A. auricula-judae*, *A. heimuer* has Asian distribution, whereas *A. auricula-judae* has a European distribution. In addition, *A. auricula-judae* usually has basidia of more than 65 µm long and basidiospores of more than 15 µm long (Wu *et al.* 2021). *Auricularia villosula* has fawn to fuscous colour when fresh and short abhymenial hairs (40–90 × 4.5–6 µm) compared to reddish brown colour

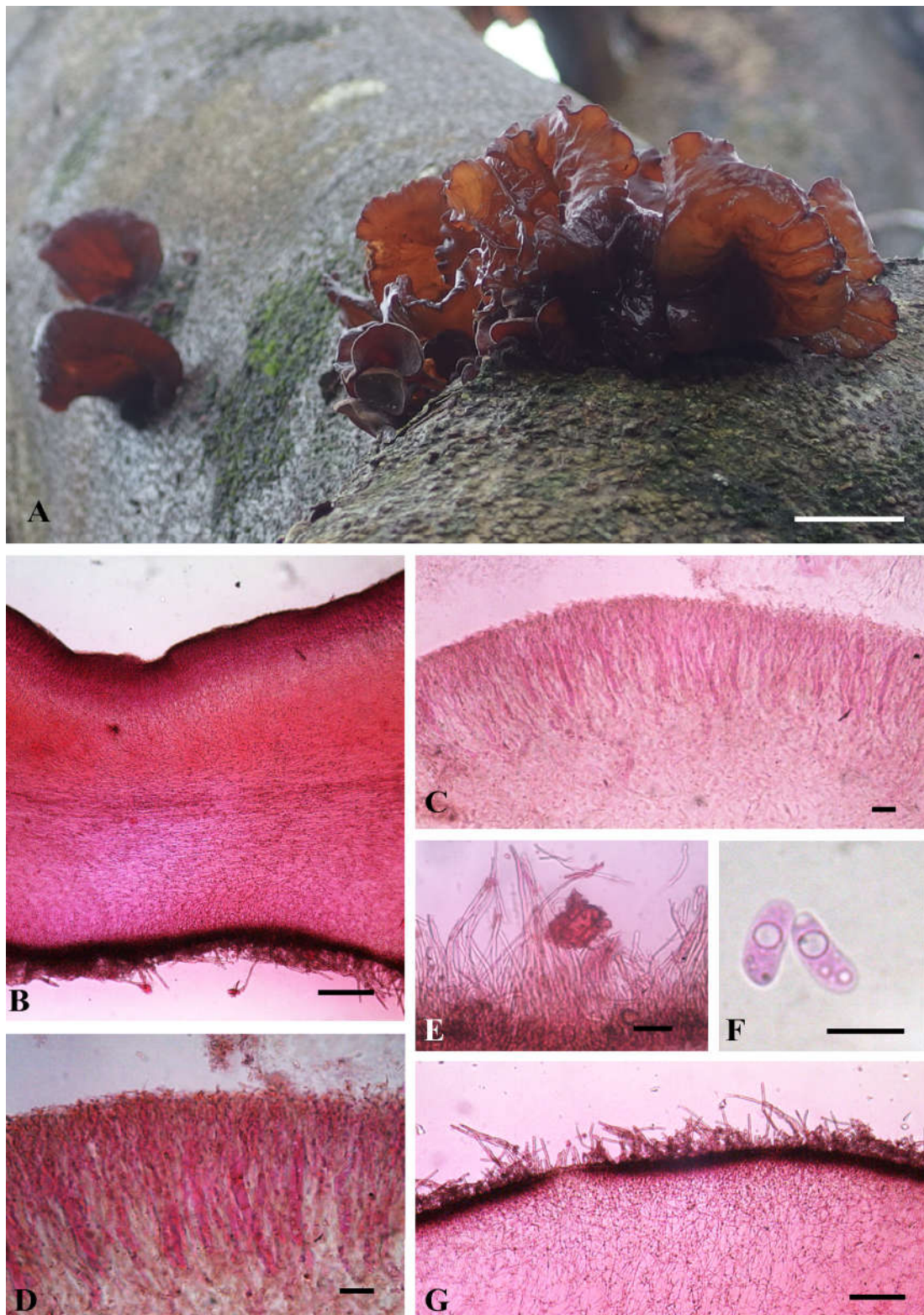


Figure 48: *Auricularia heimuer*- **A.** Basidiocarp; **B.** Cross section showing tramal zones; **C&D.** Hymenium; **E&G.** Abhymenial hairs; **F.** Basidiospores. Scale bars: A=10mm, B&G=100µm, C-F=10µm.

of *A. heimuer* and larger (90–150 × 4–6 µm) abhymenial hairs. In addition, *A. villosula* lack medulla (Malysheva and Bulakh 2014) whereas, *A. heimuer* has medulla. In *A. americana*, medulla may present or absent, and have larger basidiospores (14–16.5 µm) growth on gymnosperms (Wu *et al.* 2021), whereas, *A. heimuer* grow on angiosperms and have shorted basidiospores (11–15 µm) with medullary region in cross section. Compared to the original description of *A. heimuer*, the present collection has slightly larger basidiospores (11–15 × 4.5–5.5 µm), whereas original description has 11–13 × 4–5 µm long basidiospores. *Auricularia heimuer* is not formally reported from India till date.

Auriculariaceae taxon

Figure 49

Basidiocarp 20–60 × 3–5 mm, resupinate, rosette, initially develop as circular patches, later coalescing to form a continuous layer. Upper surface uneven, slightly cerebriform, gelatinous when fresh, becoming membraneous, margin reflexed upon drying. Greyish when fresh, becoming pale brown on drying.

Hyphal system monomitic. **Subiculum** 20–26 µm wide zone, composed of agglutinated hyphae, parallel to the substratum, yellow to brownish yellow pigmented at the region of agglutination, thin-walled, and heavily gelatinised. Ascending tramal hyphae arising from subiculum, 1.5–3 µm wide, thin-walled, hyaline with clamp-connections. Collapsed basidia distributed throughout ascending layer. **Basidia** 13.5–15 × 10–11 µm, obovoid, subglobose, ellipsoid, hyaline, guttulate, 2–4 celled, longitudinally septate, thin-walled. Younger basidia emerge from the basidial base, leads to the long zig-zag shaped fertile hyphae. Remnants of old basidia can be seen in the basal parts of fertile hypae. **Hyphidia** flexuose, branched, thin-walled, narrow, 1–2 µm wide. **Cystidia** 16–24 × 3.3–3.9 µm, hyaline, clavate with irregularly shaped projections at tip, clamp-connections at base, thin-walled. **Basidiospores** 7.5–9.5 × 4.5–6 µm (Q = 1.2–2.1 µm, Qm = 1.5 µm) hyaline, ovoid to ellipsoid, broadly cylindrical, guttulate, aseptate, thin-walled.

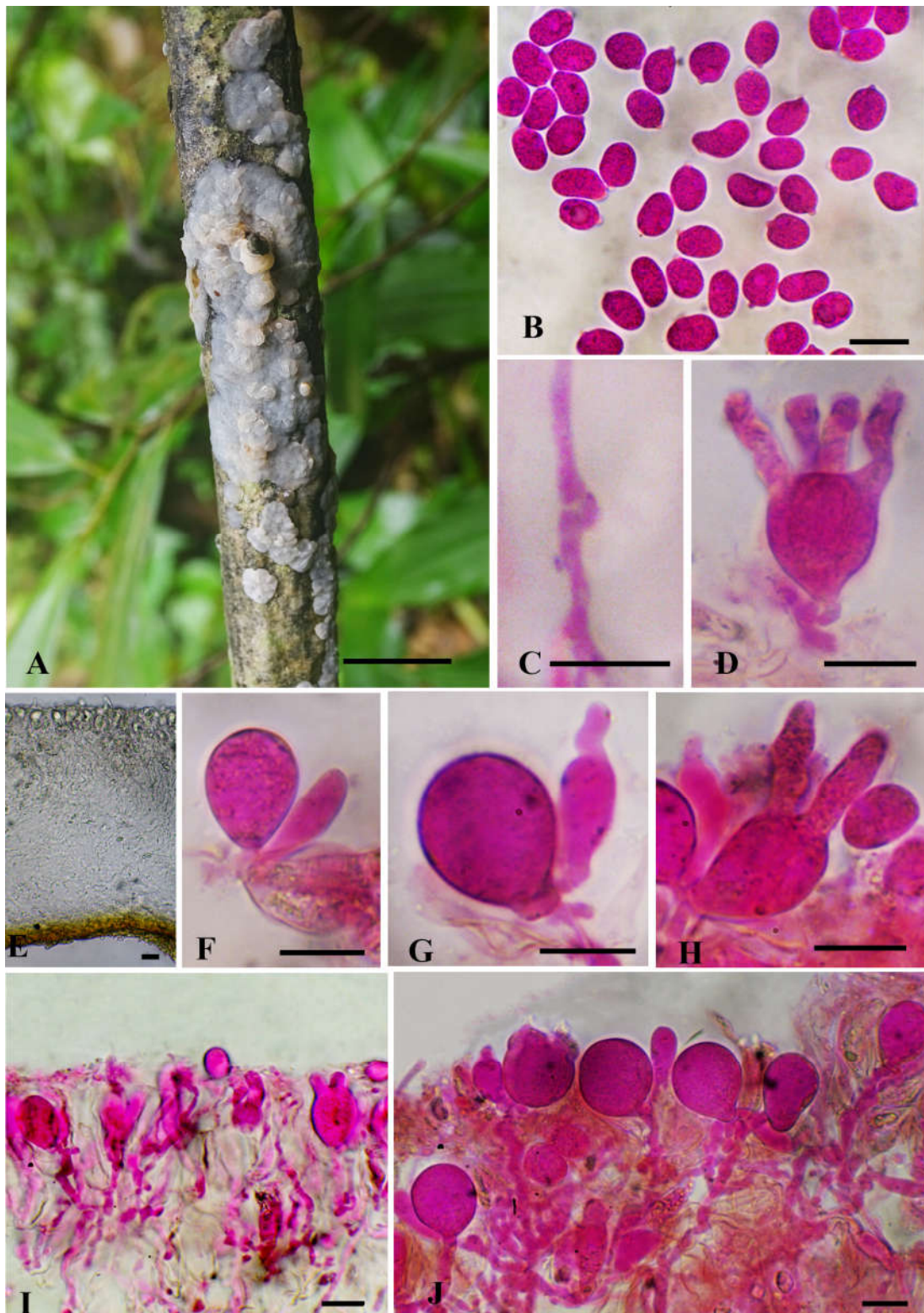


Figure 49: Auriculariaceae taxon- **A.** Basidiocarp; **B.** Basidiospores; **C.** Clamp-connection; **D.** Basidia; **E.** Cross-section of basidiocarp; **F&G.** Basidiole with cystidia; **H.** Basidia with cystidia; **I.** Hymenium with hyphidia; **J.** Hymenium showing fertile hyphae. Scale bars: A=10mm, B-J=10µm.

Specimens examined: INDIA. Kerala State, Wayanad District, 900 kandi, 12 July 2019, Anjitha Thomas, ZGCAT106; Kozhikode District, Poilkave, 14 July 2021, Anjitha Thomas, ZGCAT242.

Habitat: On dead wood.

Comments: Auriculariaceae taxon is characterised by resupinate gelatinous basidiocarp which become membranous and reflexed upon drying, monomitic hyphal system, yellow to brownish yellow pigmented at the region of agglutination in basal zone (subiculum), subglobose to ellipsoid longitudinally septate basidia, flexuose hyphidia, clavate cystidia, and ovoid to ellipsoid basidiospores.

In Auriculariales, *Exidia sensu lato* contain species with resupinate gelatinous basidiocarp, which include *Exidia*, *Myxarium*, and *Tremellochaete* (Tohtirjap *et al.* 2023). Genus *Myxarium* belongs to Hyaloriaceae. *Myxarium* is characterised by stalked basidia, which is absent in "Auriculariaceae taxon". *Exidia* and *Tremellochaete* belong to family Auriculariaceae. *Tremellochaete* is characterised by the presence of papillae on the hymenophore, which is absent in *Exidia*. But, the demarcation of these two genera is still not clear. Wang and Thorn (2021) treated *Exidia* and *Tremellochaete* as synonyms due to their phylogenetic relatedness (Tohtirjap *et al.* 2023). Phylogenetically, the unidentified Kerala taxon is distant from *Exidia sensu lato* members.

Corticoid members of Auriculariales with tough, resupinate basidiocarps were traditionally placed in genera like *Eichleriella*, *Exidiopsis*, and *Heterochaete*. Based on the molecular studies, the generic concepts were refined and new genera like *Adustochaete*, *Alloexidiopsis*, *Amphistereum*, *Crystalloдон*, *Heteroradulum*, *Proterochaete*, and *Sclerotrema* were erected to reflect monophyly (Liu *et al.* 2022). Auriculariaceae taxon is morphologically different from all these genera in having gelatinous waxy resupinate

basidiocarp. *Exidiopsis* genus was used to deposit all resupinate species with tremelloid basidia and clamp-connection. Roberts (1993) redefined *Exidiopsis* having species with resupinate, gelatinous basidiocarp with clamp-connections and hyphidia, based on the characters of the type species *Exidiopsis grisea* (Bres.) Bourdot and Maire. Roberts (1993) not mentioned anything about cystidia. According to Wells and Raitviir (1977), *Exidiopsis grisea* have larger, cylindrical, curved to allantoid basidiospores, and lack basal yellowish subiculum.

In the phylogenetic analysis, ITS sequence generated from ZGCAT106, and LSU sequence generated from ZGCAT242 showed 100 % similarity with the accessions MH178280 (He5206) and MH178257 (He4610) from China, which are also identified up to order level (Auriculariales species) only. In the phylogram (Figure 51), Kerala specimens cluster with the above mentioned sequences from China, and forms a sister clade to the genus *Auricularia*. Clade of *Elmerina*, *Aporpium* and *Protodaedalea* forms a neighbouring clade to the Auriculariaceae taxon. Morphologically the unidentified Kerala taxon differs from *Auricularia* members by the globose, longitudinally septate basidia, absence of abhymenial hairs, and zonation in basidiocarp. Genus *Protodaedalea* is characterised by the sessile annual leathery basidiocarp with dimitic hyphal system, poroid hymenophore, sphaeropedunculate basidia, and presence of gleocystidia (Seok *et al.* 2011). Genus *Elmerina* and *Aporpium* have poroid hymenophore with dimitic hyphal system (Sotome *et al.* 2014). Presence of smooth hymenophore and pigmented subiculum and monomitic hyphal system, differentiate Auriculariaceae taxon from *Protodaedalea*, *Elmerina* and *Aporpium*.

Thorough study with more collections and gene regions are necessary to confirm the taxonomic identity of the collection.

4.2.4. Taxonomic descriptions of Sebacinales

Sebacina Tul. and C. Tul.

Basidiocarps microscopic to pustulate, resupinate, stipitate, merulioid, flabellate to infundibuliform, gelatinous, cartilaginous or leathery. Basidia globose, ovate to pyriform, longitudinally septate, four-celled. Hyphidia may present or absent, simple to branched, sometimes forming a palisade like layer covers young and mature basidia in the hymenium. Cystidia may present or absent, branched or unbranched. Basidiospores broadly ovate, ellipsoid, oblong to short cylindrical or allantoid, thin-or thick-walled, capable of germinating by repetition. Resting spores may present or absent, thick-walled spores with irregular spore wall. Tramal hyphae may monomitic or dimitic, thin-or thick-walled, gelatinous, without clamp-connections.

Sebacina species

Figure 50

Basidiocarp 55–98 × 3–13 mm, resupinate, coriaceous, spongy, with a gelatinous texture on upper surface, lobed, undulate, dull white to cream when fresh, turning to yellowish brown when dry.

Hymenium 58–200 µm wide, gelatinous, composed of basidia and hyphidia. **Hyphidia** 58–200 × 2–3 µm, numerous, branched, cylindrical, hyaline to pale grey, thin-walled, without clamp-connections, projecting beyond basidia.

Basidia 10–19 × 8–18 µm, globose to ellipsoid, 2–4 celled, longitudinally septate, thin-walled, guttulate, hyaline. **Basidiospores** 9–12 × 5–6 µm (Q = 1.58–2.1 µm, Qm = 1.88 µm) ellipsoid, broadly ellipsoid, ovoid, hyaline, thin-walled, smooth, guttulate. Spore print not observed. **Tramal hyphae** 2–4 µm wide, thick-walled, gelatinous, agglutinated, densely packed, yellow to yellowish brown, septate, without clamp-connections. Densely packed hyphae are interspersed with air spaces.

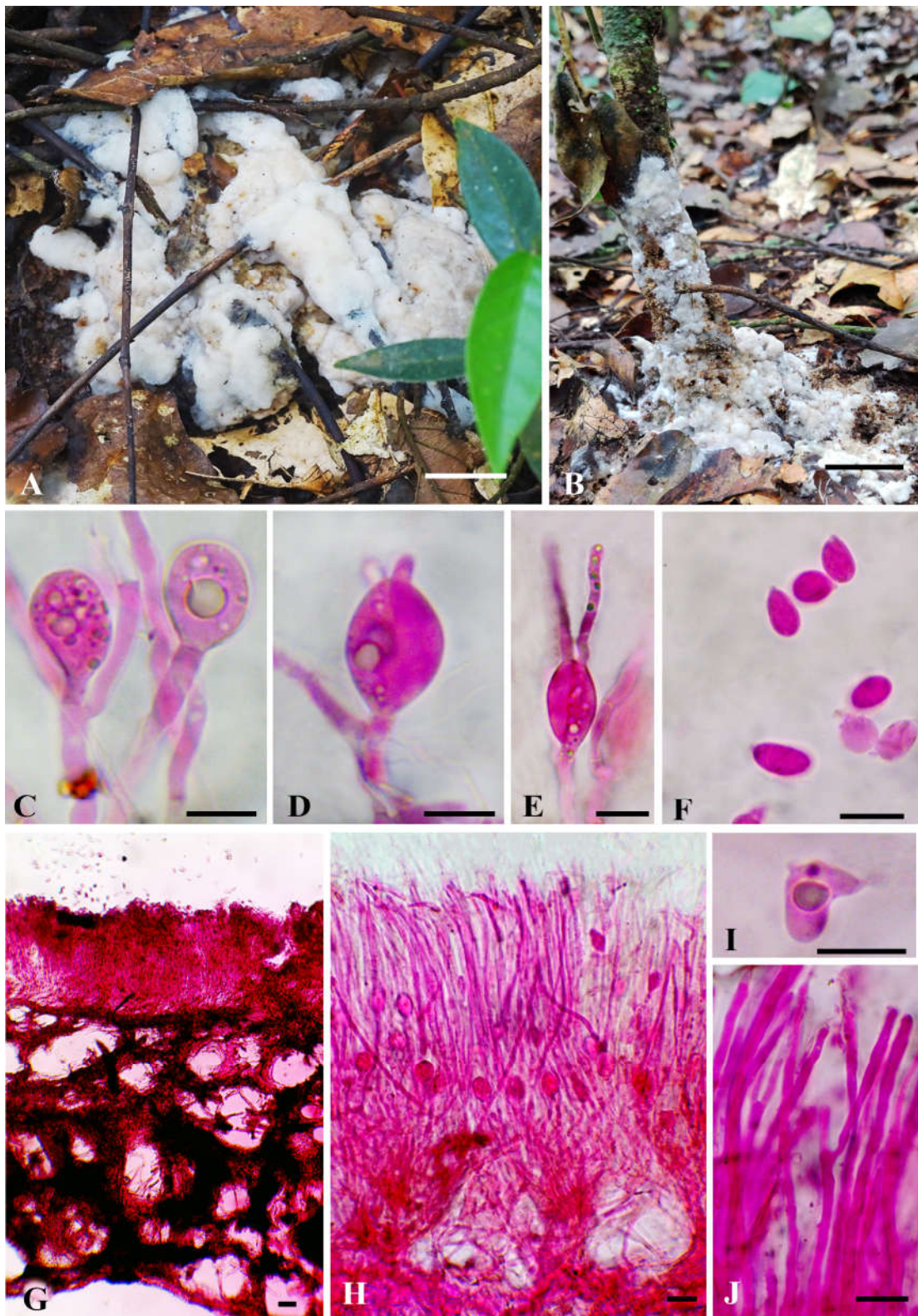


Figure 50: *Sebacina* species- **A&B.** Basidiocarps; **C-E.** Basidia; **F.** Basidiospores; **G.** Cross section of basidiocarp; **H.** Hymenium with basidia and hyphidia; **I.** Basidiospore with ballistospore formation; **J.** Hyphidia. Scale bars: A&B=10mm, C-J=10µm.

Specimens examined: INDIA, Kerala State, Malappuram District, Nilambur, 23 October 2021, Anjitha Thomas, ZGCAT301; ZGCAT302.

Habitat: on soil, incrusting stones, leaves, twigs.

Comments: *Sebacina* species has thick-walled tramal hyphae, which are agglutinated and densely packed, with well defined cavity-like spaces resulting in a spongy texture. Hymenium is compactly arranged, gelatinous, with thin-walled basidia and occasionally branched, thin-walled hyphidia. *Sebacina* species is morphologically related to *S. epigaea* and *S. incrustans* with the incrusting and terricolous nature (Riess *et al.* 2013, Oberwinkler *et al.* 2014). According to Riess *et al.* (2013), the basidiocarp of *S. epigaea* are opalescent and becoming membranous when drying, and has thin-walled hyphae. Whereas, *Sebacina* species has thick-walled tramal hyphae densely packed with gaps which results in a spongy texture of the basidiocarp. In addition, *S. epigaea* has an irregularly branched short hyphidia (up to 60 μm) in the hymenial region (McNabb 1966). *Sebacina* species has dense, occasionally branched, cylindrical, long (58–200 \times 2–3 μm) hyphidia, which projects beyond the basidial zone. *Sebacina incrustans* have incrusting and terricolous nature, with unchanging cream to ochre coloured basidiocarp, similar to *S.* species. But the former has irregularly branched hyphidia, and larger basidiospores 10–20 \times 6–10 μm (Burt 1915, Henkel *et al.* 2004, Riess *et al.* 2013) compared with short basidiospores (9–12 \times 5–6 μm) of *S.* species. In addition, *S. incrustans* has 2–3 mm thick basidiocarp with loosely intertwined tramal hyphae whereas, *S.* species has 3–13 mm thick basidiocarp and agglutinated, densely packed tramal hyphae with gaps in tramal region.

Phylogenetically, *S.* species is distinct from *S. epigaea* and *S. incrustans*. In the phylogenetic tree constructed with the combined ITS and LSU sequences, the accessions of *Sebacina* species clustered with accessions of uncultured *Sebacina* species with 91% bootstrap support value, and together they form a sister clade to *S. dimitica* with 99% bootstrap support value. *Sebacina* species differs from *S. dimitica* by the absence of dimitic hyphal system (Dueñas 2005).

4.3 Pure culture establishment

As part of conservation of heterobasidiomycetous taxa from Kerala, pure cultures of 20 species have been generated. The live cultures have been catalogued and maintained in the refrigerator in the Mycology laboratory of The Zamorin's Guruvayurappan College.

Table 6: List of species having pure cultures generated in the present study

| Sl. No. | Taxon | Culture isolate number |
|---------|----------------------------------|--------------------------|
| 1. | Auriculariaceae taxon | ZGCATCUL242 |
| 2. | <i>Calocera cornea</i> | ZGCATCUL55 |
| 3. | <i>Dacrymyces cerebriformis</i> | ZGCATCUL170 |
| 4. | <i>Dacrymyces falcatus</i> | ZGCATCUL241 |
| 5. | <i>Dacrymyces san-augustinii</i> | ZGCATCUL357 |
| 6. | <i>Dacrymyces</i> species 1 | ZGCATCUL134, ZGCATCUL226 |
| 7. | <i>Dacrymyces</i> species 2 | ZGCATCUL131, ZGCATCUL232 |
| 8. | <i>Dacrymyces spathularia</i> | ZGCATCUL144 |
| 9. | <i>Dacryopinax petaliformis</i> | ZGCATCUL37, ZGCATCUL313 |
| 10. | <i>Phaeotremella foliaceae</i> | ZGCATCUL350 |
| 11. | <i>Sebacina</i> species | ZGCATCUL302 |
| 12. | <i>Tremella armeniaca</i> | ZGCATCUL180 |
| 13. | <i>Tremella erythrina</i> | ZGCATCUL314 |
| 14. | <i>Tremella fuciformis</i> | ZGCATCUL292 |
| 15. | <i>Tremella poilkavensis</i> | ZGCATCUL187, ZGCATCUL243 |
| 16. | <i>Tremella</i> species 1 | ZGCATCUL244 |
| 17. | <i>Tremella sairandriana</i> | ZGCATCUL181 |
| 18. | <i>Tremella seclusa</i> | ZGCATCUL183 |
| 19. | <i>Tremella taiwanensis</i> | ZGCATCUL316 |
| 20. | <i>Vishniacozyma</i> species | ZGCATCUL354 |

Frequent contamination and lack of sufficient quantity of basidiocarps were the major problems encountered during the culture establishment of heterobasidiomycetous taxa.

4.4. Molecular characterization

The study generated 55 DNA sequences representing 24 species of heterobasidiomycetes fungi and 2 DNA sequences from the hosts of *Naematelia encephaloidea* and *Tremella poilkavensis*. This includes 35 ITS sequences and 20 LSU sequences.

Table 7: Molecular sequences generated in the study

| Sl. No. | Taxon | Voucher number | ITS | LSU |
|---------|----------------------------------|----------------|----------|----------|
| 1 | <i>Auricularia cornea</i> | ZGCAT227 | PP380396 | - |
| 2 | <i>Auricularia srilankensis</i> | ZGCAT155 | PP380394 | - |
| 3 | Auriculariaceae taxon | ZGCAT242 | PP380637 | - |
| 4 | Auriculariaceae taxon | ZGCAT106 | - | PP818916 |
| 5 | Cryptococcaceae taxon | ZGCAT323 | - | PP188486 |
| 6 | Cryptococcaceae taxon | ZGCAT324 | PP188483 | PP188481 |
| 7 | <i>Dacrymyces microsporus</i> | ZGCAT336 | PP760154 | - |
| 8 | <i>Dacrymyces san-augustinii</i> | ZGCAT266 | PP760155 | - |
| 9 | <i>Dacrymyces</i> species 1 | ZGCAT134 | PQ014733 | - |
| 10 | <i>Dacrymyces</i> species 1 | ZGCAT226 | PQ014734 | PQ012568 |
| 11 | <i>Dacrymyces</i> species 2 | ZGCAT232 | PP758320 | - |
| 12 | <i>Dacrymyces</i> species 2 | ZGCAT208 | PP758322 | - |
| 13 | <i>Dacryopinax primogenitus</i> | ZGCAT92 | PP758341 | - |
| 14 | <i>Dacryopinax primogenitus</i> | ZGCAT89 | PP758342 | - |
| 15 | <i>Naematelia encephaloidea</i> | ZGCAT325 | OQ621803 | - |
| 16 | <i>Naematelia encephaloidea</i> | ZGCAT326 | OQ621795 | OQ621978 |
| 17 | <i>Naematelia encephaloidea</i> | ZGCAT327 | OQ621748 | - |
| 18 | <i>Naematelia encephaloidea</i> | ZGCAT329 | OQ621704 | OR068134 |
| 19 | <i>Sebacina</i> species | ZGCAT301 | PP388210 | - |
| 20 | <i>Sebacina</i> species | ZGCAT302 | PP388209 | PP388211 |
| 21 | <i>Sirobasidium brefeldianum</i> | ZGCAT189 | PP976611 | PP976613 |
| 22 | <i>Sirobasidium japonicum</i> | ZGCAT167 | PP179382 | - |
| 23 | <i>Sirobasidium magnum</i> | ZGCAT26 | - | PP179309 |
| 24 | <i>Tremella erythrina</i> | ZGCAT305 | OR457653 | OR453163 |
| 25 | <i>Tremella erythrina</i> | ZGCAT314 | OR453169 | - |

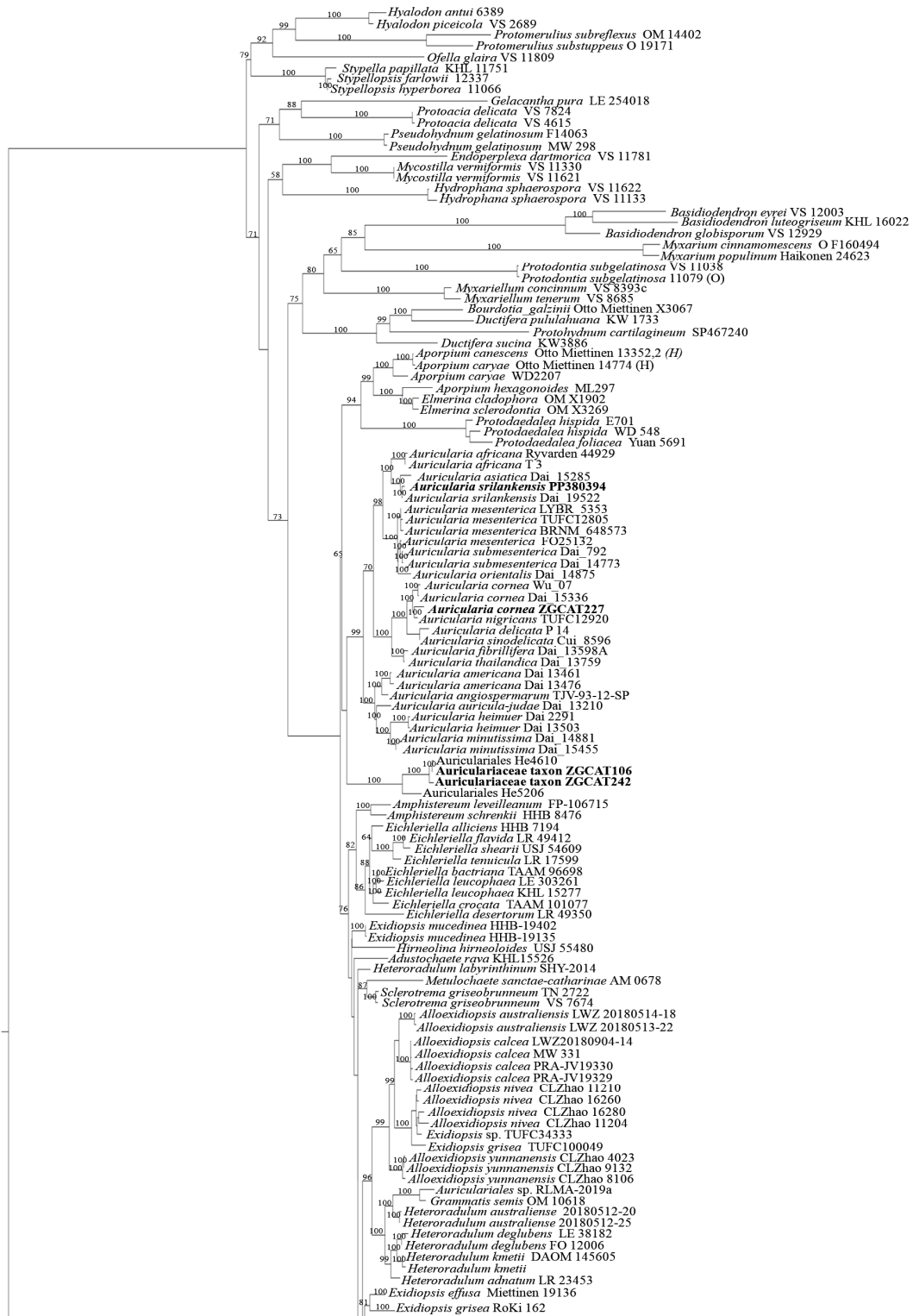
Result and Discussion

| | | | | |
|---|--|------------|----------|----------|
| 26 | <i>Tremella laurisilvae</i> | ZGCAT271 | - | OR461202 |
| 27 | <i>Tremella laurisilvae</i> | ZGCAT276 | OR478036 | OR478037 |
| 28 | <i>Tremella mesenterica</i> | ZGCAT139 | - | PP179305 |
| 29 | <i>Tremella poilkavensis</i> | ZGCAT14 | OQ096659 | - |
| 30 | <i>Tremella poilkavensis</i> | ZGCAT243 | OL616066 | OL616061 |
| 31 | <i>Tremella sairandhrana</i> | ZGCAT89 | ON668075 | ON668076 |
| 32 | <i>Tremella seclusa</i> | ZGCAT183 | OR452983 | OR452985 |
| 33 | <i>Tremella</i> species 1 | ZGCAT52 | OR452937 | OR452957 |
| 34 | <i>Tremella</i> species 1 | ZGCAT108 | OR452981 | OR457652 |
| 35 | <i>Tremella</i> species 1 | ZGCAT335 | OR453173 | |
| 36 | <i>Tremella</i> species 3 | ZGCAT195 | PP179218 | OR452984 |
| 37 | <i>Tremella</i> species 3 | ZGCAT32 | PP179217 | - |
| 38 | <i>Tremella taiwanensis</i> | ZGCAT316 | OR453171 | - |
| 39 | <i>Vishniacozyma</i> species | ZGCAT354 | - | PP724435 |
| 40 | <i>Vishniacozyma</i> species | ZGCAT359 | - | PP724719 |
| Sequences generated from host organism | | | | |
| 41 | <i>Stereum</i> species Host of <i>N. encephaloidea</i> | ZGCATHS326 | OR083274 | - |
| 42 | <i>Biscogniauxia</i> species Host of <i>T. poilkavensis</i> | ZGCATHS243 | OQ983831 | - |

4.5. Phylogenetic analysis

4.5.1. Phylogenetic tree of Auriculariales

Figure 51



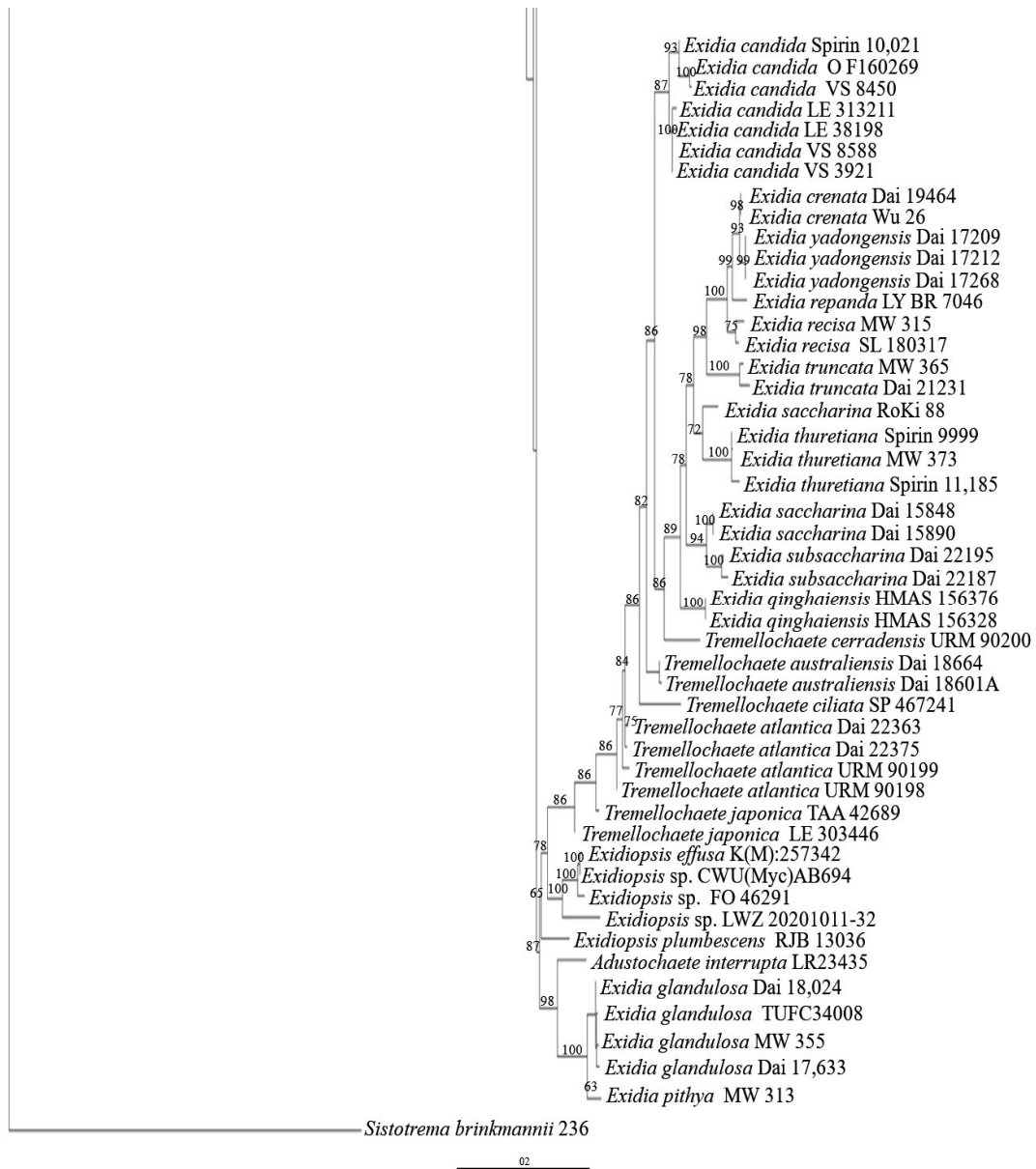


Figure 51: Maximum likelihood tree of Auriculariales generated using combined ITS-LSU sequence data. Values at the branches indicating Maximum Likelihood bootstrap support. Bootstrap support values above 50% are shown. Bold names indicating sequences generated in the present study. Voucher names are provided along with taxon name.

4.5.2. Phylogenetic tree of Sebaciales

Figure 52

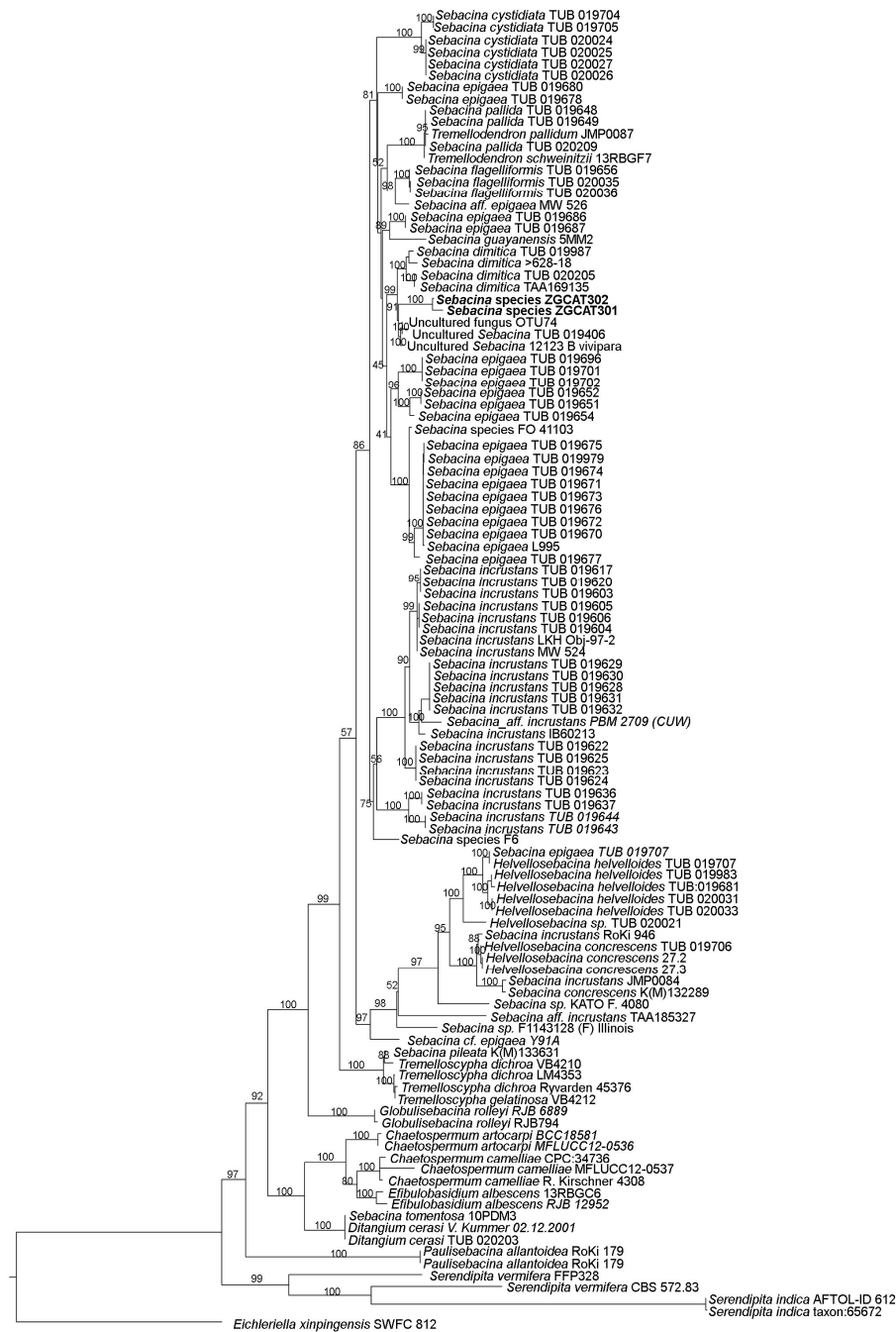


Figure 52: Maximum likelihood tree of Sebaciales generated using combined ITS-LSU sequence data. Values at the branches indicating Maximum likelihood bootstrap support. Bootstrap support values above 50% are shown. Bold names indicating sequences generated in the present study. Voucher names are provided along with taxon name.

4.5.3. Phylogenetic tree of Dacrymycetes

Figure 53

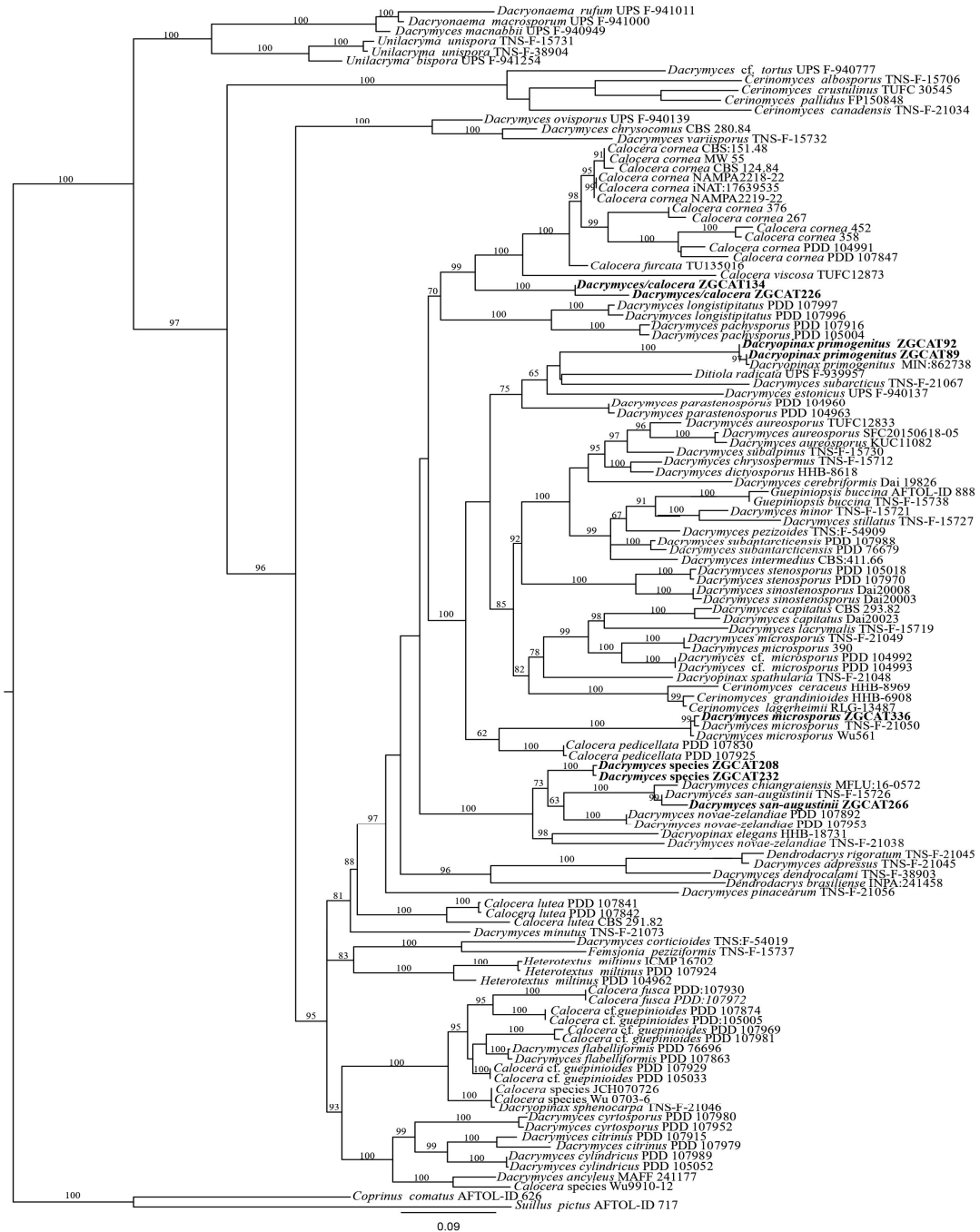
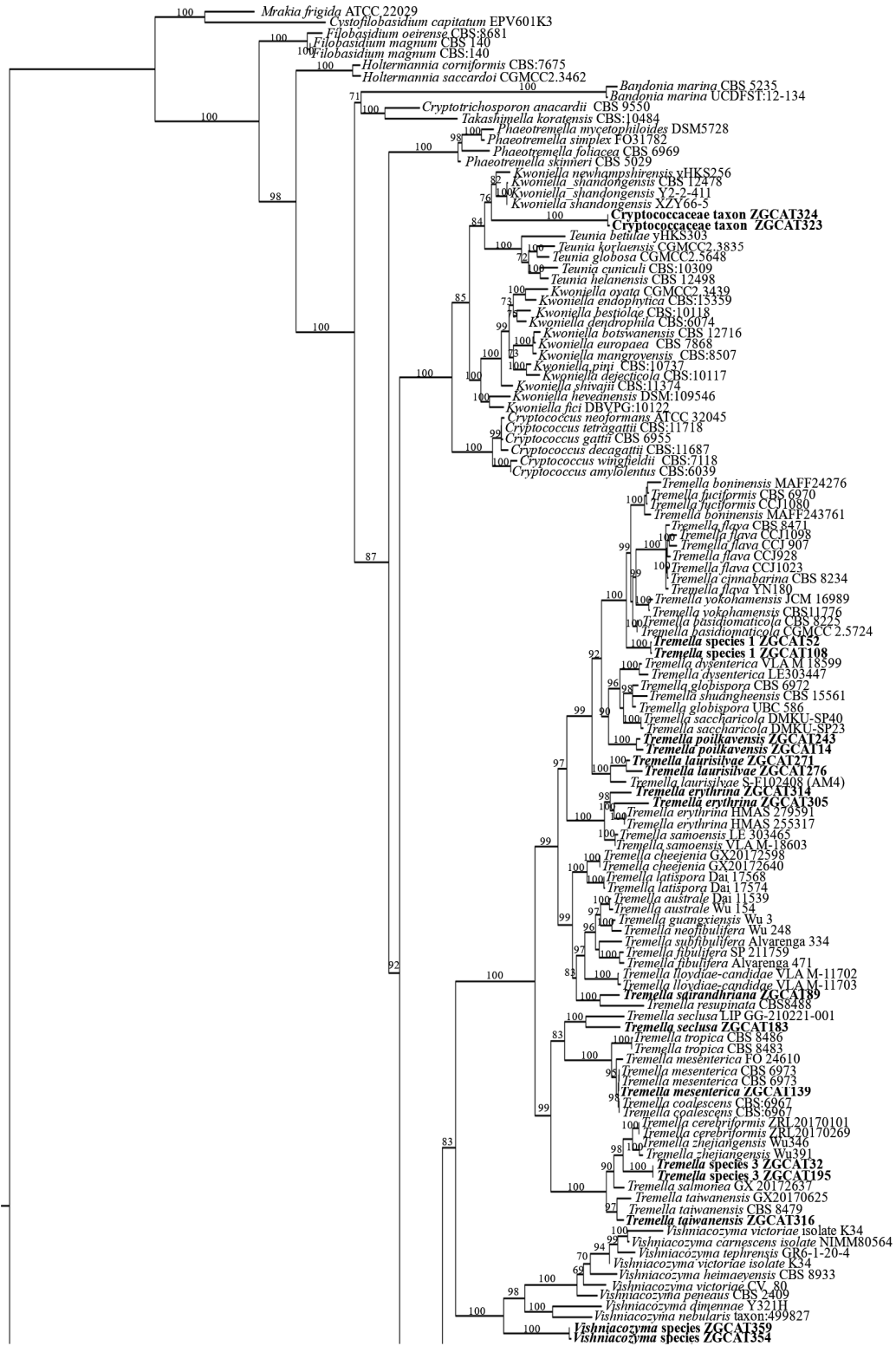


Figure 53: Maximum likelihood tree of Dacrymycetes generated using combined ITS-LSU sequence data. Values at the branches indicating Maximum likelihood bootstrap support. Bootstrap support values above 50% are shown. Bold names indicating sequences generated in the present study. Voucher names are provided along with taxon name.

4. 5. 4. Phylogenetic tree of Tremellomycetes

Figure 54



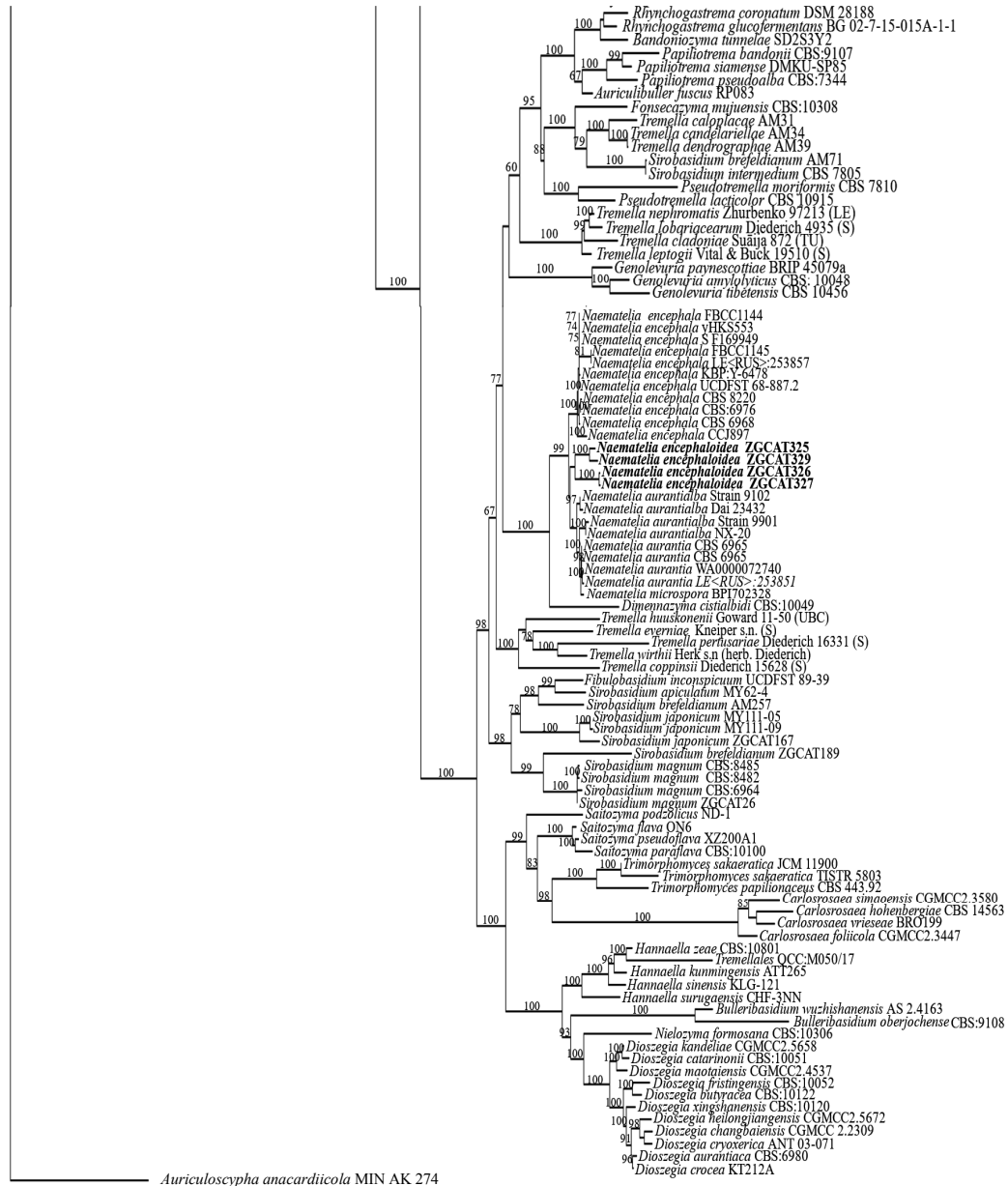


Figure 54: Maximum likelihood tree of Tremellomycetes generated using combined ITS-LSU sequence data. Values at the branches indicating Maximum likelihood bootstrap support. Bootstrap support values above 50% are shown. Bold names indicating sequences generated in the present study. Voucher names are provided along with taxon name.

New species collected during the study are, *Naematelia encephaloidea* A. Thomas and T.K.A. Kumar, *Tremella poilkavensis* A. Thomas and T.K.A. Kumar, and *Tremella sairandhriana* A. Thomas and T.K.A. Kumar, *Dacrymyces* species 1, *Dacrymyces* species 2, *Sebacina* species, *Tremella* species 1, *Tremella* species 2, *Tremella* species 3, and *Vishniacozyma* species. Two taxa (Auriculariaceae taxon and Cryptococcaceae taxon) could be only identified up to generic level. Designation of taxonomic rank of these two should be finalised with additional specimens and molecular data.

New record to Asia:

Tremella seclusa

The study has documented two new genus records and 24 new species records to India. The following are the new genus records to India:

Dendrodacrys and *Vishniacozyma*

Following are the new species records to India:

Auricularia heimuer, *A. sinodelicata*, *A. subglabra*, *Dacrymyces cerebriformis*, *D. dacryomitriiformis*, *D. falcatus*, *D. microsporus*, *D. novae-zelandiae*, *D. san-augustinii*, *D. sinostenosporus*, *D. cupularis*, *Dacryopinax indacocheae*, *Da. petaliformis*, *Da.primogenitus*, *Da. yungensis*, *Dendrodacrys paraphysatum*, *Phaeotremella yunnanensis*, *Sirobasidium japonicum*, *S. magnum*, *Tremella armeniaca*, *T. erythrina*, *T. laurisilvae*, *T. seclusa*, *T. taiwanensis*

The study also documented 8 new genus records and 31 new species records to Kerala. Following are the new genus records to Kerala:

Sebacina, *Dacrymyces*, *Dendrodacrys*, *Guepiniopsis*, *Naematelia*, *Phaeotremella*, *Sirobasidium* and *Vishniacoozyma*

Following are the new species records to Kerala:

Auricularia fibrillifera, *A. heimuer*, *A. sinodelicata*, *A. srilankensis*, *A. subglabra*, *Dacrymyces capitatus*, *D. cerebriformis*, *D. dacryomitriiformis*, *D. falcatus*, *D. lacrymalis*, *D. microsporus*, *D. novae-zelandiae*, *D. san-augustinii*, *D. sinostenosporus*, *D. cupularis*, *Dacryopinax indacocheae*, *Da. petaliformis*, *Da. primogenitus*, *Da. yungensis*, *Dendrodacrys paraphysatum*, *Guepiniopsis buccina*, *Phaeotremella yunnanensis*, *Sirobasidium brefeldianum*, *S. japonicum*, *S. magnum*, *Tremella armeniaca*, *T. erythrina*, *T. fuciformis*, *T. laurisilvae*, *T. seclusa*, *T. taiwanensis*

All heterobasidiomycetes (except *Sebacina* species) collected and examined in this study were growing on dead and decaying wood (either as mycoparasitic on host fungi or saprobic). Auriculariales and Dacrymycetales are wood inhabiting members, which play active role in wood decomposition. Tremellaceous members were mostly observed as growing on other fungi especially ascomycete fungi. *Naematelia encephaloidea* were collected as growing on *Stereum* species (basidiomycete fungi). *Sebacina* species were collected directly from soil and as incrustated on twigs, dried leaves and stones.

Although dacrymycetous fungi are generally described as causing brown rot decay, some dacrymycetous collections (*Dacrymyces microsporus*: ZGCAT102) were observed as causing white rot (just a preliminary field observation). More studies are required to understand such properties of Dacrymycetes fungi.

Among the diverse collection localities including natural forests, sacred groves, college campuses, plantations and abandoned areas of Kerala state, natural forests and sacred groves were observed as with abundance of heterobasidiomycetes. Silent valley National Park (Palakkad District) and Poilkave Sacred grove (Kozhikode District) provided maximum number of specimens during monsoon seasons.

This is the first attempt from Kerala State to document the diversity of heterobasidiomycetes, and is the major comprehensive study of heterobasidiomycetes from India after Mahamulkar *et al.* (2003) and Patil *et al.* (2003).

Systematic studies using the collections from Kerala included a phylogenetic comparison of molecular data available so far on heterobasidiomycetes from around the world.

Extensive documentary studies using morpho-molecular techniques are essential to reveal the complete diversity status of the group in Kerala. Culture studies and bioprospecting of the heterobasidiomycete diversity should be the topics of further research.

SUMMARY

Heterobasidiomycetes are a polyphyletic group of fungi having jelly-like basidiocarp, complex dolipore septum with parenthesomes, septate basidia, and basidiospores capable of producing secondary spores and/or yeast-like cells. Heterobasidiomycete taxa (Agaricomycotina), generally called as jelly fungi are distributed in the following classes: Agaricomycetes, Dacrymycetes, and Tremellomycetes. Jelly fungi are ecologically and economically important.

Basidiocarps of heterobasidiomycetes were collected from different parts of Kerala State during the monsoon seasons of 2018-2023, and were systematically studied. Both morphological and molecular characterization was done for the collected specimens. As part of the study, 47 species belonging to 11 genera, 7 families, 4 orders, were documented. Three species collected during the study have been formally proposed as new (Thomas and Kumar 2023, 2024; Liu *et al.* 2024). Seven species were found as hitherto undescribed and may represent species new to science (*Sebacina* species, *Dacrymyces* species 1, *Dacrymyces* species 2, *Tremella* species 1, *Tremella* species 2 and *Tremella* species 3 and *Vishniacozyma* species). Two taxa were identified only up to family level and belonged to Auriculariaceae, and Cryptococcaceae. These two taxa could not be placed in a genus because they exhibited phylogenetic distinction from all the heterobasidiomycete genera described so far. Among the total 47 taxa documented, one is a new record to Asia, 24 are new records to India, and 31 are new records to Kerala. Pure cultures of twenty species were established and are maintained in the Fungal Diversity laboratory of the Zamorin's Guruvayurappan College as part of conservation efforts. Fifty five molecular sequences were newly generated and phylogenetic analysis of Auriculariales, Sebaciniales, Dacrymycetes, and Tremellomycetes were conducted for accurate identification of species.

Summary

Only a few systematic studies have been conducted on heterobasidiomycetes of India so far. After the major taxonomic accounts of jelly fungi from south-west Maharashtra (Mahamulkar *et al.* 2003, Patil *et al.* 2003), this group is studied from Kerala State. The study is based on extensive collection of fresh fruit bodies. Systematic documentation of heterobasidiomycetes from Kerala is done using combined morphological and molecular characterization. This study forms the first phylogenetically supported comprehensive treatment of heterobasidiomycetes from India.

RECOMMENDATIONS

This systematic study on heterobasidiomycete has documented 47 species from Kerala State during the 5 year period (2018–2023). The number of new species and new reports to Kerala documented during the present study indicate the diversity richness of heterobasidiomycetes of Kerala State. Jelly fungi need not form basidiocarps throughout the seasons at fixed habitats. Many species may have been evaded collection due to the absence of formation of basidiocarp during the five-year study period. Hence, there may be more species of heterobasidiomycetes remaining to be characterized and identified. Further extensive studies with extended time period and more environmental sampling (other than basidiocarps) are highly recommended, which will further increase the number of heterobasidiomycete reports from Kerala State.

Basidiocarps of heterobasidiomycetes are difficult to handle and preserve. The lack of sufficient quantity of basidiocarp is another problem while dealing with heterobasidiomycetes. Most of the specimens do not retain their original shape and texture after drying. This makes microscopic examination of dried materials difficult. Dried specimens also do not yield sufficient DNA. Hence, isolation of pure culture is important. Pure cultures will also provide taxonomically relevant information. Maintenance of cultures are also extremely important from a conservation point of view. This study has isolated pure cultures from 20 species, which is only 42.5% of documented species. This is due to high contamination rate from basidiocarps and the difficulty to obtain spore prints. More field isolation techniques should be used to increase the success rate of culture establishment. Studies involving mycochemical screening and bioprospecting of jelly fungi using basidiocarps and live cultures can be recommended as having scope for extended future studies.

Heterobasidiomycetes is a group of ecologically and economically important fungi. Members of the genus *Auricularia* and *Tremella* are well known with their edibility. Spawn production protocols and cultivation techniques of these edible species should be standardized according to the climatic conditions of Kerala in further studies. Heterobasidiomycetes, especially Auriculariales and Dacrymycetales members, are ecologically important because of their wood decomposition properties. Natural habitat destruction and deforestation affects the survival of this group. Spawn production, proper environmental protection strategies and conservation methods should be employed for long term *in vitro* and *in vivo* conservation of heterobasidiomycetes.

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APPENDICES

APPENDIX- I - List of figures

1. Figure 1 : Map of Kerala State, India, showing major collection localities
2. Figure 2 : Cell types in Tremellales: photographic plate
3. Figure 3 : Cell types in Tremellales: drawing
4. Figure 4 : *Vishniacozyma* species
5. Figure 5 : *Sirobasidium magnum*
6. Figure 6 : *Sirobasidium japonicum*
7. Figure 7 : *Sirobasidium brefeldianum*
8. Figure 8 : *Naematelia encephaloidae*
9. Figure 9 : *Tremella poilkavensis*
10. Figure 10: *Tremella fuciformis*
11. Figure 11: *Tremella* species 1
12. Figure 12: *Tremella* species 2
13. Figure 13: *Tremella laurisilvae*
14. Figure 14: *Phaeotremella yunanensis*
15. Figure 15: *Tremella seclusa*
16. Figure 16: *Tremella armeniaca*
17. Figure 17: *Tremella sairandhriana*
18. Figure 18: *Tremella mesenterica*
19. Figure 19: *Tremella erythina*
20. Figure 20: *Tremella taiwanensis*
21. Figure 21: *Tremella* species 3
22. Figure 22: *Cryptococcaceae* taxon
23. Figure 23: *Calocera cornea*
24. Figure 24: *Guepiniopsis buccina*
25. Figure 25: *Dacryopinax indacocheae*
26. Figure 26: *Dacryopinax primogenitus*
27. Figure 27: *Dacryopinax yungensis*
28. Figure 28: *Dacryopinax petaliformis*
29. Figure 29: *Dendrodacrys paraphysatum*

30. Figure 30: *Dacrymyces spathularia*
31. Figure 31: *Dacrymyces dacryomitriiformis*
32. Figure 32: *Dacrymyces microsporus*
33. Figure 33: *Dacrymyces* species 1
34. Figure 34: *Dacrymyces lacrymalis*
35. Figure 35: *Dacrymyces cupularis*
36. Figure 36: *Dacrymyces capitatus*
37. Figure 37: *Dacrymyces falcatus*
38. Figure 38: *Dacrymyces novae-zelandiae*
39. Figure 39: *Dacrymyces san-augustinii*
40. Figure 40: *Dacrymyces* species 2
41. Figure 41: *Dacrymyces cerebriformis*
42. Figure 42: *Dacrymyces sinostenosporus*
43. Figure 43: *Auricularia srilankensis*
44. Figure 44: *Auricularia sinodelicata*
45. Figure 45: *Auricularia subglabra*
46. Figure 46: *Auricularia cornea*
47. Figure 47: *Auricularia fibrillifera*
48. Figure 48: *Auricularia heimuer*
49. Figure 49: Auriculariaceae taxon
50. Figure 50: *Sebacina* species
51. Figure 51: Maximum likelihood tree of Auriculariales
52. Figure 52: Maximum likelihood tree of Sebacinales
53. Figure 53: Maximum likelihood tree of Dacrymycetes
54. Figure 54: Maximum likelihood tree of Tremellomycetes

APPENDIX- II - List of tables

1. Table 1: Generic concept of Dacrymycetaceae according to different workers
2. Table 2: List of species used in the phylogenetic analysis of Auriculariales
3. Table 3: List of species used in the phylogenetic analysis of Sebaciales
4. Table 4: List of species used in the phylogenetic analysis of Dacrymycetes
5. Table 5: List of species used in the phylogenetic analysis of Tremellomycetes
6. Table 6: List of species having pure cultures generated in the present study
7. Table 7: Molecular sequences generated in the study