Systematic studies on the boletoid fungi (Agaricomycetes, Basidiomycota) 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

SALNA N.
(U.O.No. 10060/2018/Admn. Dtd. 29/08/2018)

Post Graduate & Research Department of Botany
The Zamorin's Guruvayurappan College
Kozhikode-673 014, Kerala

August 2024

THE ZAMORIN'S GURUVAYURAPPAN COLLEGE
(Established in 1877, Affiliated to the University of Calicut.
Re-accredited by NAAC with A Grade)
Guruvayurappan College P.O., Kozhikode-673014, Kerala
Website: www.zgcollege.org, Phone: 0495-2331516, Email: zgckozhikode@gmail.com

August 2024

CERTIFICATE

This is to certify that the thesis entitled "**Systematic studies on the boletoid fungi (Agaricomycetes, Basidiomycota) of Kerala**", submitted to the University of Calicut by Ms. Salna N., for the award of Ph. D. 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

POST GRADUATE & RESEARCH DEPARTMENT OF BOTANY
THE ZAMORIN'S GURUVAYURAPPAN COLLEGE
(Established in 1877, Affiliated to the University of Calicut.
Re-accredited by NAAC with A Grade)
Guruvayurappan College P.O., Kozhikode-673014, Kerala
Website: www.zgcollege.org, Phone: 0495-2331516, Email: zgckozhikode@gmail.com

Dr. Arun Kumar T. K.
Assistant Professor of Botany

August 2024

CERTIFICATE

This is to certify that the thesis entitled "**Systematic studies on the boletoid fungi (Agaricomycetes, Basidiomycota) of Kerala**" submitted to the University of Calicut by Ms. Salna N., in partial fulfillment of the requirements for the award of the degree of Doctor of Philosophy in Botany, has been carried out by her under my supervision and guidance, and that no part of this thesis has formed the basis for the award of any degree or diploma or other similar title or recognition.

Dr. Arun Kumar T. K.

POST GRADUATE & RESEARCH DEPARTMENT OF BOTANY
THE ZAMORIN'S GURUVAYURAPPAN COLLEGE
(Established in 1877, Affiliated to University of Calicut.
Re-accredited by NAAC with A Grade)
Guruvayurappan College P.O., Kozhikode-673014, Kerala
Website: www.zgcollege.org, Phone 0495-2331516, Email: zgckozhikode@gmail.com

August 2024

CERTIFICATE

This is to certify that the thesis entitled "**Systematic studies on the boletoid fungi (Agaricomycetes, Basidiomycota) of Kerala**" submitted to the University of Calicut by Ms. Salna N., in partial fulfillment of the requirements for the award of the degree of Doctor of Philosophy in Botany, has been carried out by her under the supervision and guidance of Dr. Arun Kumar T. K., Assistant Professor of this department, and that no part of this thesis has formed the basis for the award of any degree or diploma or other similar title or recognition.

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

DECLARATION

I hereby declare that the thesis entitled "**Systematic studies on the boletoid fungi (Agaricomycetes, Basidiomycota) of Kerala**" submitted to the University of Calicut in partial fulfillment of the requirements for the award of the degree of Doctor of Philosophy in Botany, has been carried out by me under the supervision and 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 have undergone plagiarism check using iThenticate software at C.H.M.K. Library University of Calicut, and the similarity index found was within the permissible limit. I also declare that the thesis is free from AI generated contents.

Place: Kozhikode **Salna N.**
Date:

ACKNOWLEDGEMENTS

I express my sincere gratitude to Dr. Arun Kumar T. K. (Assistant Professor, P. G. & Research Department of Botany, The Zamorin's Guruvayurappan College, Kozhikode) for his excellent guidance, inspiring comments, consistent supervision, and encouragement extended throughout my work.

I am grateful to the Management of the Zamorin's Guruvayurappan College, Principal of the College, Dr. B. Rajani, former Principals Dr. P. T. Malini, Dr. G. Indiradevi, and Dr. T. Ramachandran, for providing all facilities, and whole-hearted support for carrying out my PhD. studies.

My sincere thanks to KSCSTE (Kerala State Council for Science and Technology) for providing financial assistance, Chief Wildlife Warden, Kerala for granting me permission for fieldwork in the forest areas of Kerala. I also thank staff members of the Kerala Forest Department for giving facilities during the field trips to various forest areas of Kerala.

Thanks are due to my Research Advisory Committee members, Dr. R. V. M. Divakaran, Dr. A. K. Pradeep, Professor (Dr). P. Manimohan, Dr. P. P. Rajan, Dr. K. P. Rajesh and Dr. Sanoj E. for critically evaluating the progress of my research work and for providing suggestions for improvement.

I record my special gratitude to Prof. (Dr.) P. Manimohan (Department of Botany, University of Calicut) for introducing me to fungal taxonomy and for his invaluable advices and suggestions.

I extend my heartfelt thanks to Dr. C. K. Pradeep (Principal Scientist & Head

Microbiology Division Jawaharlal Nehru Tropical Botanic Garden & Research Institute (JNTBGRI) Palode, Thiruvananthapuram, for his invaluable advices and suggestions.

I am thankful to Dr. P. Indulekha, Head of the Department of Botany, and Dr. P.P. Rajan (former HoD) for giving all the facilities and support during my studies. I am thankful to the faculty members Dr. K. P. Rajesh, Dr. Sanoj E., Dr. Anoop K., Dr. Sreejith P. E. and former faculty Dr. Manju C. Nair of the Zamorin's Guruvayurappan College for their support. I am thankful to all teaching and non-teaching staff of the College for their help and support.

I have great pleasure to record the valuable help and constant encouragement extended to me by the Research Scholars of the Department of Botany, Ms. Anjitha Thomas, Dr. Krishnapriya K., Ms. Anju John V., Dr. Vinjusha N., Ms. Jeena Rose Pious, Ms. Vaishnavi M., Dr. Chandini V. K., Dr. Vijisha P., Ms. Manju A. C., Ms. Thulasi R., Ms. Vafa A. Latheef, Ms. Nishida P. P., Ms. Sruthy O.M., Ms. Sajitha Menon S., Ms. Vinisha, and *Ms. Aswathy C.S. I also thank Research Scholars of other Departments of the college for their support.*

I thank my family members and friends for their valuable help, encouragement, cooperation and support to bring this work to a successful end. I sincerely appreciate my husband's support, love, and tolerance during the research process.

Above all, I thank the almighty God for the grace and blessings showered on me throughout my work, and for giving me strength for the successful completion of my work.

Salna N.

ABSTRACT

Boletoid fungi are a monophyletic group (Boletales Agaricomycetes, Basidiomycota) with members producing basidiomata that are usually fleshy, stipitate-pileate and with poroid or lamellate hymenophore. Most of the species form ectomycorrhizal associations with higher plants. Many are edible. Boletoid fungi have been studied in detail from around the world. In India, boletoid fungi have been fairly documented from northern states. However, there are no comprehensive studies on the Boletales of South India. Hence, a documentary study of the boletoid fungi of Kerala was conducted during the period 2018-2024.

Morphological characterisation along with molecular phylogenetic analyses of the collected specimens were conducted. Boletoid specimens were collected from different parts of Kerala State. Molecular characterization of collected specimens were done using various gene regions (ITS, 28S and *RPB2*). Phylogenetic trees were generated by using Maximum Likelihood method.

A total of 185 boletoid taxa were collected during the five-year period. Significant number of bolete collections were obtained from Kuruva Islets and the Thurayilkotta Sacred grove. Forty bolete species belonging to 29 genera of eight families (Boletaceae, Boletinellaceae, Gyroporaceae, Paxillaceae, Pisolithaceae, Serpulaceae, Sclerodermataceae, Suillaceae) were recorded. Fourteen species were found to be hitherto undescribed. Five species were formally published and other undescribed species are in the process of publication. A collection was found to belong to a genus new to science. Out of the total taxa documented, nine were new records to India and 18 were new records to Kerala. All the specimens, including holotypes are maintained at Zamorin's Guruvayurappan College Herbarium (ZGC). A total of 50 gene sequences were generated from the collections during the study and were used for molecular phylogenetic analyses. Newly generated gene sequences were deposited in open repository. This taxonomic treatment provides descriptions, comparisons, taxonomic keys and molecular phylogenetic analyses of boletes along with macroscopic and microscopic photographs.

Key words: Biodiversity, Boletales, Ectomycorrhizal, Taxonomy, Phylogeny.

സംഗ്രഹം

ബൊളീറ്റോയ്ഡ് ഫംഗസുകൾ ബൊളീറ്റേയ്ൽസ് എന്ന മോണൊഫൈലെറ്റിക് ഓർഡറിന് കീഴിലാണ് വരുന്നത്. അവ സാധാരണയായി സസ്യങ്ങളുമായി എക്ടോമൈകോറൈസൽ ബന്ധം കാണിക്കുന്നു. ചില ബൊളീറ്റുകൾ ഭക്ഷ്യയോഗ്യവുമാണ്. ബോളീറ്റേയ്ൽസ് ഓർഡറിന്റെ ടാക്സോണമി, ഫൈലോജനി, ബയോജോഗ്രഫിക് വശങ്ങൾ ഇന്ന് വളരെയധികം പ്രധാനപ്പെട്ട ഗവേഷണ മേഖലകളാണ്. ഇതിനെയെല്ലാം സഹായിക്കാൻ ഉഷ്ണമേഖലാ പ്രദേശങ്ങളിൽ, പ്രത്യേകിച്ച് ഇന്ത്യൻ ഉപഭൂഖണ്ഡത്തിൽ നിന്നുള്ള പഠനങ്ങൾ അത്യാവശ്യമാണ്. അതിനാൽ 2018-2024 കാലയളവിൽ കേരളത്തിലെ ബൊളീറ്റുകളെ കുറിച്ച് പഠനം നടത്തി.

ബോളീറ്റോയിഡ് ടാക്സകൾ ശേഖരിക്കുകയും അവയുടെ മോർഫോളജിക്കൽ പഠനത്തോടൊപ്പം മോളിക്യുലാർ ഫൈലൊജനറ്റിക് വിശകലനവും നടത്തി. പഠനകാലത്ത് 185 ടാക്സകൾ ശേഖരിച്ചു. അവയിൽ നിന്ന്, എട്ട് ഫാമിലികളിലായി 29 ജീനസ്സുകളിൽപ്പെടുന്ന 40 ബോളീറ്റ് സ്പീഷീസുകൾ തിരിച്ചറിഞ്ഞു. പതിനാല് പുതിയ സ്പീഷുകൾ ഇതിൽ ഉൾപ്പെടുന്നു. ഒമ്പത് ടാക്സകൾ ഇന്ത്യയിൽ ആദ്യത്തെ റെക്കോഡും, 8 എണ്ണം കേരളത്തിൽ പുതിയ റെക്കോഡുമാണ്. ഹോളോടൈപ്പുകൾ ഉൾപ്പെടെ, എല്ല ബോളീറ്റോയിഡ് ഫംഗസുകളെയും സാമൂതിരി ഗുരുവായൂരപ്പൻ കോളേജിലെ ഹെർബേറിയത്തിൽ സൂക്ഷിക്കുന്നുണ്ട്. അൻപത് പുതിയ ജീൻ സീക്വൻസുകളും ജനറേറ്റ് ചെയ്തു. ദക്ഷിണേന്ത്യയിൽ നിന്നുള്ള ആദ്യത്തെ സമഗ്രമായ പഠനമാണ് ഈ ഗവേഷണത്തിന്റെ ഭാഗമായി നടത്തിയിരിക്കുന്നത്.

സൂചക പദങ്ങൾ : ജൈവ വൈവിധ്യം, ബോളീറ്റേയ്ൽസ്, എക്ടോമൈക്കോറൈസൽ, ടാക്സോണമി, ഫൈലോജനി.

CONTENTS

1. INTRODUCTION

Boletes, commonly known as fleshy pored mushrooms, are considered as one of the most fascinating and iconic components of larger mushroom-forming fungi. They are having worldwide distribution (Gelardi 2021). Boletoid fungi were first identified as a distinct group by Chevallier in 1826. Now they belong to an extraordinarily rich monophyletic order Boletales E.-J. Gilbert (Agaricomycetes, Baisdiomycota). Most species of Boletales have the conspicuous stipitate-pileate fruiting body with tubular or lamellate hymenophore (Gilbert 1931, Binder and Hibbett 2006). To a lesser extent, epigeous and hypogeous sequestrate, agaricoid and pleurotoid lamellate, corticioid and polyporoid forms are also present (Binder and Hibbett 2006). Currently, Boletales is subdivided into 5 suborders, 18 families and 150 accepted genera with approximately 2194 species worldwide (Gelardi 2021).

As far as the nutritional status is concerned, most boletes are ectotrophically mycorrhizal, occasionally ericoid or tuberculate ectomycorrhizal with roots of a large variety of living green woody plants belonging to gymnosperms and angiosperms (Binder and Hibbett 2006, Halling et al. 2007, Tedersoo et al. 2010). Boletes show ectomycorrhizal relationships mainly with families like Fagaceae Dum., Pinaceae Lindley, Myrtaceae Juss., Dipterocarpaceae Blume, Casuarinaceae R.Br., Fabaceae Lindl. and Betulaceae Gray (Gelardi 2021). A few genera such as *Chalciporus* Bataille are species-specific mycoparasites (Xu et al. 2021). Species of *Phlebopus* (R. Heim) Singer and *Boletinellus* Murrill establish a tripartite nutritional relationship through the formation of fungus-insect galls (Raghoonundon et al. 2021). Corticioid genera (*Coniophora* DC., *Serpula* (Pers.) Gray, *Leucogyrophana* Pouzar, etc.) in Boletales are having most dangerous wood-destroying fungal species (Hibbett and Binder 2002, Binder et al. 2005, Binder and Hibbett 2006).

Various types of chemical compounds, pigments and secondary metabolites are present in many of the boletes (Nelsen 2010, Zhou et al. 2010). Identification of boletes using the color change of the flesh is useful and important. Derivatives of the pulvinic acid are responsible for the yellow, red and brown pigments and they provide enzymatic bluing oxidation phenomenon evident in many of the boletes (Gelardi 2021). Boviquinones, carboxylic aromatic acids, terphenyl quinones, atromentinic acid like chemical compounds are also present in bolete species (Besl and Bresinsky 1997, Besl et al. 1986).

Many bolete species are highly nutritive, edible and delicious. Members of the genus *Boletus* L. (commonly called "king boletes", "ceps" or "porcini mushrooms") are the most utilized wild edible mushrooms. Due to the great demand, they are constantly harvested for consumption and trading in different parts of the world. Several rural populations in Asia generate income from the selling of these edible mushrooms (Kirk et al. 2008, Sitta and Floriani 2008, Feng et al. 2012, Mello 2013, Sitta and Davoli 2013, Peintner et al. 2013, Dentinger and Suz 2014, Gelardi 2020). *Phlebopus* species are widely used as edible and they are cultivated on a large scale in Asian countries (Raghoonundon et al. 2021). Some boletes like *Rubroboletus satanas* (Lenz) Kuan Zhao and Zhu L. Yang, are toxic and cause gastrointestinal problems. *Pulveroboletus ravenelii* (Berk. and M.A. Curtis) Murrill is a well-known bolete in Chinese medicines. Some boletes have antioxidant properties (Zeng et al. 2017).

Gilbert (1931) formed the foundation for the modern study of boletoid mushrooms. Then after, a lot of major taxonomic treatments on the group were published, and now, molecular phylogenetic reconstruction is attaining more attention in Boletales (Kühner and Romagnesi 1953, Hongo 1960, Watling 1970, Smith and Thiers 1971, Corner 1972, Pilát and Dermek 1974, Singer 1986, Pegler and Young 1981, Moser and Kibby 1983, Binder and Hibbett 2006, Matheny et al. 2006, Wu et al. 2014, 2016, He et al. 2019, Varga et al. 2019, Tremble et al. 2023).

Boletoid fungi have worldwide distribution and they are present in most terrestrial biomes in all continents except Antarctica (Smith and Thiers 1971, Corner 1972, Horak 1983, Binder and Bresinsky 2002, Wu et al. 2014, 2016, Gelardi 2021). A high number of bolete species were reported from the pantropical belt of the northern hemisphere with biodiversity hotspots located in North America (especially north-eastern North America), in neotropical montane cloud forests of Central America and the Caribbean and even more in eastern and south-eastern Asia (Smith and Thiers 1971, Corner 1972, Horak 1983, Binder and Bresinsky 2002, Wu et al. 2014, 2016).

India represents one of the largest biodiversity-rich countries of the world, consisting of different types of ecosystems. The Eastern Himalayan region of India has lots of suitable ectomycorrhizal host plants, hence many boletes have been reported so far. A total of 110 boletoid species were reported from different parts of India (Mohanan 2011, Lakhanpal 1996, 1998, Chakraborty and Das 2015, Das and Dentinger 2015, Das et al. 2012, 2013, 2014, 2023, Chakraborty et al. 2017, Kumar et al. 2019).

Kerala is a small state located between 8º15´ N and 12º50´ N latitudes and between 74º50´E and 77º30´ E longitudes, and one of the highly diverse areas of India (Krishnakumar et al. 2008). It is hemmed in between the Western Ghats on the east side and the Arabian Sea on the west side. Western Ghats, one of the biodiversity hotspots of the world, is home to more than 5,000 angiosperms. Many of the flora and fauna of this geographically unique area are endemic. Only 29 boletes were recorded from Kerala so far (Mohanan 2011, Pradeep et al. 2015, Kumar et al. 2019). The rich host plant diversity of the Western Ghats and favorable tropical climate leads to the assumption of the presence of a high number of boletes in Kerala State. Documentation of tropical boletes is crucial for an accurate understanding of the phylogeny and biogeography of boletes.

Objectives of the study:

1. To prepare systematic account of the boletoid fungi (Agaricomycetes, Basidiomycota) of Kerala.
2. Morphological and molecular characterization of the documented data.
3. Elucidation of phylogenetic relationships of the boletoid fungi of Kerala.

2. REVIEW OF LITERATURE

Boletoid fungi (Boletales) are characterized by large, fleshy, and colored basidiomata having tubulose, lamellate, or loculus hymenophore (Wang et al. 2023). As per the recent morphological and molecular analyses, the order Boletales consists of 5 suborders, 18 families, 150 accepted genera and more than 2194 species worldwide (He et al. 2019, Gelardi 2021). A sclerodermatoid fossil genus *Palaeogaster* Poinar, Alfredo and Baseia is also included in Boletales (Poinar et al. 2014).

Boletales was extensively studied in the temperate regions (Gilbert 1931, Kühner and Romagnesi 1953, Singer 1960, Moser 1983, Klofac 2007). The classification of different boletoid groups was developed in to a more natural system, with the accumulation of morphological data in the twentieth century (Bozok et al. 2019). The most accepted classification system based on morphology of boletoid fungi was Singer's (1986) concept. Hibbett and Thorn (2001) published a preliminary phylogenetic classification of homobasidiomycetes, which included the establishment of a boletoid clade based on molecular data.

Kirk et al. (2008) listed 15 families in Boletales. Boletaceae Chevall. is the largest family of the order consisting more than 800 species (Kirk et al. 2008, Wu et al. 2014, Bozok et al. 2019). Phylogenetic treatment of the order identified large clades instead of sections (Binder and Hibett 2006, Wu et al. 2014). Molecular phylogenetic studies also reconstructed many of the genera based on the evolutionary relationships (Binder and Hibett 2006, Nuhn et al. 2013, Gelardi et al. 2014, Wu et al. 2014).

Boletoid members have ectomycorrhizal associations with more than ten plant families (Sato et al. 2007, Kennedy et al. 2012). The host plant families include Fabaceae, Casuarinaceae, Dipterocarpaceae, Myrtaceae, Pinaceae, and

Ericaceae Juss. (Newman and Reddell 1987, Binder and Hibbett 2006). Boletes having ectomycorrhizal associations are host specific or host non-specific. The species in Suillineae show obligate ectomycorrizal associations with Pinaceae (Singer 1986, Binder and Bresinsky 2002). Genera like *Boletinellus* and *Phlebopus* are root parasites (Singer 1986, Binder and Bresinsky 2002). A few species in the family Gomphidiaceae Maire ex Jülich are mycoparasites (Agerer 1991).

Boletoid fungi were studied for their anticancerous and medicinal properties (Kim et al. 2017, Malinowska and Falandysz 2004). *Boletus edulis* Bull. or the king bolete is a highly prized mushroom in different parts of the world (Feng et al. 2012). But, *Rubroboletus satanas* (Lenz) Kuan Zhao and Zhu L. Yang, *Sutorius venenatus* (Nagas.) G. Wu and Zhu L. Yang, *Heimioporus japonicus* (Hongo) E. Horak etc. are toxic and causes gastrointestinal problems (Patocka 2018).

Boletoid fungi have a worldwide distribution (Binder and Hibbett 2006, Halling 2007). But tropical forests are least explored and expected to have more undescribed species. India has several mega diversity hotspots like Western Ghats. 110 boletoid species were reported from India (Manjula 1983, Verma and Pandro 2018, Kumar et al. 2019, Das et al. 2024). Eighty Five species belonging to 24 genera in Boletaceae are known from Indian Himalaya (Das et al. 2024).

2.1. Boletales E.-J. Gilbert.

Boletales, is one of the largest fungal groups in homobasidiomycetes (Binder and Hibbett 2006). The order contains mushrooms with a tubulose, sometimes lamellate hymenial surface (Gilbert 1931, Binder and Hibbett 2006, Wu et al. 2014). Boletales also includes fungi having gasteroid (puff-ball like), resupinate, merulioid or hydnoid hymenophore (Besl and Bresinsky 1997, Jarosch 2001).

Boletales is a monophyletic assemblage of boletoid fungi (He et al. 2019, Gelardi 2021). The tribe Bolétés was first recognized by Patouillard (1900). However, Gilbert (1931) erected Boletales as an independent order from Agaricales and included both poroid and lamellate genera. Gilbert (1931) established two suborders under Boletales, Boletineae E.-J. Gilbert and Strobilomycetineae E.-J. Gilbert, by studying European and American boletes. The classification of the group was done on the basis of morphological data for more than two centuries before the emergence of molecular phylogenetic studies (Gelardi 2021). Establishment of order Boletales was not uniformly accepted (Horak 1968). Kühner and Romagnesi (1953) studied Europian boletes and divided the members in to two informal groups, lamellate boletes and poroid boletes. Japanese boletes were grouped in to four families (Paxillaceae Lotsy, Gomphidiaceae, Boletaceae and Strobilomycetaceae) under Agaricales Underw. by Hongo (1960). Watling (1970) classified British boletes in to three familes (Boletaceae, Gomphidiaceae and Paxillaceae), without specifying the order to which they belong. Smith and Thiers (1971) proposed Boletaceae family for placing all the fleshy pored boletes of Michigan (USA) in agreement with Watling (1970). South-east Asian boletes were studied by Corner (1972) by giving importance to Indo-Malayan region, and recognized only four genera, *Boletus*, *Gyroporus* Quél, *Heimiella* Boedijn and *Strobilomyces* Berk. Soon, Pilát and Dermek (1974), published a monograph of European boletes, which included two subfamilies, Strobilomycetoideae Snell and Boletoideae Burnett. Kühner (1977) recognized Boletales order by including two families, Boletaceae and Paxillaceae. Boletaceae included *Strobilomyces, Gyroporus, Boletus, Suillus* Gray and *Gomphidius* Fr. Paxillaceae had *Hygrophoropsis* (J. Schröt.) Maire ex Martin-Sans and *Paxillus* Fr. *Boletus* divided into subgenera *Gyrodon* Opat., *Phylloporus* Quél., *Xerocomus* Quél., *Boletus, Tylopilus* P. Karst., *Porphyrellus* E.-J. Gilbert and *Leccinum* Gray. Pegler and Young (1981) retained Boletales order and broadly classified the accepted members in to the following families:

Boletaceae, Paxillaceae, Gyrodontaceae Heinem., Xerocomaceae Pegler and T.W.K. Young, Strobilomycetaceae, Gomphidiaceae, Rhizopogonaceae Gäum. and C.W. Dodge and Chamonixiaceae Jülich. Moser and Kibby (1983) also accepted the order status of Boletales and described 21 European genera in four different families (Strobilomycetaceae, Boletaceae, Paxillaceae and Gomphidiaceae). However, Singer (1986) in his book 'The Agaricales in modern taxonomy' included the 34 boletoid genera within the suborder Boletineae E.-J. Gilbert of order Agaricales. All the subsequent studies retained the order Boletales, and molecular phylogenetic studies confirmed the monophyly of Boletales (Agerer 1987, Besl and Bresinsky 1997, Ginns 1998, Watling and Li 1999, Bessette et al. 2000, Ladurner and Simonini 2003, Muñoz 2005, Zang 2006, Klofac 2007, Knudsen and Taylor 2008, Bernicchia and Gorjón 2010, Zang et al. 2013, Nuhn et al. 2013, Wu et al. 2016a, Gelardi et al. 2021). The Boletes of Michigan (Smith and Theirs 1971), Boletaceae of New Zealand (McNabb 1968), Boletus in Malaysia (Corner 1972), Agaricoid and Boletoid fungi from Malawi and Zambia (Pegler 1982) and Revison of Malaysian species of Boletales (Horak 2011) are the major monographic works that exist. Singer (1936, 1983, 1986), Watling (1970), Smith and Thiers (1971), Agerer (1987), Moser (1983), Besl and Bresinsky (1997) were the major taxonomists who contributed to the taxonomy of Boletales based on morphology.

Chemotaxonomic studies also contributed to the classification of Boletales (Bresinsky 1974, Besl and Bresinsky 1977). The important chemicals detected in Boletales were pulvinic acid derivatives, grevillins and boviquinones (Høiland 1987). Pigments in the species were used to separate Suillineae from Boletineae (Besl and Bresinsky 1997, Binder and Hibbett 2006). Agerer (1999) explained Tapinellineae and Coniophorineae in Boletales with the characters of rhizomorphs and substrate hyphae. Pegler and Young (1981) had removed Coniophoraceae from Boletales and had maintained in Aphyllophorales.

However, chemotaxonomic studies along with morphological data placed Coniophoraceae in Boletales (Besl and Bresinsky 1986).

Molecular phylogenetic studies using nuclear and mitochondrial genes changed the classical taxonomic views of Boletales (Bruns et al. 1989). The phylogenetic treatments indicated that Boletales is a monophyletic group (Binder and Bresinsky 2002, Binder et al. 2005, Binder and Hibbett 2006). Hibbet and Thorn (2001) gave a breakthrough in the classification of homobasidiomycetes and established different clades in homobasidiomycetes with molecular data. Boletales was retained as bolete clade in their phylogenetic treatment. In Dictionary of Fungi by Kirk et al. (2008) boletoid species maintained in the Boletales order. Binder and Hibbet (2006) published their findings of biological diversification of Boletales by using nuclear encoded large subunit (nuc-LSU) gene region for broad sampling and a multigene dataset (nuclear encoded small subunit (nuc-SSU), nuc-LSU, 5.8s, mitochondrial large subunit (mt-LSU), *atp6*) for sampling 42 key species of Boletales. Six major lineages were recognized (Boletineae, Paxillineae, Sclerodermatineae Manfr. Binder and Bresinsky, Suillineae Besl and Bresinsky, Tapinellineae Agerer and Coniophorineae Agerer and C. Hahn) and Boletineae and Suillineae were found monophyletic in their analyses. A comprehensive taxonomic treatment of Kingdom Fungi was proposed by Hibbett et al. (2007) based on molecular phylogenetic data. Their classification followed Linnaen hierarchy and boletoid fungi was placed in Boletales under Class Agaricomycetes Doweld. Multilocus analyses of Agaricomycotina Doweld by Matheny et al. (2006) found that Agaricales, Boletales and Atheliales Jülich originates from a single node. Subsequently, Atheliales was considered as the sister group of Boletales. The families Pisolithaceae Ulbr. and Truncocolumellaceae Agerer were combined with Sclerodermataceae and Suillaceae Besl and Bresinsky, respectively by Kirk et al. (2008) and He et al. (2019). However, studies by Wu et al. (2020) and Gelardi (2021) considered them as separate families. Several phylogenetic treatments of boletoid groups were published and numerous novel taxa were described in the past ten years (Nuhn et al. 2013, Wu et al. 2014, Wu et al. 2016a, He et al. 2019, Magnago et al. 2022).

The order Boletales includes 5 suborders, 17 families and 150 accepted genera (including the sclerodermatoid fossil genus *Palaeogaster*) and 2022 species according to recent phylogenetic analyses by He et al. (2019). Accepted suborders and families according to He et al. (2019) are given in the Table 1.

Table 1. Boletales according to He et al. (2019).

Suborder	**Family**
Tapinellineae Agerer	Tapinellaceae C. Hahn
Coniophorineae Agerer and C. Hahn	Coniophoraceae Ulbrich Hygrophoropsidaceae Kühner
Suillineae Besl and Bresinsky	Gomphidiaceae R. Maire ex Jülich Rhizopogonaceae Gäumann and C.W. Dodge Suillaceae (Singer) Besl and Bresinsky Truncocolumellaceae Agerer
Sclerodermatineae Manfr. Binder and Bresinsky	Boletinellaceae P.M. Kirk, P.F. Cannon and J.C. David Calostomataceae E. Fischer Diplocystidiaceae Kreisel Gyroporaceae (Singer) Manfr. Binder and Bresinsky Pisolithaceae Ulbrich Sclerodermataceae Corda
Boletineae E.-J. Gilbert	Boletaceae Chevallier Paxillaceae Lotsy
incertae sedis	Gasterellaceae Zeller Serpulaceae Jarosch and Bresinsky

According to Binder et al. (2010), the suborders Tapinellineae and Coniophorineae Agerer and C. Hahn are evolutionarily the first diverging lineages of the Boletales, and they occupy a basal position. These two suborders mainly consist of lignicolous corticioid, pleurotoid and polyporoid genera (Gelardi 2021). Suborder Suillineae includes four families, in which Suillaceae and Gomphidiaceae consist of boletoid and agaricoid taxa respectively, and Rhizopogonaceae and Truncocolumellaceae are composed of sequestrate species. Boletinellaceae and Gyroporaceae are the families, which include boletoid genera, and Calostomataceae E. Fisch., Diplocystidiaceae Kreisel, Pisolithaceae and Sclerodermataceae Corda, are the families which include epigeous gasteroid genera under the suborder Sclerodermatineae. Sato and Toju (2019) established Sclerodermatineae as polyphyletic, and revealed the group to be composed of Sclerodermatineae s.str. and Boletinellaceae P.M. Kirk, P.F. Cannon and J.C. David. Suborder Boletineae includes most diverse families like Boletaceae. Boletaceae consist of 108 genera with over 1270 species distributed worldwide. Boletaceae includes members with a basidiomata, whereas, Paxillaceae contains boletoid, agaricoid, hypogeous sequestrate, polyporoid and corticioid basidiomata (Gelardi 2021).

Hibbett et al. (1997) suggested that the order Boletales descended from a boletoid ancestor. But, later phylogenetic studies rejected this suggestion and found that the ancestral species of order Boletales may be a saprotrophic resupinate or more probably polyporoid basidiomata forming fungus responsible for brown rot on conifer wood (Binder and Hibbett 2006, Larsson et al. 2004). This is substantiated by the placement of suborders Tapinellineae and Coniophorineae in the basal position of Boletales (Sato and Toju 2019). Suborder Boletineae suggested to be originated in the Upper Cretaceous, around 91–71 million years ago (Dentinger et al. 2010). The Boletineae is considered to have undergone rapid radiation in the evolutionary history (Binder and Hibbett 2006, Halling et al. 2007, Nuhn et al. 2013). Sclerodermatinae also originated in the upper Cretaceous in eastern and south-eastern Asia and North America during 82–80 million years ago. However, the diversification of this suborder was in middle and Early Cenozoic (Wilson et al. 2011). Suborder Suillineae originated in Early Cenozoic, around

56–53 mya (Wilson et al. 2011). Family Serpulaceae clusterd near the suborder Tapinellinae as a sister taxon, and may be due to the separation of two groups during the upper Cretaceous around 64 mya (Skrede et al. 2011). The study of Tremble et al. (2023) provided extended knowledge on Boletaceae phylogeny and biogeography by using multigene data. They found that Boletaceae likely arose before Gondwanan breakup, and present-day distributions are partly due to vicariance.

2.1.1. Taxonomic characters

2.1.1.1. Macroscopic basidiomatal characters

The order Boletales includes mainly mushroom forming homobasidiomycetes (Gelardi 2021). Fruiting bodies may be annual, ephemeral, short-lived, or easily putrescent. They grow as solitary, scattered to gregarious, or in infrequently caespitose pattern. Basidiomata may be small to massive. Most of the species are fleshy, stipitate-pileate, with varying colors. However, some genera like *Scleroderma* Pers. and *Pisolithus* Alb. and Schwein. posses secotioid or gasteroid structures, with both epigeous (earthballs and earthstars) and hypogeous (false truffles) habit. A very few members show corticioid or crust-like habit (Hibbett and Thorn 2001).

Pileus may be scaly, fibrillose, tomentose, velutinous or glabrous, dry or viscid. The hymenophore structure is tubular-poroid in most of the genera. Lamellate boletes with decurrent lamellae are present in seven genera of Boletinaeae, such as *Paxillus*, *Phylloporus*, *Phyllobolites* Singer (Boletaceae), *Phylloboletellus* Singer (Boletaceae), *Phylloporopsis* Angelini, *Erythrophylloporus* Ming Zhang and TH Li and *Paxilloboletus* Furneaux, De Kesel and FK Khan. (Badou et al. 2022). Poroid or lamellate hymenophore under the pileus is attached to the stipe, and are easily detachable from the pileal context. Poroid or lamellate hymenophore show depressed, sinuate-adnexed, adnate to decurrent attachment. Sequestrate species of Boletales have hymenophore region as gleba, which is enclosed or exposed, convoluted, labyrinthine, lacunose or chambered. Corticioid taxa show smooth, folded to meruloid or raduloid or even hydnoid hymenophore (Gelardi 2021).

Stipe is usually fleshy, central, eccentric, cylindrical or subcylindrical. Stipe surface may be glabrous, fibrillose, tomentose, pruinose, distinctly reticulated or striated. Stipe is often absent or coverd by gleba in sequestrate froms. Context characters of pileus and stipe are important in bolete taxonomy (Wu et al. 2016a). Context colors occur as white, yellowish, orange, brownish or greyish and shows bluing, reddening, browning, blackening on brusing or when cut, due to auto-oxiadation in many boletes.

Odour is generally mild, fungoid or not distinct. Some boletes possess peculiar smell like sweetish, garlic or shallot-like, chicory or licorice-like, of vinyl glue, iodoform, naphthalene, vanilla, boiled milk, roasted potatoes, and rotting meat smells. Edible species are many, while some species may taste bitter (*Tylopilus* felleus (Bull.) P. Karst.), peppery or sour (*Chalciporus piperatus* (Bull.) Bataille) (Mei et al. 2021, Raghoonundon et al. 2021, Xu et al. 2021). Spore prints of bolete species are usually olive-brown but can also be white, cream yellowish, yellow ochraceous, flesh pink, brownish pink, reddish, rusty brown, purplish brown, dark sooty brown to blackish (Horak 2011, Gelardi 2021).

2.1.1.2. Microscopic basidiomatal characters

Basidiospores

Basidiospores of Boletales members are generally ellipsoid-fusiform, but also elongate fusoid to cylindrical, broadly ellipsoid to ovoid or globose to subglobose, or rarely amygdaliform. Walls may be thin to thick. Many of the species have guttulate spores. Spores may be hyaline to pigmented with yellowish, brownish or darker contents. The distal end of spores may be rounded, pointed, sometimes truncate, with or without germ pore. Members of Boletales generally have smooth spores, however, striate, longitudinally costate or winged, rugulose-verrucose, pustulate-tuberculate, echinulate, cristate, reticulate-alveolate, pitted, denticulate, and bacillate spores are also present. The discharging mechanism is ballistosporic in pileate-stipitate forms and statismosporic in sequestrate representatives. All the basidiospores are generally cyanophilic in cotton blue, inamyloid, dextrinoid or very rarely amyloid in Melzer's reagent. The length of spores varies from small (smaller than 10 µm, *Suillus* Gray) to large (larger than 20 µm, Gomphidiaceae).

Hyphal system

Majority of bolete species possess monomitic hyphal system. Hyphae are frequently septate, thin- to thick-walled, smooth or incrusted, hyaline to variously pigmented. Dimitic hyphal system and oleipherous hyphae are characteristic of the genus *Serpula.*

Basidia

Basidia are generally 4-spored, but 1-, 2- or 3-spored are also present. Rarely, 6–10-spored basidia is present in some gasteroid genera such as *Pisolithus*, *Scleroderma*, *Rhizopogon* Fr., and *Alpova* C.W. Dodge. Basidia may be clavate or broadly clavate. Caulobasidia is present in some genera like *Tylopilus* and *Boletellus* Murrill.

Hymenophoral trama

Hymenophoral trama is bilaterally divergent in majority of boletes. Bilateral diveregence is generally grouped in to '*Boletus* type', '*Phylloporus* type' or intermediate.

Cystidia

Hymenial cystidia, pleurocystida and cheilocystidia are present in most of the genera of Boletales. The common shapes of cystidia are lageniform, ventricose-fusiform, cylindrical, clavate, capitate, mucronate and sphaeropedunculate. Caulocystidia present on the stipe surface of many species resemble the shape of hymenial cystidia. Pseudocystidia can be seen occasionally in genera like *Alessioporus* Gelardi, Vizzini and Simonini and *Cupreoboletus* Simonini, Gelardi and Vizzini.

Pileipellis/peridium structure

Pileipellis in the stipitate-pileate and sequestrate forms can be of the subcutis, ixosubcutis, trichodermium, hyphoepithelium, ixotrichodermium, ixohyphoepithelium, or interwoven types. Peridium of sequestrate species can be soilid or powdery, blackish or brownish.

Clamp-connections

Clamp-connections are absent in most of the poroid genera, except in the family Boletinellaceae. Lamellate genera in Paxillaceae and some gasteroid genera of Sclerodermatineae are characterized by clamp-connections in all tissues.

2.1.1.3. Pigments, bioactive chemical compounds and secondary metabolites

Most of the boletes consist of several types of pigments and secondary metabolites. They will add color to the basidiomata and cause oxidation reactions. Derivatives of pulvinic acid such as variegatic acid, xerocomic and isoxerocomic acid, vulpinic acid, variegatorubin and xerocomorubin are the common compounds. Genera like *Gyroporus*, Leccinum, *Chamonixia* Rolland, *Paxillus*, *Gyrodon*, *Melanogaster* Corda, *Rhizopogon, Suillus, Gomphidius* possess boviquinones, terphenyl quinones, atromentinic acid, phenolic metabolites, prenylated phenols and grevillins (Besl and Bresinsky 1997, Besl et al. 1986, Liu 2007, Nelsen 2010).

2.1.2. Ultrastructural characters

Boletales exhibits perforate parenthesomes (wall next to the dolipore with holes). Ultrastructural features of *Suillus* is studied by Jenkinson et al. (2008).

2.1.3. Molecular characters

The taxonomy of Boletales radically changed after the emergence of molecular phylogenetic techniques. The most commonly used gene regions for sequencing of Boletales are ITS, 28S, *RPB1, RPB2,* tef-1α and *atp6* (Wu et al. 2016a, He et al. 2019, Gelardi 2021, Magnago et al. 2022). Molecular analysis of Boletales was done by Binder and Hibbett (2006) using nuc-ssu, nuc-lsu, 5.8S, atp6 and mt-lsu gene regions for resolving the sister-group relationships among Boletales. The recent phylogenetic studies have utilized 28S, *RPB1, RPB2, TEF1 α* gene regions more than other genes (Gelardi et al. 2023, Magnago et al. 2022, Wang et al. 2023). It is preferable to perform multigene analysis on species to accurately classify the Boletales (Wu et al. 2014, 2016, He et al. 2019).

2.1.4. Biogeographic aspects of boletes

Fungi are suitable organisms for studying the biogeographic pattern and evolutionary radiations (Tremble et al. 2023). Species of the family Boletaceae were taken as model organisms to analyse the divergence pattern of boletoid fungi (Halling et al. 2007). Boletaceae includes ectomycorrhizal species that can be unique systems to identify the genetic mechanisms that contribute to diversification (Tremble et al. 2023). Many large-scale molecular analyses were published to explain the evolutionary history in the Boletaceae (Halling et al. 2007, Nuhn et al. 2013, Dentinger et al. 2015, Tremble et al. 2023, Tremble et al. 2024).

The family is thought to have undergone an early evolutionary radiation between 60-100 mya (Binder et al. 2006, Dentinger et al. 2010, Wu et al. 2014, 2016). Halling et al. (2008) analysed many bolete species to describe the migration pattern from North America to South America. Halling et al. (2008) suggested three possible hypotheses to account for apparent disjunction among the boletes: 1. Long distance dispersal of basidiospores, 2. post-Cretaceous migration of co-symbionts over land bridges with a change or shift in symbiotic partners, 3. Relictual Pangaean distribution. Halling et al. (2008) suggested *Tylopilus balloui* (Peck) Singer as a promising model species for examining the biogeography and population genetics of ectomycorrhizal basidiomycetes based on molecular phylogenetic data.

The latest evolutionary study by Tremble et al. (2023) based on multigene phylogenetic analyses of large number of boletes provides more informations about the origin and diversification of boletes. Their divergence dating analyses support a Gondwanan origin of the Boletaceae. Subsequent divergence may have occured through continental drift based vicariance events and possible long-distance dispersals. Origin and divergence of Boletaceae correlates with that of symbiotic plant species (Wilf et al. 2019). So, Tremble et al. (2023) suggest that vicariance may have played a strong role in the distribution of ectomycorrhizal fungal taxa, despite the long-distance dispersal capacity of airborne spore. This is substantiated by the "Southern Route to Asia" hypothesis (Wilf et al. 2019). Hypothesis proposes ectomycorrhizal Fagaceae and their symbiotic fungi originated in Gondwana and were carried on Australia north to Asia. Tremble et al. (2023) also suggested a strong migration event happened recently over the past 50 mya between the Indo-Malaysian and Holarctic regions.

2.1.5. Ecological and economic importance

Most of the species in Boletales are known to establish mycorrhizal associations with plants such as Betulaceae, Casuarinaceae, Dipterocarpaceae, Ericaceae, Fagaceae, Myrtaceae, and Pinaceae (Newmann and Reddell 1987, Osmundson et al. 2007, Halling et al. 2007). Ectomycorrhizal fungi are important components of forest ecosystems and provide suitable conditions for the enhanced growth of plants (Gelardi 2021). Recent phylogenetic analyses of ectomycorrhizal boletes revealed that ectomycorrhizal associations arose independently and asynchronously at least five times in the stem positions of the Suillineae, Sclerodermatineae s. str., Boletaceae, Paxillaceae and in *Austropaxillus* Bresinsky and Jarosch (Hibbett and Matheny 2009, Skrede et al. 2011, Sato and Toju 2019). Mycorhhizal association can occur as ectotrophically mycorrhizal (eg: *Boletus* species) or tuberculate mycorrhizal (eg: Suillaceae and Rhizopogonaceae) (Newman and Reddell 1987, Binder and Hibbett 2006, Tedersoo et al. 2010). These associations help for the rapid growth of plants in their habitats. Many mycorrhizal boletes like *Suillus* Gray, *Scleroderma, Pisolithus, Rhizopogon* are used as biotechnology tools for studying and enhancing plant growth, seedling establishment and nutrient uptake (Agerer 2006, Watling 2008). Majority of the species in suborder Suillineae are exclusively obligate symbionts of Pinaceae. Gomphidiaceae members establish association with Pinaceae species, however, they can also facultatively parasitize rhizomorphs and ectomycorrhizas of the Suillaceae and Rhizopogonaceae (Singer 1986, Agerer 1987, 2006, Olsson et al. 2000, Binder and Hibbett 2006). Wilson et al. (2012) studied the ectomycorrhizal host associations of Sclerodermtineae group. *Pisolithus* and *Scleroderma* can form ectomycorrhizal relationship with different plants (Sanon et al. 2009). *Pulveroboletus* species in Boletaceae are thought to be in association with Pinaceae, Casuarinaceae and Fagaceae (Halling 2001, Wilson et al. 2012). Boletaceae, Gyroporaceae, Melanogastraceae E. Fisch., Paxillaceae, Rhizopogonaceae, Sclerodermataceae and Suillaceae exhibit most advanced type of rhizomorphs and plectenchymatous (consisting of interwoven filamentous hyphae) ectomycorrhizal mantle for effective association (Agerer, 1999, 2006).

Mycoparasites are present in some of the genera of Boletales. *Chalciporus*, *Pseudoboletus* Šutara and *Buchwaldoboletus* Pilát includes species-specific mycoparasites. *Chalciporus piperatus* is a parasite on *Amanita muscaria* (L.) Lam. Genera such as *Phlebopus* and *Boletinellus* show tripartite association between trees and some bugs (Zhang et al. 2015, Fang et al. 2020, Yu et al. 2020, Raghoonundon et al. 2021).

Saprotrophic members of Boletales degrade stumps, debris, fallen twigs or branches and dead standing trees (Gelardi 2021). *Coniophora* members show a special rot called Coniophoraceae-type brown rot. Other saprophytic members make dry rot or brown rot. The normal white rot and soft rot fungi are not at all present in the Boletales (Hibbett and Binder 2002, Binder et al. 2005, Binder and Hibbett 2006). Ascomycete fungi like *Hypomyces chrysospermus* (Bull.) Tul. and C. Tul. infects some bolete members suggesting a co-evolution specialization between parasite and host species (Rogerson and Samuels 1989, Sahr et al. 1999). Many members of *Coniophora*, *Serpula*, and *Leucogyrophana* are wood destroying fungi (Hibbett and Binder 2002, Binder et al. 2005, Binder and Hibbett 2006). *Serpula lacrymans* (Wulfen) J. Schröt. in Europe and Asia, and *Serpula incrassata* (Berk. and M.A. Curtis) Donk in North America are important brown rot wood decomposers (Watkinson and Eastwood 2012).

Many species of Boletales are edible, highly nutritive and medicinally important (Dentinger et al. 2010). The collection of edible boletes provides income and it is also becoming a recreational activity in the developed countries (Power et al. 2015). Evidence for the consumption of boletes dates back to Upper Paleolithic (Magdalenian period), based on the identification of the spores of boletoid and agaricoid species from a tooth plaque of a 18,700 years old woman found at El Miron Cave, Cantabria, northern Spain (Power et al. 2015). The most popular and sought-after edible wild mushrooms globally are those of the genus *Boletus* s. str. They are commonly called “king boletes”, “ceps” or “porcini mushrooms” (Dentinger et al. 2010). Due to the high nutritional content they are extensively harvested and sold in the local markets (Feng et al. 2012, Mello 2012, Sitta and Davoli 2012, Peintner et al. 2013, Dentinger and Suz 2014, Wu et al. 2019, Gelardi 2020). *Phlebopus portentosus* is known as the ‘black bolete’ and it is one of the favourite edible mushrooms in Asian countries (Raghoonundon et al. 2021).

It is a common practise to cultivate edible ectomycorrhizal fungi in conjunction with their host trees (Hall et al. 2003). The most cultivated bolete species is *Phlebopus portentosus.* Experiments with this species have been successful even in the absence of host trees (Kumla et al. 2012). *Phlebopus spongiosus* Pham and Har. Takah. is also artificially cultivated using rice seed mixed with sawdust as substrate (Kumla et al. 2020). *Rhizopogon roseolus* (Corda) Th. Fr. and *Suillus granulatus* (L.) Roussel were cultivated in the field by inoculating the host plants with sporal suspensions or pure cultures (Hall et al. 2003).

The collection, preservation and trade of boletoid fungi were pioneered by the ancient Greeks and Romans (Gelardi 2021). Edible boletes are an integral part of fungal diet of several rural ethnic groups in Europe, Mexico and Central America (Flores Arzù 2020). For marketing, the boletes are sliced and dried, brined, powdered, processed or otherwise preserved perfectly (Sitta and Floriani 2008, Feng et al. 2012, Dentinger and Suz 2014). Epigeous members of *Astraeus* Morgan and *Rhizopogon* are also used as edible and are traded in local mushroom markets of China (Wang et al. 2020). *Phlebopus portentosus* and *P. spongiosus* are successfully cultivated under artificial conditions in south-western China, Thailand and Vietnam (Kumla et al. 2012, Raghoonundon et al.

2021). *Suillus* and *Rhizopogon* species are cultivated in Pine plantations in the Patagonian Andean forests of Chile and Argentina and trading them in local markets (Sitta et al. 2007, Barroetaveña and Toledo 2020).

Tribal communities of China use boletes as medicines (Liu 1984). *Pulveroboletus ravenelii* is used for treating lumbago and skelalgia. *Paxillus involutus* (Batsch) Fr., *Psiloboletinus lariceti* (Singer) Singer and *Fistulinella wolfeana* Singer and J. García are having antioxidant properties (Tsai et al. 2007, Ahmed et al. 2015). The species of *Hortiboletus* Simonini, Vizzini and Gelardi*, Gyroporus, Rhizopogon* and *Tapinella* E.-J. Gilbert posess anticancer properties (Sasek and Musilek 1967, Zheng et al. 2006). Antibacterial activities were observed in the compouds isolated from some *Buchwaldoboletus* species (Madhosingh, 1966).

Normally toxic or inedible, red-pored boletes can occasionally be made edible with the right cooking methods (eg: *Suillellus luridus* (Schaeffer) Murrill, *S. queletii* (Schulzer) Kuntze). However, some other species are poisonous even after cooking (Sarc et al. 2013, Chen et al. 2016). *Rubroboletus satanas* and Zhu L. Yang (Devil's bolete) and *Neoboletus venenatus* (Nagasawa) G. Wu and Zhu L. Yang, can cause nausea, violent vomiting and diarrhea and sometimes also sweating, headache, fever and hyperprocalcitonemia (Kretz et al. 1991). *Boletus venenatus, Heimioporus japonicas*, species of *Scleroderma* and some *Pulveroboletus* are also poisonous (Bau et al. 2014, Wu et al. 2014, Chen et al. 2016). *Tylopilus felleus*, *Gyroporus ammophilus* M.L. Castro and L. Freire and *Hygrophoropsis aurantiaca* (Wulfen) Maire have bitter taste and are doubtfully poisonous (Castro and Freire 1995). The species of species of *Leccinum* and *Leccinellum* Bresinsky and Manfr. Binder make gastrointestinal poisoning when eaten raw or in case of incomplete cooking (Bessette et al. 2000, Sitta et al. 2020). Basidiospores of *Serpula* species are capable of causing asthma (Watling 2008). *Paxillus involutus* is capable of causing Paxillus syndrome (also known as hemolytic syndrome or allergic cytotoxic syndrome (Gelardi 2021).

2.1.5. Distribution

Distribution is cosmopolitan, and they occur in different habitats such as arid or semiarid environments to wetlands and from the sea level to the timberline or even above in specific ecological conditions (Zang 2006, Gelardi 2021). Bolete species are reported from every continent except Antarctica (Gilbert 1931, McNabb 1968, Heinemann and Rameloo 1982, Singer 1983, Singer 1986, Halling et al. 2007, Wu et al. 2016a).

The majority of the world's diversity hotspots for Boletales are found in the northern hemisphere, with more reports coming from North America (particularly north-eastern North America), the neotropical montane cloud forests of Central America and the Caribbean, and even more from eastern and south-eastern Asia, as well as peninsular and insular Malaysia (Singer 1965, Smith and Thiers 1971, Corner 1972, Binder and Bresinsky 2002, Wu et al. 2014, 2016). More than 500 species belonging to around 55 genera were reported from China (Li and Song 2000, Li et al. 2011, Wu et al. 2016a).

Majority of the members of Boletales are ectomycorrhizal, hence the host species always determine their distribution pattern (Gelardi 2021). Ectomycorrhizal species and their symbiotic partners migrated successfully between Asia and North America (Wu et al. 2000). The presence of phylogenetically similar species in these two continents and geographic distribution of some species like *Suillus decipiens* (Peck) Kuntze, *S. spraguei* (Berk. and M.A. Curtis) Kuntze, *S. americanus* (Peck) Snell, *S. clintonianus* (Peck) Kuntze, *Aureoboletus mirabilis* (Murrill) Halling, *Harrya chromapes* (Frost) Halling and *Sutorius eximius* are the evidences for such migration (Wu et al. 2019, Gelardi 2021). Genera *Erythrophylloporus* and *Rugiboletus* G. Wu and Zhu L. Yang also showed the disjunct geographic distribution between paleotropics (eastern and south-eastern Asia) and neotropics (Central and northern South America) (Vadthanarat et al. 2019).

Table 2. Boletales taxa reported from Kerala State.

Sl. No.	Name	Family
1	*Austroboletus gracilis* (Peck) Wolfe	Boletaceae
2	*Austroboletus gracilis* var. *laevipes* (Peck) Wolfe (Synonymised to *A. gracilis*)	Boletaceae
3	*Boletus patriciae* A.H. Sm. and Thiers	Boletaceae
4	*Boletus alutaceus* var. *subalutaceus* T.N. Lakh. and Sagar (Synonymised to *Boletus alutaceus)*	Boletaceae
5	*Boletus edulis*	Boletaceae
6	*Boletus edulis* subsp. *clavipes* (Peck) Singer (Synonymised to *Boletus edulis)*	Boletaceae
7	*Boletus hongoi* T.N. Lakh. and Sagar	Boletaceae
8	*Boletus huronensis* A.H. Sm. and Thiers	Boletaceae
9	*Boletus pallidus* Frost (Synonymised to *Imleria pallida*)	Boletaceae
10	*Boletus reticulatus* Schaeff.	Boletaceae
11	*Leccinum scabrum* (Bull.) Gray	Boletaceae
12	*Rubinoboletus caespitosus* T.H. Li and Watling	Boletaceae
13	*Strobilomyces annulatus* Corner	Boletaceae
14	*Strobilomyces mollis* Corner	Boletaceae
15	*Strobilomyces strobilaceus* (Scop.) Berk.	Boletaceae
16	*Tylopilus alboater* (Schwein.) Murrill	Boletaceae
17	*Phylloporus septocystidiatus* C.K. Pradeep and K.B. Vrinda	Boletaceae
18	*Boletinellus merulioides* (Schwein.) Murrill	Boletinellaceae
19	*Phlebopus portentosus* (Berk. and Broome) Boedijn	Boletinellaceae
20	*Gyroporus castaneus* (Bull.) Quél.	Gyroporaceae
21	*Pisolithus albus* (Cooke and Massee) Priest	Pisolithaceae
22	*Scleroderma areolatum* Ehrenb.	Sclerodermataceae
23	*Scleroderma bovista* Fr.	Sclerodermataceae
24	*Scleroderma citrinum* Pers.	Sclerodermataceae
25	*Scleroderma verrucosum* (Bull.) Pers.	Sclerodermataceae
26	*Scleroderma polyrhizum* (J.F. Gmel.) Pers.	Sclerodermataceae
27	*Suillus brevipes* (Peck) Kuntze	Suillaceae
28	*Suillus placidus* (Bonord.) Singer	Suillaceae
29	*Suillus tomentosus* Singer, Snell and E.A. Dick	Suillaceae

Porcini mushrooms are mostly distributed in south eastern Asia (Dentinger et al. 2010) They were thought to be originated in Australasia or the Indo-Malayan area and ungergone several migratory events to Europe and North and Central America (Feng et al. 2012). Many Sclerodermatineae members are having south-eastern Asian origin and are also distributed in other continents (*Calostoma* Desvaux, *Astraeus, Gyroporus, Pisolithus*, *Scleroderma*). The genus *Strobilomyces* exhibit restricted geographical distribution and shows high degree of endemism (Han et al. 2018).

Around 120 boletoid fungi have been reported from India (Lakhanpal 1996, Natarajan et al. 2005, Das 2009, 2012, 2013, Varghese et al. 2010, Mohanan 2011, Farook et al. 2013, Chakraborty and Das 2015, Das et al. 2014, Das and Dentinger 2015, Pradeep et al. 2015, Verma and Pandro 2018, Das et al. 2024). Most of them are from northeast regions of India (Verma and Pandro 2018). Nearly 92 species belonging to 24 genera were reported from Indian Himalayan regions (Das et al. 2024). *Strobilomyces*, *Tylopilus, Aureoboletus, Boletus* and *Xerocomus* are the most representing genera in India (Das and Dentinger 2015, Verma and Pandro 2018, Das et al. 2024).

More than 850 macromycetes have been reported from Kerala so far (Mohanan 2011, Farook et al. 2013, Adarsh et al. 2018, Kumar et al. 2019). Among them, only 29 bolete species were reported (Varghese et al. 2010, Mohanan 2011, Farook et al. 2013, Kumar et al. 2019) and given in Table 2.

2.2. Boletecaeae Chevall.

Boletaceae is one of the most studied families of Boletales (Yang 2011, Wu et al. 2014). Species of Boletaceae are mainly characterized by fleshy context, and tubulose or lamellate or loculate hymenophore (Wu et al. 2014). Most of the species are ectomycorrizal and many of them are highly priced edible mushrooms (Binder and Hibbett 2006, Halling et al. 2007, Dentinger et al. 2010). According to Kirk et al. (2008), only 35 genera are included in Boletaceae with 787 species. But, the recent studies added more genera and species to the family (Arora and Frank 2014, Gelardi et al. 2014, Li et al. 2011, Vizzini 2014a, 2014b, Zeng et al. 2014, Zhao et al. 2014, Wu et al. 2016a, Vásquez et al. 2018). Boletaceae currently includes approximately 1000 species in 89 genera, with a worldwide distribution (He et al. 2019). *Hemilanmaoa* Yang Wang, Bo Zhang and Yu Li, *Tropicoboletus* Angelini, Gelardi and Vizzini, *Brasilioporus* A.C. Magnago, Alves-Silva and T.W Henkel, *Neotropicomus* A.C. Magnago, Alves-Silva and T.W Henkel, *Nevesoporus* A.C. Magnago, Alves-Silva and T.W. Henkel and *Paxilloboletus* Furneaux, De Kesel and FK Khan are the very recently described other genera in Boletaceae (Wang et al. 2023, Gelardi et al. 2023, Magnago et al. 2022, Badou et al. 2022).

Most of the previous studies on the taxonomy of Boletaceae were based on chemical or/and morphological features (Snell 1941, Smith and Thiers 1971, Corner 1972, Pegler and Young 1981, Singer 1986, Høiland 1987, Watling and Li 1999, Li and Song 2000, Binder and Bresinsky 2002, Zang 2006, Horak 2011). The original Friesian classification of Boletaceae included almost all the pored fleshy species (McNabb 1968). It was modified by many mycologists like Murrill (1909), Gilbert (1931) Snell and Dick (1941) and Singer (1945). Murrill's (1909) work was based on North American species and he included 11 genera in Boletaceae. Singer (1936) accepted Gilbert's system with some modifications. Snell (1941) also followed Gilbert's system and he applied it for North American species. But additionally, he grouped the species with ornamented spores in a new family Strobilomycetaceae.

Singer (1936) published a comparison of the European and North American species of *Suillus, Phylloporus* and *Boletinus* Kalchbr., that was widely accepted. Based on that, Singer revised the concepts of the Boletaceae in 1946, and included 15 genera under 4 sub families. Singer (1945) considered

Boletaceae as a well-defined family having close affinities with Strobilomycetaceae, Paxillaceae and Gomphidiaceae. From China, Chiu (1948, 1957) reported 57 boletes, including 22 new species, and it was a major contribution from the Asian region (Wu et al. 2016a). McNabb (1968) published a monograph of Boletaceae with 14 genera. Another major work on boletales was that of Smith and Thiers (1971). They placed poroid members including that of Suillinae and Sclerodermatinae in the concept of Boletaceae. The concept of Smith and Thiers (1971) was more conservative than that of Singer (Nuhn et al. 2013). Singer recognized 22 genera while Smith and Thiers (1971) recognised only 12 genera. In Smith and Thiers (1971) classification *Boletus* was treated as an easily recognizable genus. However, Singer (1986) accommodated the species of *Boletus* in many other genera. Then, the basidiospore ornamentations along with the other characters were applied in the taxonomy of Boletaceae by Pegler and Young (1981). Comprehensive studies on this family in tropical region mainly started in the late 20th century. Chen and Yeh (2000) reported 72 species from Taiwan.

Several issues have been brought forth by the disagreements over the taxonomic classification of boletoid fungi based on morphological and chemotaxonomical evidence (Binder and Hibbett 2006, Wu et al. 2014, 2016). The emergence of molecular phylogenetic analyses completely changed the traditional treatment of this family. Singer’s (1986) concept of the Boletineae is almost identical to the modern concept of Boletales (Singer 1986, Binder and Hibbett 2006). The modern Boletineae members are distributed in the Paxillaceae and Boletaceae in Singer’s (1986) classification. The classification system proposed by Pegler and Young (1981) based on the basidiospore ornamentation was not supported by phylogenetic treatment.

Major phylogenetic studies of Boletaceae were based on the specimens from China (Wu et. al 2013, 2014, Zeng et al. 2014, Zhao et al. 2014, Zhu et al.

2014, Wu et al. 2016a). Nuhn et al. (2013) elucidated generic relationships in the suborder Boletineae using nrLSU, tef1-α and *RPB1* sequences and identified 17 clades with four major groups in the family Boletaceae. Phylogenetic studies helped to revise the concepts of many genera such as *Xerocomus, Boletus, Phylloporus* and *Tylopilus*. Subfamilies of Boletaceae such as Strobilomycetoideae (E.-J. Gilbert) Snell, Boletoideae and Xerocomoideae Singer were also revised after phylogenetic treatments (Binder and Hibbett 2006, Nuhn et al. 2013). Wu et al. (2014) redefined the family Boletaceae based on the data from nrLSU, *tef1-α*, *RPB1*, and *RPB2* gene regions. Wu et al. (2014) found seven major clades at subfamily level including four new subfamilies (Austroboletoideae G. Wu and Zhu L. Yang, Chalciporoideae G. Wu and Zhu L. Yang, Leccinoideae G. Wu and Zhu L. Yang, Zangioideae G. Wu, Yan C. Li and Zhu L. Yang) and reported 59 generic lineages. Wu et al. (2015) described four new genera such as *Baorangia* G. Wu and Zhu L. Yang, *Lanmaoa* G. Wu and Zhu L. Yang, *Parvixerocomus* G. Wu and Zhu L. Yang, and *Rugiboletus*. *Alessioporus*, *Butyriboletus* D. Arora and J. L. Frank, *Caloboletus* Vizzini, *Crocinoboletus* N.K. Zeng, Zhu L. Yang and G. Wu, *Cyanoboletus* Gelardi, Vizzini and Simonini, *Imleria* Vizzini, *Neoboletus* Gelardi, Simonini and Vizzini, *Pseudoaustroboletus* Yan C. Li and Zhu L. Yang, *Pulchroboletu*s Gelardi et al. and *Rubroboletus* Kuan Zhao et Zhu L. Yang were the recently reported genera. One hundred boletes were reported from China based on morphological and molecular studies (Wu et al. 2016a). Wu et al. (2016) proposed four genera, 46 species and 26 combinations as new to science. Molecular phylogeny also redefined the taxonomy of sequestrate genera in Boletaceae (Binder and Hibbett 2006, Halling et al. 2012, Lebel et al. 2012, Orihara et al. 2012, Trappe et al. 2013, Wu et al. 2014). Tremble et al. (2023) published a multigene phylogenetic study that redefined Boletaceae in to eight subfamilies (Austroboletoideae, Boletoideae, Chalciporoideae, Leccinoideae, Phylloboletelloideae Dentinger, Tremble, Halling, T.W. Henkel and Moncalvo, Suillelloideae Dentinger, Tremble, Halling, T.W. Henkel and Moncalvo, Xerocomoideae Singer, and Zangioideae). A new genus, *Indoporus* A. Parihar, K. Das, Hembrom and Vizzini, was reported from India with *I. shoreae* A. Parihar, K. Das, Hembrom and Vizzini as the type species based on molecular and morphological data (Parihar et al. 2018).

2.2.1. Taxonomic characters

The family Boletaceae has members with fleshy, boletoid or sequestrate, and occasionally lamellate basidiomata. The members show different patterns of color and color changes. Pileus is small to large, scaly, fibrillose, tomentose, velutinous or glabrous, dry or viscid, margin sometimes projecting, context fleshy, unchanging, bluing, browning, blackening, or reddening when bruised, hymenophore depressed, sinuate-adnexed, adnate to decurrent, lamellate or tubular whitish, pinkish, yellowish to yellow, red, or brown, unchanging or staining blue, brown, black, or red when bruised, when sequestrate, the gleba loculate, chambered or tubulose. Stipe is usually fleshy, central to eccentric, cylindrical or ventricose-bulbous, solid, glabrous, or ornamented with furfuraceous to scabrous squamules, or with reticulate lines, when sequestrate, stipe often absent or surrounded by the gleba. Basidia ballistosporic (when stipitate-pileate) or statismosporic (when sequestrate), clavate. Basidiospores roundish, broadly ellipsoid, ovate, subfusiform, or elongate subfusoid, yellowish brown, brown, or olivaceous brown to pinkish, smooth, or with different types of ornamentations. Cystidia more or less fusoid-ventricose. Hymenophoral trama boletoid or phylloporoid or intermediate. Pileipellis subcutis, ixosubcutis, trichodermium, hyphoepithelium, ixotrichodermium, ixohyphoepithelium, or composed of interwoven hyphae. Hyphae without clamp-connections. Mostly ectomycorrhizal, occasionally mycoparasitic/saprotrophic (Singer 1945, Wu et al. 2014). The spore ornamentations in this group are striate, pitted, perforated, reticulated or bascillated (Vasques et al. 2018).

2.2.2. Ecological and economic importance

Ecologically, Boletaceae members are important as ectomycorrhizal fungi (Halling et al. 2007). They are proven as being an integral part of forest ecosystems and help in nutrient recycling, nutrient uptake and decomposition (Halling et al. 2007). Boletaceae species form ectomycorrhizal relationships with different plant families such as Betulaceae, Casuarinaceae, Ericaceae, Fagaceae, Myrtaceae Juss., and Pinaceae (Osmundson et al. 2007).

Boletaceae family has some of the most widely collected and highly priced edible mushrooms, which are having dietary and health values (Dentinger et al. 2010, Feng et al. 2012, Wu et al. 2014). The edible *Boletus edulis* Bull. s. l. and its allies are known as "porcini mushrooms", and approximately 20000-100000 metric tons of these fungi are consumed annually (Dentinger et al. 2010). Porcini are one of the important sources of income for rural people in many parts of the world, such as China, Thailand and North America (Dentinger 2010, Wu et al. 2014). Almost 25 species were placed in the porcini group including *Boletus rex-veris* D. Arora and Simonini and *Boletus pinophilus* Pilát and Dermek (Dentinger 2010). *Pulveroboletus ravenelli* is commonly used as edible in China, Japan and Korea (Kim et al. 2017). Some species are used in traditional medicines (Kim et al. 2017). *Pulveroboletus ravenelli* is a component in the Chinese traditional medicines.

Apart from these delicious boletes, some of the Boletaceae members are poisonous (Wu et al.2014, Patocka 2018). *Boletus satanas* is known as Devil's mushroom due to its poisonous nature. *Boletus venenatus, Heimioporus japonicas*, some *Pulveroboletus* species are also toxic boletes (Li et al. 2011, Bau et al. 2014, Wu et al. 2014).

2.2.3. Distribution

Boletaceae members have known distribution in every continent except Antartica (Gilbert 1931, Snell 1941, McNabb 1968, Singer 1986, Wu et al. 2014, Wu et al. 2015). Species of this family reported from Asia, Europe, Africa, Central, North and South America (Li et al. 2011, Zeng et al. 2014, Zhao et al. 2014, Gelardi et al. 2015, Zhu et al. 2015, Wu et al. 2016ab). A monograph of North American boletes was published by Murril (1909). McNabb (1968) described 22 species from New Zealand. Malaysian species of Boletaceae were recorded by Corner (1972) and gave detailed descriptions of *Boletus*, *Gyroporus, Strobilomyces* and *Heimeilla*. Corner (1972) recorded 140 species from the Malay Peninsula and Borneo. Boletes from south and east central Africa was published by Watling and Turnbull (1992). Most of the recent novel reports were from tropical and subtropical regions (Wu et al. 2014, Wu et al. 2016a, Verma and Pandro 2018). Many studies were published based on the distributional pattern of Boletaceae (Halling et al. 2007, Lumbsch 2008, García-Jiménez 2019).

Boletaceae species from India were reported in scattered studies (Manjula 1982, Mohanan 2011, Farook et al. 2013, Kumar et al. 2019). Most of the reports were from northern India (Das et al. 2016, Chakraborty et al. 2018, Parihar et al. 2018, Chakraborty et al. 2022, Das et al. 2023, 2024). Nearly 92 species belonging to 24 genera were reported from Indian Himalayan regions (Das et al. 2024).

2.2.4. ***Anthracoporus*** Yan C. Li and Zhu L. Yang

Anthracoporus is a recently described genus from China (Li and Yang 2021). The genus was erected based on the morphological and molecular phylogenetic analyses of *Boletus holophaeus* Corner and its allies. *Anthracoporus* consist of only three species, *A. holophaeus* (Corner) Yan C. Li and Zhu L. Yang and *A. nigropurpureus* (Hongo) Yan C. Li and Zhu L. Yang, and *A. cystidiatus* Yan C. Li and Zhu L. Yang. *Anthracoporus holophaeus* is the type species and it was formerly described as *B. holophaeus* by Corner in 1972. Then, this species was transferred to *Tylopilus* as *T. holophaeus* (Corner) E. Horak based on the revision work by Horak (2011) on Malaysian boletes described by Corner. However, Li and Yang (2011) considered this species in the genus *Porphyrellus* as *P. holophaeus* (Corner) Yan C. Li and Zhu L. Yang. The morphological study along with multilocus phylogenetic analyses of Chinese collections led to the reconstruction of *Tylopilus* s. l. (Li and Yang 2021) and proposed *A. holophaeus* as a combination novum. Another species, *A. nigropurpureus* was initially described in the genus *Boletus* by Corner (1972). Horak (2011) considered this species as *T. purpureoniger* E. Horak and Li and Yang (2011) considered as *P. nigropurpureus* (Hongo) Yan C. Li and Zhu L. Yang. *A. cystidiatus* was a new species described from China (Li and Yang 2021).

2.2.4.1. Taxonomic characters

Anthracoporus is characterized by the following characters: Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical to applanate, surface tomentose, usually rugose, dry, context solid, white to greyish white, becoming reddish then blackish when injured. Hymenophore adnate or depressed around apex of stipe, hymenophoral surface black to greyish black when young, greyish wihte to greyish pink when mature, tubes concolorous with hymenophoral surface, pores angular, fine, staining reddish firstly then blackish finally when injured. Stipe central, glabrous or reticulate, concolorous with pileus, becoming reddish then blackish when injured, context white to cream, becoming reddish then blackish when bruised, basal mycelia cream, becoming reddish then blackish when bruised. Basidiospores smooth, subfusiform, yellow to brownish yellow. Pleuro- and cheilocystidia fusiform to subfusoid-ventricose. Pileipellis often a trichoderm or epithelium. Clamp-connections absent (Li and Yang 2021).

2.2.4.2. Ecological and economic importance

An informative study on the poisoning of *Anthracoporus nigropurpureus* was published by Ma et al. (2023). Poisoning was reported in five adults and one child who ingested wild boletoid mushrooms known locally as "Yanyoujun", which were identified as *A. nigropurpureus* by morphological and molecular studies. The symptoms included dizziness, blurred vision, muscle weakness, red eyes, headache, muscle cramps, even tremors in the extremities (Ma et al. 2023).

2.2.4.3. Distribution

Anthracoporus holophaeus was first recorded from Malaysia (Corner 1972). Later, the species reported from China (Li and Yang 2011, 2021). *Anthracoporus nigropurpureus* reported from Central Africa (Watling and Turnbull 1994), Malaysia (Corner 1972) and China (Li and Yang 2011, 2021). *Anthracoporus cystidiatus* have been reported from only China (Li and Yang 2021).

2.2.5. ***Aureoboletus*** Pouzar

Synonymy:

Sinoboletus M. Zang, Mycotaxon 45: 223 (1992)

Aureoboletus is a genus in the family Boletaceae with *Aureoboletus gentilis* (Quél.) as the type species (García-Jiménez et al. 2019). The species included in this genus forms ectomycorrhizal associations with many plants such as *Fagaceae, Betulaceae* and *Pinaceae* (Newman and Reddell 1987, Tedersoo et al. 2010, García-Jiménez et al. 2019). *Aureoboletus* species differ from other Boletaceae members by having glutinous pileus, brightly yellow colored hymenophore which is unchanging on bruising, ixotrichodemis pileipellis (rarely trichodermis), and smooth basidiospores (Chakraborty et al. 2017). *Index Fungorum* (www.indexfungorum.com, accessed on 20 May 2022) records 44 species under this genus. *Aureoboletus* differs from all other genera of Boletaceae in its usually viscid pileus and brilliant yellow hymenophore without color change when bruised or cut, an ixotrichodermium or occasionally trichodermium pileipellis and smooth basidiospores (Wu et al. 2016a).

Singer (1942) established a section called *Auripuri* in the genus *Xerocomus,* which was later transferred to the section of *Pulveroboletus*. Based on these concepts, *Aureoboletus* was erected as a genus by Pouzar in 1957 to include enigmatic species that made confusions in the section *Auripuri*. But many mycologists, including Singer, did not accept the generic rank and maintained all *Aureoboletus* species within *Pulveroboletus.* Singer (1986) broadly described the features of *Aureoboletus* (as section *Auripori*) as 'pileus or stipe or both viscid, pores golden yellow or brightly olive-gold even in dried condition, elements of the trama often filled with deep lemon yellow soluble (NH4OH) pigment, stipe covered by a gelatinous layer'. Klofac (2010) in his monographic treatment described *Aureoboletus* as "pileus often viscid, but also subtomentose, tubes and pores with all shades of yellow, carpophores small to medium-sized, hymenophoral surface more or less depressed around the stipe, broadly adnate or with decurrent tube walls, stipe subequal or fusoid, nearly always slightly to distinctly swollen in the middle and more or less rooting or attenuated to the base, not distinctly reticulate and neither scabrous nor glandulose". Some other studies of that time recognized polyphyletic nature of *Pulveroboletus* and recommended to consider *Aureoboletus* as an independent genus (Smith and Thiers 1971, Corner 1972).

Molecular phylogenetic studies revealed the independent position of *Aureoboletus* in Boletaceae (Binder and Hibbett 2006, Nuhn et al. 2013, Wu et al.

2014, W u et al. 2016a). Binder and Hibbett (2006) placed the genus in the sub order Boletinae of Boletales. The Boletinae was revised by Nuhn et al. (2013) based on studies using nuc-LSU, *tef1-alpha* and *RPB1* gene sequences. Nuhn et al. (2013) classified the Boletaceae family in to large groups or clades and *Aureoboletus* found clustered with *Boletellus, Boletus* (non-porcini), *Hemileccinum, Phylloporus,* and *Xerocomus* in hypobolete clade*.* Wu et al. (2014) recognized seven major clades at sub family level in Boletaceae by molecular studies. The sub family Xerocomoideae accommodated *Aureoboletus* along with *Boletellus, Corneroboletus* N.K. Zeng and Zhu L. Yang, *Hemileccinum* Šutara, *Heimioporus, Phylloporus, Sinoboletus* M. Zang and *Xerocomus.* Studies have suggested that *Sinoboletus* and *Aureoboletus* should be synonymized because the type species of *Sinoboletus* nested within the *Aureoboletus* clade (Wu et al. 2014*.*). *Boletellus projectellus* (Murrill) Singer, *B. mirabilis* (Murrill) Singer, *B. russellii* (Frost) E.-J. Gilbert and *Pulveroboletus auriflammeus* (Berk. and M.A. Curtis) Singer) were transferred to *Aureoboletus* by phylogenetic analysis (Halling et al. 2015, Wu et al. 2016a). Zhang et al. (2019) proposed eight major clades in the monophyletic *Aureoboletus* group based on morphological characteristics along with molecular phylogenetic inference.

2.2.5.1. Taxonomic characters

Aureoboletus can be distinguished by the following characters: Basidioma stipitate-pileate with tubular hymenophore. Pileus convex to applanate, surface usually glabrous and viscid when wet, context yellowish to yellow, without color change when injured. Hymenophore adnate to sinuate, surface bright yellow to yellow, without color change when injured, pores angular to nearly round, tubes concolorous with pores, unchanging in color when injured. Stipe central, without color change when injured, basal mycelium usually white. Basidiospores usually smooth, rarely longitudinally striate, subfusiform, light yellow to yellow. Pleurocystidia and cheilocystidia fusiform-ventricose or clavate, sometimes with long-broad beak, yellowish to yellow in KOH but soon dissolving in the medium. Pileipellis usually an ixotrichodermium, sometimes trichodermium. Clamp-connections absent (Wu et al. 2016a).

2.2.5.2. Ecological and economic importance

The species of *Aureoboletus* show ectomycorrhizal associations with plants such as Fagaceae, Betulaceae and Pinaceae and they play important role in nutrient cycle (Binder and Hibbett 2006, García-Jiménez et al. 2019). Some of them, such as *Aureoboletus mirabilis* (Murrill) Halling, are edible (Bessette et al. 2017).

2.2.5.3. Distribution

Most of the species were reported from Asia, Europe and North America (Wang and Yao 2005, Klofac 2010, Zhang et al. 2019, Wu et al. 2016a, García-Jiménez et al. 2019). Klofac (2010) reported 12 species from Europe and America. Nine species were reported from Mexico (García-Jiménez et al. 2019). *Aureoboletus projectellus* (Murrill) Halling was native to North America and then introduced to Europe (Banasiak et al. 2019). *Aureoboletus clavatus* N.K. Zeng and Ming Zhang was reported from Asian countries (Zeng et al. 2015). The Malaysian bolete *A. longicollis* (Ces.) N.K. Zeng and Ming Zhang and distributed in Singapore, Japan and China (Zeng et al. 2015). *Aureoboletus projectellus* and *A. mirabilis* were found to have disjunctive distributions in North America, Asia and Europe (Chen et al. 1988, Motiejūnaitė et al. 2013, Halling et al. 2015, Zhang et al. 2019). *Aureoboletus gentilis* G. Wu and Zhu L. Yang was originally described from Europe and it is not found in any other continents.

Aureoboletus was poorly recorded from India (Chakraborty et al. 2017). *Aureoboletus nephrosporus* is the only authentically reported species from India and it was formerly reported from China only (Chakraborty et al. 2017).

2.2.6. *Austroboletus* (Corner) Wolfe

Austroboletus was introduced by Corner in 1972, with *Porphyrellus dictyotus* Boedijn as type species. Corner (1972) considered *Austroboletus* as a subgenus of *Boletus* s. l. and included Malaysian boletes with ornamented spores. Later, Horak (1968) preferred to consider *Austroboletus* as an independent genus. Following that, *Austroboletus* was given the genus rank by Wolfe's (1980) comparative analysis of *Porphyrellus* s. l. and *Boletus* subgenus *Austroboletus*. Corner (1980) did not accept the recognition of *Austroboletus* as a genus. But Pegler and Young (1981), Singer (1986), and Horak (1983) followed the concept of Wolfe (1980). Now, *Austroboletus*, typified by *A. dictyotus* (Boedijn) Wolfe, consists of 41 species (*Index Fungorum*, accessed on 22 March 2023). The phylogenetic studies revealed *Austroboletus* as a monophyletic group and the back born of the subfamily *Austroboletoideae* (Nuhn et al. 2013, Wu et al. 2014, 2016a). *Austroboletus* shows close morphological similarities with genera such as *Tylopilus* and *Fistulinella* Henn. However, *Austroboletus* has ornamented spores, while others posess smooth spores.

2.2.6.1. Taxonomic characters

Austroboletus is characterized by the following features: Basidiomata stipitate-pileate. Pileus hemispherical to subhemispherical or convex, surface subtomentose or glabrous, dry to gelatinous, margin extending and embracing the stipe in younger basidiomata then breaking into pieces and hanging on the pileal margin, context white, without color change when injured. Hymenophore poroid, depressed around apex of stipe, hymenophoral surface pinkish when young, becoming pink to purplish pink when mature, pores angular or approximately spherical, tubes concolorous with hymenophoral surface, unchanging in color when injured. Stipe central, distinctly reticulate, basal mycelium white. Basidiospores elongate amygdaliform, ornamented with warts, reticulate ridges or shallow and irregularly furrowed pits. Pleurocystidia and cheilocystidia abundant, morphologically similar or greatly different. Pileipellis subrepent to trichodermium composed of filamentous interwoven hyphae, sometimes strongly gelatinous. Clamp-connections absent (Wu et al. 2016a, Gelardi et al. 2020).

2.2.6.2. Ecological and economic importance

Most of the species are ectomycorrhizal with different plants such as members of Fagaceae, Pinaceae, Dipterocarpaceae, Myrtaceae, and caesalpinoid legumes (Bessette et al. 2016a). A very few species are saprotrophic or only facultative ectomycorrhizal (Watling 2008).

2.2.6.3. Distribution

Austroboletus species are distributed worldwide. Seven species were reported from China (Li and Yang 2021). Many species were described from Australia, Guyana and Taiwan (Fulgenzi et al. 2010, Fechner 2017). Four species have been reported from Brazil (Magnago and Neves 2014). Two species, *A. gracilis* (Peck) Wolfe and *A. olivaceoglutinosus* K. Das and Dentinger, were reported from India till now (Lakhanpal 1996, Das and Dentinger 2015).

2.2.7. ***Baorangia*** G. Wu and Zhu L. Yang

Baorangia G. Wu and Zhu L. Yang is a genus recently described to accommodate *Boletus pseudocalopus* Hongo based on morphological and molecular phylogenetic studies (Wu et al. 2015). The genus is characterized by a thin hymenophore (3 – 5 times thinner than the pileal context), which indicates the name, slowly bluing yellowish pileal context, and a trichodermium to interwoven trichodermium type of pileipellis (Wu et al. 2015, Zhang et al. 2021). *Baorangia* includes seven described species that are reported from China, Japan, North America, India and Mediterranean area (Wu et al. 2016a,b, Crous et al. 2018).

2.2.7.1. Taxonomic characters

The genus characters are the following: Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical, convex or applanate, subtomentose, dry, usually incurved at the margin when young, context pale yellow to yellow, slowly staining pale blue when cut. Hymenophore relatively thin (thickness of hymenophore 1/3 – 1/5 times that of pileal context at the position halfway to the pileus center), usually decurrent, hymenophoral surface and tubes yellow, immediately staining light blue to greenish blue when injured, pores angular, or sometimes nearly round, tubes short. Stipe smooth or occasionally with reticulations at the upper part, context pale yellow to yellow, staining pale blue, basal mycelia white to pale yellow. Pileipellis a trichodermium to an interwoven trichodermium. Pleuro- and cheilocystidia present. Basidiospores smooth, subfusiform to elongated subfusiform, light yellow to brownish-yellowish. Clamp-connections absent (Wu et al. 2016a,b).

2.2.7.2. Ecological and economic importance

Ectomycorrhizal and edibility status unknown.

2.2.7.3. Distribution

All the species except *Baorangia major* Raspé & Vadthanarat and *B. duplicatopora* N.K. Zeng, Xu Zhang & S. Jiang have been found in temperate or subtropical areas of the world (Vizzini 2015, Wu et al. 2015, Bessette et al. 2016a, Wu et al. 2016a, Crous et al. 2018, Phookamsak et al. 2019). *Baorangia major* has been reported from Thailand and China (Phookamsak et al. 2019). *Baorangia duplicatopora* reported from China (Zhang et al. 2021).

2.2.8. ***Boletellus*** Murrill

Synonymy:

Boletogaster Lohwag, Beih. bot. Zbl., Abt. 2 42(2): 274 (1926)
Frostiella Murrill, Contr. Herb. Univ. Fla. Agr. Exp. Stat. Gainesville: Jan. 5 1942: 6 (1942)
Strobilofungus McGinty, in Lloyd, Mycol. Writ. (Cincinnati) 4(Letter 59): 7 (1915)

The genus *Boletellus* was erected by Murrill in 1909 (Halling et al. 2015). Murrill (1909) included only one species, *B. ananas* (M.A. Curtis) Murrill. Most of the species in this genus are ectomycorrhizal and some grow on rotten woods (Singer 1986, Sato and Hattori 2015). The genus is characterized by yellow hymenophore staining blue immediately, or without color changing when cut or bruised, a trichodermium pileipellis with broad hyphae, and longtitudinally striate basidiospores (Wu et al. 2016a). *Boletellus* was formerly placed in Strobilomycetaceae family (McNabb 1968). Pegler and Young (1981) treated *Boletellus* within Xerocomaceae based on the basidiospore morphology. Singer (1986) considered it as a separate genus and erected seven sections with 33 species. He included species having both smooth and ornamented spores. Sections like *Boletellus, Chrysenteroidei, Ixocephali,* and *Dictyopodes* were included with longitudinally winged spores, section *Mirabilis* had smooth-spored species, section *Allospori* had species with spores having imbedded short spines, section *Retispori* with species having reticulate spores (Singer 1986, Sato and Hattori 2015).

Phylogenetic works on Boletales inferred *Boletellus* as a polyphyletic group (Dentinger et al. 2010, Nuhn et al. 2013, Wu et al. 2014, 2016a). Nuhn et al. (2013) included *Boletellus* in hypoboleteus group of Boletinae suborder along with *Aureoboletus, Boletellus, Boletus, Hemileccinum, Phylloporus,* and *Xerocomus.* But they could not resolve the phylogenetic relationships of these groups (Sato and Hattori 2015). Based on the multigene analyses of Wu et al. (2014), *Boletellus* s. l. with ornamented spores, olivaceous spore print, and yellow tubular hymenophore, was found to be polyphyletic. They suggested rearranging all the sections in *Boletellus* created by Singer (1986) based on molecular and morphological data. Section *Boletellus* and section *Chrysenteroidei* were retained in *Boletellus* s. str. and section *Ixocephali* transferred to *Aureoboletus* (Wu et al. 2014). All other sections also found to be uncertain (Nuhn et al. 2013, Wu et al. 2014, 2016a).

2.2.8.1 Taxonomic characters

The genus *Boletellus* is characterized by stipitate-pileate basidiomata with tubular hymenophore. Convex to broadly convex pileus, which is glabrous or tomentose, or fibrillose, or velvety, dry, sometimes with marginal veil, yellowish to yellow context, usually staining bluish, blue to dark blue when cut or bruised, sometimes unchanging. Hymenophore adnate to sinuate, hymenophoral pores and tubes concolorous, yellowish to yellow, staining bluish, blue to dark blue, sometimes unchanging when injured. Stipe central, glabrous or surface pruinosefurfuraceous. Basidiospores longitudinally striate, subfusiform, brownish yellow. Pleuro- and cheilocystidia subfusiform-ventricose or clavate, with subacute apex or long beak. Pileipellis a trichodermium to an intricated trichoderm with broadly filamentous hyphae. Clamp-connections absent (Wu et al. 2016a).

2.2.8.2. Economic and ecological importance

Most of the species in *Boletellus* show ectomycorrhizal associations with angiosperms (Tedersoo et al. 2010).

2.2.8.3. Distribution

It is estimated that 50 species in *Boletellus* have been reported worldwide (McNabb 1968, Pegler and Young 1981, Singer 1986, Halling et al. 2015, Wu et al. 2016a, Loizides et al. 2019). Majority of them were from tropical regions (Heinemann and Goossens-Fontana 1954, Snell and Dick 1970, Smith and Thiers 1971, Corner 1972, Singer 1986, Singer et al. 1992, Gómez 1996, Watling 2001, Fulgenzi et al. 2008, Halling and Ortiz-Santana 2009, Halling et al. 2015, Sato and Hattori 2015). Eight species were reported from India (Berkeley 1851, Horak 1980, Harsh and Bisht 1982, Verma and Pandro 2018, Parihar et al. 2018).

From India, eight species were reported as follows: *Boletellus dissiliens, B. ananas, B. corner, B. emodensis, B. squamatus, B. verrucarius, B. chrysenteroides, B. pseudochrysenteroides* (Berkeley 1851, 1852, 1854, Harsh and Bisht 1982, Verma and Pandro 2018, Parihar et al. 2018). *Boletellus ananas* was the only species reported from Kerala (Kumar et al. 2019).

2.2.9. *Boletus* L.

Boletus L. is a historical genus which was established at the time of formation of Boletaceae family (Gelardi et al. 2022). *Boletus edulis* is the type specimen. Gilbert (1931) included the genus in suborder Boletineae based on the presence of smooth spores. Kühner and Romagnesi (1953) studied European boletes and considered them in two informal groups, bolétacées lamellées" (lamellate boletes) (encompassing Phylloporus, Gomphidius and Paxillus) and "bolétacées porées" (poroid boletes). All poroid boletes were included under *Boletus* and divided in to ten subgenera (*Strobilomyces, Gyroporus, Krombholzia* (Fr.) P. Karst.*, Tylopilus, Tubiporus* P. Karst. (= Boletus), *Porphyrellus, Xerocomus, Ixocomus* Quél., *Boletinus* Kalchbr., *Gyrodon*). Singer (1986) divided *Boletus* s. l. in to seven sections such as *Boletus*, *Ornatipedes*, *Grisei*, *Subpruinosi*, *Appendiculati*, *Calopodes* and *Luridi.*

Molecular phylogenetic analyses redefined the concept of *Boletus* and sections described by Singer (1986) has been proved to be polyphyletic (Binder and Bresinsky 2002b, Binder and Hibbett 2007, Dentinger et al. 2010). Present *Boletus* s. str. includes only the members of sect. *Boletus*. Species of sections *Ornatipedes* and *Grisei* were transferred to a new genus *Retiboletus* Manfr. Binder & Bresinsky (Binder and Bresinsky 2002). Sections *Appendiculati*, *Calopodes*, and *Luridi* were clustered within the *Pulveroboletus* Group in phylogenetic analysis by Wu et al. (2014). sect. *Luridi* was the largest section and included around 40 species. *Caloboletus*, *Crocinoboletus*, *Exsudoporus* Vizzini, Simonini & Gelardi, *Neoboletus, Suillellus* Murrill and *Rubroboletus* are the genera formed from the molecular analysis of sect. *Luridi* (Zhao et al. 2014). *Boletus edulis* and allies in sect. *Boletus* are commonly known as Porcini and they include some of the widely and frequently collected edible mushrooms in the world (Dentinger et al. 2010). The biogeography and origin of monophyletic Porcini group was studied by Dentinger et al. (2010).

2.2.9.1. Taxonomic characters

Boletus s. str. is characterised by the following characters: Basidioma fleshy, boletoid, or sequestrate, occasionally phylloporoid. Pileus small to large, scaly, fibrillose, mealy, tomentose, velutinous or glabrous, dry or viscid, margin sometimes projecting, context fleshy, unchanging, bluing, browning, blackening, or reddening when bruised, hymenophore depressed, sinuate-adnexed, adnate to decurrent, lamellate or tubular whitish, pinkish, yellowish to yellow, red, or brown, unchanging or staining blue, brown, black, or red when bruised, when sequestrate, the gleba loculate, chambered or tubulose. Stipe usually fleshy, central to eccentric, cylindrical or ventricose-bulbous, solid, glabrous, or ornamented with furfuraceous to scabrous squamules, or with reticulate lines, when sequestrate, stipe often absent or surrounded by the gleba. Basidia ballistosporic (when stipitate-pileate) or statismosporic (when sequestrate), clavate. Basidiospores roundish, broadly ellipsoid, ovate, subfusiform, or elongate subfusoid, yellowish brown, brown, or olivaceous brown to pinkish, smooth, or with different types of ornamentations. Cystidia more or less fusoid-ventricose. Hymenophoral trama boletoid or phylloporoid or intermediate. Pileipellis subcutis, ixosubcutis, trichodermium, hyphoepithelium, ixotrichodermium, ixohyphoepithelium, or composed of interwoven hyphae. Clamp-connections absent.

2.2.9.2. Ecological and economic importance

Boletus species can form ectomyrrizhal associtaions with plants of several families, such as Pinaceae, Fagaceae and Dipterocarpaceae. *Boletus* s.

str. includes worlds most iconic edible species like *B. edulis.* Porcini mushrooms are having prized flavor and delicious taste and are commonly used as an exquisite ingredient for a large variety of processed foods (Gelardi 2021). The economic value of wild harvested porcini and allied species is clearly substantial, since an estimated 20,000–100,000 metric tons are consumed annually (Dentinger et al. 2010). They are an important source of revenue for rural economies in several regions of the world (Cui et al. 2015). Young basidiomata of *B. huronensis* is using as edible by Chinese people (Gelardi 2021). *Boletus edulis* has antioxidant properties (Ahmed et al. 2015). *Boletus kumaeus* R. Heim, *B. flammeus* R. Heim, *B. manicus* R. Heim, and *B. nigroviolaceus* R. Heim have long been considered hallucinogenic by local indigenous tribes in Papua New Guinea (Watling 2001).

2.2.9.3. Distribution

Dentinger et al. (2010) showed that the main hotspot for porcini mushrooms diversity is unquestionably south-eastern Asia. Many species of this genus have been reported from North America and Europe (Singer 1965, 1967, 1986, Watling 1970, Smith and Thiers 1971, Bessette et al. 2000, Horak 2011). Around 20 species were reported from China (Cui et al. 2015). Thirty seven species have been reported from India (Verma and Pandro 2018).

2.2.10. ***Buchwaldoboletus*** Pilát

Buchwaldoboletus is the saprotrophic and lignicolous genus in Boletaceae (Jo et al. 2019). The genus was erected by Pilát in 1969. The genus is proposed to accommodate *Boletus lignicola* Kallenb. and *B. hemichrysus* Berk. & M.A. Curtis*. Buchwaldoboletus lignicola* (Kallenb.) Pilát is the type species, which was reported as *Boletus lignicola* by Kallenbach in 1929 (Ortiz-Santana and Both 2011, Jo et al. 2019). Pilát transferred *B. lignicola* and *B. hemichrysus* based on characters like lignicolous habit, lack of veil, decurrent and arcuate hymenophore, the stipes with yellow mycelium, the bluing yellow context and the absence of hyphal clamp-connections (Pilát 1969, Ortiz-Santana and Both 2011).

Singer (1947) created a section called *Sulphurei* in genus *Phlebopus* for accommodating *Boletus sulphureus* and other related genera. He also considered *B. lignicola* to be a synonym of *B. sulphureus* (Singer 1947, Ortiz-Santana and Both 2011). Later, the section *Sulphurei* was transferred to *Pulveroboletus* (Singer 1947). However, Pilát (1969) rejected this accommodation and created a separate genus, *Buchwaldoboletus.* In 1988 Watling and Gregory transferred *B. sulphureus* to *Buchwaldoboletus*. Currently, the genus includes 13 species (Jo et al. 2019). Members of *Buchwaldoboletus* accommodated to three stirpes in Europe such as *Lignicola, Sphaerocephalus, and Hemichrysus* (Watling and Hills 2005, Ortiz-Santana and Both 2011).

Molecular phylogenetic studies revealed *Buchwaldoboletus* as a basal group of Boletaceae (Binder and Hibbett 2006, Nuhn et al. 2013, Wu et al. 2014). It is more related to genera like *Chalciporus* and *Heimioporus* (Nuhn et al. 2013, Wu et al. 2016a). Caifa and Smith (2022) studied the phylogenetic relationships among taxa in *Chalciporoideae* clade which includes *Chalciporus* and *Buchwaldoboletus.* They also tested the effect of *Buchwaldoboletus* species on wood decay and elucidated the trophic mode. *B*. *hemichrysus* and *B. sphaerocephalus* (Barla) Watling & T.H. Li produce conidia and *B. lignicola* produces sclerotia in cultures *(*Caifa and Smith 2022).

2.2.10.1. Taxonomic description

The genus *Buchwaldoboletus* is characterized by the following features: Basidioma stipitate-pileate with tubular hymenophore. Pileus convex or applanate, surface subtomentose to tomentose or pulverulent, dry, usually incurved at the margin, context light yellow to yellow, staining bluish when injured. Hymenophore slightly decurrent to sinuate, hymenophoral pores and tubes concolorous, light yellow to ochraceous yellow, staining bluish to dark blue when injured. Stipe central, subcylindrical. Basidiospores smooth, subfusiform, pale yellow to brownish-yellowish. Pleuro- and cheilocystidia subfusiform-ventricose or clavate, with subacute apex or long beak. Pileipellis composed of matted interwoven hyphae (subcutis). Clamp-connections absent (Jo et al. 2019).

2.2.10.2. Economic and ecological importance

The species in *Buchwaldoboletus* are mostly saprotrophic and they normally grow near coniferous trees (Ortiz-Santana and Both 2011, Xie et al. 2021). *Buchwaldoboletus lignicola* is a mycoparasite and have been found to be associated with another fungus *Phaeolus schweinitzii* (Fr.) Pat. (Migliorini and Santini 2011, Caifa and Smith 2022). *Buchwaldoboletus lignicola* grow mostly near trees like *Larix* Mill. and *Pinus* L. (Migliorini and Santini 2011). It can degrade fragments of *Pinus silvestris* L. in artificial condition (Migliorini and Santini 2011). *Buchwaldoboletus sphaerocephalus* mostly found on old dying *Pinus* trees (Migliorini and Santini 2011). *Buchwaldoboletus xylophilus* (Petch) Both & B. Ortiz is a widely distributed species in Asia (Corner 1972, Pegler 1986, Xie et al. 2021). *Buchwaldoboletus xylophilus* was reported among Bamboo trees, but they do not form ectomycorrhizal associations (Xie et al. 2021).

Caifa and Smith (2022) studied the effect of wood decay by *Buchwaldoboletus* species. *Buchwaldoboletus lignicola* and *B. hemichrysus* cause brown rot and they can grow in cultures under laboratory conditions (Caifa and Smith 2022).

2.2.10.3. Distribution

Buchwaldoboletus have species with worldwide distribution (Ortiz-Santana and Both 2011, Venturella 2017, Jo et al. 2019). *Buchwaldoboletus* *lignicola* have been reported from Europe, eastern North America, South Korea, China (Ortiz-Santana and Both 2011, Xie et al. 2021). The genus consists of species, which occur predominantly in Northern hemisphere, Australia and New zealand (Robinson and Gates 2020). *B. lignicola, B. hemichrysus* and *B. sphaerocephalus* have wide distribution in Europe (Ortiz-Santana and Both 2011)*. Buchwaldoboletus lignicola* is considered as a potentially endangered species (Jo et al. 2019). *Buchwaldoboletus parvulus* (Natarajan and Purushothama) Both and B. Ortiz is the only species reported from India.

2.2.11. ***Chalciporus*** Bataille

Synonymy:

Chalciporus subgen. *Rubinoboletus* (Pilát and Dermek) Klofac and Krisai, Öst. Z. Pilzk. 15: 33 (2006)
Rubinoboletus Pilát and Dermek, Česká Mykol. 23(2): 81 (1969)

Chalciporus Bataille (Boletaceae, Boletales) is a small genus consisting of 35 species (*Index Fungorum* accessed on 5 January 2023) distributed world-wide. The genus was introduced with *C. piperatus* as type species in 1908 (Bataille 1908). Singer (1938, 1962) treated the genus as a subsection of *Suillus.* The subsequent studies included *Chalciporus* members under *Pulveroboletus* Murrill (Coker and Beers 1943, Smith and Thiers 1971). Morphological similarities of *Chalciporus* with *Rubinoboletus* Pilát and Dermek confirmed them as a single genus, and so *Chalciporus* was retained as an independent genus (Pegler and Young 1981, Singer 1986, Klofac 2006 Zhang et al. 2016a). *Rubinoboletus* is now considered as synonym of *Chalciporus.* Molecular phylogenetic studies proved the monophyly of *Chalciporus* (Wu et al. 2014).

2.2.11.1. Taxonomic description

Chalciporus is characterized by the following features: a stipitate-pileate basidiomata with tubular hymenophore. Pileus convex to broadly convex, glabrous to obscurely subtomentose, dry, but sometimes subviscid when wet. Context whitish to light yellow, unchanging or staining bluish slowly when injured. Hymenophore decurrent, pinkish red to reddish brown. pleurocystidia and cheilocystidia subfusiform-ventricose. Pileipellis a trichodermium. Basidiospores subfusiform. Clamp-connections absent (Wu et al. 2016a).

2.2.11.2. Economic and ecological importance

Secondary metabolites like sclerocitrin (the yellow pigment in the stipe base and mycelium), variegatic acid, variegatorubin, chalcitrin, and the unusual 2H-azepine derivative chalciporone (responsible for the pungent taste of the basidioma) have been isolated from *Chalciporus* species (Winner et al. 2004).

Chalciporus piperatus is the only mycoparasite species in this genus, which colonizes *Amanita muscaria* and all others are ectomycorrhizal with different plant groups such as conifers, Betulaceae and Fagaceae (Singer 1962, 1986, Degreef and Kesel 2008, Xu et al. 2021). The host range of *C.* species is wide, including *Pinus*, *Fagus* L., *Quercus* L., *Betula* L., *Nothofagus* Blume and *Cistus* L. (Degreef and De Kesel 2008)*. Chalciporus africanus* Degreef & De Kesel is always found under *Uapaca guineensis* Müll.Arg. *(*Degreef and De Kesel 2008)*. Chalciporus pseudopiperatus* Klofac and Krisai is also a suspected mycoparasite on *Amanita muscaria. Chalciporus rubinus* (W.G. Sm.) Singer is exclusively associated with deciduous trees (Singer 1965).

2.2.11.3. Disrtribution

The species of *Chalciporus* are distributed worldwide (Desjardin et al. 2009, Nuhn et al. 2013, Xu et al. 2021). Two species, *C. piperatus* and *C. rubinellus* (Peck) were reported from India (Verma and Pandro 2018). Six species have been reported from China (Zhang et al. 2016, 2017, Chai et al. 2019, Xu et al. 2021). The genus has representations from Austria, Australia, Poland, Africa, and USA (Degreef and Kesel 2008, Klofac and Krisai-greilhuber 2020).

2.2.12. ***Erythrophylloporus*** Ming Zhang and T.H. Li

Molecular phylogenetic studies revealed more generic groups in the Boletaceae family (Binder and Hibbett 2006, Dentinger et al. 2010, Wu et al. 2014, Wu et al. 2016a). *Erythrophylloporus* is one of the recently recognized genera from China with *Erythrophylloporus cinnabarinus* Ming Zhang and T.H. Li as the type species (Zhang and Li 2018). Boletaceae family has a few numbers of lamellate genera such as *Phylloboletellus*, *Phyllobolites* and *Phylloporus*. *Erythrophylloporus* is closely related to *Phylloporus* and it is an addition to the lamellate genera in Boletaceae.

Zhang and Li (2018) proposed the genus with a single species (*Erythrophylloporus cinnabarinus*) collected from sub tropical and tropical regions of China. Zhang and Li (2018) used nrLSU, *tef1-α*, *RPB1* and *RPB2* gene regions in phylogenetic studies for supporting the independent nature of *Erythrophylloporus.* Vadthanarat et al. (2019) studied the new genus with four-gene dataset (atp6, tef1, rpb2 and cox3) and established two new species of *Erythrophylloporus, E. paucicarpus* Raspé, Vadthanarat and Lumyong and *E. suthepensis* Vadthanarat, Raspé and Lumyong. The collections were made from the northern Thailand. Zhang and Li (2018) reported that *Erythrophylloporus* had close affinities to *Rugiboletus* and *Lanmaoa* based on multilocus molecular study. But Vadthanarat et al. (2019) revised this concept with atp6, *tef1*, *RPB2* and cox3 multilocus dataset by stating *Erythrophylloporus* was more related to *Singerocomus.*

Vadthanarat et al. (2019) proposed two new combinations based on morphological and molecular analysis. *Phylloporus aurantiacus* Halling and G.M. Mueller was changed to *Erythrophylloporus aurantiacus* (Halling and G.M. Muell.) Raspé and Vadthanarat. *Erythrophylloporus fagicola* (Montoya and Bandala) Raspé and Vadthanarat was *Phylloporus fagicola* Montoya and Bandala (Montoya and Bandala 2011, Vadthanarat et al. 2019).

2.2.12.1. Taxonomic characters

Erythrophylloporus is characterized by small to medium-sized basidiomata, stipitate-pileate with lamellate hymenophore. Pileus convex to applanate, dry, pruinose or velutinous, subtomentose to faintly squamulose or subfloccose towards the center, orange, deep orange, yellowish red to reddish orange, pileus context vivid yellow to yellowish orange gradually changing dark violet, blackish blue to dark blue when exposed. Hymenophore lamellae, slightly thick, decurrent, deeply yellowish orange to deep orange or reddish orange to orange red or brownish orange to red. Stipe central, solid, subcylindrical or clavate, orange, yellow, reddish orange to yellowish red, with orange, reddish orange to orange red pruinose squamules on surface, basal mycelium vivid yellow. Basidiospores broadly ellipsoid, ellipsoid to nearly ovoid, smooth, thinwalled. Pleuro and cheilocystidia present, usually containing yellowish brown pigment, slowly dissolving in KOH. Pileipellis a subcutis to trichoderm, becoming a subcutis when mature. Clamp-connections absent (Zhang and Li 2018).

2.2.12.2. Economic and ecological importance

Erythrophylloporus forms ectomycorrhizal associations with plants in the family Fagaceae (Vadthanarat et al. 2019).

2.2.12.3. Distribution

The distribution of *Erythrophylloporus* species have been reported only from Asia (China and Thailand), North America (Mexico) and Central America (Costa Rica) (Montoya and Bandala 2011, Zhang and Li 2018, Vadthanarat et al. 2019).

2.2.13. ***Indoporus*** A. Parihar, K. Das, Hembrom and Vizzini

Indoporus is a recently described genus from India (Parihar et al. 2018). This genus differs from all other genera in the Boletaceae in its extended pileal margin, grey or greyish white to greyish pink hymenophore, big hymenophoral pores (up to 4 mm wide), initially reddish then blackish discoloration in the context when injured, and smooth basidiospores (Parihar et al. 2018, Li and Yang 2021). Indoporus was erected to include a bolete species, *I. shoreae* which is commonly found near *Shorea robusta* C. F. Gaertn. plants (Dipterocarpaceae). Recently another species, *I. squamulosus* Yan C. Li and Zhu L. Yang has been described from China (Li and Yang 2021).

2.2.13.1. Taxonomic characters

Indoporus species have the following characters. Pileus grey with black squamules, non-glutinous, context yellowish white, quickly becoming dull red to greyish red then slowly becoming black to charcoal black. Hymenophore tubulose, depressed at the juncture of stipe, reddish grey or paler brownish orange on bruising, finally black after 5 minutes, pores angular, simple. Stipe cylindrical to clavate, becoming narrow towards base, smooth, greyish violet at upper half, then grey to blackish brown, context greyish violet to dark violet in upper half and dark blackish brown on lower half, slowly becoming black to charcoal black on exposure. Basidiospores greyish brown in deposit, smooth, inamyloid. Pleurocystidia rare, lanceolate to ventricose, hyaline. Cheilocystidia frequent, narrowly lanceolate with rounded to capitate apex, hyaline. Pileipellis a trichoderm, with irregular and inflated terminal cells with brownish-black intracellular pigmentations (Parihar et al. 2018).

2.2.13.2. Ecological and economic importance

Indoporus shoreae is found to be associated with *Shorea robusta* trees (Parihar et al. 2018).

2.2.13.3. Distribution

Only two species have been reported in *Indoporus. I. shoreae* from India (Parihar et al. 2018) and *I. squamulosus* from China (Li and Yang 2021).

2.2.14. ***Lanmaoa*** G. Wu and Zhu L. Yang

Lanmaoa is a recently erected genus based on molecular phylogenetic analysis (Wu et al. 2016a) with *Lanmaoa asiatica* G. Wu and Zhu L. Yang as the type species. This genus is morphologically similar to *Baorangia* and *Cyanoboletus*. The generic description of *Lanmaoa* by Wu et al. (2016b) includes thin hymenophore (thickness of hymenophore 1/3 – 1/5 times that of pileal context at the position halfway to the pileus center) which stains blue when bruised, a light-yellow context which stains pale blue slowly when cut, and an interwoven trichodermium to a subcutis pileipellis. However, recent studies indicate that the thickness of hymenophore is not a consistent character and it is thicker in some newly designated species (Chai et al. 2018). In phylogenetic analysis, *Lanmaoa* inferred as a sister group of *Cyanoboletus* and *Baorangia.* Wu et al. (2016b) observed that species of *Lanmaoa* have short hymenophoral tubes (thickness of hymenophore 1/3 – 1/5 times that of pileal context at the position halfway to the pileus center) and a slow color change when injured, while *Cyanoboletus* is characterized by dark basidioma and quick bluing when injured and always gelatinized pileus. However, Chai et al. (2018) indicated close morphological and molecular similarities of *Lanmaoa* and *Cyanoboletus*, and suggested a possibility of synonymisation. Studies by Chai et al. (2018) and Farid et al. (2021) treated *Lanmaoa* and *Cyanoboletus* independently. Currently, *Lanmaoa* consists of 12 described species according to *Index Fungorum* (www.indexfungorum.org, accessed on 09 January 2024).

2.2.14.1. Taxonomic characters

Lanmaoa is characterized by the following characters: Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical, convex or applanate, subtomentose, dry, slightly incurved at themargin when young, context off-white to cream yellow, slowly staining pale blue to light blue when injured. Hymenophore adnexed or sinuate, thickness of hymenophore 1/3 – 1/5 times that of pileal context at the position halfway to the pileus center, hymenophoral surface cream yellow to lemon yellow, staining dull blue when injured, pores angular or nearly round, tubes concolorous with hymenophoral surface or light red, staining dark blue when injured. Stipe central, cream yellow, light yellow to lemon yellow at the apex and light to dark purple red towards the base, basal mycelia yellowish white to white. Pileipellis often an interwoven trichodermium to subcutis, rarely ixosubcutis. Pleurocystdia and cheilocystidia subfusiform-ventricose or clavate. Basidiospores smooth, narrowly suboblong to subfusoid, light yellow to brownish yellow. Clamp-connections absent (Wu et al. 2016a)

2.2.14.2. Ecological and economic importance

All species of *Lanmaoa* are suggested to posess ectomycorrhizal association with different plants, mostly with Fagaceae members (Chai et al. 2018). *Lanmaoa macrocarpa* is an edible species (Zheng et al. 2023).

2.2.14.3. Distribution

Lanmaoa species are distributed in North America, USA and China (Wu et al. 2015, Chai et al. 2019, Farid et al. 2021). All the recently described species were reported from China.

2.2.15. *Leccinum* Gray

Leccinum is a widely studied and a species-rich group in Boletales (Meng et al. 2021). It is estimated that the genus possesses 150 species distributed worldwide (Smith and Thiers 1971, Sutara 1989, Meng et al. 2021). The genus was introduced by Gray in 1821 with *L. aurantiacum* (Bull.) Gray as type species and accommodated several species, which now belong to other genera such as *Gyroporus*, *Boletus*, *Suillus*, *Chalciporus* and *Xerocomus* (Den Bakker and Noordeloos 2005). Members of the genus are mainly characterized by whitish or yellow hymenophore, a white to cream context unchanging or staining blue or red when injured, a brown to blackish scabrous to dotted squamules on the surface of the stipe, and comparatively long and smooth basidiospores (Meng et al. 2021). *Leccinum* species can be easily distinguished from other boletes due to the presence of peculiar stipe ornamentations (Bakker and Noordeloos 2005). Important taxonomic works on the genus are Smith and Thiers (1971), Smith et al. (1967), Singer (1986) and Den Bakker and Noordeloos (2005). Smith and Thiers (1971) proposed three sections in *Leccinum* (section *Leccinum* Smith and Thiers, section *Luteoscabra* Smith and Thiers and section *Scabra*). Singer (1986) introduced four sections (section *Luteoscabra*, section *Leccinum*, section *Roseoscabra* and section *Eximia*) in this genus by studying the European species. (Bakker and Noordeloos 2005, Meng et al. 2021).

Leccinum was found to be polyphyletic in early molecular phylogenetic analysis, with the species being suggested to be limited to the sections *Leccinum* and *Scabra* (Binder and Besl 2000). Subsequent studies suggested to retain the genus *Leccinum* by including members present in section *Leccinum* of Singer's infrageneric classification (Bakker and Noordeloos 2005, Meng et al. 2021).

2.2.15.1. Taxonomic characters

The genus *Leccinum* is characterized by the following features: Basidiomata stipitate-pileate. Pileus hemispherical, convex or applanate, glabrous to fibrillose, dry, sometimes subviscid when wet, context whitish, always staining brownish, pinkish, reddish, or occasionally bluish when cut. Hymenophore adnexed, surface concolorous with that of tubes, whitish, tubes and pores staining yellowish, brownish, brown, vinaceous to blackish when hurt. Stipe central, whitish to dirty white, covered with brown to blackish dots or squamules and sometimes additionally with longitudinal ridges, context same to that of pileus, basal mycelium whitish to white. Basidiospores smooth, subfusiform, pale olive-brownish. Pleuro- and cheilocystidia subfusiform-ventricose. Pileipellis an interwoven trichodermium or interwoven subcutis, rarely ixosubcutis. Clamp-connections absent (Wu et al. 2016a).

2.2.15.2. Ecological and economic importance

Most members of *Leccinum* are ectomycorrhizal and highly host-tree specific (Den Bakker et al. 2004, Stasinska et al. 2014). Host specific relationship is used for the identification of many species (den Bakker et al. 2004). Species in the *Leccinum* section *Scabra* are associated with plants of *Betula*, while species of section *Fumosa* and section *Leccinum* are associated with plants of *Populus* L., *Betula,* Pinaceae and Ericaceae (Meng et al. 2021). Species like *L. aurantiacum* are not host-specific and they found associated with different plant groups (Den Bakker and Noordeloos, 2005). *Leccinum quercinum* (Pilát) E.E. Green andWatling, *L. scabrum* (Bull.) Gray and *L. versipelle* (Fr. and Hök) Snell are well-known edible species (Meng et al. 2021).

2.2.15.3. Distribution

North America has the richest *Leccinum* diversity and 118 species reported from this region (Both 1993). Smith and Thiers (1967,1971) reported 68 species from Michigan. 12 species were reported from Central America by many workers (Ortiz-Santana and Halling 2009, Halling and Mueller 2003, Meng et al. 2021). den Bakker and Noordelos (2005) revised and described 16 European species based on morphology and molecular data.

Most of the Asian species of *Leccinum* have been reported from China and a total of 34 species present in China (Wu et al. 2020, Meng et al. 2021). *L. ustale* (Berk.) E. Horak is the only species reported from India so far (Verma and Pandro 2018).

2.2.16. ***Neotropicomus*** A.C. Magnago, Alves-Silva and T.W Henkel

Neotropicomus is a recently described genus from Brazil, with *N. australis* A.C. Magnago as the type species. The genus is represented by two species, *N.*

australis and *N. parvogracilis* (T.W. Henkel and Husbands) A.C. Magnago and T.W. Henkel. *N. parvogracilis* was originally described as *Xerocomus parvogracilis* T.W. Henkel and Husbands (Husbands et al. 2013, Magnago et al. 2022). *Neotropicomus* was included in the subfamily Boletoideae of Boletaceae with Tengioboletus G. Wu and Zhu L. Yang as sister clade (Magnago et al. 2022).

2.2.16.1. Taxonomic characters

The diagnostic features of the genus are the following: Basidiomata epigeous. Pileus smooth to rugulose. Hymenophore tubulose-poroid, pale olivaceous yellow, pores 1–2 mm wide, isodiametric to subangular. Context pale yellowish, unchanging. Stipe smooth to minutely scabrous. Basidiospores olivaceous in deposit, subfusoid to fusoid, smooth. Pleuro- and cheilocystidia fusiform. Pileipellis a trichodermium. Hymenophoral trama phylloporoid. Clamp-connections absent (Magnago et al. 2022).

2.2.16.2. Economic and ecological importance

Neotropicomus australis was collected from the vicinity of *Guapira* Aubl. and *Pisonia* L. (Husbands et al. 2013, Magnago et al. 2022).

2.2.16.3. Distribution

Neotropicomus australis have been reported from Brazil's Atlantic Forest. *Neotropicomus parvogracilis* described from Guyana (Husbands et al. 2013, Magnago et al. 2022).

2.2.17. ***Parvixerocomus*** G. Wu and Zhu L. Yang

Parvixerocomus is a recently established genus erected by Wu et al. (2015), having smaller basidiomata (20 – 40 mm), subdecurrent, yellow hymenophore without stuffed pores, context bluing on bruising and smooth, ovoid to ellipsoid basidiospores. The genus comprised of only three species, *Parvixerocomus aokii* (Hongo) G. Wu, N.K. Zeng and Zhu L., *P. pseudoaokii* G. Wu, Kuan Zhao and Zhu L. Yang and *P. matheranensis* P.B. Patil, Senthil., S.K. Singh and S.A. Vaidya. *Parvixerocomus pseudoaokii* is the type species. The name indicates its close resemblances to the genus *Xerocomus* (Wu et al. 2015).

Boletus aokii Hongo was reported as *Parvixerocomus aokii* by Wu et al. (2015) based on morphological and molecular data. The species was originally reported from Japan in 1984 (Wu et al. 2015, Patil et al. 2021). *Parvixerocomus pseudoaokii* is closely similar to *P. aokii* at morphological and molecular level. However, *P. aokii* have larger basidiospores than *P. pseudoaokii. Parvixerocomus matheranensis* P. B. Patil, Senthil., S.K. Singh & S.A. Vaidya was reported from Maharashtra, India (Patil et al. 2021).

Molecular phylogenetic studies with nrLSU, tef1-α, rpb1, andrpb2 revealed that *Parvixerocomus* was the basal group of *Boletoideae* subfamily (Wu et al. 2016a). Patil et al. (2021) also confirmed that *Parvixerocomus* was a sister clade to other genera in Boletoideae subfamily.

2.2.17.1. Taxonomic characters

Parvixerocomus is characterized by the following: Basidioma small, stipitate-pileate with tubular hymenophore. Pileus convex to applanate, subtomentose, dry, context yellowish to yellow, staining blue immediately when injured. Hymenophore subdecurrent, often with teeth on the apex of stipe, surface yellowish to yellow, staining blue immediately when injured, pores irregular, angular to round, often compound, tubes concolorous with hymenophoral surface, staining blue immediately when injured. Stipe central, lightbrown, brownish red to reddish brown, surface often pruinose, basal mycelia cream to greyish yellowish. Pileipellis an epithelium composed of submoniliform to moniliform hyphae with cystidioid terminal cells. Pleuro- and cheilocystidia subfusiform-ventricose or clavate, with subacute apex or with long beak. Basidiospores smooth, ovoid to ellipsoid, yellowish to brownish yellow. Clamp-connections absent (Wu et al. 2015).

2.2.17.2. Ecological and economic importance

The species in the genus *Parvixerocomus* have not been studied for its ectomycorrhizal associations (Wu et al. 2016a, Patil et al. 2021).

2.2.17.3. Distribution

Parvixerocomus has tropical to subtropical distribution (Wu et al. 2015, Patil et al. 2021). *Parvixerocomus aokii* was distributed in Japan and South China (Wu et al. 2015). *Parvixerocomus psuedoaokii* was reported from China (Wu et al. 2015). *Parvixerocomus* matheranensis was originally reported from Matheran Hills, Maharashtra, India (Patil et al. 2021).

2.2.18. ***Phylloporus*** Quél.

Phylloporus is a genus, which consist of lamellate to somewhat poroid hymenophore in Boletaceae (Neves et al. 2012, Chuankid et al. 2019). *Phylloporus pelletieri* (Lév.) Quél is the type species. More than 90 species have been reported in this genus from all over the world (Chuankid et al. 2019). Most of the species were reported from subtropical or tropical regions (Zeng et al. 2013, Hosen and Li 2015).

Corner (1972) considered *Phylloporus* as a primitive genus of Boletaceae due to the presence of lamellate hymenophore. The lamellate hymenophore and smooth basidiospores led Pegler and Young (1981) to consider *Phylloporus* as a derived genus. But, *P. pelletieri* has bacillate ornamentation in spores. Later, Heinemann and Rammeloo (1986) supported the concept of Pegler and Young (1981) by extensive taxonomic study. Multigene molecular studies also supported the concept of *Phylloporus* as a derived genus that closely related to *Xerocomus* (Binder and Hibbett 2006).

Bresinsky and Besl (2003) suggested synonymising *Phylloporus* with *Xerocomus* based on the phylogeny of the two *Phylloporus* species. Phylogenetic analysis in a broad scale by Neves et al. (2012) supported the monophyly of *Phylloporus.* They stated that the group is distinct from *Xerocomus* by morphological and molecular data. Based on a three-locus molecular data obtained from East Asian collections by Zeng et al. (2013) supported the monophyly and they obtained nine major clades.

2.2.18.1. Taxonomic description

Phylloporus is characterised by the following features: Basidiomata small to medium-sized. Pileus convex, plano-convex to applanate, sometimes with shallow depression at the center, brown, orange, or yellow, surface glabrous or tomentose. Pileal context whitish to yellowish, unchanging or changing to blue or grey on bruising. Hymenophore lamellate, adnate to slightly decurrent, lamellae subclose, ventricose, or shallowly intervenose to somewhat anastomosing. Stipe equal or tapering downward. Basidiospores smooth or finely bacillate to slightly rugulose. Basidia narrowly clavate to clavate, 4-spored or 2-spored. Hymenophoral trama bilateral. Cystidia fusoid to narrowly fusoid, sometimes clavate to nearly mucronate. Pileipellis trichodermium or interwoven trichodermium. Clamp-connections absent (Neves et al. 2012, Chuankid et al. 2019).

2.2.18.2. Economic and ecological importance

Many *Phylloporus* species are showing ectomycorrhizal associations with different plants in Fagaceae, Pinaceae, Fabaceae, Myrtaceae and Dipterocarpaceae (Hosen and Li 2017).

2.2.18.3. Distribution

A large number of *Phylloporus* species reported from tropical to subtropical areas (Corner 1972, Heinemann and Rammeloo 1986, Neves et al.

2012, Zeng et al. 2013, Pradeep et al. 2015). Two species, *P. gajari* Hosen and Zhu L. Yang and *P. septocystidiatus* C.K. Pradeep and K.B. Vrinda were reported from India (Pradeep and Vrinda 2015, Ghosh et al. 2023). *Phylloporus septocystidiatus* was reported as a new species from Kerala State.

2.2.19. ***Retiboletus*** Manfr. Binder and Bresinsky

Retiboletus was described Binder and Bresinsky (2002) with *R. ornatipes* (Peck) Manfr. Binder and Bresinsky as type species. The genus can be distinguished from other genera of Boletaceae by its usually reticulate stipe with a base darker than the apex, and yellow-orange to rusty brown color change of basidiomata (Chuankid et al. 2021). The genus was erected to accommodate *Boletus retipes* Berk. and M.A. Curtis, *B. ornatipes* Peck, *B. flavoniger* Halling, G.M. Muell. and L.D. Gómez, *B. griseus* Frost, and *B. nigerrimus* R. Heim. A unique class of metabolites, retipolides, is present in species of *Retiboletus* (Justus et al. 2007). Molecular phylogentic analysis and presence of retipolides were the major features for erecting this genus (Binder and Bresinsky 2002). Now, 17 species have been described so far in this genus (Zhou et al. 2022, *Index Fungorum* accessed on 17 November 2023). *Retiboletus kauffmanii* (Lohwag) N.K. Zeng and Zhu L. Yang is the only species reported from India (Chakraborty et al. 2017).

2.2.19.1. Taxonomic characters

Basidioma stipitate-pileate with tubular hymenophore. Pileus hemispherical to subhemispherical, surface subtomentose, dry, context white to pallid or yellow, unchanging or becoming brownish in color when injured. Hymenophore adnate or depressed around apex of stipe, hymenophoral surface pallid to greyish pink or yellow, pores angular or roundish, tubes concolorous with hymenophoral surface, unchanging or brownish in color when injured. Stipe central, wholly reticulate, rarely nonreticulate, basal mycelium white to yellow. Basidiospores smooth, subfusoid. Pleuro- and cheilocystidia abundant, subfusiform to fusoid-ventricose. Pileipellis subrepent to trichodermium composed of filamentous interwoven hyphae. Clamp-connections absent (Wu et al. 2016a).

2.2.19.2. Economic and ecological importance

Edibility and ectomycorrhizal status of the genus unknown.

2.2.19.3. Distribution

Most of the species have been reported from North America and eastern Asia (Zeng et al. 2016). 10 species have been reported from China (Binder and Bresinsky 2002, Wu et al. 2016a, Zeng et al. 2016, Liu et al. 2020). *Retiboletus kauffmanii* was reported from Sikkim, India (Chakraborty et al. 2017).

2.2.20. *Rostrupomyces* Vadthanarat and Raspé

Rostrupomyces is very recently described genus to accommodate *Xerocomus sisongkhramensis* Khamsuntorn, Pinruan and Luangsa-ard. The genus erected based on multiple protein-coding genes (atp6, cox3, tef1, and rpb2) analyses of a wide taxon sampling of Boletaceae (Vadthanarat et al. 2024). The genus is morphologically closely similar to *Xerocomus,* but differs by the shape and size of basidiospores. Hymenophore of *Xerocomus* always turn more or less bluish to blue when bruised or cut (Wu et al. 2016a), however, color change upon bruising does not occur in any part of Rostrupomyces basidiomatas (Vadthanarat et al. 2024). *Rostrupomyces* clustered as a sister taxon to *Rubinosporus* in the subfamily Xerocomoideae. The genus is phylogenetically distatnt from *Xerocomus* in the phylogram (Vadthanarat et al. 2024).

2.2.20.1. Taxonomic characters

Basidiomata stipitate-pileate. Pileus initially convex becoming plano-convex to applanate, surface at first rugulose then subrugulose in age, finely tomentose to tomentose, dark brown to reddish brown, becoming light brown to brown to greyish orange, unchanging when bruised, context off-white then yellowish to dull pale orange in age, unchanging when cut. Stipe central, terete, cylindrical, surface subscabrous, yellowish white to pale yellow to orange white, with scattered brown to dark brown to reddish brown granulose squamules, unchanging when bruised, basal mycelium white, context solid, white becoming off-white to yellowish white in age, unchanging when cut. Hymenophore tubulate, slightly depressed to depressed around the stipe. Tubes pale yellow then greyish yellow, separable from the pileus context, unchanging when cut. Pores roundish then subangular to angular with age, when young white then yellowish white becoming greyish yellow, unchanging when touched. Spore print yellowish brown. Basidiospores ellipsoid to broadly ellipsoid, thin-walled, smooth under light microscope and SEM. Basidia 4-spored, clavate without basal clamp connection. Cheilo- and pleurocystidia narrowly fusiform to fusiform or narrowly utriform, thin-walled. Pileipellis an intricate trichoderm, made of moderately interwoven to loosely interwoven, thin-walled hyphae. Stipitipellis arranged parallel to the surface of the stipe, composed of moderately interwoven, thin-walled hyphae, with scattered groups of rising cells to clusters of narrowly clavate to clavate cells. Clamp-connections not seen in any tissue (Vadthanarat et al. 2024).

2.2.20.2. Ecological and economic characters

Rostrupomyces sisongkhramensis (Khamsuntorn, Pinruan & Luangsa-ard) Vadthanarat, Raghoonundon & Raspé is always found near Dipterocarpaceae members, suggesting that it may have ectoycorrhizal associations.

2.2.20.3. Distribution

The single species *Rostrupomyces sisongkhramensis* is currently known only from northern and northeastern Thailand (Vadthanarat et al. 2024).

2.2.21. ***Rubroboletus*** Kuan Zhao and Zhu L. Yang

Rubroboletus is a recently erected genus typified by *R. sinicus* (W.F. Chiu) Kuan Zhao and Zhu L. Yang (Zhavo et al. 2014). The genus is characterized by a brown, pinkish to reddish pileal surface, an orange-red to blood-red surface of the hymenophore, yellow tubes, pink to red reticula or spots on the stipe, a blue color change of tissues when injured, and smooth basidiospores (Zhang et al. 2022).

Boletus s. l.was a polyphyletic group and traditional sections (Singer 1986) of the genus were revisited with phylogenetic analyses (Wu et al. 2014). *Boletus* section *Luridi* was the largest section in Boletus s. l. (Singer 1986). Molecular phylogenetic studies proved that this section was polyphyletic and contains independent clades (Wu et al. 2014, Zhao et al. 2014). The members of section *Luridi* were transferred to other genera such as *Caloboletus, Crocinoboletus, Exsudoporus, Neoboletus, Suillellus,* and *Rubroboletus* which included *R. sinicus*. Members of *Rubroboletus* can be clearly distinguished from other related genera by morphological characters also.

2.2.21.1. Taxonomic characters

Basidioma stipitate-pileate with tubular hymenophore. Pileus hemispherical, convex or applanate, greyish, pinkish to red, context white, yellowish to lemon-yellow, bluing quickly when exposed. Hymenophore surface orange red to blood red, sometimes orange-yellow when mature, rapidly bluing when bruised, tubes yellow to olivaceous green, turning blue promptly when injured, then back to the original color slowly. Stipe central, covered with pinkish, red to brownish red reticula or spots. Pileipellis an interwoven trichoderm composed of more or less vertically arranged, sometimes gelatinized filamentous hyphae. Hymenophoral trama boletoid. Basidiospores smooth, subfusiform to ovoid-ellipsoid, slightly thick-walled. Pleuro- and cheilocystidia lageniform, thin-walled. Clamp-connections absent (Zhao et al. 2015).

2.2.21.2. Ecological and economic characters

Rubroboletus legaliae (Pilát and Dermek) Della Maggiora and Trassini, *R. lupinus* (Fr.) Costanzo, Gelardi, Simonini and Vizzini, *R. pulcherrimus* (Thiers and Halling) D. Arora, N. Siegel and J.L. Frank, *R. rhodoxanthus* (Krombh) Kuan Zhao and Zhu L. Yang, and *R. satanas* (Lenz) Kuan Zhao and Zhu L. Yang are reported as poisonous species (Zhang et al. 2022). *Rubroboletus esculentus* Kuan Zhao, H.M. Shao and Zhu L. Yang, and *R. sinicus* have been collected and as edibles in markets of southwestern China (Zhang et al. 2022). *Rubroboletus himalayensis* Sarwar and Khalid is thought to have medicinal properties (Sarwar et al. 2021).

2.2.22.3. Distribution

The species of *Rubroboletus* have been reported from worldwide including Europe, USA, China, Italy, France and Germany (Thiers and Halling 1976, Muñoz 2005, Frank 2015, Halama 2015, Maggiora 2015, Vizzini 2015, Wu et al. 2016a, Zhao and Shao 2017, Sarwar et al. 2021, Zhang et al. 2022). No species has been reported from India to date.

2.2.22. ***Strobilomyces*** Berk.

Synonymy:

Eriocorys Quél., Enchir. fung. (Paris): 163 (1886)

The genus *Strobilomyces* was introduced by Berkeley (1851). It is one of the easily identifiable bolete genera characterized by dark brown to blackish basidiomata with coarsely fibrillose or conical to patch-like squamules on the pileal surface, wooly to shaggy stipe, with or without partial veil, blackish brown globose to subglobose basidiospores with reticulate or verrucose to echinate ornamentation (Singer 1986, Sato et al. 2011). *Strobilomyces strobilaceus* (Scop.)

Berk. is the type species. *Strobilomyces* is known for their ectomycorrhizal associations with trees belonging to Fagaceae and Pinaceae (Sato et al. 2011). *Index Fungorum* (accessed on 30 November 2023) records 47 species of *Strobilomyces*. Nine species have been reported from India (Verma and Pandro 2018). Han et al. (2017) published their studies on the phylogeny and biogeographical analyses of *Strobilomyces* mainly based on African collections. They recognized that *Strobilomyces* probably originated in Africa during Eocene, and spore dispersal played an important role in the distribution of the species.

Gilbert (1931) erected a family, Strobilomycetaceae to accommodate some flesy, pore bearing fungi with ornamented spores, which were previously considered in the family Boletaceae. Gilbert (1931) initially included two genera, *Strobilomyces* and *Boletinellus.* The system proposed by Gilbert (1931) got universal acceptance after the revision of Strobilomycetaceae by Singer (1945, 1962). Singer (1945) revised *Strobilomyces* and *Boletinellus* with more morphological data. *Porphyrellus* Gilb. and *Phyllobolites* Singer (a lamellate genus) was also placed in Strobilomycetaceae by Singer (1945). Singer and Digilio (1951) added one more lamellate genus *Phylloboletellus* Singer to this family. McNabb (1967) published a monograph Strobilomycetaceae in New Zealand and indicated the close similarity of Boletaceae and Strobilomycetaceae. On the basis of spore ornamentations, Singer (1975) divided Strobilomycetaceae in to two sections: section *Strobilomyces* with reticulate, semireticulate or verrucose spores, and section *Pterospori* with spores having longitudinal costae. Pegler and Young (1981) transferred the species in section *Pterospori* to a new genus *Afroboletus.* Molecular phylogenetic studies revealed the close affinities of Strobilomycetaceae with Boletaceae (Binder and Hibbett 2006, Han et al. 2017, Wu et al. 2014). Then, removed the family status of strobilomycetaceae (Binder and Hibbet 2006, Wu et al. 2014, Wu et al. 2016a).

2.2.22.1. Taxonomic characters

The genus is characterized by the following features. Basidioma stipitate-pileate with tubular hymenophore, dark brown to blackish. Pileus hemispherical, convex or applanate, coarsely squamose or squamulose, dry, margin often appendiculate, context whitish to greyish or pale greyish cream, quickly staining reddish then slowly blackish when injured. Hymenophore adnate or adnexed, hymenophoral surface whitish cream, greyish brown or vinaceous drab, staining reddish then blackish when injured, pores angular, tubes concolorous with hymenophoral surface, staining reddish then blackish when injured. Stipe central, ornamented with woolly or fibrillose squamules, apical or upper part usually reticulate, partial veil often present, persistent as an annulus on the stipe apex or as an appendiculate margin on the pileus or fugacious, basal mycelium whitish to blackish. Basidiospores comparatively small, subglobose to obtusely ellipsoid, blackish brown, echinulate, reticulate or longitudinally striate. Pleuro- and cheilocystidia subfusiform, ventricose or clavate. Pileipellis often an intricated trichodermium, composed of loosely branching hyphae. Clamp-connections absent (McNabb 1967, Singer 1986, Wu et al. 2016a).

2.2.22.2. Ecological and economic importance

Strobilomyces species are ectomycorrhizal with plants belonging to Fagaceae and Pinaceae (Sato et al. 2011).

2.2.22.3. Distribution

Strobilomyces species are distributed in most of the continents except Antartica and most of the reports are from tropical and sub-tropical areas of Asia and Africa (Heinemann 1954, Corner 1972, Pegler 1977, Zang 1985, Han et al. 2017). *Strobilomyces seminudus* and *S. hongoi* were two new species reported from Japan (Sato 2011).

Nine species were reported from India, *Strobilomyces echinocephalus* Gelardi & Vizzini from Jammu and Kashmir (Kour et al. 2013), *S. kalimpongensis* Bose from West Bengal (Bose 1946), *S. mollis* Corner from Jammu and Kashmir (Lakhanpal 1996, Kour et al. 2013), *S. montosus* Berk. from Meghalaya (Berkeley 1851), *S. nigricans* Berk. from West Bengal and Meghalaya (Berkeley 1851), *S. strobilaceus (*Scop.) Berk. from Nagaland, and *S. velutipes* Cooke & Massee from Uttarakhand (Lloyd 1925). *S. polypyramis* was reported earlier from India in 1851 by Berkley and it was rediscovered by Das et al. (2014).

Strobilomyces floccopus (Vahl) P. Karst., *S. annulatus, S. strobilaceous* and *S. mollis* have been reported from Kerala state (Mohanan 2011, Vrinda and Pradeep 2014).

2.2.23. *Tylopilus* P. Karst

Synonymy:

Leucogyroporus Snell, Mycologia 34(4): 408 (1942)
Phaeoporus Bataille, Bull. Soc. Hist. nat. Doubs 15: 31 (1908)
Rhodobolites Beck, Z. Pilzk. 2: 147 (1923)
Rhodoporus Quél. ex Bataille, Bull. Soc. Hist. nat. Doubs 15: 31 (1908)

Tylopilus is one of the largest and widespread genera in Boletaceae family (Magnago et al. 2017), with *T. felleus* as the type species. *Tylopilus* species are known from Africa, Australia, Asia, Europe and the Americas (Singer et al. 1983, Wolfe and Bougher 1993, Amtoft et al. 2002, Halling et al. 2007, Osmundson and Halling 2010). Most of the species in this genus were recognized as ectomycorrhizal with many plant species (Osmundson and Halling 2010, Sarwar et al. 2014). The traditional treatment of boletoid species placed pink spored members with adnate tubes in the genus *Tylopilus* (Karsten 1881).

The genus *Tylopilus* was established by Karsten (1881) to accommodate a single species *T. felleus* (Bull.) P. Karst*.* Smith and Thiers (1968, 1971) suggested for considering Singer's *Porphyrellus* as a subgenus within the

Tylopilus. Corner (1972) didn't accept *Tylopilus* as an independent genus and he included it as a subgenus under *Boletus.* Corner (1972) also suggested including smooth spored taxa of *Porphyrellus* in *Boletus* subg. *Tylopilus.* Many *Tylopilus* species were described by Singer (1986) and he expanded the morphological data of the species. Based on Singer's (1986) concept, *Tylopilus* s. l. is characterized by a dry pileus, a light colored hymenophore when young, usually depressed around the stipe, a sordid pink to dull flesh ocher spore print, pale basidiospores, well-developed cystidia with plasmatic pigments, boletoid tube trama, and a whitish context.

The molecular phylogenetic studies concluded that *Tylopilus* s. l. was polyphyletic in Boletaceae family (Binder and Hibbett 2006, Dentinger et al. 2010, Nuhn et al. 2013, Wu et al. 2014). Li et al. (2010) proposed a new genus *Zangia* for accommodating species which are morphologically similar but phylogenetically distant from *Austroboletus, Fistulinella,* and *Tylopilus* s. str. *Tylopilus* s. str. was grouped in to *Boletoideae* sub family (Wu et al. 2014). A monographic treatment of Asian *Tylopilus* species was published in the book 'The boletes of China: *Tylopilus* s. l.' by Li and Yang (2021). Based on morphological and molecular studies, the wider concept of the genus was circumscribed by Li and Yang (2021), where they distributed 105 species of *Tylopilus* s. l. in to 19 genera. Several new species and new combinations were introduced in this study. Six species of *Tylopilus* s. str. have been reported from India so far (Das et al. 2012, Chakraborty et al. 2018, Verma and Pandro 2018, Chakraborty et al. 2022). Among these, *T. neofelleus* Hongo, *T. himalayanus* D. Chakr., K. Das and Vizzini and *T. pseudoballoui* D. Chakr., K. Das and Vizzini, were reported from China also (Li and Yang 2021).

2.2.23.1. Taxonomic characters

The following are the peculiar features of *Tylopilus*: Basidioma stipitate-pileate with tubular hymenophore. Pileus hemispherical to subhemispherical or applanate, surface subtomentose or glabrous, dry to gelatinous, context white, without color change when injured, mostly with a bitter taste. Hymenophore depressed around the apex of stipe, hymenophoral surface white when young, and becoming pinkish when mature, pores angular or roundish, tubes concolorous with hymenophoral surface, unchanging in color when injured. Stipe central, glabrous or distinctly reticulate, basal mycelium white. Basidiospores ellipsoid to oblong. Pleurocystidia and cheilocystidia abundant, subfusiform. Pileipellis subcutis to trichodermium. The bitter taste of the context can be used as an easy way to recognize *Tylopilus* speices. Clamp-connections absent (Wu et al. 2016a).

2.2.23.2. Ecological and economic importance

Most of the species in *Tylopilus* are ectomycorrhizal (Wu et al. 2016a). Species like *T. felleus* have bitter taste, so they are commonly known as the bitter bolete. Bitter taste makes them inedible (Verma and Pandro 2018).

2.2.23.3. Distribution

Species of *Tylopilus* were reported from Africa, Australia, Asia, Europe and the America (Magnago 2017). More reports are from paleotropical and neotropical regions (Fulgenzi et al. 2007). About 20 species have been reported from neotrpics (Wolfe and Bougher 1993, Amtoft et al. 2002, Halling et al. 2007, Osmundson and Halling 2010). Thirteen species were described from China with morphological and molecular data (Wu et al. 2016a). Thirty four species and four combinations were described from China recently (Li and Yang 2021).

Eight species have been reported from India (Mohanan 2011, Verma and Pandro 2018). *Tylopilus himalayanus* and *T. pseudoballoui* were reported from India (Sikkim and Uttarakhand res) as new species (Chakraborty et al. 2018). *Tylopilus alboater* (Schwein.) Murrill from Kerala (Mohanan 2011), *Tylopilus chromipes* (Frost) A.H. Sm. & Thiers from West Bengal (Verma and Pandro 2018), *T. indecisus* (Peck) Murrill from Uttarakhand (Harsh and Bisht 1982), *T. neofelleus* from Sikkim (Chakraborty et al. 2018) and *T. plumbeoviolaceus (*Snell & E.A. Dick) Snell & E.A. Dick (Lakhanpal and Sharma 1988) are the other distributional reports from India.

2.2.24. ***Xerocomellus*** Šutara

The genus *Xerocomellus* was erected by Šutara (2008) to accommodate *X. chrysenteron* and its relatives. *Xerocomellus* includes species with boletoid or hypogeous to secotioid basidiomata (Garza-Ocañas et al. 2022). *Xerocomellus* members are commonly known as "cracked-cap boletes" due to their tendency to develop areolate pileus surfaces (Frank et al. 2020). *Xerocomellus* species are characterized by red to purple-red tinged pileus and stipe, dry and subtomentose pileal surface and angular and large pores (Martínez-reyes et al. 2023). *Xerocomellus* has a worldwide distribution and most of the reports were from Europe and North America (Frank et al. 2020).

Xerocomus s. l., typified by *X. subtomentosus* (L.) Quél. is a polyphyletic group in phylogenetic analyses (Šutara 2008, Frank et al. 2020). Šutara (2008) erected *Xerocomellus* from *Xerocomus* based on morphological and phylogenetic data. Several multi-gene studies also supported the placement of the genus in Boletaceae (Gelardi et al. 2015, Wu et al. 2016a, Frank et al. 2020). Thirty three taxa are coming under *Xerocomellus* in *Index Fungorum* (accessed on 01 Feb 2024). Two species of *Xerocomellus, X. chrysenteron* and *X. himalayanus* D. Chakr. and A. Ghosh have been reported from India (Verma and Pandro 2018, Das et al. 2023).

2.2.24.1. Taxonomic characters

Xerocomellus is characterized by the following features: Basidioma stipitate-pileate with tubular hymenophore. Pileus hemispherical, convex or applanate, surface velvety, dry, context white to yellowish, slowly staining bluish when injured. Hymenophore adnate to sinuate, sometimes depressed around the stipe, surface oliveyellow to brownish yellow, becoming ochraceous with age, staining blue immediately when bruised, pores compound, angular, comparatively large (1 – 2.5 mm in diam.), tubes concolorous with hymenophoral surface, staining blue when injured. Stipe comparatively slender, red to brownish red, longitudinally fibrillose, basal mycelium dirty white. Basidiospores subfusiform to slender amygdaliform in side view with poor suprahilar depression, subfusoid in ventral view, brownish yellow, smooth (under SEM), rarely with indistinctly longitudinal ridges. Pleuro- and cheilocystidia fusoid to lageniform, thin-walled. Pileipellis a palisadoderm consisting of vertically arranged, yellowish brown, more or less broadened and often incrusted hyphal elements, terminal cells of which reach almost at the same level. Clamp-connections absent (Wu et al. 2016a).

2.2.24.2. Ecological and economic importance

Xerocomellus species form ectomycorrhizas with members of Fagaceae and Pinaceae (Tedersoo et al. 2010).

2.2.24.3. Distribution

Majority of the *Xerocomellus* species are reported from North America. Fourteen species have been reported from North America and 12 species have been recorded from Europe and Asia (Martínez-reyes et al. 2023). Two species, *X. himalayanus* (Verma and Pandro 2018, Das et al. 2023) and *X. chrysenteron* (Mohanan 2011), reported from India.

2.3. Boletinellaceae P. M. Kirk, P. F. Cannon and J. C. David

Boletinellaceae is a small family comprising of only two genera, *Boletinellus* and *Phlebopus* (Pham et al. 2012). Seven species of *Boletinellus* and 17 species of *Phlebopus* are listed in *Index Fungorum* (www.indexfungorum.com, accessed on 14 November 2023). Molecular phylogenetic studies revealed the independent status of Boletinellaceae in Boletales (Binder and Bresinsky 2002). Most of the species in this family are ectomycorrhizal (Bougher 1994, Miller et al. 2000, Binder and Bresinsky 2002).

Genera such as *Boletinellus, Gyrodon, Gyroporus* and *Paragyrodon* (Singer) Singer were included in Gyrodontaceae Heinem. based on morphological data and the family was considered as an artificial taxon (Bruns et al. 1998). The phylogenetic analyses of boletoid fungi revealed the polyphyletic nature of Gyrodontaceae, and its affinities with *Calostoma, Pisolithus* and *Scleroderma* (Binder and Bresinsky 2002). Binder and Bresinsky (2002) studied the phylogenetic relationship of Gasteromycetes and Hymenomycetes using 28S gene region. In their study, Paxillineae and Boletineae were not resolved as separate clades due to the polyphyly of Gyrodontaceae. *Boletinellus* and *Phlebopus* were inferred as sister clades. Based on these observations, Binder and Bresinsky (2002) made a new suborder, Sclerodermatinae. In this sub order, Binder and Bresinsky (2002) proposed two families, Boletinellaceae and Gyroporaceae. *Boletinellus* and *Phlebopus* were placed in Boletinellaceae based on morphological characters, nutritional modes, habitats preferences and molecular phylogeny (Binder and Bresinsky 2002).

2.3.1. Taxonomic characters

Boletinellaceae is characterized by the following features. Basidiocarps stipitate-pileate. Pileus glabrous to subtomentose, olive brown to yellow brown. Stipe olive brown to yellow brown, darkening towards the base, almost smooth, without reticulate ornamentation, eccentric or central. Boletinoid basidiocarps show eccentric stipe decurrent tubular hymenophore (*Boletinellus*). Basidiocarps with central stipe (*Phlebopus*) show a narrow tubular hymenophore, which is depressed around the stipe. Color of hymenophore yellow to olive yellow or yellow brown. Flesh pale olive yellow, with pinkish flush, unchanging or slightly changing to pale bluish green, context of the stipe often turning blue, reddish brown or black towards the base. Spores smooth, ellipsoid to subglobose, inamyloid and dextrinoid. Spore print yellowish, yellow brown to olive brown. Hyphae with clamp-connections (Binder and Bresinsky 2002).

2.3.2. Ecological and economic importance

Boletinellus merulioides is also known as ash-tree bolete, as they are commonly found under ash-trees (*Fraxinus* species) in North America (Singer 1945, Snell and Dick 1970) and they were assumed to be in ectomycorrhizal relationship (Brundrett and Kendrick 1987). *Boletinellus merulioides* also shows a peculiar mutualistic association with an aphid *Meliarhizophagus fraxini-folii.* The fungus provides a living space for the aphid, and in return, fungus gets nutrients from the excreted honeydew of aphid (Brundrett and Kendrick 1987). Most of the *Phlebopus* species are ectomycorrhizal with plants like *Eucalyptus* and *Quercus* (Kumla et al. 2012). *Phlebopus portentosus* is one of the delicious mushrooms and it is commonly known as the 'black bolete' (Kumla et al. 2012).

2.3.3. Distribution

Boletinellaceae members have been reported mainly from tropical and subtropical regions of the world (Heinemann and Rammeloo 1982, Li and Watling 1999, Pham et al. 2012).

2.3.4. ***Boletinellus*** Murrill

Boletinellus is a small genus consisting of ectomycorrhizal species (Murrill 1909, Singer 1945, Smith and Thiers 1971, Watling 2008). The nutritional mechanism of the *Boletinellus* species exhibits complicated strategies. Many species are facultative ectomycorrhizal, some are saprotrophic, and species like *B. merulioides* (Schwein.) Murrill shows a three-way interaction of fungi, plants, and different species of insects like mealy bugs and arthropods (Brundrett and Kendrick 1987, Miller et al. 2000, Binder and Bresinsky 2002, Wilson et al. 2012).

Mei et al. (2020) included three species in *Boletinellus* (*B. exiguous* (Singer and Digilio) Watling, *B. merulioides* and *B. rompelii* (Pat. and Rick) Watling). Later, Liu et al. (2022) reassigned *Paxillus rhytidophyllus* M. Zang as *B. rhytidophyllus* (M. Zang) Li R. Liu, Yan C. Li and Zhu L. Yang. According to *Index Fungorum* (www.indexfungorum.org, accessed on 21 March 2023), there are six species in *Boletinellus,* including *B. proximus* (Singer) Murrill and *B. monticola* (Singer) Watling apart from the other four species. *Boletinellus proximus* was originally described as *Gyrodon proximus* by Singer (1945), and later transferred to *Boletinellus* by Murrill (1946). Some authors followed the concept of Singer (1945) and did not consider this species under *Boletinellus* (Singer and Digilio 1960, Mei et al. 2020). However, recent studies retain this species in *Boletinellus* (Magnago 2014, Magnago et al. 2022). *Boletinellus monticola* was another species that was originally described as *Gyrodon monticola* Singer (Singer and Digilio 1957), and transferred to *Boletinellus* by Watling (Watling and Meijer 1997). However, Halling and Mueller (2005) retained the species in the mycorrhizal genus *Gyrodon,* mainly because of its strict ectomycorrhizal association. Ecological and molecular phylogenetic studies supported the placement of *G. monticola* in *Gyrodon* (Becerra et al. 2005, Nuhn et al. 2013). *Boletinellus monticola* seems to be better placed in *Gyrodon*.

2.3.4.1. Taxonomic characters

Members of the genus *Boletinellus* are characterized by small to medium-sized basidiomata with a brownish pileus with fulvous or olivaceous tinge, and minutely tomentose to floccose-tomentose surface, white or yellowish fleshy context, deeply decurrent, large and gyrose to alveolate hymenophore, which is yellowish to olivaceous brown, tissues unchanging or staining blue very slowly on bruising, central, eccentric or lateral stipe tinged yellowish brown to brownish black, smooth and ellipsoid to sub-reniform basidiospores, fusoid to ventricose cheilocystidia and pleurocystidia, and the presence of clamp-connections in all tissues (Murrill 1909, Singer 1945, Smith and Thiers 1971, Liu et al. 2022).

2.3.4.2. Ecological and economic importance

Boletinellus species exhibit a complex nutritional mode. Many species are facultative ectomycorrhizal, some are saprotrophic, and species like *B. merulioides* (1909) show a three-way interaction of fungi, plants, and insects like mealy bugs and arthropods (Brundrett and Kendrick 1987, Bougher 1994, Miller et al. 2000, Binder and Bresinsky 2002, Wilson et al. 2012).

2.3.4.3. Distribution

Boletinellus species have been reported from Brazil, USA, Canada, China, Mexico, Australia, Thailand and India (Nanu et al. 2023). Only two species of *Boletinellus*, *B. merulioides* and *B. viridianus* Salna Nanu and T.K.A. Kumar have been recorded so far from India (Mohanan 2011, Karun and Sridhar 2017, Kumar et al. 2019, Nanu et al. 2023).

2.3.5. ***Phlebopus*** (R. Heim) Singer

Synonymy:

Boletus subgen. *Phlebopus* R. Heim, Revue Mycol., Paris 1: 9 (1936)
Phaeogyroporus Singer, Mycologia 36(4): 360 (1944)

Boletinellaceae is a small family in Boletales, comprising of only two genera, *Phlebopus* and *Boletinellus* (Kirk et al. 2008). Heim (1936) proposed *Phlebopus* as a subgenus of *Boletus* to accommodate *Boletus colossus* R. Heim. Singer (1936) elevated *Phlebopus* to genus with *P. colossus* (R. Heim) Singer as the type species (Pham et al. 2012). *Phlebopus* is a tropical to subtropical genus with typically robust basidiomata stature producing an olivaceous brown spore print, non-hollow stipe, ellipsoidal, smooth basidiospores, and hyphae with clamp-connections (Singer 1986, Watling 2008, Baroni et al. 2015). *Phlebopus* was classified in the Boletinellaceae family by Binder and Bresinsky (2002).

Singer (1936) transferred *Boletus colossus* R. Heim to *Phlebopus colossus* (R. Heim.) Singer and elevated the subgenus status of *Phlebopus* in genus level. Subsequently, most of the species included in the genus *Phaeogyroporus* Singer were transferred to *Phlebopus* (Heinemann and Rammeloo 1982, Singer et al. 1983, Singer 1986, Pham et al. 2012). Heinemann and Rammeloo (1982) provided a global survey report of this genus and provided key for 12 species.

The closest relatives of *Phlebopus* were *Boletinellus* and *Gyroporus* based on morphological and chemical data (Bruns et al. 1998). So, these three genera were grouped in the family Gyrodontaceae (Binder and Bresinsky 2002). There was some ambiguity in the placement of *Phlebopus* in Gyrodontaceae (Singer 1986, Smith and Thiers 1971, Binder and Bresinsky 2002). Based on the molecular phylogenetic studies, Binder and Bresinsky (2002) suggested that *Phlebopus* should be excluded from Gyrodontaceae. Now, *Phlebopus* is placed in Boletinellaceae under suborder Sclerodermatineae (Binder and Hibbett 2006). According to Kirk et al. (2008), 12 species of *Phlebopus* were included in Boletinellaceae. *Index Fungorum* (accessed on 25 March 2024) records 17 species.

2.3.5.1. Taxonomic characters

Major taxonomic characters of this genus are medium- to large-sized pileus with light brown, reddish brown or dark brown with olivaceous or yellowish tinge, yellowish or cream context changes to blue or without color change, small to wide pores having yellowish pore surface with or without bluing on bruising, sturdy stipe, sub globose to ellipsoid basidiospores, and presence or absence of hymenial cystidia (Raghoonundon et al. 2021).

2.3.5.2. Ecological and economic importance

According to Singer (1986), *Phlebopus* can form facultative ectomycorrhizal association and sometimes non- ectomycorrhizal habit. The studies of Bougher (1994), Binder and Bresinsky (2002), and Miller et al. (2000) suggested that many species of this genus show ectomycorrhizal associations with different plant species. *Phlebopus beniensis,* is suspected to form ectomycorrhizal relationship with leguminous plants (Miller et al. 2000), and *P. marginatus* Watling and N.M. Greg. is found to have association with *Eucalyptus* species (Bougher, 1995). Binder and Bresinsky (2002) showed that the nutritional mode in the species of *Phlebopus* and *Boletinellus* was a transition between mutualistic and parasitic models based on molecular data. Some species show relationships with scale insects (Pham et al. 2012, Baroni et al. 2015).

Some of the *Phlebopus* species are edible. In Southeast Asia, *P. portentosus* and *P. marginatus* are regarded as conspecific (Watling and Gregory 1988, Watling and Li 1999). *Phlebopus portentosus* is considered as a highly priced edible bolete in Thailand, China and other parts of the world (Kumla et al. 2012, Zhang et al. 2017). This species is known as "Hei-ben-ma-lang" in Thailand and "black bolete" in China due to its dark brown fruit body (Zhang et al. 2017). *Phlebopus portentosus* are normally found near trees like *Dimocarpus longan* Lour., *Elaeocarpus hygrophilus* Kurz, *Mangifera indica* L., *Mimosa pigra* L., *Quercus* species, but ectomycorrhizal status is unknown (Kumla et al. 2012). Even though *Phlebopus* species were thought to be ectomycorrhizal, *P. portentosus* is an artificially cultivable boletus mushroom under controlled conditions (Jiang et al. 2017). This species may be saprotrophic, parasitic or a facultative ectomycorrhizal mushroom, and further studies are needed to confirm the nutritional mode (Kumla et al. 2012). Different types of pyrole alkaloids were identified from *P. portentosus* (Sun et al. 2018).

2.3.5.3. Distribution

The distribution of *Phlebopus* species is tropical or sub-tropical. *Phlebopus* species have been reported from Central and South America, Africa, Asia and Austarlia (Singer 1936, Heinemann and Rammeloo 1982, Li and Watling 1999, Pham et al. 2012). Six species have been reported from Brazil: *Phlebopus beniensis* (Singer and Digilio) Heinem. and Rammeloo, *P. brasiliensis* Singer, *P. braunii* (Bres.) Heinem., *P. harleyi* Heinem. and Rammeloo, *P. portentosus* and *P. tropicus* (Rick) Heinem. and Rammeloo (Singer et al. 1983, Putzke et al.1994, Watling and Meijer 1997). From Australia, a gigantic basidiomata, *P. marginatus* was reported (Watling and Gregory 1988). *Phlebopus spongiosus* was reported from Vietnam (Pham et al. 2012), *P. mexicanus* was reported from Mexico (Baroni et al. 2015).

2.4. **Gyroporaceae** Manfr. Binder and Bresinsky

Binder and Bresinsky (2002) studied Boletales with morphological and molecular phylogenetic data, and proposed Sclerodermatineae as a suborder. Gyroporaceae is a monotypic family in the suborder Sclerodermatineae (Binder and Hibbett 2002). The family is phylogenetically close to gasteromycete genera like *Scleroderma* and *Calostoma*. Gyroporaceae includes a single ectomycorrhizal genus, *Gyroporus,* which is distributed worldwide.

2.4.1. Taxonomic characters

Basidiomata stipitate-pileate. Pileus subtomentose to subsquamose, with yellowish, brownish or reddish colors. Stipe glabrous to fibrous, without reticulate ornamentation, partly with hollow chambers. Tubular hymenophore depressed around the stipe, whitish to straw yellow. Flesh white, unchanging or turning to blue. Spores smooth and elliptic, straw yellow, inamyloid. Spore print yellowish. Clamp-connections present (Binder and Hibbett 2002).

2.4.2. Ecological and economic importance

Species in *Gyroporus* show ectomycorrhizal associations with many plants in Fagaceae, Pinaceae and Myrtaceae (Xie et al. 2022*). Gyroporus castaneus* is a well-known edible species.

2.4.3. Distribution

Members of Gyroporaceae are widely distributed and have been reported from temperate, subtropical and tropical regions of the world (Zhang et al. 2022).

2.4.4. *Gyroporus* Quél.

Gyroporus is a widely distributed genus in Gyroporaceae (Zhang et al. 2022). The genus is typified by *G. cyanescens* (Bull.) Quél. *Gyroporus* is a monophyletic genus, however, infrageneric classification is extremely difficult due to the overlap of phenotypic variation among species (Xie et al. 2022). The genus was initially included in the family Gyrodontaceae Heinem. Binder and Hibbett (2002) transferred *Gyroporus* to Gyroporaceae based on phylogeny. The genus is closer to gasteromycete genera in molecular phylogeny. Zhang et al. (2022) divided *Gyroporus* in to four sections (*Castaneus*, *Cyanescens*, *Longicystidiatus* and *Pallidus*).

2.4.4.1. Taxonomic characters

Gyroporus is characterized by small to middle-sized basidiomata, whitish, yellowish, yellow-brown to red-brown villous or scaly pileus, white to light yellow pores, chambered or completely hollow and brittle stipe, white context unchanging or turning blue or purple when injured, short ellipsoid basidiospores, and the presence of clamp-connections (Zhang et al. 2022).

2.4.4.2. Ecological and economic importance

The species of *Gyroporus* show ectomycorrhizal association with many plant families such as Fagaceae, Pinaceae, and Myrtaceae (Xie et al. 2022).

2.4.4.3. Distribution

Gyroporus species were reported from every continent, except Antarctica (Singer et al. 1983, Halling and Mueller 2005, Vizzini et al. 2015, Das et al. 2017, Xie et al. 2022). Twenty-one species have been reported from China (Zhang et al. 2022). A single species, *G. paramjitii* K. Das, D. Chakraborty and Vizzini was reported from India (Das et al. 2017).

2.5. **Paxillaceae** Lotsy

Paxillaceae is one of the families in Boletales, which includes lamellate species (Alvarado et al. 2021, Gelardi 2021). Ten genera are included in this family according to He et al. (2019). *Paxillus* is the type genus and *Alpova*, *Austrogaster* Singer, *Gyrodon*, *Hoehnelogaster* Lohwag, *Hydnomerulius* Jarosch and Besl, *Meiorganum* R. Heim, *Melanogaster* Corda, *Neoalpova* Vizzini, *Paragyrodon* are the other genera included in this family (He et al. 2019, Gelardi 2021). The family consists of diverse fruiting bodies such as lamellate in *Paxillus*, tubular in *Gyrodon*, with a veil in *Paragyrodon,* and resupinate in *Hydnomerulius* (Nuhn et al. 2013).

Maire (1902) considered two genera, *Paxillus* and *Phylloporus* in Paxillaceae. Maire (1902) believed that Paxillaceae had a connection between lamellate and tubulose members of Agaricales (McNabb 1968). Singer (1942) was the first taxonomist who updated this family. Singer (1942) described *Phyllobolites* and included the genus in Paxillaceae. Later *Hygrophoropsis, Linderomyces* Singer and *Neopaxillus* Singer were added to this family (Singer 1947). Singer (1962) transferred *Phyllobolites* to Strobilomycetaceae. Paxillaceae was placed in the order Agaricales by Hongo (1960) to accommodate lamellate boletes in Japan (Gelardi 2021). McNabb (1968) followed Singer's concept (1946) of Paxillaceae with five genera, *Paxillus*, *Neopaxillus* and *Linderomyces* with brown spores, and *Hygrophoropsis* and *Cheimonophyllum* with white or faintly tinted spores. The placement of *Hygrophoropsis* and *Cheimonophyllum* was not accepted by many taxonomists (Corner 1966, Horak 1968, McNabb 1968). Singer (1964) and McNabb (1968) observed the close affinity of Paxillaceae with Boletaceae in their studies. Both of them considered these families in the order Agaricales (McNabb 1968, Gelardi 2021). Kühner (1977) recognized order Boletales with two families Boletaceae and Paxillaceae. Kühner (1977) considered Paxillaceae including two genera *Hygrophoropsis* and *Paxillus*. Pegler and Young (1981) and Moser (1983) also followed Kühner (1977). Singer (1986) incorporated Paxillaceae in the suborder Boletineae within the order Agaricales. Poroid genera *Gyrodon* and *Paragyrodon* were placed in this family based on similar microscopic features (Singer 1986). *Hydnomerulius* was transferred to Paxillaceae based on the similarities of secondary metabolites (Jarosch and Besl 2001, Alvarado et al. 2021). Binder and Hibbett (2006) and Binder et al. (2010) did not consider this inclusion and rejected it based on extended molecular data. Pegler and Young (1981) placed the gasteroid genus *Austrogaster* in this family due to the presence of hyphae with clamp-connections and elliptic to amygdaliform brownish basidiospores (Alvarado et al. 2021). *Hoehnelogaster* is the monotypic gasteroid genus in Paxillaceae, and its placement needs confirmation (Alvarado et al. 2021). *Melanogaster* was included in in Melanogasteraceae and transferred to Paxillaceae (Alvarado et al. 2021). The recent phylogenetic classification of Basidomycota by He et al. (2019) accepted ten genera in Paxillaceae.

Major phylogenetic studies of family Paxillaceae were done by Bresinsky et al. 1999, Binder and Hibbett 2006, Nuhn et al. 2013, and He et al.2019. *Paragyrodon* and *Gyrodon* were included in Paxillaceae was confirmed by molecular studies using nuc rDNA 28S data (Bresinsky et al. 1999, Alvarado et al. 2021). Jarosch (2001) transferred *Hydnomerulius* to Paxillaceae with 28S data. Later, phylogenteic studies of Binder and Hibbett (2006) rejected this transfer. Binder and Hibbett (2006) recognized Paxillineae as a suborder of Boletales, and they proposed to include Gyrodontaceae and Melanogastraceae in Paxillaceae. The molecular phylogenetic study of Nuhn et al. (2013) using a combined 28S, *RPB1*, and tef1 alpha dataset, rejected the suborder Paxillineae and restricted Paxillaceae under suborder Boletineae. Nuhn et al. (2013) excluded *Hydnomerulius* from Paxillaceae due to the lack of molecular support. Later, He et al (2019) did phylogenetic analyses with combined 28S, SSU, 5.8s, *RPB1*, *RPB*2, and ef1 alpha datasets and replaced *Hydnomerulius* again in Paxillaceae.

2.5.1. Taxonomic characters

The family comprises morphologically diverse taxa. The major taxonomic characters of Paxillaceae members are: basidiomata consists of lamellate (*Paxillus*) or tubular hymenophore (*Gyrodon, Paragyrodon*), and presence of clamp-connections on all hyphae (Nuhn et al. 2013). *Paragyrodon sphaerosporus* (Peck) Singer consists of basidiomata with an annulus.

2.5.2. Ecological and economic importance

The members of Paxillaceae are ectomycorrhizal (Sato and Toju 2019, Gelardi 2021). Sato and Toju (2019) revealed that ectomycorrhizal symbiosis independently evolved in Paxillaceae. *Paxillus* species showectomycorrhizal associations with numerous trees including conifers (Jargeat et al. 2013). *Paxillus rubicundulus* has association with *Alnus* species. Other tree hosts are coniferous and deciduous species like *Picea abies* (L.) H. Karst., *Populus* species, *Betula pendula* Roth, and *Pinus contorta* Douglas (Taylor et al. 2000). The genus *Alpova* includes species growing mostly under *Alnus* trees (Moreau et al. 2013).

2.5.3. Distribution

Paxillaceae members have been reported worldwide (McNabb 1969, Gelardi et al. 2014, Jargeat et al. 2016). *Paxillus involutus* was reported from India by Roy et al. 2022.

2.5.4. ***Paxillus*** Fr.

The genus *Paxillus* comprises of ectomycorrhizal lamellate fungi (Jargeat et al. 2014, Jargeat et al. 2016). *Paxillus involutus* is the type species and one of the important fungi in experimental research (Jargeat et al. 2014). The genus was established by Fries in 1821. Fries (1821) included fungi with decurrent lamellae, brown spores and easily separable soft hymenophore (Jargeat et al. 2016). *Paxillus* was placed in Agaricales for many years (Singer 1946, McNabb 1969, Singer 1986). But some taxonomists clearly indicated the relationship of this genus with Boletales (Watling 1970, Linzerkirchner and Besl 1993, Watling and Hills 2005, Agerer 2006). Phylogenetic studies also clarified the placement of *Paxillus* in the family Paxillaceae within the suborder Boletineae of order Boletales (Bresinsky et al. 1999, Binder and Hibbett 2006, Drehmel et al. 2008, Nuhn et al. 2013, He et al. 2019). Bresinsky et al. (1999) conducted a comprehensive phylogentic study of *Paxillus* with 28S data. They separated *Paxillus* s. l. to three independent genera, *Paxillus* s. str., *Tapinella* and *Austropaxillus,* based on morphological, anatomical, ecological, chemical and phylogenetic data. According to Kirk et al. (2008), *Paxillus* s. str. includes about 15 species.

Hedh et al. (2008) studied Europian species of *Paxillus* with phylogentic data. They recognized two clusters within the species, as *P. rubicundulus* P.D. Orton complex [= P. filamentosus (Scop.) Fr. ss. auct., *P. leptopus* Fr.] and *P. involutus* (Batsch) Fr. complex. *P. invlotus* complex of Hedh et al. (2008) includes *P. invlotus* I and *P. invlotus* II (Gelardi et al. 2013). *Paxillus orientalis* was reported as a new species from China by Gelardi et al. (2013) and they included it in *P. rubicundulus* s. l. Based on their phylogenetic study with ITS data, Gelardi et al. (2013) confirmed that there were two main species lineages in *Paxillus*, the subg. *Alnopaxillus* consisting of the *P. rubicundulus* complex and of *P. orientalis* and the subg. *Paxillus* comprising the species referred to the *P. involutus* complex. The members of subg. *Alnopaxillus* shows association with *Alnus* species and normally shows host specificity (Gelardi et al. 2013). However, the species in subg. *Paxillus* shows no host specificity and show association with Betulaceae, Corylaceae, Fagaceae, Pinaceae, Salicaceae, etc. (Hedh et al.2008, Gelardi et al. 2013). Gelardi et al. (2013) suggested that, there are three distinct species in the *P. rubicundulus* complex. Jargeat et al. (2014) studied the Europian species of *Paxillus* as a continuation of Gelardi et al. (2013). Jargeat et al. (2014) gave a key for European species and clarified the *P. involutus* complex. *P. involutus* complex comprised of *P. involutus, P. ammoniavirescens, P. obscurisporus* and *P. cuprinus*. Jargeat et al. (2016) reconstructed *P. rubicundulus* complex with morphological and phylogenetic analyses of ITS gene regions. Studies of Bon (1977) preferred to reject the names for any *Alnus a*ssociated *Paxillus* species. Finally, Jargeat et al. (2016) confirmed that the name *P. filamentosus* could not apply to any of the new species in the genus *Paxillus* based on their studies on type materials and molecular data. According to Kirk et al. (2019), the genus comprised of 38 valid species.

2.5.4.1. Taxonomic characters

The genus possesses medium- to large-sized basidiomata with colors ranging from ochraceous-yellow to chestnut brown or dark brown, a funnel-shaped pileus with typically involute margin at least in young specimens, deeply decurrent and easily detachable lamellae which are interveined towards the stipe, more or less intensely reddening/browning tissues on exposure or handling and rusty brown to reddish-brown spore print. Broadly ellipsoid, smooth, cyanophilic basidiospores, a trichodermal pileipellis consisting of filamentous hyphae, bilateral divergent hymenophoral trama and presence of clamp-connections (Moser 1983, Singer 1986, Watling 2008, Knudsen and Taylor 2012, Gelardi et al. 2013).

2.5.4.2. Ecological and economic importance

The members of the genus *Paxillus* are ectomycorrhizal with conifers (Jargeat et al. 2014). The species in *P. rubicundulus* complex shows host specificity and they are associated with alder trees (*Alnus* species, Betulaceae) (Orton 1969, Jargeat et al. 2014). The members in *P. involutus* complex are associated with plants such as *Betulaceae, Fagaceae, Pinaceae, Salicaceae, etc.* and showed least host specificity (Bresinsky et al. 1999, Hedh et al.2008). *Paxillus involutus* can produce antifungal compounds when grown in the presence of root exudates of *Pinus resinosa* Sol. ex Aiton (Duchesne et al. 1988). Mycorrhizal association between *P. involutus* and *Pinus sylvestris* L. detected that *P. involutus* can enhance more fructose production (Timonem et al. 1998).

Many species in *Paxillus* are poisonous and causes gastrointestinal problems (Bresinsky et al. 1990). Poisoning of *P. involutus* may lead to acute kidney failure (Schmidt et al. 1971).

2.5.4.3. Distribution

Paxillus members have been reported from a variety of habitats in Europe, North America and Asia (Bresinsky 1999, Gelardi et al. 2013, Jargeat et al. 2014, 2016). Most of the species were reported from Northern hemisphere (Jargeat et al. 2014). *Paxillus involutus* have been reported from different habitats of Northern Hemisphere, Europe, India, China, Japan, Iran, North America, and Turkey (Ammirati 1985, Gelardi et al. 2013). *Paxillus cuprinus* has been reported from France and Italy (Jargeat et al. 2014). *Paxillus rubicundulus* complex members were mainly reported from Europe and also from China

(Henrici and Kibby, 2014, Gelardi et al. 2013). The species related to *P*. *involutus* such as *P. ammoniavirescens* were reported from different localities of Europe, North America and Asia (Corner 1971, Heinemann and Rammeloo 1985, Gelardi et al. 2013).

2.6. Pisolithaceae Ulbr.

Pisolithaceae consist of gasteroid boletes like *Pisolithus.* Most members of Pisolithaceae are showing ectomycorrhizal associations with plants (Lebel et al. 2018). The family was extensively studied and redefined by Agerer (1999) and transferred this family in to the order Boletales. Agerer (1999) also concluded that Pisolithaceae more closely related to the Paxillaceae and included in Paxillineae by studying features of hyphae and clamp-connections. However, Binder and Bresinsky (2002) rejected the placement of Pisolithaceae under Paxillineae. Kirk et al. (2008) and He et al. (2019) merged Pisolithaceae in Sclerodermataceae. Phylogenetic analysis of Sato and Toju (2019) found that Pisolithaceae can be treated as an independent family under the suborder Sclerodermatineae of Boletales. Binder and Hibbett (2006), Wu et al. (2020), Gelardi (2021) are the other taxonomists who treated Pisolithaceae as a separate family.

2.6.1. Taxonomic characters

Major taxonomic characters of Pisolithaceae are the following: Basidiomata gasteroid, basidiomata epigeous or subhypogeous, globose or subglobose or turbinate, sessile, pseudostipitate or shortly stipitate. Peridium simple or complex, thin or thick, corky or membranaceous. Gleba divided regularly or irregularly by means of thin or thick sterile tramal plates, becoming peridioles. Columella absent, no hymenial layer, at maturity the tramal plates, remain divided into peridioles. Dehiscence either by an irregular apical pore or by fracture or by splitting at the apical portion. Capillitium absent. Peridium simple, thin and brittle. Spores not amyloid, subspherical to spherical, ornamented (Guzmán 1971, Lebel et al. 2018).

2.6.2. Ecological and economic importance

Members of the genus *Pisolithus* are ectomycorrhizal commonly with many plants such as *Pinus, Eucalyptus* L'Hér., and *Cistus* L. (Kasuya et al. 2010).

2.6.3. Distribution

Pisolithaceae members ae distributed worldwide (Marx 1977, Malloch and Kuja 1979, Chambers and Cairney 1999).

2.6.4. ***Pisolithus*** Alb. and Schwein.

Synonymy:
Durosaccum Lloyd, Mycol. Writ. 7(Letter 73): 1306 (1924)
Endacinus Raf., Précis Découv. Trav. Somiologiques Palermo: 51 (1814)
Eudacnus Raf. ex Merr. (1943)
Eudacnus Raf. (1815)
Lycoperdodes Haller ex Kuntze, Revis. gen. pl. (Leipzig) 2: 858 (1891)
Pisocarpium Link, Beschreib. Natur.-Samml. Univ. Rostock, (Diss.) 1: 33 (1808)
Pisomyces Fr., in Fries and Nordholm, Symb. gasteromyc. (Lund) 1: 4 (1817)
Polypera Pers., Traité champ. Comest. (Paris): 116 (1818)
Polysaccum F. Desp. and DC., in de Candolle, Mém. Agric. Soc. Agric. Dép. Seine 11: 8 (1807)

Pisolithus is a gasteromycete genus in the Sclerodermtaceae family under Sclerodermatinae suborder of Boletales (Binder and Hibbett 2006). *Pisolithus* species form ectomycorrhizal associations with angiosperms and gymnosperms (Marx 1977). The type species is *Pisolithus arhizus* (Scop.) Rauschert. They were reported from different types of habitats such as forests, plantations and highly disturbed sites (Garbaye et al. 1988, Grand 1976, Momoh and Gbadegesign 1980, Singla et al. 2004). *Pisolithus indicus* Natarajan & Senthil. is a new species reported from India (Reddy et al. 2005).

Petri (1909) included four taxa (*P. crassipes* (DC.) J. Schröt., *P. tuberosus* (P. Micheli ex Fr.) Mig., *P. arenarius* Alb. & Schwein) in *Pisolithus*. All these taxa were synonymised with *P. arhizus* (Gargano et al. 2018). Taxa within the

Pisolithus were regarded as conspecific and most of them were grouped as *Pisolithus tinctorius* (Pers.) Coker and Couch (Coker and Couch 1928, Chambers and Cairney 1999). Kope and Fortin (1990) proposed that the genus have many biological species based on basidiospore morphology and mating incompatibility tests. Farmer and Sylvia (1998) suggested that the genus represents a complex species based on the analysis of ITS sequences.

Molecular analyses clarified and delimited the taxa in *Pisolithus* more accurately (Taylor et al. 2000, Wu et al. 2000, Kanchanaprayudh et al. 2003, Moyersoen et al. 2003, Singla et al. 2004, Binder and Hibbett 2006). Many species were thought to be *Pisolithus tinctorius* (Reddy et al. 2005). Anderson et al. (2001) obtained ITS sequences of the taxa from different geographical regions. Biogeographical patterns and ectomycorrhizal host affiliations of *Pisolithus* were studied by Martin et al. (2002) and two major lineages were identified. *Pisolithus tinctorius* s. str., and *P. arhizus* were applied as basic lineages in their study and they found new genetic lineages. Binder and Bresinsky (2002) and Binder and Hibbett (2006) presented comprehensive molecular phylogeny of boletoid fungi and most of gasteroid fungi were included in suborder Sclerodermatinae. They found the close affinities of *Pisolithus* with *Scleroderma, Calostoma* and *Boletinellus.* Further studies also followed this concept and now *Pisolithus* is included in Sclerodermatinae (Matheny et al. 2007). Two new species from Australia were published by Lebel et al. (2018) and they resolved the confusion in the nomenclature of *P. tinctorius* reported in Australia. Now, *Index Fungorum* (30 January 2024) records 16 species of *Pisolithus.*

2.6.4.1. Taxonomic characters

Basidiocarp epigeous or subhypogeous, globose or subglobose or turbinate, sessile, pseudostipitate or shortly stipitate. Peridium simple or complex, corky or membranaceous. Gleba divided regularly or irregularly by means of thin or thick sterile tramal plates, columella absent, no hymenial layer, at maturity the tramal plates, are divided into peridioles. Dehiscence either by an irregular apical pore or by fracture or by splitting in the apical portion, sometimes stellate. Capillitium absent. Gleba divided into periodioles at maturity. Peridium simple, thin and brittle. Spores not amyloid, subspherical to spherical, ornamented (Guzmán 1970, Lebel et al. 2018).

2.6.4.2. Ecological and economic importance

Pisolithus members are vital components in nutrient recycling and forming ectomycorrhizal associations (Smith and Read 1987). *Pisolithus* species are ectomycorrhizal commonly with many plants such as *Pinus, Eucalyptus*, and *Cistus* (Kasuya et al. 2010). They can form ectomycorrhizal with members of Myrtaceae, Pinaceae, Fagaceae, Mimosaceae and Dipterocarpaceae (Pradhan et al. 2011). Ectomycorrhizal relationship of *Pisolithus* species can increase root branching in angiosperms and gymnosperms (Chambers and Cairney 1999). Different isolates of this genus are used as inoculants to enhance the tree growth in many plantations (Brundrett et al. 1996). Spores of *Pisolithus* used to inoculate seeds for plantations (Lebel et al. 2018). In some local communities *Pisolithus* species were used as coloring agents in leather tanning and cooked with eggs at the early stages of growth (Venturella and Saitta 2003).

2.6.4.3. Distribution

Pisolithus has been reported from a variety of habitats such as forest, urban and disturbed sites (Marx 1977, Malloch and Kuja 1979, Chambers and Cairney 1999). The genus is distributed in all continents except Antartica. The most of the reports were from Europe, South America, Africa and Asia (Garbaye et al. 1988, Singla et al. 2004, Reddy et al. 2005, Kasuya et al. 2010). *Pisolithus arhizus*, and *P. tinctorius* have been reported from *Eucalyptus* plantations in Africa, Australia, Europe, India, North and South America, and South East Asia

(Bougher and Syme 1998, Martín et al. 2013, Marx et al. 1977, Singla et al. 2004).

From India, *Pisolithus arhizus* was reported from Tamilnadu and West Bengal (Natarajan et al. 1988, Pradhan et al. 2011). *Pisolithus albus* distributed in many *Eucalyptus* plantations overall India (Singla et al. 2004). *Pisolithus indicus* is a new species described from India from (Reddy et al. 2005).

2.7. Sclerodermataceae Corda

The monophyletic Boletales is classdified in to six suborders, Boletinaeae, Paxillineae, Sclerodermatineae, Suillineae, Tapinellineae and Coniophorineae (Binder and Hibbett 2006). Four families were included in Sclerodermatineae (Boletinellaceae, Diplocystaceae, Gyroporacea and Sclerodermatceae). Sclerodermatceae includes species with a variety of fruiting bodies, including gelatinous fruit bodies with numerous peridial layers (*Calostoma* species), compact peridia enclosing gleba (*Scleroderma* apecies), and spores containing peridioles (*Pisolithus* species) (Binder and Hibbett 2006).

The initial classification of Sclerodermataceae was done by Fries (1829) by including *Scleroderma, Pisolithus, Melanogaster* and *Elaphomyces* in a group known as Sclerodermei. Fischer (1900) modified the concepts of Fries (1829) and established Sclerodermatceae family to include six genera (*Melanogaster, Corditubera* Henn*., Sclerangium* Lév*., Pompholyx* Corda, *Pisolithus* and *Scleroderma).* Coker and Couch (1928) excluded all genera except *Pisolithus* and *Scleroderma* from Strobilomycetaceae. Cunningham (1942), Bottomley (1948) and Demoulin (1968) followed the concept of Coker and Couch (1928) and considered only two genera (*Pisolithus* and *Scleroderma*) in Sclerodermataceae. *Pisolithus* was removed from Sclerodermataceae by Zeller (1948) and placed in separate family, Pisolithaceae. Guzmán (1969) added a new genus to the family, *Veligaster* Guzmán and he continued to study the taxonomy of this family. In 1971, Guzmán published a comprehensive work on Sclerodermataceae.

Guzmán (1971) included *Scleroderma, Pisolithus, Tremellogaster* E. Fisch. and *Veligaster* in the family based on morphological data. Guzmán (1971) also presented a key for the genera in Sclerodermataceae and a basic phylogeny.

The major phylogentic studies of Sclerodermatinae were included in the studies of Binder and Hibbett (2006). Currently, the Sclerodermatceae family has six genera, *Calostoma, Chlorogaster* Læssøe & Jalink*, Favillea* Fr.*, Horakiella* Castellano & Trappe*, Pisolithus* and *Scleroderma* (Binder and Hibbett 2006).

2.7.1. Taxonomic characters

Sclerodermataceae members have the following characteristics: Basidiomata gasteroid, epigeous or subhypogeous, globose or subglobose, sessile, pseudostipitate or stipitate. Peridium gelatinous, thin or thick, corky or membranaceous. Gleba divided regularly or irregularly, at maturity break down into powdery gleba or remain divided into peridioles. Dehiscence either by an irregular apical pore or by fracture or by splitting in the apical portion, sometimes stellate. Basidia vesiculose or pyriform, two-, four- or six-spored, and readily collapsing. Spores not amyloid, short-pedunculate when immature, subspherical to spherical, smooth to echinulate or reticulate, subhyaline to brownish or brown, commonly with a gelatinous sheath Guzmán (1971).

2.7.2. Ecological and economic importance

Pisolithus, Calostoma and *Scleroderma* are ectomycorrhizal with different plant species (Sanon et al. 2009, Wilson et al. 2012). *Caesalpiniaceae, Dipterocarpaceae, Fagaceae, Myrtaceae, Phyllanthaceae* Martynov, and *Pinaceae* are the major host plants of Sclerodermataceae members (Sims et al. 1997, Sanon et al. 2009).

2.7.3. Distribution

Sclerodermatceae species are distributed in tropical, subtropical and temperate regions (Wilson et al. 2012). From India, ten species have been reported in this family (Mohanan 2011, Pradhan et al. 2011, Kumar et al. 2019).

2.7.4. ***Scleroderma*** Pers.

Synonymy:
Actigea Raf., Précis Découv. Trav. Somiologiques Palermo: 52 (1814)
Actinodermium Nees, Syst. Pilze (Würzburg): 135 (1816) [1816-17]
Caloderma Petri, Malpighia 14: 136 (1900)
Goupilia Mérat, Nouv. Fl. Environs Paris, Edn 3 1: 91 (1834)
Lycoperdastrum P. Micheli, Nov. pl. gen. (Florentiae): 219, tab. 99 (1729)
Mycastrum Raf., Ann. Bot. (Desvaux) 1: 236 (1813)
Neosaccardia Mattir., Annali Fac. Med. vet. Torino 56: 32 (1921)
Nepotatus Lloyd, Mycol. Writ. 7(Letter 75): 1355 (1925)
Phlyctospora Corda, in Sturm, Deutschl. Fl., 3 Abt. (Pilze Deutschl.) [7](19-20): 51 (1841)
Pirogaster Henn., Hedwigia 40(Beibl.): (27) (1901)
Pompholyx Corda, in Sturm, Deutschl. Fl., 3 Abt. (Pilze Deutschl.) [7](19-20): 47 (1841)
Sclerangium Lév., Annls Sci. Nat., Bot., sér. 3 9: 130 (1848)
Stella Massee, J. Mycol. 5(4): 185 (1889)
Sterrebekia Link, Mag. Gesell. naturf. Freunde, Berlin 8: 44 (1816) [1815]
Veligaster Guzmán, Mycologia 61(6): 1117 (1970) [1969]

Scleroderma is an ectomycorrhizal genus distributed in temperate and tropical regions (Guzmán 1971, Kasuya et al. 2002). The genus was introduced by Persoon (1801) with 11 species. Type Species is *Scleroderma verrucosum* (Bull.) Pers*. Scleroderma* is the largest and best known gasteromycete genus in the Sclerodermtaceae family (Guzmán 1970, Cortez et al. 2011). *Scleroderma* species are thick skinned earth-balls having definite openings to eject their spores (Sims et al. 1995, Jeffries 1999).

Persoon (1801) recognized 11 species of *Scleroderma*. Among the 11 species, six species were transferred to other genera (Guzmán 1971). Now, *Scleroderma citrinum* and *S. verrucosum* represents the original descriptions of Persoon (1801). Šebek (1953) published a comprehensive work on Czechoslovakian *Scleroderma* species. Guzmán (1971) monographed Sclerodermataceae members and changed the concepts of Šebek (1953). Guzmán (1971) divide the genus in to three sub genera based on the basidiospore ornamentations. The species with spiny basidiospores were placed in *Aculeatispora,* species with subreticulate basidiospores placed in *Sclerangium* and those with distinctly reticulate basidiospores were placed in *Scleroderma.*

Binder and Bresinsky (2002) published the phylogenetic studies of gasteromycetes inferred from nuc-lsu and 28s gene sequences. Binder and Bresinsky (2002) encountered polyphyletic nature of the existed gasteromycete group and proposed a new suborder Sclerodermatinae. *Scleroderma* and related genera were placed in Sclerodermatinae. They retrieved ITS gene sequences of 43 *Scleroderma* basidiomatas collected from different geographical regions. In their study, *Scleroderma areolatum* Ehrenb., *S. Bovista* Fr., *S. cepa* Pers., *S. citrinum* Pers., *S. polyrhizum* (J.F. Gmel.) Pers., *S. sinnamariense* Mont., *S. verrucosum* (Bull.) Pers., *S. michiganense* (Guzmán) Guzmán and *S. septentrionale* Jeppson formed as a coherent group. Wilson et al. (2012) studied the diversity and evolution of ectomycorrhizal associations in Sclerodermatinae.

2.7.4.1. Taxonomic characters

The genus *Scleroderma* is characterized by the following features: Basidiomata leathery to very hard when dry, globose, subglobose, pyriform, sessile, pseudostipitate or with a well-developed stipe, with a large basal compact mass of mycelium. Exoperidium thin or thick, dry, smooth, cracked, scaly or cover by small or large squamules. Sometimes membranaceous veil-like or patches on the basidiomata or stipe or pseudostipe is present. Endoperidium thin, with a membrane covering the gleba. Both exoperidium and endoperidium frequently rufescent. Gleba leathery, compact, dusty, white, soon purple or dark greyish-brown or reddish-brown. Dehiscence by cracking the apical part of the basidiomata, or through an irregular apical pore. Capillitium absent. Basidiospores globose, thick-walled, yellowish-brown, echinulated, subreticulated or reticulated, with a visible apiculus. Basidia 4 - 6(-8) spored, pyriform, sometimes claviform, thin or thickwalled, hyaline, discharging early the basidiospores in an immature stage. Odor and taste in general strong like rubber (Guzmán et al. 2013).

2.7.4.2. Ecological and economic importance

Scleroderma species show ectomycorrhizal associations with Pinaceae, Betulaceae, Fagaceae, and Salicaceae (Binder and Hibbett 2006, Wilson et al. 2012). *Scleroderma* species are participating in nutrient recycling and decomposition in the forest ecosystems (Alexopoulose 1996, Binder and Hibbett 2006).

2.7.4.3. Distribution

Scleroderma species have worldwide distribution (Wilson et al. 2012). *Scleroderma sinnamariense* Mont. is a common species in Thailand, Malaysia, Indonesia and the Philippines. It is also known from Fiji, Central America, New Guinea, etc. (Guzmán 1970, Watling and Sims 2004). In India, *Scleroderma cepa* was reported from Southern states, Uttar Pradesh, Mharashtra, (Bottomley 1948, Lloyd 1904-1919, Thapa et al. 1967, Patil et al. 1978). *Scleroderma macrorhizon* was reported from West Bengal (Pradhan et al. 2011). *Scleroderma areolatum, S. bovista, S. citrinum, S. polyrrhizum, S. citrinum, S. verrucosum* were reported from Kerala state (Mohanan 2011, Florence 2004).

2.8. Serpulaceae Jarosch and Bresinsky

Serpulaceae is a recently formed monophyletic family consisting of saprotrophic brown rot taxa that mainly degrade the conifer substrates (Binder and Hibbett 2006, Skrede et al. 2011, Watkinson and Eastwood 2012). The family includes three genera, *Serpula, Austropaxillus* and *Gymnopaxillus* (Watkinson and Eastwood 2012). Molecular phylogenetic studies were confirmed the close relationship between these three genera and erected the family Serpulaceae (Binder and Hibbett 2006). Binder and Hibbett (2006) placed the family in boletales truly based on phylogentic studies. *Serpula lacrymans* is a popular species, which causes dry rot in woods (Watkinson and Eastwood 2012). According to *Index Fungorum* records (30 July 2024), 26 species are included in Serpulaceae family. *Serpula* have 13 species, *Austropaxillus* includes nine species and four species placed in *Gymnopaxillus.*

Austropaxillus and *Gymnopaxillus* E. Horak were placed in *Paxillus* earlier due to its morphological and ecological similarities with *Paxillus* species (Bresinsky et al. 1999). These two genera are ectomycorrhizal with roots of *Nothofagus* and *Eucalyptus* trees (Skrede et al. 2011). The transition between nutritional modes within Boletales inferred from phylogenetic studies revealed the relationship of Serpulaceae with boletoid fungi (Binder and Hibbett 2006). It is assumed that *Austropaxillus* and *Serpula* had splitted 34.9 mya and changed their nutritional modes (Watkinson and Eastwood 2012).

Skrede et al. (2011) studied the evolutionary history of Serpulaceae species and clarified the monophyletic nature of this family. Late Cretaceous origin of the Serpulaceae was again proved in their study. A single transition occurred from brown rot to ectomycorrhizal habit in Serpulaceae. Skrede et al. (2011) supported close relationship of ectomycorrhizal *Austropaxillus* and saprotrophic *Serpula. Gymnopaxillus* was found to be within the Australian *Austropaxillus* clade and the final conclusion was to construct a family, Serpulaceae with three genera. *Serpula dendrocalami* C.L. Zhao is a recently identified species in the family (Wang et al. 2019).

2.8.1. Taxonomic characters

Basidiomata resupinate to effuse-reflexed, or pileate basidiocarps mostly with merulioid to poroid hymenophore, a dimitic hyphal system with clamp-connections on generative hyphae, presence of skeletal hyphae in the context, clavate basidia, and ellipsoid to ovoid, smooth, thick-walled, brownish, not or weakly dextrinoid, cyanophilous basidiospores, and causing brown rot (Wang et al. 2019).

2.8.2. Ecological and economic importance

Serpulaceae members include ectomycorrhial (*Gymnopaxillus, Austropaxillus*) and saprobic (*Serpula*) genera (Watkinson and Eastwood 2012). Ectomycorrhizal associations were encountered with *Nothofagus* and *Eucalyptus* trees (Skrede et al. 2011). *Serpula lacrymans* is a brown rot fungus distributed more in Europe and Asia (Watkinson and Eastwood 2012). *Serpula incrassata* causes dry rot, predominantly found in North America (Watkinson and Eastwood 2012). *Serpula himantoides* also causes brown rot. But, *Serpula lacrymans* is more damaging than other brown rot fungi because of its affinity grow and survive with limited nutrients and moisture supply (Watkinson and Eastwood 2012).

2.8.3. Distribution

Austropaxillus and *Gymnopaxillus* species were reported only from temperate Southern Hemisphere (Skrede et al. 2011). *Serpula lacrymans* was reported from Europe and Asia (Watkinson and Eastwood 2012).

2.8.4. ***Serpula*** (Pers.) Gray

Synonymy:

Gyrophana Pat., Cat. Rais. Pl. Cellul. Tunisie (Paris): 53 (1897)
Gyrophora Pat., Hyménomyc. Eur. (Paris): 143 (1887)
Merulius sect. Serpula Pers., Syn. meth. fung. (Göttingen) 2: 496 (1801)
Plicaturella Murrill, N. Amer. Fl. (New York) 9(3): 172 (1910)
Xylomyzon Pers., Mycol. eur. (Erlanga) 2: 26 (1825)
Xylophagus Link, Mag. Gesell. naturf. Freunde, Berlin 3(1-2): 38 (1809)

Serpula is a small genus comprising of saprotrophic, brown rot causing taxa (Vizzini et al. 2019). *Serpula* was included in the family Serpulaceae of Boletales by molecular phylogenetic studies (Binder and Hibbett 2006, Skrede et al. 2011). *Serpula lacrymans* (Wulfen) J. Schröt is the type species and it is one of the most damaging brown rot (Skrede et al. 2011). *Serpula* species was intensly studied for its impact on the wood and buildings (Watkinson and

Eastwood 2012, Walach et al. 2015). *Index Fungorum* (www.indexfungorum.com, 01 January 2024) records 13 species of this genus.

Molecular phylogenetic treatments confirmed the close affinities of *Serpula* with Boletales (Binder and Hibbet 2006, Skrede et al. 2011, Watkinson and Eastwood 2012). Binder and Hibbett (2006) found that *Serpula* members clustered in to Serpulaceae family and grouped with *Coniophora marmorata* Desm. and *Tapinella atrotomentosa* (Batsch) Šutara. But the further studies proved the Coniophoraceae members are more distant from *Serpula* and they form a separate clade (Watkinson and Eastwood 2012). Zmitrovich and Spirin (2002) synonymized *Serpula* with *Leucogyrophana* based on morphological resemblences. Larsson (2007) studied phylogenetic analysis of corticoid fungi and rejected this synonymisation. *Serpula* species showed close relationships with *Austropaxillus* and *Gymnopaxillus* in phylogenetic studies and so placed in Serpulaceae (Watkinson and Eastwood 2012).

2.8.4.1. Taxonomic characters

Basidiomata resupinate to effuse-reflexed, or pileate, membranaceous, soft, easily detachable, hymenophore merulioid to poroid, orange to brownish or with olivaceous tints, margin rhizomorphic. Hyphal system dimitic, hyphae polymorphic, generative hyphae with clamps, skeletoid hyphae present in the context, true skeletal hyphae occur in the rhizomorphs. Cystidia absent, hyphoid cystidiols may be present. Basidia clavate, with 4-sterigmata and a basal clamp. Basidiospores ellipsoid to ovoid, smooth, thick-walled (double layered), brownish, not or weakly dextrinoid, cyanophilous (Bernicchia and Gorjón 2010, Wang et al. 2019).

2.8.4.2. Ecological and economic importance

Serpula genus is saprotrophic and possesses wood decaying capacity (Skrede et al. 2011). *Serpula lacrymans* was studied for its unique mechanism of wood decay and the species was found to have different wood decaying enzymes (Eastwood et al. 2011). *Serpula lacrymans* together with other dry rot fungi, *Serpula himantoides, S. similis,* causes huge economic damage in many countries around the world (Watkinson and Eastwood 2012).

2.8.4.3. Distribution

Distribution pattern of *Serpula lacrymans* is worldwide (Watkinson and Eastwood 2012). *Serpula lacrymans* is more common in indoor habitats of Europe and Asia (Watkinson and Eastwood 2012). *Serpula incrassata* is common in North American buildings than other species (Watkinson and Eastwood 2012). Another species, *Serpula similis,* were reported from Sri Lanka, India, Nepal, China, Tropical Asia and North America (Wang et al. 2019). *Serpula dendrocalami* is a recently identified species from China (Wang et al. 2019). *Serpula himantioides* is another common species in European countries and also reported from China (Wang et al. 2019).

2.9. Suillaceae Besl and Bresinsky

The family Suillaceae established by Besl and Bresinsky (1997) based on their chemotaxonomic studies. Suillaceae was proposed under the suborder Suillineae to include *Suillus, Boletinus* and *Gastrosuillus* Thiers*.* Besl and Bresinsky (1997) explained the close relationship of Suillaceae, Rhizopogonaceae and Gomphidiaceae. Kirk et al. (2008) and He et al. (2019) combined Truncocolumellaceae and Suillaceae in their studies. According to He et al. (2019), three genera (*Psiloboletinus*, *Suillus* and *Truncocolumella* Zeller) present in Suillaceae. However, Gelardi (2021) retained Suillaceae and Truncocolumellaceae separately by following Binder and Hibbett (2006) and Wu et al. (2020). According to Gelardi (2021), Suillaceae have *Suillus, Psiloboletinus* and *Rhopalogaster* J.R. Johnst., and he placed the family under *incertae sedis*. *Psiloboletinus* and *Rhopalogaster* are monotypic genera (Wu et al. 2020).

2.9.1. Taxonomic characters

Species of Suillaceae are characterized by fleshy pileus, glutinous or tomentose cap (in the presence or absence of a veil), and small, glandular dots on the stipe, elongate, smooth basidiospores, and presence of cystidia (Dahlberg and Finlay 1999).

2.9.2. Ecological and economic importance

Suillus consist of ectomycorrhizal and edible members (Min et al. 2014). *Suillus* species exhibit ectomycorrhizal association mostly with *Pinus* species (Nguyen et al. 2016). They also show high host specificity (Klofac 2013). *Suillus bellini*, *S. luteus* and *S. granulatus* are well-known edible boletes. *Psiloboletinus* is a monotypic genus with a single species, *P. lariceti*, which is associated with *Larix* species (Wu et al. 2020). *Suillus* species are used as a model system for studying ectomycorrhizal fungal diversity, ecosystem function, population genetics, and host-symbiont coevolution (Dahlberg and Finlay 1999).

2.9.3. Distribution

Most of the species in Suillaceae are distributed in northern hemisphere (Wu et al. 2000, Nguyen et al. 2016). Some species are repoted from Southern hemisphere also. A compherehensive work on North American *Suillus* taxa was published by Smith and Thiers (1964). In India, seven species have been described from northwestern Himalayan region (Verma and Reddy 2015).

2.9.4. ***Suillus*** Gray

The genus *Suillus* consist of 101 species which include ectomycorrhizal, as well as edible boletes (Min et al. 2014). Gray (1821) erected the genus with *S. luteus* as type species. But, then *Suillus* was considered as as subgenus of *Boletus* for a long time (Singer 1951). Singer (1951) again upgraded *Suillus* to genus level. Hawksworth et al. (1995) placed *Suillus* in Boletaceae. Based on chemosystematic studies, Besl and Bresinsky (1997) erected a separate family, Suillaceae, to accommodate *Suillus*. The important taxonomic treatments on this genus are those by Singer (1945), Smith and Thiers (1971), Both (1993), and Bessette et al. (2000)

One of the comprehensive studies on *Suillus* was by Smith and Thiers (1964) of North American taxa. Kretzer et al. (1996) inferred the association of some *Suillus* species with *Pinus* trees based on ITS sequence data analysis. Nguyen et al. (2016) published a comprehensive molecular phylogenetic assessment of global *Suillus* species with ITS sequence data.

2.9.4.1. Taxonomic characters

Basidiomata medium-sized to large-sized. Pileus dry, viscid or glutinous. Hymenophore poroid, pores small or large, sometimes radial. Stipe subcylindrical, equal or clavate, solid. Pileal context pale yellow to yellowish, slowly changing to orange, pink or blue or without any color change on bruising. Basidiospores subcylindric to ellipsoidal Smith and Thiers (1971).

2.9.4.2. Economic and ecological importance

Ectomycorrhizal species of *Suillus* are mostly associated with coniferous trees in northern temperate and boreal regions (Min et al. 2014). Most members are host specific and grow with *Pinus*, *Larix,* and *Pseudotsuga* Carrière (Kretzer et al. 1996, Smith and Thiers 1964, 1971). *Suillus* species are known to improve the growth of plants by enhancing water and nutrient uptake, resistance to drought, plant pathogens and salinity (Sanchez-Zabala et al. 2013). *Suillus granulatus* and *S. luteus* are edible species (Reis et al. 2014).

2.9.4.3. Distribution

Suillus species are mostly distributed in temperate, boreal, and Mediterranean regions (Verma and Reddy 2014). A very few of them were reported from tropical areas (Halling and Mueller 2002). Most species known from Southern hemisphere are associated with introduced pine species (McNabb 1968). Ding and Wen (2003) listed 36 *Suillus* species from China and most of them were associated with *Laryx* species. *Suillus indicus* B. Verma and M.S. Reddy, *S. triacicularis* B. Verma and M.S. Reddy, *S. himalayensis* B. Verma and M.S. Reddy, *S. marginielevatus S. Sarwar*, Khalid and Dentinger, *S. lariciphilus* K. Das, D. Chakr., K.P.D. Latha and Cotter, and *S. adhikarii* K. Das, D. Chakr. and Cotter have been described from Pakistan and the Himalayan regions of India and Nepal (Verma and Reddy 2015, Adamcˇík et al. 2015, Verma and Pandro 2018).

3. MATERIALS AND METHODS

3.1. STUDY AREA

3.1.1. Physiography of Kerala

Kerala is a biodiversity-rich state, which is located in the southwest part of peninsular India (Vinod 2017). It lies in between north latitudes 8°17’30” and 12°47’40” and east latitudes 74°51’57” and 77°24’47”. Kerala covers an area of 38,817 sq. km. The state is surrounded by Western Ghats on the east and Arabian Sea on the West (Kumar et al. 2019). The state is popularly known as the “Gateway of summer monsoon” in India (Krishnakumar et al. 2009). Geographically, Kerala has three different regions: the highlands (600–1800 m high), the midlands (300–600 m high) and the lowlands (6–300 m high). The highlands include dense forest areas and plantations including the parts that slope down from the Western Ghats in the eastern highlands. The central midlands are covered with hills and broad valleys. The western lowlands are popular for different types of water resources such as shallow lagoons, river deltas, backwaters and the shores of the Arabian Sea (Krishnakumar et al. 2009).

3.1.2. Vegetation of Kerala

Kerala possesses the most luxuriant vegetation in India due to its peculiar tropical climate. Kerala is covered by 11,125.59 km^2 of forest area. 28.88% of the total land area of the state belongs to forests (Aravindakshan and Manimohan 2015). Evergreen forests, deciduous forests, shola forests and grasslands are the major types of forest in Kerala (Champion and Seth 1968). Evergreen forests may group under wet evergreen and semi-evergreen climax forests, west coast tropical evergreen forests, southern hilltop tropical evergreen forests and semi-evergreen forests. Secondary dry deciduous forests, southern dry deciduous forests, secondary moist deciduous forests and dry deciduous forests are various types of deciduous forests. Mangroves, littoral forests, *Myristica* swamps, mixed deciduous forests and teak forests are also present in this small state. Tropical rain forest is the natural climax vegetation here (Nair 2011). Kerala harbors almost 25% of India's total plant species because of the diverse vegetation. Due to the peculiar edaphic, physiographic and climatic conditions, many endemic species are found in Kerala (Sasidharan 2012). Kerala possess a part of Western Ghats. This is one of the biodiversity hotspot regions of the world and it harbors many endemic flora and fauna (Aravindakshan and Manimohan 2015).

3.1.3. Climate of Kerala

Kerala experiences tropical, maritime and monsoonal climates (Farook et al. 2013, Aravindakshan and Manimohan 2015). Kerala gets annual rainfall of around 3000 mm and the average monthly temperature except in December and February is 24-39° C. The average monthly temperature December – February is 22-33° C (Adarsh et al. 2018). Occasionally, in some areas of the plains, the summertime maximum day temperature rises beyond 40°C, while in the highlands, the wintertime lowest nighttime temperature falls below 0°C. Kerala has its unique climatic condition because of two monsoon seasons (Thomas 1979). South-West monsoon from June to September and North-East monsoon from October to December are the monsoon seasons.

3.2. FIELD STUDY AND COLLECTION OF SPECIMENS

Field collections of specimens were done during the five-year period (2018-2023). Most of the bolete collections were obtained during the rainy season (Southwest monsoon season - June to September, Northeast monsoon season - October to December) and summer rain (March – May). For collecting materials, field trips were conducted to different types of vegetations in Kerala such as natural forests, sacred groves, private plantations and botanical gardens (Figure 1 and Figure 2).

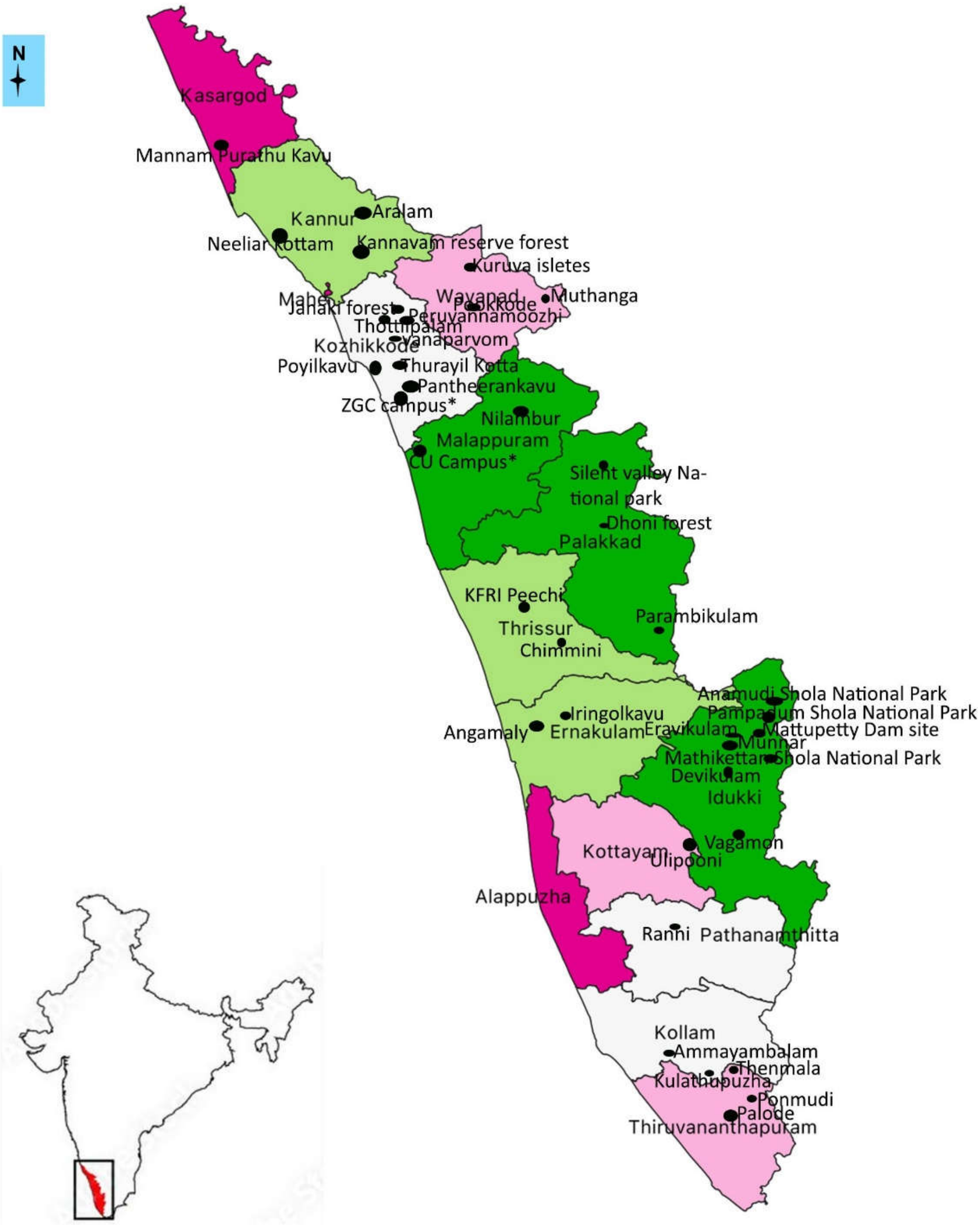
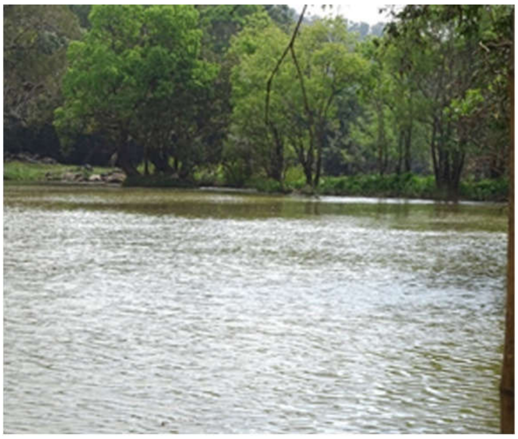


Figure 1. Map of Kerala State, India, showing major collection localities

Munnar

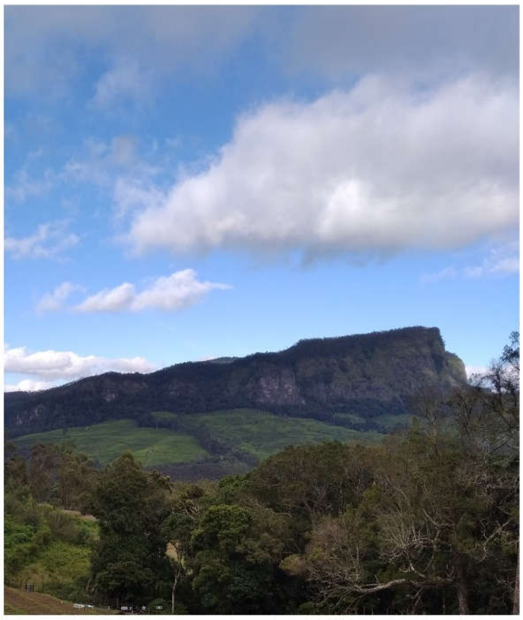


Kuruva isletes

Vagamon pine valley

Janaki forest

Thurayilkotta sacredgrove



Anamudi Shola National Park

Figure 2: Photographs of some major collection localities

3.3. MORPHOLOGICAL CHARACTERIZATION

3.3.1. Macroscopic analysis

The macroscopic characters of boletoid fungi were noted in the field as far as possible. Basidiomata of various stages were collected and recorded. The color photographs of all the collections were taken using a digital camera (SONY DSC-HX400V). The size and color of pileus, stipe, pores and tubes or lamellae were noted. Color changes of different parts of basidiomata before and after bruising were noted from the fruit bodies. Pileus and stipe surfaces were checked at the time of collection under a stereo microscope at the laboratory. Features of basal mycelium were also noted. Odor and taste of the collections were checked whenever possible. The mycorrhizal associations and nearby plants were recorded. Spore print of the specimens were taken whenever possible. After recording the macroscopic characters, most of the specimens were dried in hot-air oven for 4 – 12 hours at 50 – 70º C for preservation. Some specimens were dried under a hot bulb placed in a small box. This type of drying is useful for small specimens and can do it at basecamps.

3.3.2. Microscopic analysis

For observing the microscopic characters, thin, free-hand sections from tissues of the fruiting bodies were made with the aid of a razor blade and a stereo microscope. Pileus, tubes and stipe were sectioned. These sections were mounted in a drop of water to observe the color and the nature of pigments. Sections were also stained with one drop each of 1% aqueous solutions of phloxine and Congo red. Excess stain removed and sections were mounted in 5% KOH on a microscopic slide overlaid by a coverslip. The coverslip was gently tapped with the butt of a pencil to disperse the structures in a thin optical plane. Melzer's reagent (iodine 1.5 g, potassium iodide 5 g, chloral hydrate 100g and H_2O 100 ml) was used to study the amyloidity of the basidiospores and tissues.

From the sections of tubes or lamellae presence or absence of basidia, pleurocystidia and cheilocystidia were noted. The shape, dimensions and features of both the cystidia and the basidia were recorded. The arrangement of hyphae and their width was noted from the pileus trama and stipe trama.

Length and breadth of 20 randomly selected basidiospores from each specimen were measured to find out the range of size of the basidiospores. Spore Quotient (Q value) was calculated for 20 randomly selected basidiospores from each specimen. Spore Quotient is the ratio of the spore length to its width. The average of these values was calculated as the Qm. The arithmetic mean of both the length and breadth of the basidiospores was calculated using the formula $M_m = \sum M_0/n$, where M_0 is the individual observation and 'n' is the number of observations. The root mean square deviation was calculated using the formula,

$$S = \sqrt{\sum \frac{(M_n - M_0)^2}{n-1}}$$

Radial sections were made from the central, middle, and marginal regions of pileus and the type of pileipellis structure was noted including the squamules when present. The shape and size of pileocystidia were also noted if they were present. The structure of stipitipellis and the presence or absence of caulocystidia were noted from the stained longitudinal-tangential sections made from the upper, middle and basal regions of the stipe. All types of hyphae were examined for clamp-connections.

Binocular compound microscopes (Magnus MX21i-LED, LEICA DM 2000 LED) were used for the microscopic examination. Measurements were taken with the oil-immersion (100 X), 40X and 20X objectives of the same microscopes with the aid of a calibrated micrometer. A digital camera fixed to these compound microscopes were used to obtain the microphotographs.

3.3.3. Classification systems, taxonomic concepts and terminology followed

Macroscopic and microscopic descriptions, and microphotographs were prepared for all the studied taxa. Microscopic photographs were processed using the IS CAPTURE software. Based on macroscopic and microscopic observations, taxonomic description sheets were prepared for all taxa examined. The descriptions of multiple collections of each species were later compiled. Photographic plates were prepared using the Adobe Photoshop 2020 (Carlson 2019). Identification of the studied bolete collections was made down to the species-level using taxonomic keys, comparative studies with similar species described in the available literature and phylogenetic analyses. The classification system followed is that of Nuhn et al. (2013), Wu et al. (2016a), He et al. (2019), Wu et al. (2020), Magango et al. (2022) and Gelardi et al. (2023). Here, we treated Pisolithaceae and Truncocolumellaceae as independent families following by Wu et al. (2020) and Gelardi (2021). The terminologies for describing the morphological features of boletes like pileus, pores, tubes, stipe, basal mycelium, basidiospores, basidia, cystidia, and pellis were used in this study were those of Noordeloos et al. (1999) and Wu et al. (2016).

3.3.4. Preservation of herbarium materials

Specimens are well preserved at Zamorin's Guruvayurappan College Fungarium (ZGC) after macroscopic and microscopic studies. All specimens were packed in separate brown packets with proper labelling after drying. Label includes the details about species name, collection locality, date of collection, and name of the collector. The packets were arranged according to an accepted classification and are preserved in plastic covers after vacuumed.

3.3.5. Scanning electron microscopy

Basidiospores of some specimens were observed under a scanning electron microscope (SEM) for understanding the surface ornamentation. The procedure includes sample preparation, data collection, results and presentation. Dried fungal samples were used for taking SEM photographs. Hymenial part of fungal specimens were used for gold coating. The specimen was mounted on a metal stub using a sticky carbon disc which increases conductivity. Gold coating was applied in a controlled manner using a sputter coater. Gold coated stubs were used for observing through scanning electron microscope (Zeiss Gemini 1) at 15 Kv. Images were taken with the help of an inbuilt camera (Zeiss).

3.4 MOLECULAR ANALYSIS

Molecular phylogenetic analyses of the collections were performed during this study to confirm the species identification. Molecular analysis includes DNA isolation, PCR amplification, agarose gel electrophoresis, DNA sequencing, BLAST search and formation of phylogenetic tree.

3.4.1. DNA extraction, PCR amplification and DNA sequencing

DNA extraction was carried out under sterile conditions. To avoid contamination, all the equipment and the working table for the DNA isolation was surface sterilized before the extraction of DNA. The DNA extraction was carried out employing the protocol described by Izumitsu *et al.* (2012) for many samples. DNA extraction of other samples was done by using REDExtract-N-Amp kit by Sigma-Aldrich Company (India) according to the manufacturer's instructions. ITS1F and ITS4R were the two primers for the amplification of nrITS gene region (White et al. 1990). For nuclear large subunit (28 S) region, the primers LROR and LR7 were used (Vigalys and Hester 1990). 983F and 2212R were used for the translation elongation factor 1-alpha (TEF1 α), RPB1-B-F and

RPB1-B-R for *RPB2* gene region (Wendland and Kothe 1997, Magnago et al. 2022). The PCR amplification was carried out in a PCR thermal cycler (GeneAmp PCR System 9700, Applied Biosystems). Sequencing was done by Barcode BioSciences Private Limited, Bangalore, India, Rajiv Gandhi Centre for Biotechnology (RGCB), Thiruvananthapuram, India, and Enfys Lifesciences, Kochi, India. The newly generated sequences were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/).

3.4.2. BLAST Search

The retrieved and edited sequences were used for BLAST searches in the GenBank database (www.ncbi.nlm.nih.gov) to compare closely related taxa.

3.5 PHYLOGENETIC ANALYSIS

Phylogenetic analyses were carried out by using ITS, 28S, *RPB2* and *tef1α* gene sequences. Sequences generated in this study (Table 9), obtained from GenBank, and based on previously published studies (Wu et al. 2016a, Magnago et al. 2022) were used for the analysis. Sequences retrieved from GenBank included the sequences that showed more than 80% similarity in the BLAST search. Details of the sequences used in this study is given in Table 3, Table 4, Table 5, Table 6, Table 7 and Table 8. The sequence alignments were carried out by the MAFFT web tool (https://mafft.cbrc.jp/alignment/server/). The MAFFT aligned datasets were corrected manually by using MEGA X64 (Kumar et al. 2018). The fully aligned dataset was used for the Maximum Likelihood (ML) analysis using IQ-TREE (Nguyen et al. 2015) program and MEGAX64 program (Kumar et al. 2018). IQTREE program generated the phylogram using parameters like auto-detecting the substitution model, 1000 bootstrap in ultrafast approach (UFBoot) and SH-like approximate likelihood ratio test (SHaLRT) (Nguyen et al. 2015, Hoang et al. 2018, Kalyaanamoorthy et al. 2017). MEGAX64 program generated phylogenetic trees using parameters like

Tamura-Nei model and bootstrap method with 1000 bootstrap replications. The obtained phylogenetic trees were viewed with FigTree v1.4.4 (Rambaut 2018). Bootstrap values (BS) of ≥ 60% were displayed in the ML trees.

3.5.1. Phylogenetic analysis of Boletaceae

Phylogenetic analysis of the family Boletaceae has been done by using ITS, 28S and *rpb2* gene sequences. Gene sequences of 156 Bolete taxa (containing 19 taxa collected from Kerala) have been included to make data matrix. Sequences that were newly generated for this study, those from earlier studies (Magnago et al. 2022, Mao et al. 2023), and those that showed more than 80% similarity in a BLAST search were used to construct the data matrices. Concatenated dataset of ITS, 28S, and *RPB2* was prepared to assemble phylogenetic tree of Boletaceae family. Data matrix includes 243 gene sequences (ITS=19, 28S= 140, *RPB2*=84) including that of outgroups (Table 3). Species of *Suillus* (Suillaceae), *Gyrodon* (Paxillaceae) and *Gyroporus* (Gyroporaceae) were used as outgroups by following Mao et al. (2023). Phylogram was generated by using IQTree program (Nguyen et al. 2015, Hoang et al. 2017, Kalyaanamoorthy et al. 2017). The obtained phylogenetic trees were viewed with FigTree v1.4.4 (Rambaut 2018). Bootstrap values (BS) of ≥ 60% alone are displayed in the ML trees.

Table 3. Taxa, voucher ID and GenBank accession numbers of the DNA sequences used in the phylogenetic analysis of Boletaceae from ITS, 28S and *RPB2* dataset. Newly generated sequences are indicated in bold.

Taxon	**Voucher ID**	**GenBank accession numbers**		
		ITS	**28S**	***RPB2***
Afroboletus luteolus	00-436	-	KF030238	-
Alessioporus ichnusanus	AMB12756	-	KJ729504	-
Amoenoboletus granulopunctatus	HKAS56280	-	KF112418	KF112708
Anthracoporus nigropurpureus	**ZGCSN104**	**PP504488**	**PP504487**	-

Anthracoporus holophaeus	**ZGCSN224**	**-**	**PP504682**	-
Aureoboletus duplicatoporus	HKAS 50498		KF112361	KF112754
Aureoboletus gentilis	Pug1	-	DQ534635	-
Austroboletus fusisporus	HKAS 75207	-	JX889720	-
Austroboletus gracilis	112/96	-	DQ534624	-
Austroboletus olivaceoglutinosus	HKAS 57756		KF112383	KF112764
Austroboletus species	HKAS 59624	-	KF112485	KF112765
Australopilus palumanus	REH6791		JX889650	-
Baorangia albostipitata	**ZGCSN211 holotype**	**OR990613**	**PP499214**	
Baorangia albostipitata	**ZGCSN228**	**OR990614**	-	-
Baorangia bicolor	MB07-001	-	-	-
Boletus aereus	REH8721	-	KF030339	-
Boletus edulis	HMJAU4637	-	KF112455	KF112704
Boletus sp.	HKAS59660	-	KF112358	KF112664
Boletus sp.	HKAS63598	-	KF112317	KF112663
Boletus subalpinus	27882	-	KF030340	-
Boletellus aurocontextus	MRC10	PP582903	-	-
Boletellus aurocontextus	**ZGCSN174**	**-**	**ON707625**	
Boletellus chrysenteroides	3838	-	KF030312	-
Boletellus dissiliens	REH9435	-	JX889674	-
Boletellus indistinctus	HKAS 90215	-	KT990533	KT990369
Bothia fujianensis	HKAS82694	-	KM269193	-
Borofutus dhakanus	HKAS 73789	-	JQ928616	JQ928597
Bothia castanella	MB03-053	-	DQ867117	-
Buchwaldoboletus xylophilus	FHMU5933-1	MW783446	-	-
Buchwaldoboletus xylophilus	**ZGCSN110**	**ON707263**	-	-
Butyriboletus pseudoroseoflavus	HMJAU59470	-	OL587853	OL739126
Butyriboletus pseudoroseoflavus	HMJAU59471	-	OL587852	OL739125

Butyriboletus subregius	HMJAU60200	-	OM237339	OM285109
Butyriboletus subregius	HMJAU60201	-	OM237340	OM285110
Caloboletus yunnanensis	HKAS63040	-	KJ605676	KT990395
Caloboletus yunnanensis	HKAS69214	-	KJ184556	KT990396
Caloboletus calopus	HKAS74739	-	KF112335	KF112667
Chalciporus piperatus	MB04-001	-	DQ534648	-
Chalciporus rubrostipitatus	**ZGCSN153**	**OQ225690**	**OQ193026**	**OQ993343**
Chalciporus rubrostipitatus	**ZGCSN160**	**OQ231504**	-	-
Chalciporus species	HKAS 53400	-	KF112352	KF112821
Chalciporus species	HKAS 74779	-	KF112351	KF112820
Costatisporus cyanescens	Henkel 9061	-	-	LC053664
Crocinoboletus laetissimus	HKAS50232	-	KT990567	-
Crocinoboletus rufoaureus	HKAS59820	-	KF112434	KF112709
Crocinoboletus rufoaureus	HKAS53424	-	KF112435	KF112710
Cupreoboletus poikilochromus	GS 11008	-	KT157059	KT157067
Cupreoboletus poikilochromus	GS 10070	-	KT157060	KT157068
Cyanoboletus brunneoruber	HKAS 63504	-	KF112368	KF112702
Cyanoboletus brunneoruber	HKAS 80579	-	KT990568	KT990401
Cyanoboletus pulverulentus	MG 628a	-	KT157064	KT157069
Fistulinella olivaceoalba	HKAS 53367	-	KF112439	KF112790
Fistulinella prunicolor	REH9502	-	JX889648	-
Gymnogaster boletoides	REH9455	-	KT990572	KT990406
Gyrodon lividus	REG Gl1	-	AF098378	GU187786
Gyrodon species	HKAS 57588	-	KF112348	KF112817
Gyrodon species	HKAS 59448	-	KF112349	KF112818
Gyroporus castaneus	HKAS 76672	-	KF112478	KF112827
Gyroporus species	HKAS 52520	-	KF112475	KF112825

Gyroporus species	HKAS 63505	-	KF112476	KF112826
Harrya chromapes	HKAS 50527	-	KF112437	KF112792
Hemileccinum impolitum	Bim1	-	AF139715	-
Hemileccinum rugosum	HKAS 84355	-	KT990578	KT990413
Hemileccinum subglabripes	72206	-	KF030303	-
Heimioporus subretisporus	HKAS 52236	-	KF112346	KF112807
Heimioporus retisporus	HKAS 52237	-	KF112347	KF112806
Hiranmaya indica	**ZGCSN221**	**PP979450**	**PP977529**	-
Hiranmaya indica	**ZGCSN139**	**PP979451**	**PP977190**	-
Hourangia cheoi	HKAS52269	-	KF112385	KF112773
Hourangia nigropunctata	HKAS76657	-	KF112388	KF112774
Imleria badia	Xb2	-	KF030357	-
Kaziboletus rufescens	HKAS 74705	-	JQ928620	JQ928599
Kaziboletus rufescens	HKAS 74706	-	JQ928618	JQ928600
Lanmaoa angustispora	HKAS 74765	-	KF112322	KF112680
Lanmaoa asiatica	HKAS 54094	-	KF112353	KF112682
Lanmaoa flavorubra	NY775777	-	JQ924339	KF112681
Lanmaoa pseudosensibilis	DS615-07	-	KF030257	-
Lanmaoa rubriceps	N.K.Zeng2774	MG030476		
Lanmaoa rubriceps	N.K.Zeng2766	MG030472		
Lanmaoa species	HKAS52518	-	KF112354	KF112683
***Lanmaoa* species**	**ZGCSN211**	**PP979452**	**-**	-
Leccinum albellum	MB06-040	-	JQ327007	-
Leccinum quercinum	HKAS 63502	-	KF112444	KF112724
Leccinum monticola	HKAS 76669	-	KF112443	KF112723
Leccinum scabrum	Ls1	-	AF139705	-
Leccinellum aff. *crocipodium*	HKAS 76658	-	KF112447	KF112728
Leccinellum albellum	KUO-07241101	-	MK601746	MK766308
Leccinellum corsicum	Buf4507	-	KF030347	-
Leccinellum crocipodium	KUO-07050707	-	MK601749	MK766311
Leccinellum lepidum	K(M)-142974	-	MK601751	MK766312
Leccinellum pseudoscabrum	DPL-11432	-	MK601752	MK766313

Leccinellum species	HKAS 53427	-	KF112488	KF112727
Leccinellum species	HKAS 57592	-	KF112446	KF112726
Leccinellum viscosum	BOS-478	-	MK601755	-
Mucilopilus castaneiceps	HKAS 75045	-	KF112382	KF112735
Neoboletus ferrugineus	HKAS 77718	-	KT990596	KT990431
Neoboletus flavidus	HKAS 58724	-	KU974140	KU974145
Neoboletus hainanaensis	HKAS 63515	-	KT990614	KT990449
Octaviania japonimontana	KPM-NC-0017812	-	JN378486	-
Octaviania tasmanica	OSC132097	-	JN378494	-
Parvixerocomus matheranensis	**ZGCSN165**		**PP504561**	
Parvixerocomus matheranensis	**ZGCSN74**	-	**OQ650291**	
Parvixerocomus matheranensis	SV63	-	MH521245	
Phylloporus imbricatus	HKAS 68642	-	KF112398	KF112786
Phylloporus luxiensis	HKAS 75077	-	KF112490	KF112785
Phylloporus pelletieri	Pp1	-	AF456818	-
Porphyrellus porphyrosporus	HKAS 76671	-	KF112482	KF112718
Pseudoboletus parasiticus	Xpa1	-	AF050646	-
Pulchroboletus roseoalbidus	AMB12757	-	KJ729499	-
Pulveroboletus aff. *ravenelii*	HKAS 53351	-	KF112406	KF112712
Pulveroboletus species	HKAS 57665	-	KF112409	KF112715
Pulveroboletus species	HKAS 74933	-	KF112407	KF112713
Retiboletus griseus	202/97	-	AF456834	-
Retiboletus nigerrimus	HKAS 59699	-	JQ928627	JQ928603
***Retiboletus* species**	**ZGCSN126**	-	**PP504510**	
Rossbeevera bispora	GDGM 45612	-	MK036346	-
Rossbeevera cryptocyanea	KPM-NC-0017845	-	KC552030	MK350308
Rossbeevera eucyanea	TNSF36986	-	HQ693880	-
Rostrupomyces sisongkhramensis	**ZGCSN124**	-	**PP504509**	

Royoungia boletoides	REH8774	-	JX889660	-
Rubroboletus latisporus	HKAS63517	-	KP055022	KP055028
Rubroboletus latisporus	HKAS80358	-	KP055023	KP055029
***Rubroboletus* species**	**ZGCSN100**	**OQ504748**	**OQ472490**	**OQ689073**
Rugiboletus brunneiporus	HKAS83009	-	KM605133	KM605168
Rugiboletus brunneiporus	HKAS83209	-	KM605134	KM605168
Rugiboletus extremiorientalis	HKAS63635	-	KF112403	KF112720
Solioccasus polychromus	REH9417	-	JQ287642	-
Spongiforma thailandica	DED7873	-	EU685108	-
Strobilomyces giganteus	HKAS74967	MG832061	-	-
Strobilomyces giganteus	**ZGCSN205**	**PP510435**	-	-
Suillus aff. *granulatus*	HKAS 57622	-	KF112429	KF112726
Suillus aff. *luteus*	HKAS 57748	-	KF112430	KF112824
Sutorius eximius	REH9400	-	JQ327004	-
Sutorius eximius	HKAS52672	-	KF112399	KF112802
Turmalinea chrysocarpa	HKAS 70601	-	NG_059488	*KF112729*
Turmalinea mesomorpha	KPM-NC-0018016	-	KC552049	-
Turmalinea persicina	KPM-NC-0018001	-	KC552038	-
Tylopilus glutinosus	AGDC_21-14	OM903877		-
Tylopilus glutinosus	**ZGCSN149**	**PP504524**	**-**	**-**
Tylopilus purpureus	**ZGCSN145**	**OQ198445**	-	-
***Tylopilus* species**	**ZGCSN203**	-	**PP504625**	
Veloporphyrellus alpinus	HKAS 57490	-	KF112380	KF112733
Xanthoconium affine var. *maculosum*	BD217	-	HQ161854	-
Xanthoconium purpureum	BD228	-	HQ161864	-
Xanthoconium stramineum	3518	-	KF030353	-
Xerocomus magniporus	HKAS 58000	-	KF112392	KF112781
Xerocomus perplexus	MB00-005	-	JQ003702	-
Xerocomus	Xs1	-	AF139716	-

subtomentosus				
Veloboletus limbatus	BRI	-	MN393700	MT747397
Veloboletus limbatus	NY 1393645	-	MN393699	-
Villoboletus persicinus	BJTC FM1869	-	OP793898	OP792032
Villoboletus persicinus	BJTC FM1904	-	OP793899	OP792033
Villoboletus persicinus	BJTC FM1906	-	OP793900	OP792034
Zangia olivacea	HKAS 45445	-	HQ326945	-
Zangia olivaceobrunnea	HKAS 52275	-	HQ326947	-
Zangia roseola	HKAS 51137	-	HQ326949	-

3.5.2. Phylogenetic analysis of Boletinellaceae

Phylogenetic analysis of *Boletinellaceae* included the taxa from two genera present in the family (*Boletinellus* and *Phlebopus*). Molecular analysis (Maximum Likelihood) was done by using ITS and 28S gene regions. A total of 26 ITS sequences and 8 28S sequences were used (Table 4). Three newly generated 28S and two ITS sequences from Kerala collections were included in the dataset. *Suillus punctipes* (Peck) Singer was used as the outgroup by following Nanu and Kumar (2023). Phylogram was generated by using IQTree program (Nguyen et al. 2015, Hoang et al. 2017, Kalyaanamoorthy et al. 2017). The obtained phylogenetic tree was viewed with FigTree v1.4.4 (Rambaut 2018). Bootstrap values (BS) of ≥ 60% alone are displayed in the ML tree.

Table 4. Taxa, voucher ID, locations and GenBank accession numbers of the DNA sequences used in the phylogenetic analysis of Boletinellaceae from ITS and 28S dataset. Newly generated sequences are indicated in bold.

Taxon	**Voucher ID**	**Location**	**GenBank accession numbers**	
			ITS	nrLSU
Boletinellus exiguus	CHC 053	Brazil	MG996738	-
Boletinellus exiguus	MA-Fungi 47677	Brazil	AJ419185	-
Boletinellus	MA-Fungi 49401	Brazil	AJ419183	-

exiguus				
Boletinellus merulioides	BHI-F353a	USA	MF161227	-
Boletinellus merulioides	2630a	Canada	KM248952	-
Boletinellus merulioides	FLAS-F-61630	USA	MH212011	-
Boletinellus merulioides	FLAS-F-61785	USA	MH399882	-
Boletinellus merulioides	AFTOL-ID-575	USA	DQ200922	DQ534581
Boletinellus rhytidophyllus	KUN-HKAS113221	China	MZ470250	OL614952
Boletinellus rompelii	AH 01	Brazil	MG996741	-
Boletinellus rompelii	MAN 1064	Brazil	MG996740	-
Boletinellus rompelii	MA-Fungi 49405	Brazil	AJ419192	-
Boletinellus rompelii	MAN 1091	Brazil	MG996739	-
Boletinellus viridianus	**ZGCSN163**	**India**	**OP542551**	**OP526842**
Boletinellus viridianus	**ZGCSN186**	**India**	**OP901718**	-
Phlebopus beniensis	VO1891	Mexico	MT939284	-
Phlebopus beniensis	DS 1056	Brazil	MG996748	-
Phlebopus marginatus	REH8883	USA	EU718109	EU718145
Phlebopus mexicanus	S.Cappello-2009-233	Mexico	KM675999	KM676001
Phlebopus mexicanus	UJAT:S.Cappello2507	Mexico	KM676000	-
Phlebopus portentosus	REH8795	USA	EU718111	-
Phlebopus portentosus	CY_336	China	KJ439035	-
Phlebopus portentosus	**ZGCSN15**	**India**	**-**	**PP504687**

Phlebopus portentosus	**ZGCSN63**	**India**	**-**	**PP504702**
Phlebopus roseus	MY2017275	China	MK734171	MK734302
Phlebopus roseus	MY2017277	China	MK734172	-
Phlebopus spongiosus	CMUB39826	Thailand	KX575661	-
Suillus punctipes	SYKOf2669	USA	MF773628	-

3.5.3. Phylogenetic analysis of *Gyroporus*

The genus *Gyroporus* is placed in the family Gyroporaceae. The single collection obtained was studied phylogenetically by generating two ITS and one 28S gene sequences. 26 ITS sequences and 31 28S sequences (Table 5) were used to form data matrix. Phylogenetic inferences made using Maximum likelihood method. Phylogram was generated by using IQTree program (Nguyen et al. 2015, Hoang et al. 2017, Kalyaanamoorthy et al. 2017). The obtained phylogenetic tree was viewed with FigTree v1.4.4 (Rambaut 2018). *Phlebopus portentosus* was used as the outgroup taxon by following Xie et al. (2022). Bootstrap values (BS) of ≥ 60% alone are displayed in the ML tree.

Table 5. Taxa, voucher ID, locations and GenBank accession numbers of the DNA sequences used in the phylogenetic analysis of *Gyroporus* from ITS and 28S dataset. Newly generated sequences are indicated in bold.

Taxon	**Voucher ID**	**Location**	**GenBank accession number**	
			ITS	28S
Gyroporus castanaeus	Gc1	Germany	AF336252	-
Gyroporus aff. *cyanescens*	OKM23719	-	EU718104	EU718140
Gyroporus aff. *cyanescens*	REH8819	-	-	EU718172
Gyroporus aff. *cyanescens*	E486	-	-	EU718173
Gyroporus pseudolacteus	AH 39364	Spain	-	KX869880
Gyroporus flavocyanescens	WXL1182	China	MW440550	MW442950
Gyroporus	GDGM75894	China	ON502909	ON502932

atrocyanescens				
Gyroporus atrocyanescens	GDGM85841	China	-	ON502934
Gyroporus subcaerulescens	GDGM60494-1	China	ON502924	ON502947
Gyroporus alpinus	Li1478b	China	MW149435	MW151269
Gyroporus alpinus	Li1478a	China	MW149438	MW151268
Gyroporus brunneofloccosus	Wu2644a	China	MW149436	MW151267
Gyroporus brunneofloccosus	GDGM74550	China	ON502904	ON502927
Gyroporus brunneofloccosus	GDGM74638	Guangdong, southern China	MW149437	MW151266
Gyroporus longicystidiayus	N.K.Zeng1390 (FHMU937)	*China*	-	MW352972
Gyroporus longicystidiatus	FHMU900	China	MW380852	MW352975
Gyroporus pseudolongicystidiatus	GDGM42787	China	ON502916	ON502940
Gyroporus pseudolongicystidiatus	GDGM42986	China	-	ON505946
Gyroporus memnonius	FHMU929	China	MW380856	MW352979
Gyroporus memnonius	FHMU3369	China	MW380858	MW352981
Gyroporus memnonius	FHMU929	China	MW380856	MW352979
Gyroporus memnonius	GDGM44779	China	ON502914	ON502938
Gyroporus memnonius	FHMU3369	China	MW380858	MW352981
Gyroporus memnonius	FHMU929	China	MW380856	MW352979
Gyroporus cf. *castaneus*	FHMU3368	China	MW38086	MW352984
Gyroporus pallidus	GDGM46275	China	ON502918	ON502942
Gyroporus alboluteus	GDGM25474-1	China	-	ON502925
Gyroporus castanaeus	239-97	USA	-	AF336253
Gyroporus porphyreus	FHMU917	China	MW380854	MW352977
Gyroporus porphyreus	FHMU926	China	MW380855	MW352978
Gyroporus purpurinus	Chpn776	USA	KX389110	-
Gyroporus purpurinus	PRL3737	-	EU718105	EU718141
Gyroporus castaneus	239-97	USA	EU718100	-
Gyroporus aff. *castaneus*	CM061	Algeria	KP826761	-
Gyroporus castanea	G_cast_1-1-2R	USA	JX030211	-
Gyroporus cf. castaneus	Y.G. Fan3814 (FHMU3368)	China	MW380861	MW352984
Gyroporus aff. *subalbellus*	HONDURAS19-F036a	Honduras	MT57152	-
Gyroporus cyanescens	FLAS-F-61545	USA	MH211963	-

Gyroporus cyanescens	FLAS-F-61592	USA	MH211984	-
Gyroporus cyanescens	2837	-	KM248948	-
Gyroporus paramjitii	CAL KD 162–002	India	MF120284	MF120285
Gyroporus paramjitii	GDGM52188	China	ON502917	ON502941
Gyroporus paramjitii	FHMU2243	China	MW380847	MW352968
Gyroporus paramjitii	FHMU2240	China	MW380846	MW352967
Gyroporus ammophilus	AH:45842	Spain	KX869876	KX869890
Gyroporus ammophilus	AH:45814	Spain	-	KX869892
Gyroporus ammophilus	AH:45843	Spain	-	KX869891
Gyroporus porphyreus	FHMU905	China	MW380853	MW352976
Gyroporus porphyreus	FHMU917	China	MW380854	MW352977
Gyroporus austrobrasiliensis	ICN 184399	Brazil	MF436999	MF437014
Gyroporus austrobrasiliensis	ICN 184400	Brazil	MF437000	MF437015
Gyroporus aff. *cyanescens*	E486	-	-	EU718173
Gyroporus subglobosus	FHMU3364	China	-	MW352985
***Gyroporus* species**	**ZGCSN225**	**India**	**PP486355**	**PP474257**
***Gyroporus* species**	**ZGCSN230**	**India**	**PP510438**	**-**
Gyroporus subglobosus	FHMU859	China	MW380851	MW352974
Phlebopus portentosus	REH8795	Thailand	-	FJ153623

3.5.4. Phylogenetic analysis of Paxillaceae

Dataset for the phylogenetic analysis of *Paxillaceae* included taxa of four genera, *Paxillus*, *Alpova*, *Paragyrodon, Gyrodon* and *Melanogaster.* 28S gene region including the newly generated one were used for constructing the dataset and it included 29 sequences (Table 6) in total. *Boletus subviolaceofuscus* B. Feng, Y.Y. Cui, J.P. Xu and Zhu L. Yang was used as the outgroup taxon. Phylogram was generated by using MEGAX64 program (Kumar et al. 2018). Bootstrap values (BS) of ≥ 60% alone are displayed in the ML trees.

Table 6. Taxa, voucher ID, locations and GenBank accession numbers of the DNA sequences used in the phylogenetic analysis of Paxillaceae from 28S dataset. Sequence in bold was generated in this study.

Taxon	**Voucher ID**	**Location**	**GenBank accession number 28S**
Alpova australis	CORD LSD 2291	USA	AY377575
Alpova olivaceotinctus	-	-	AF352036

Boletus subviolaceofuscus	HKAS 83149	China	NG_058676
Gyrodon species	HKAS 59448	China	AY177257
Gyrodon lividus	420526MF0500	China	MH141335
Melanogaster ambiguus	Ma2	-	AF352046
Melanogaster ambiguus	JC180719NR	Spain	MN594299
Paragyrodon sphaerosporus	MB06-066	USA	GU187593
Paragyrodon sphaerosporus	TDB-420	USA	AF071531
Paxillus ammoniavirescens	Pou09.2	-	OM337575
Paxillus ammoniavirescens	JAC10247	New Zealand	OP141505
Paxillus ammoniavirescens	JAC12332	New Zealand	OP141517
Paxillus cuprinus	JAC8820	New Zealand	OP141494
Paxillus cuprinus	PDD 103789	New Zealand	OP141598
Paxillus cuprinus	JAC15966	New Zealand	OP141567
Paxillus filamentosus	PfM	-	AF167681
Paxillus involutus	Pi1	-	AF098385
Paxillus involutus	Pi1	-	AF098385
Paxillus involutus	PiM2	-	AF167686
Paxillus involutus	RV98.135	-	AY612815
Paxillus involutus	420526MF0799	China	MG696609
Paxillus involutus	Pi3	-	AF167682
Paxillus involutus	Pi2	-	AF167683
Paxillus involutus	Pi5	-	AF167684
Paxillus obscurosporus	-	-	AY177256
Paxillus rubicundulus	Ve08.2h10	-	OM238150
***Paxillus* species**	**ZGCSN82**	**India**	**PP510439**
Paxillus vernalis	AFTOL-ID 715	-	AY645059
Paxillus vernalis	AFTOL-ID 715	-	AY662662
Paxillus vernalis	Pv2	-	AF167685

3.5.5. Phylogenetic analysis of Sclerodermataceae and Pisolithaceae

A single phylogenetic analysis was done using taxa from two families, Sclerodermataceae and Pisolithaceae. Dataset was constructed by using 63 ITS sequences (Table 7). These comprise 56 species of *Scleroderma*, 6 species of *Pisolithus*, and an outgroup taxon *Calostoma*. Phylogram was generated by using IQTree program (Nguyen et al. 2015, Hoang et al. 2017, Kalyaanamoorthy et al. 2017). The obtained phylogenetic tree was viewed with FigTree v1.4.4 (Rambaut 2018). Bootstrap values (BS) of ≥ 60% alone are displayed in the ML trees.

Table 7. Taxa, voucher ID, and accession numbers of the DNA sequences used in the phylogenetic analysis of Sclerodermataceae and Pisolithaceae from ITS dataset. Sequence in bold was generated in this study.

Taxon	Voucher ID	Genbank accession number ITS
Calostoma sp.	MDO-2018b	MF521440
Pisolithus arhizus	Watling139161	FR748132
Pisolithus arhizus	BCN:MPM2676	FM213365
Pisolithus orientalis	BBH 28597	NR_119745
Pisolithus orientalis	BBH:28598	FR748149
Pisolithus tinctorius	05MCF5506	LK024184
Pisolithus tinctorius	-	FR748139
Scleroderma anomalosporum	INPA:271001	KX792084
Scleroderma areolatum	ARESCL2	FM213352
Scleroderma areolatum	K(M)54413	EU784416
Scleroderma areolatum	ARESCL3	FM213353
Scleroderma areolatum	RT00036	EU819518
Scleroderma areolatum	02MCF4202_E10/42-02	HF933231
Scleroderma cf. *areolatum*	FH:BHI-F107	KM875555
Scleroderma bermudense	BZ3961	EU718118
Scleroderma bovista	-	AB099901
Scleroderma bovista	K(M)105588	EU784409
Scleroderma bovista	K80S09	GQ267487

Scleroderma bovista	Li 160723-42	MH513628*
Scleroderma camassuense	INPA:271114	KX792085
Scleroderma capeverdeanum	MA:Fungi:87406	KU747110
Scleroderma cepa	UNSCL7	FM213343
Scleroderma cepa	SOC541	DQ453694
Scleroderma cepa	CEPSCL5	FM213355
Scleroderma citrinum	K(M)17485	EU784413
Scleroderma citrinum	CITSCL1	FM213344
Scleroderma dictyosporum	IR215	FJ840443
Scleroderma dictyosporum	SD-4901	FJ840449
Scleroderma duckei	INPA:272127	KX792086
Scleroderma duckei	UFRN:Fungos 2795	KX792087
Scleroderma dunense	UFRN:Fungi 1361	KU747114
Scleroderma dunense	UFRN:Fungi 2551	KU747116
Scleroderma macalpinei	OSC24605	EU718122
Scleroderma meridionale	05MCF5505_1_E10/44-04_1	HF933238
Scleroderma meridionale	CCMA-21	AY935514
Scleroderma michiganense	MICSCL1	FM213346
Scleroderma michiganense	MICSCL3	FM213348
Scleroderma nastii	JKR-2014	KJ740390
Scleroderma nitidum	UFRN:Fungos 1759	KU759907
Scleroderma nitidum	UFRN:Fungos 2034	KU759904
Scleroderma nitidum	UFRN:Fungos 2500	KU759909
Scleroderma patagonicum	Trappe 26232 (CORD)	HQ688789
Scleroderma patagonicum	Trappe 26236 (CORD)	HQ688788
Scleroderma polyrhizum	POLSCL1	FM213349
Scleroderma polyrhizum	POLSCL2	FM213350
Scleroderma septentrionale	UNSCL5	FM213342
Scleroderma septentrionale	SEPSCL1	FM213337
Scleroderma sinnamariense	SINSCL2 (SCLP3)	FM213357
Scleroderma sinnamariense	SINSCL6 (SCLD1)	FM213361
Scleroderma sinnamariense	**ZGCSN101**	**PP364562**
Scleroderma sinnamariense	Li 150728-29	MH513635
Scleroderma suthepense	CMU55-SC2	JX205215
Scleroderma suthepense	Li 180508-08	MH513625
Scleroderma venenatum	A27	JX434679

Scleroderma venenatum	EMF38	JF273540
Scleroderma venenatum var. *macrosporum*	Li 150829-04 Holotype!	MH513634
Scleroderma venenatum var. *macrosporum*	MLMY20160808-009 Paratype	MH513632
Scleroderma venenatum var. *macrosporum*	MLMY20160808-016 Paratype	MH513630
Scleroderma verrucosum	CEPSCL2	FM213354
Scleroderma verrucosum	89MCF4709_E10/43-10	HF933237
Scleroderma verrucosum	08MCF10124_E10/42-08	HF933233
Scleroderma yunnanense	Ji001A	JQ639040
Scleroderma yunnanense	Ji002B	JQ639045

3.5.6. Phylogenetic analysis of Suillaceae

Phylogenetic analysis of the family Suillaceae has been done by using ITS gene sequences. Only one collection of *Suillus* obtained during the collection period and analyzed the specimen morphologically and phylogenetically. Phylogenetic analysis included taxa of all major genera in Suillaceae (*Suillus*, *Psiloboletinus,* and *Truncocolumella*). 24 ITS sequences of these genera including the newly generated ITS sequence of Kerala collections used for constructing phylogenetic tree. Sequences used in this study are given in Table 8. *Boletus bainiugan* Dentinger was used as the outgroup taxon. Phylogram was generated by using IQTree program (Nguyen et al. 2015, Hoang et al. 2017, Kalyaanamoorthy et al. 2017). The obtained phylogenetic trees were viewed with FigTree v1.4.4 (Rambaut 2018). Bootstrap values (BS) of ≥ 60% alone are displayed in the ML trees.

Table 8. Taxa, vouchers ID, locations and GenBank accession numbers of the DNA sequences used in the phylogenetic analysis of Suillaceae from ITS dataset. Sequence in bold was generated in this study.

Taxon	Voucher ID	Location	GenBank accession number ITS
Boletus bainiugan	K 189052	China	NR137845
Psiloboletinus lariceti	NSK 1005345	Russia	MK940821
Psiloboletinus lariceti	LE 325744	Mongolia	MK940820
Suillus americanus	RZ07291202	China	KU663189
Suillus americanus	2077-QFB-25893	-	KM248957
Suillus decipiens	BKr1029002	Belize	KU721495
Suillus flavidus	Chu36	China	DQ407264
Suillus granulatus	KA17-0554	South Korea	MN294845
Suillus granulatus	JBRI-M22-086	-	OP928180
Suillus granulatus	SFC20120922-10	-	KJ415099
Suillus granulatus	**ZGCSN217**	**India**	**PP510437**
Suillus grevillei	-	-	OM865366
Suillus grevillei	2712	-	KM248955
Suillus huapi	FHMU838	China	MH208358
Suillus indicus	PUN 6590	India	KJ675501
Suillus indicus	PUN 6576	India	KJ675502
Suillus intermedius	TENN066904	USA	KU721166
Suillus kwangtungensis	HKAS71979	China	KU721539
Suillus kwangtungensis	HKAS90666	China	KU721540
Suillus phylopictus	RZ07281202	China	KU721529
Suillus phylopictus	RZ08111203	China	KU721530
Suillus flavidus	Chu36	China	DQ407264
Suillus flavidus	YSU-F-3981	Russia	OP866186
Truncocolumella sp.	OSC 67369	USA	KT968570
Truncocolumella citrina	JLF2149	USA	MH217566

4. RESULTS AND DISCUSSION

Boletoid fungi were collected from Kerala during the period 2018-2023. A total of 185 boletoid specimens were collected during the five-year period. Forty bolete species belonging to 29 genera of eight families (Boletaceae, Boletinellaceae, Gyroporaceae, Paxillaceae, Pisolithaceae, Serpulaceae, Sclerodermataceae, Suillaceae) were recorded and identified. The most represented family is Boletaceae and the genus is *Scleroderma* with five species. Boletaceae comprises of twenty-eight species under twenty-one genera. *Tylopilus* is the second most represented genus with four species.

Among the 40 species described, five species have been formally proposed as new to science. They are *Baorangia albostipitata* Salna Nanu and T. K. A. Kumar, *Boletinellus viridianus* Salna Nanu and T. K. A. Kumar, *Chalciporus rubrostipitatus* Salna Nanu and T. K. A. Kumar, *Neotropicomus indicus* Salna Nanu and T. K. A. Kumar, and *Tylopilus purpureus* Salna Nanu and T. K. A. Kumar. Some collections were found belonging to an undescribed genus in the family Boletaceae, based on morphological and multigene molecular phylogenetic analyses. Eight species, *Aureoboletus* species, *Indoporus* species, *Lanmaoa* species, *Retiboletus* species, *Rubroboletus* species, *Tylopilus* species, *Gyroporus* species and *Paxillus* species are hitherto undescribed.

The following nine taxa are new records to India:

Anthracoporus holophaeus, *Anthracoporus nigropurpureus*, *Boletellus aurocontextus* Hirot. Sato, *Buchwaldoboletus pseudolignicola* (Neda) Both & B. Ortiz, *Buchwaldoboletus xylophilus*, *Erythrophylloporus suthepensis*, *Leccinum intusrubens* (Corner) Høil., *Rostrupomyces sisongkhramensis*, and *Tylopilus griseipurpureus* (Corner) E. Horak.

The following eighteen taxa are new records to Kerala:

Anthracoporus holophaeus, *Anthracoporus nigropurpureus*, *Austroboletus fusisporus* (Kawam. ex Imazeki & Hongo) Wolfe, *Boletellus aurocontextus*, *Boletellus emodensis* (Berk.) Singer, *Buchwaldoboletus pseudolignicola*, *Buchwaldoboletus xylophilus*, *Erythrophylloporus suthepensis*, *Leccinum intusrubens*, *Parvixerocomus matheranensis*, *Rostrupomyces sisongkhramensis*, *Strobilomyces giganteus* M. Zang, *Tylopilus glutinosus* Iqbal Hosen, *Tylopilus griseipurpureus*, *Xerocomellus corneri* Xue T. Zhu & Zhu L. Yang, *Scleroderma sinnamariense*, *Scleroderma nitidum* Berk., and *Suillus granulatus.*

A total of 50 gene sequences generated during this study (Table 9). Sequences include 26 ITS, 21 28S and 3 *rpb2.* The newly generated sequences from Kerala collections were used for the phylogenetic analyses of different groups of boletoid fungi. Morphological characterization along with molecular phylogenetic analysis helped to resolve the species identification of many taxa.

Table 9. Newly generated sequences during this study.

Taxa	Voucher number	Locality	GenBank accession numbers		
			ITS	28S	rpb2
Anthracoporus holophaeus	ZGCSN224	Kozhikode	-	PP504682	-
Anthracoporus nigropurpureus	ZGCSN104	Wayanad	PP504488	PP504487	-
B. viridianus	ZGCSN186	Palakkad	OP901718	-	-
Baorangia albostipitata	ZGCSN211 holotype	Kozhikode	OR990613	PP499214	-
Baorangia albostipitata	ZGCSN228	Kozhikode	OR990614	-	-
Boletellus aurocontextus	ZGCSN174		ON707625		-
Boletinellus viridianus	ZGCSN163 holotype	Palakkad	OP542551	OP526842	-
Buchwaldoboletus xylophilus	ZGCSN110	Thiruvanan-thapuram	ON707263	-	-
Chalciporus rubrostipitatus	ZGCSN160	Kozhikode	OQ231504	-	-
Chalciporus rubrostipitatus	ZGCSN153 holotype	Kozhikode	OQ225690	OQ193026	OQ993343

Gyroporus species	ZGCSN225 holotype	Kozhikode	PP486355	PP474257	-
Gyroporus species	ZGCSN230	Kozhikode	PP510438	-	-
Lanmaoa species	ZGCSN174	Thiruvananthapuram	-	PP504564	-
Lanmaoa species	ZGCSN211	Kozhikode	PP979452		-
Neotropicomus indicus	ZGCSN180	Thiruvananthapuram	OQ633210	OQ633194	-
Hiranmaya	ZGCSN221	Kozhikode	PP979450	PP977529	-
Hiranmaya	ZGCSN139	Wayanad	PP979451	PP977190	-
Parvixerocomus matheranensis	ZGCSN165	Palakkad	-	PP504561	-
Parvixerocomus matheranensis	ZGCSN74	Kozhikode	-	OQ650291	-
Paxillus species	ZGCSN82	Idukki	-	PP510439	-
Phlebopus portentosus	ZGCSN15	Kozhikode	-	PP504687	-
Phlebopus portentosus	ZGCSN63	Kozhikode	-	PP504702	-
Retiboletus species	ZGCSN126	Wayanad	-	PP504510	-
Rostrupomyces sisongkhramensis	ZGCSN124	Wayanad	-	PP504509	-
Rubroboletus species	ZGCSN100 holotype	Kollam	OQ504748	OQ472490	OQ689073
Scleroderma species			PP364562	-	-
Strobilomyces giganteus	ZGCSN205	Wayanad	PP510435	-	-
Strobilomyces giganteus	ZGCSN107	Wayanad	PP979449	-	-
Suillus granulatus	ZGCSN217	Idukki	PP510437	-	-
T. atroviolaceobrunneus	ZGCSN207	Kozhikode	PP504667	-	-
T. purpureus	ZGCSN145	Wayanad	OQ198445	-	-
T. purpureus	ZGCSN143	Wayanad	OQ198447	-	-
Tylopilus glutinosus	ZGCSN149	Thiruvananthapuram	PP504524	-	-
Tylopilus glutinosus	ZGCSN161	Kozhikode	PP504527	-	-
Tylopilus purpureus	ZGCSN130 holotype	Wayanad	OQ198446	OQ179920	OQ680710
Tylopilus species	ZGCSN203	Kozhikode	-	PP504625	-
Tylopilus species	ZGCSN206	Kozhikode	PP510436	-	-

4.1 LIST OF SPECIES DOCUMENTED DURING THE STUDY

Order Boletales

Boletaceae

1. *Anthracoporus holophaeus*
2. *Anthracoporus nigropurpureus*
3. *Aureoboletus species*
4. *Austroboletus fusisporus*
5. *Baorangia albostipitata*
6. *Boletellus aurocontextus*
7. *Boletellus emodensis*
8. *Buchwaldoboletus pseudolignicola*
9. *Buchwaldoboletus xylophilus*
10. *Chalciporus rubrostipitatus*
11. *Erythrophylloporus suthepensis*
12. *Hiranmaya indica* gen. et sp. nov
13. *Indoporus* species
14. *Lanmaoa* species
15. *Leccinum intusrubens*
16. *Neotropicomus indicus*
17. *Parvixerocomus matheranensis*
18. *Phylloporus septocystidiatus*
19. *Retiboletus* species
20. *Rostrupomyces sisongkhramensis*
21. *Rubroboletus species*
22. *Strobilomyces giganteus*
23. *Strobilomyces strobilaceus*

24. *Tylopilus glutinosus*
25. *Tylopilus griseipurpureus*
26. *Tylopilus purpureus*
27. *Tylopilus* species
28. *Xerocomellus corneri*

Boletinellaceae

29. *Boletinellus viridianus*
30. *Phlebopus portentosus*

Gyroporaceae

31. *Gyroporus* species

Paxillaceae

32. *Paxillus* species

Pisolithaceae

33. *Pisolithus albus*

Suillaceae

34. *Suillus granulatus*

Sclerodermataceae

35. *Scleroderma citrinum*
36. *Scleroderma sinnamariense*
37. *Scleroderma areolatum*
38. *Scleroderma verrucosum*
39. *Scleroderma nitidum*

Serpulaceae

40. *Serpula similis*

4.2. TAXONOMY

4.2.1. Taxonomic keys to the boletoid fungi of kerala

Key to the families of Boletales

1. Basidiomata with gasteroid hymenium 2

1'. Basidiomata without gasteroid hymenium... 3

2. Gleba heterogeneous, divided in to peridioles...........................Pisolithaceae

2'. Gleba more or less homogeneous, not divided in to peridioles..................... . ... Sclerodermataceae

3. Basidiomata with lamellate hymenophore; clamp-connections present .... Paxillaceae

3'. Basidiomata prominently with poroid or merulioid hymenophore or rarely with lamellate hymenophore; clamp-connections absent in most including lamellate forms, rarely present in poroid or merulioid forms 4

4. Basidiomata resupinate; hymenophore merulioid; hyphal system dimitic; cause wood rot.. Serpulaceae

4'. Basidiomata stipitate-pileate; hymenophore poroid or rarely lamellate; hyphal system monomitic; do not cause wood rot 5

5. Clamp-connections present... 6

5'. Clamp-connections absen 7

6. Pileal context whitish without color change on bruisng; stipe partly with hollow chambers...Gyroporaceae

6'. Pileal context pale yellow with color change to bluish on bruising; stipe without hollow chambers.. Boletinellaceae

7. Pileal surface covered by glutinous or tomentose cap; hymenophore with beaded milky droplets when young; primarily shows host-specific ectomycorrhizal relationships with *Pinus* species .... Suillaceae

7'. Pileal surface not covered by glutinous or tomentose cap; hymenophore without beaded with milky droplets; primarily shows ectomycorrhizal with other plant species .... Boletaceae

Key to the species of *Scleroderma*

1. Clamp-connections present.. 2

1'. Clamp-connections absent 3

2. Basidiospores subreticulated; peridium pale yellow to bright yellow ....*S. citrinum*

2'. Basidiospores echinulated; peridium greyish or brownish to black .... *S. sinnamariense*

3. Basidiomata sessile or shortly stipitate; basidiospores 10 – 15 µm diam ....*S. areolatum*

3'. Basidiomata pseudo or stipitate 4

4. Basidiomata pseudostipitate; basidiospores 9 – 12 µm diam .... *S. verrucosum*

4'. Basidiomata stipitate; basidiospores 7 – 11 µm diam ....*S. nitidum*

Key to the genera of Boletinellaceae

1. Basidiomata with eccentric stipe and decurrent tubular hymenophore........ ....*Boletinellus*

1'. Basidiomata with central stipe and narrow tubular hymenophore .... *Phlebopus*

Key to the genera of Boletaceae

1. Hymenophore lamellate 2

1'. Hymenophore tubular 3

2. Lamellae yellow to golden-yellow; basidiospores with bacillate ornamentation under SEM...*Phylloporus*

2. Lamellae yellowish-orange to deep orange or reddish-orange to orange red or brownish-orange to red; basidiospores without ornamentation....... ....*Erythrophylloporus*

3. Hymenophoral surface reddish, pinkish red, red to reddish brown........... .4

3'. Hymenophoral surface not the colors above 5

4. Pileal context changing to blue immediately on bruising; pore surface and tubes are of different colors; tubes yellow................................*Rubroboletus*

4'. Pileal context unchanging or changing to pale bluish slowly on bruising; pore surface and tubes are of same colors; tubes reddish, pinkish red, red to reddish brown...*Chalciporus*

5. Hymenophoral tube white, pinkish, greyish or purplish, never becomes yellow 6

5'. Hymenophoral tube yellowish to yellow.. 11

6. Basidiospores ornamented 7

6'. Basidiospores smooth 8

7. Pileal context changing to blackish or red turning blackish when bruised; basidiospores subglobose to ellipsoid, with reticulations or spines ....*Strobilomyces*

7'. Pileal context unchanging when bruised, basidiospores amygdaliform to subfusoid, with different kinds of ornamentations..................*Austroboletus*

8. Hymenophore white when young, sometimes becoming pinkish when mature.. 9

8'. Hymenophore greyish or greyish pink when young, becoming darker or reddish grey when mature.. 10

9. Stipe glabrous or distinctly reticulated; hymenophore unchanging or occasionally changing to reddish brown on bruising........................ *Tylopilus*

9'. Stipe with brown to blackish dots or squamules and sometimes additionally with longitudinal ridges; hymenophore changing yellowish, brownish, brown, vinaceous to blackish on bruising .... *Leccinum*

10. Stipe surface glabrous; stipe context greyish violet to dark violet .... *Indoporus*

10'. Stipe surface reticulated; stipe context white to cream .... *Anthracoporus*

11. Basidiospore surfaces with longitudinal striations ....*Boletellus*

11'. Basidiospore smooth 12

12. Pileal context changing to blue on bruising... 13

12'. Pileal context unchanging or changing to other than blue 17

13. Stipe surface glabrous.. 14

13'. stipe surface not glabrous 15

14. Hymenophore thin (thickness of hymenophore 1/3–1/5 times that of pileal context at the position halfway to the pileus center); stipe light yellow to lemon yellow at the apex and light to dark purple red towards the base . .. . *Lanmaoa*

14'. Hymenophore thick; yellowish to olive yellow or brownish yellow .... *Buchwaldoboletus*

15. Stipe longitudinally fibrillose; pileipellis a palisadoderm ....*Xerocomellus*

15'. Stipe with other surface features; pileipellis not palisadoderm 16

16. Pileipellis an epithelium .... *Parvixerocomus*

16'. Pileipellis trichodermium or ixotrichodermium .... *Baorangia*

17. Pileal context changing to vinaceous on bruising; pileipellis an epithelium . . .. *Hiranmaya*

17'. Pileal context unchanging or changing to brownish; pileipellis trichodermium or ixotrichodermium... 18

18. Stipe surface wholly reticulate .... *Retiboletus*

18'. Stipe surface glabrous or with other type of characters 19

19. Pileal surface always gelatinized; pileipellis usually ixotrichodermium, rarely trichodermium. .... *Aureoboletus*

19'. Pileal surface dry; pileipellis not an ixotrichodermium 20

20. Basidiospores ellipsoid to broadly ellipsoid; stipe surface with scattered brown to dark brown to reddish brown granulose squamules ....*Rostrupomyces*

20'. Basidiospores subfusoid to fusoid; stipe surface smooth to minutely pruinose .... *Neotropicomus*

Key to the species of *Strobilomyces*

1. Hymenophore white when young, changing to dark orange red to reddish immediately on bruising; cheilocystidia larger (52 – 77 × 11 – 16 μm), stipitipellis with caulobasidia; basidiospores 7 – 10 × 7.5 – 9.5 μm .... *S. giganteus*

1'. Hymenophore greyish when young, unchanging or changes to darker on bruising; cheilocystidia smaller (31 – 50 × 10 – 15 µm); stipitipellis without caulobasidia; basidiospores 8 – 11 × 8 – 10 µm........................ *S. strobilaceus*

Key to the species of *Tylopilus*

1. Pileipellis an ixotrichodermium; caulocystidia present, larger (25 – 70 × 8 – 12 µm); basidiospores 7 – 10 × 4 – 5 µm .... *T. glutinosus*

1'. Pileipellis a trichodermium; caulocystidia absent or smaller....................... 2

2. Cheilocystidia with distinct globular contents; hymenophore changing to reddish brown or brownish on bruising... 3

2'. Cheilocystidia without globular contents; hymenophore unchanging on bruising .... *T. griseipurpureus*

3. Pleurocystidia larger (45 – 70 × 10 – 15 µm); cheilocystidia larger (40– 65 × 6 – 9 µm); cystidioid elements absent in stipitipellis; basidiospores 7 – 12 × 4 – 5 µm... *T.* species

3'. Pleurocystidia smaller (27–48 × 7–9 µm); cheilocystidia smaller (24–40 × 7–9 µm); cystidioid elements present in stipitipellis; basidiospores 9.5 – 13 × 4 – 6 µm... *T. purpureus*

Key to the species of *Anthracoporus*

1. Tubes smaller (up to 3 mm long); stipe surface not reticulated; terminal cells of pileipellis with encrustations; basidiospores 11 – 13.5 × 4 – 5 µm ... .*A. nigropurpureus*

1'. Tubes larger (up to 15 mm long); stipe surface reticulated; terminal cells of pileipellis without encrustations; basidiospores 9 – 13 × 5.5 – 7 µm......... . ... *A. holophaeus*

Key to the species of *Boletellus*

1. Basidia larger (38 – 60 × 9.5 – 16 µm); cystidia fusiform; basidiospores 13.5 – 23 × 6 – 8.5 µm .... *B. emodensis*

1'. Basidia smaller (35– 40 × 8 – 18 µm); cystidia utriform; basidiospores 17 – 20 × 7 – 9 µm .... *B. aurocontextus*

Key to the species of *Buchwaldoboletus*

1. Pileipellis an ixocutis; stipitipellis with caulobasidia; pleurocystidia smaller (17 – 48 × 6 – 11); basidiospores 4.5 – 5.5 × 3 – 3.5 µm............... *B. xylophilus*

1'. Pileipellis a trichodermium; stipitipellis without caulobasidia; pleurocystidia larger (32 – 52 × 7 – 12 µm); basidiospores 5 – 6.5 × 4 – 4.5 µm.. *B. pseudolignicola*

4.2.2 TAXONOMIC DESCRIPTIONS

4.2.2.1 Pisolithaceae

Pisolithus Alb. and Schwein.

Basidomata gateroid, subglobose to ellipsoid or pyriform. Pseudostipe normally narrower towards the base. Peridium yellowish or brownish, becoming darker at maturity. Gleba developing within small isolated ellipsoid-ovoid or lens-shaped peridioles, sometimes enclosed in separated by a gelatinous or sticky, tar-like, dark brown or blackish matrix. Peridoles collapse at maturity and gleba transforms into a powdery mass. Basidiospores globose, echinulate, yellowish or brownish. Clamp-connections present.

Pisolithus albus (Cooke and Massee) Priest, Phytotaxa 348: 167 (2018)

Synonymy:

Pisolithus albus (Cooke and Massee) Priest, in Bougher and Syme, Fungi of Southern Australia (Nedlands): 122 (1998)

Polysaccum album Cooke and Massee, Grevillea 20 (no. 94): 36 (1891)

Figure 3

Basidomata gasteroid; gasterocarp subglobose or pyriform, 35 – 45 mm broad, with short pseudostipe up to 8 mm long. **Peridium** irregular, thick at young stage becoming thin when mature, disintegrating and leaving small patches above yellowish background. **Gleba** blackish; periodioles 1 – 1.5 mm diam., thin-walled, small, embedded in tier like sticky, dark matrix, breaking down to powdery mass on maturation. **Psuedostipe** arising from agglutinated mycelial base, with whitish to yellowish rhizomorphs.

Basidiospores 6.5 – 12 × 6.5 – 11.5 µm (Q = 1.01 – 1.12, Qm = 1.03), globose, ornamented with distinctive erect spines (up to 1 µm long). **Peridial hyphae** 3 – 8 µm wide, thick-walled with faint yellowish contents. **Basidia** not observed. Clamp-connections present.

Figure 3. *Pisolithus albus*. A. Basidiomata B. Basidiospores C. Basidium D. Peridial hyphae. Scale bars: A = 10 mm, B-D = 10 µm.

Habitat: On soil, scattered, near *Acacia* species, *Terminalia paniculata,* and *Eucalyptus* species.

Specimens examined: INDIA, Kerala State, Kozhikode District, Zamorin's Guruvayurappan College campus, 16 May 2022, Salna Nanu, ZGCSN152; 12 June 2023, Salna Nanu, ZGCSN200.

Comments: *Pisolithus albus* is characterised by subglobose basidiomata with thin membraneous peridium, peridioles embedded in tar like material, globose basidiospores with spines, and presence of clamp-connections. The macroscopic and microscopic characters of our collections agree with the other taxonomic descriptions of *P. albus* (Gargano et al. 2018, Lebel et al. 2018).

4.2.2.2 Sclerodermataceae

Scleroderma Pers.

Basidiomata leathery to very hard when dry, globose, subglobose, pyriform, sessile, pseudostipitate or with a well-developed stipe, with a large basal compact mass of mycelium. Exoperidium thin or thick, dry, smooth, cracked, scaly or cover by small or large squamules. Sometimes membranaceous veil-like or patches on the basidiomata or stipe or pseudostipe. Endoperidium thin, with a membrane covering the gleba. Both exo- and endoperidium frequently rufescent. Gleba compact, dusty, white, soon purple or dark greyish-brown or reddish-brown, then with thin whitish or yellowish laments. Dehiscence by cracking the apical part of the basidiomata, or through an irregular lacerated apical pore or stellated by tearing off all the peridium, in this latter case all the gleba is lost. Hymenium not developed. Basidiospores globose, thick-walled, yellowish-brown, echinulated, sub-reticulated or reticulated, when immature and subglobose, smooth, with a visible apiculus. Basidia 4 – 6 spored, pyriform, sometimes claviform, thin or thickwalled, hyaline, discharging early the basidiospores in an immature stage. Odor and taste in general strong like rubber.

Scleroderma citrinum Pers., Syn. meth. fung. (Göttingen) 1: 153 (1801)

Synonymy:

Scleroderma aurantium var. *macrorhizum* (Fr.) Šebek [as 'macrorrhizum'], Sydowia 7(1-4): 170 (1953)
Scleroderma vulgare Hornem., Fl. Danic. 10: tab. 1969, fig. 2 (1819)
Scleroderma vulgare subsp. macrorrhizon (Wallr.) Sacc. [as 'macrorhizon'], in Berlese, De Toni and Fischer, Syll. fung. (Abellini) 7(1): 135 (1888)
Scleroderma vulgare var. bogoriense Henn. and E. Nyman, in Hennings in Warburg, Monsunia 1: 159 (1899) [1900]
Scleroderma vulgare var. novoguineense Henn., Bot. Jb. 18(4 (Beibl. 44)): 37 (1894)
Scleroderma vulgare ß macrorhizum Fr., Syst. mycol. (Lundae) 3(1): 47 (1829)

Figure 4

Basidiomata 30 – 80 mm in diam., globose to ovoid, sessile or shortly pseudostipitate with compact mycelial base. **Peridium** 2 – 4 mm thick, coarsely scaly, squamules arranged in rosette form in the centre; exoperidium breaks in some parts as balck patches; endoperidium pale yellow to bright yellow, rubescent when cut. **Dehiscence** through irregular apical breaking, finishing as an irregular cup-like fruit body. Gleba whitish or pale yellow when young, dark brownish, compact, powdery when mature.

Basidiospores 6 – 9 × 5.5 – 9 µm (Q = 1 – 1.16, Qm = 1.004), globose, reticulate to subreticulate, reticulum up to 3 µm long, pale yellow with dark brown reticulations in water. **Basidia** not observed. **Exoperidium** consist of 2.5 – 12 µm wide, thin to thick-walled (wall thickness up to 1 µm), pale yellow to yellowish hyphae. **Endoperidium** consist of 3 – 8 µm wide, pale yellow to yellow, thin-walled hyphae. **Oleiferous hyphae** present on both exoperidium and endoperidium. **Clamp-connections** present.

Habitat: On soil**,** solitary, near *Terminalia* species.

Figure 4. *Scleroderma citrinum*. A-C. Basidiomata D-E. Basidiospores F. Peridial hyphae. Scale bars: A-C = 10 mm, D-F = 10 µm.

Specimens examined: India, Kerala State, Kannur district, Aralam Wildlife Sanctuary, 28 June 2019, Salna Nanu, ZGCSN27; Kozhikode district, Janaki forest, near *Terminalia* species, 11 Jan 2021, Salna Nanu, ZGCSN72; 01 June 2021, Salna Nanu, ZGCSN73; Idukki district, Devikulam forest range, on soil, under *Pinus* species, 07 Aug 2021, Salna Nanu, ZGCSN84.

Comments: *Scleroderma citrinum* is characterized by thick peridium with frequently arranged squamules, whitish to yellowish endoperidium, and dehiscence through irregular apical breaking. Our collections morphologically agree with descriptions of previously reported collections of *S. citrinum* (Guzmán et al. 2013). This species is common in forests of Kerala.

Scleroderma sinnamariense Mont., Annls Sci. Nat., Bot., sér. 2 14: 331 (1840)

Figure 5

Basidomata up to 30 – 40 mm broad, globose, with very short pseudostipe. **Peridium** thick at young stage, becoming thin when mature, greyish or brownish to black, dry. **Gleba** blackish.

Basidiospores 6 – 7 × 6 – 7 µm (Q= 1 – 1.16, Qm = 1.04), globose, ornamented with distinctive erect spines (up to 1 µm long). **Peridial hyphae** 3 – 8 µm wide, thick-walled with faint yellowish contents. Basidia not observed. **Clamp-connections** present.

Habitat: On soil, scattered, near *Terminalia paniculata.*

Specimens examined: INDIA, Kerala State, Thiruvananthapuram District, 01 October 2021, Salna Nanu, ZGCSN101.

Comments: *Scleroderma sinnamariense* is characterized by its globose pseudostipitate basidiomata, greyish or brownish to black peridium, and globose reticulated basidiospores (Guzmán and Ovrebo 2000). This is a common species in the Asian countries (Baseia et al. 2016). Kerala collection cluster with other *S. sinnamariense* collections with 100% bootstrap support in the phyloegentic analysis using ITS sequences (Figure 46). Clade of *S. sinnamariense* includes *S. venenatum*, *S.* var. *macrosporum* and *S. anomalosporum*. The species identification of present collection is confirmed by morphological and molecular phylogenetic data.

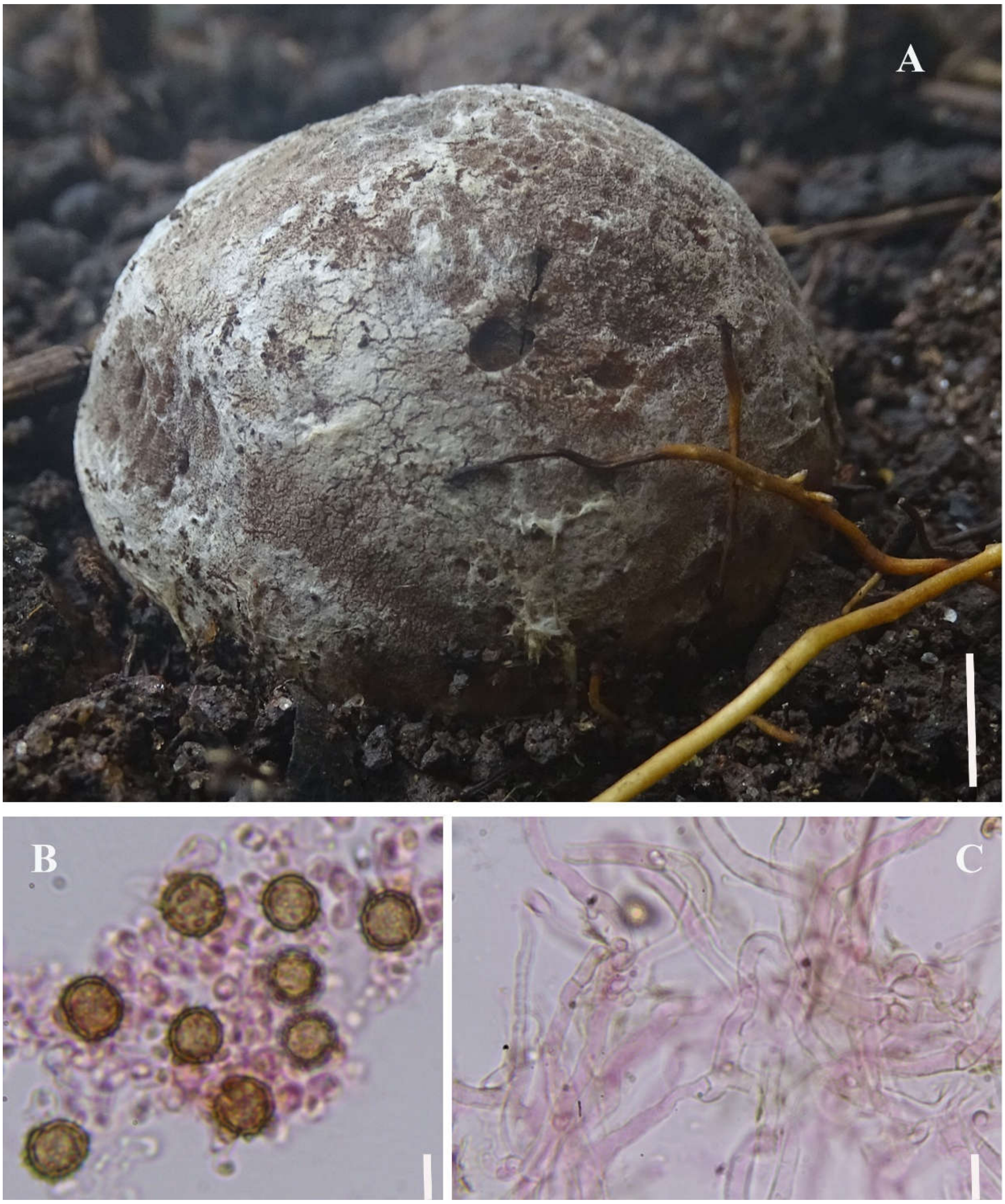


Figure 5. *Scleroderma sinnamariense*. A. Basidiomata B. Basidiospores C. clamp connection. Scale bars: A = 10 mm, B-C = 10 μm.

Scleroderma areolatum Ehrenb., Sylv. mycol. berol. (Berlin): 27 (1818)

Figure 6

Basidiomata 30 – 40 mm in diam., globose to ovoid, sessile. **Peridium** thin, membraneous when mature, yellowish brown with distinct, inherent, small, dark brown to blackish squamules. **Gleba** dark greyish to reddish brown.

Basidiospores 10.5 – 13 × 10 – 12 µm (Q= 1 – 1.17, Qm = 1.13), globose, echinulated, spines 1 – 2 µm high, brownish yellow in water. **Basidia** not observed. **Peridium** consist hyphae of of 3 – 12 µm wide, thick-walled (wall thickness up to 1 µm), hyaline in water. **Clamp-connections** not observed.

Habitat: On soil. Scattered.

Specimens examined: India, Kerala State, Idukki district, Mattupetty, 8 August 2021, Salna N., ZGCSN87.

Comments: *Scleroderma areolatum* is characterized by sessile basidiomata, thin and membraneous peridium, presence of dark brown to blackish squamules on peridium, and basidiospores 10 – 15 × 10 – 12 µm size range. *Scleroderma areolatum* is morphologically similar to *S. verrucosum*, only the size of the basidiospores separates both species (Guzmán et al. 2013).

Scleroderma verrucosum (Bull.) Pers., Syn. meth. fung. (Göttingen) 1: 154 (1801)

Synonymy:

Lycoperdon verrucosum Bull., Hist. Champ. Fr. (Paris) 1(1): 157 (1791)
Scleroderma cepa var. *maculatum* (Peck) Lloyd, Mycol. Writ. (Cincinnati) 6(Letter 63): 950 (1920)
Scleroderma maculatum (Peck) Lloyd, Mycol. Writ. (Cincinnati) 6(Letter 65): 1058 (1920) [1921]
Scleroderma verrucosum f. *angustistipitatum* Dissing and M. Lange, Bull. Jard. bot. État Brux. 32: 394 (1962)
Scleroderma verrucosum var. *fascirhizum* Šebek, Sydowia 7(1-4): 179 (1953)
Scleroderma verrucosum var. *maculatum* Peck, Ann. Rep. Reg. N.Y. St. Mus. 53: 848 (1901) [1900]
Scleroderma verrucosum var. *violascens* Herink, Sydowia 7(1-4): 176 (1953)

Figure 6

Figure 6. A-B. *Scleroderma verrucosum*. A. Basidiomata B. Basidiospores. C-F. *Scleroderma areolatum*. C. Basidiomata D-F. Basidiospores. Scale bar: A, C = 10 mm, B, D-F = 10 µm.

Basidiomata 20 – 25 mm in diam., globose to ovoid, shortly stipitate with compact mycelia at the base. **Peridium** 1.5 – 2 mm thick, yellowish brown, with frequently arranged blackish brown squamules. **Gleba** whitish to dark vinaceous with whitish filaments, compact when young, becomes dusty. **Dehiscence** through irregular cracking of the peridium.

Basidiospores 8 – 10 × 8 – 10 µm (Q= 1 – 1.1, Qm = 1.18), globose, echinulate, with spines 0.5-2 µm high. **Basidia** 23 – 25 × 10 – 11 µm, pyriform, 4 – 6 sterigmate. **Clamp-connections** absent.

Habit: On soil. Scattered. Under *Terminalia* species.

Specimens examined: India, Kerala State, Kozhikode district, Poyilkavu sacred grove, on soil, 20 June 2019, Salna Nanu, ZGCSN21; Idukki district, Ecopoint, 8 Aug 2021, Salna Nanu, ZGCSN86; Kannur district, Maloor, 10 June 2023, Salna Nanu, ZGCSN198.

Comments: *Scleroderma verrucosum* shows resemblances with *S. nitidum* and *S. areolatum*. However, *S. verrucosum* differs from *S. nitidum* and *S. areolatum* in peridium structure and basidiospore measurement (Guzmán et al. 2013).

Scleroderma nitidum Berk., Hooker's J. Bot. Kew Gard. Misc. 6: 173 (1854)

Figure 7

Basididomata 18 – 20 mm diam., globose to pyriform, shortly stipitate. **Stipe** 18 – 23 mm long. **Peridium** thin, brownish, with blackish squamules; endoperidium thin, intensely rubescent to vinaceous-red. **Gleba** pale yellowish to dark vinaceous with whitish hyphal filaments. **Dehiscence** by irregular cracking on the apical peridium.

Basidiospores 7 – 11 × 7 – 11 µm (Q= 1 – 1.1, Qm = 1.01), echinulate, echinulae up to 2.5 µm, pale yellow, inamyloid. **Basidia** 15 – 34 × 7 – 12 µm, pyriform, 4 – 6 sterigmate, hyaline, inamyloid. **Clamp-connections** not observed.

Figure 7. *Scleroderma nitidum*. A-B. Basidiomata C. Basidiospores D. Peridial hyphae. Scale bar: A-B = 10mm, C-D = 10 µm.

Habit: On soil. Scattered. Under Dipterocarpaceae trees.

Specimens examined: India, Kerala State, Kozhikode district, Poyilkavu sacred grove, on soil, 20 June 2019, Salna Nanu, ZGCSN20; Palakkad district, Silent valley national park, 4 July 2019, Salna Nanu, ZGCSN40; 24 Oct 2019, Salna Nanu, ZGCSN58; Thiruvananthapuram district, Palode, JNTBGRI campus, 28 April 2022, Salna Nanu, ZGCSN158.

Comments: *Scleroderma nitidum* is distinct from other *Scleroderma* species by the presence of a peridium showing strong rubescent to vinaceous-red, pale yellowish to dark vinaceous gleba with whitish hyphal filaments, and presence of medium-sized basidiospores (Guzmán et al. 2013). Kerala collections morphologically agree with the descriptions of other reported collections of *S. nitidum*

4.2.2.3 Paxillaceae

Paxillus Fr.

Basidiomata fleshy, lamellate. Pileus convex when young, becoming plano-convex to plane with a shallow to deep depression at centre in some, rarely with a small umbo, ochraceous-yellow to chestnut brown or dark brown, funnel shaped. Lamellae decurrent, easily detaching, turn brownish on exposure or bruising. Stipe central to eccentric, solid, straight or curved, cylindrical or tapering towards the base. Basidiospores ellipsoid, smooth, thin- to thick-walled. Pleurocystidia and cheilocystidia fusiform, thin-walled, mostly with brownish yellow pigments. Pileipellis trichodermial to cutis. Clamp-connections present.

***Paxillus* species**

Figure 8

Basidiomata medium-sized. **Pileus** 40 – 140 mm in diam., convex when young, applanate with depression in the centre, becoming more flattened or irregular shape, umbo absent; surface viscid to slimy when moist, creamy white to ochraceous brown with rust brown patches, changing to brown with age; margin almost straight to slightly inrolled when young, lobed, undulating and wavy with age. **Pileal context** yellowish, becoming brownish with age. **Hymenophore** lamellate; Lamellae unequal, crowded, narrow, deeply decurrent, forked and anastomosing towards the apex of stipe, pale yellowish and creamy white towards the margin in young specimens, yellowish to rusty brown in mature becoming darker on aging. **Stipe** 30 – 7 × 4 – 7 mm, central to eccentric, cylindrical but slightly tapering towards the base, creamy white with pale brownish patches, darker towards the base, yellowish towards apex. **Stipe context** yellowish, becoming brownish with age.

Basidiospores 5 – 6.5 × 4 – 5 μm (Q= 1.2 – 1.5, Qm = 1.28), ovoid to amygdalifom, mostly uniguttulate, thin-walled, hyaline in water. **Basidia** 24 – 42 × 6 – 9μm, clavate, 4-spored, thin-walled, pale yellow to brownish in water; sterigmata up to 4.5 μm long. **Hymenophoral trama** divergent; hyphae 5 – 20 μm wide, thin-walled, hyaline to yellowish brown. **Pleurocystidia** 40 – 54 × 9 – 14 μm, cylindrical or subfusiform, thin-walled, hyaline to brownish yellow, pigments present in upper part only in some. **Cheilocystidia** 45 – 73 × 10 – 15μm, same as pleurocystidia in shape and color, thin-walled**. Pileipellis** a cutis; hyphae 3 – 8 μm wide, thin-walled, hyaline to pale yellow. **Pileal trama** interwoven; hyphae 6 – 20 μm wide, thin-walled, hyaline. **Stipitipellis** a cutis interrupted by caulocystidia. **Caulocystidia** 26 – 48 × 9 – 11 μm, subfusiform, thin-walled, hyaline to brownish yellow. **Stipe trama** interwoven; hyphae 6 – 25 μm wide, thin-walled. **Clamp-connections** present on all hyphae.

Habitat: On soil, gregarious near *Pinus* species.

Material examined: INDIA, Kerala State, Idukki District, Devikulam forest range, 07 August 2021, Salna Nanu, ZGCSN82.

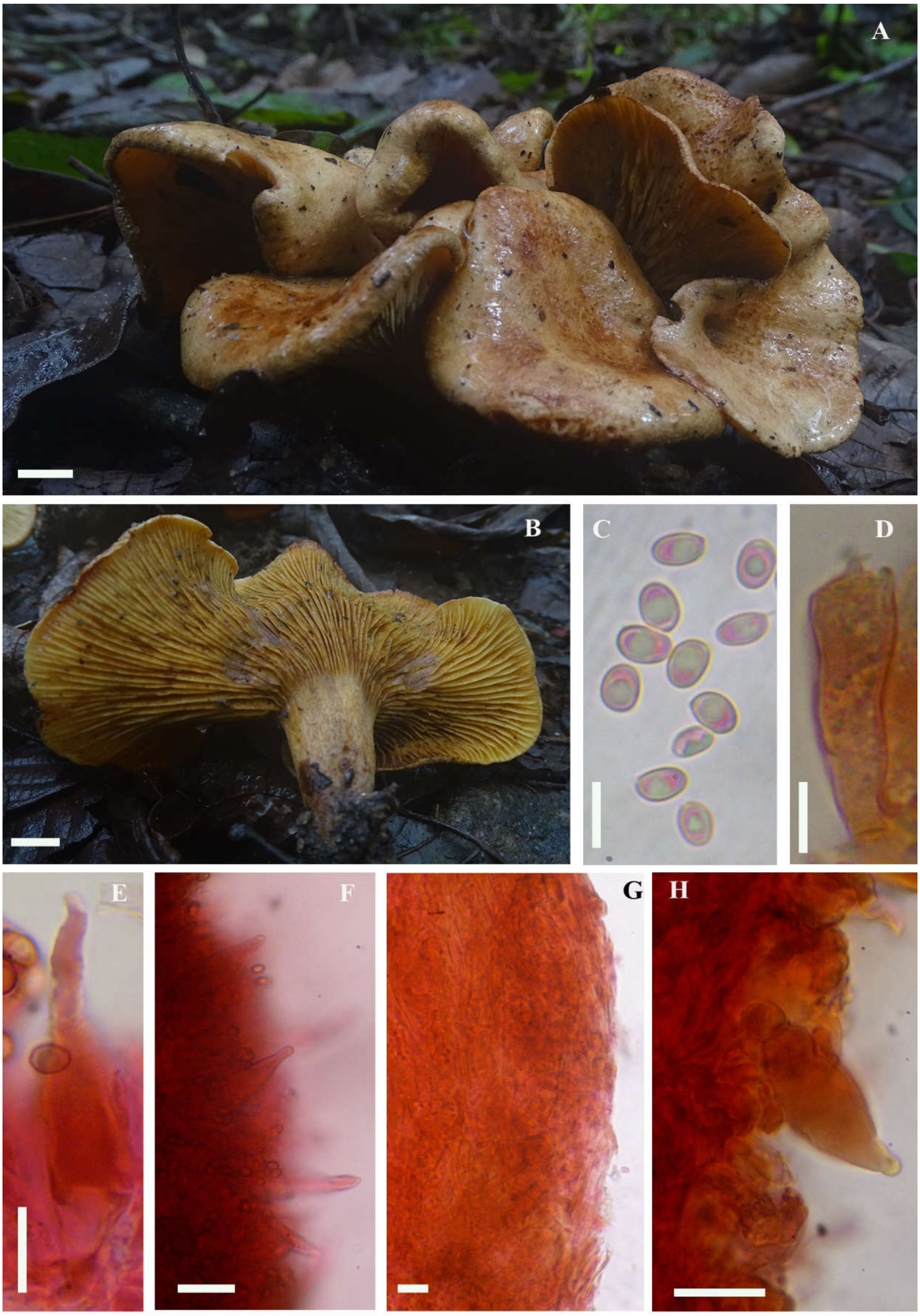


Figure 8. *Paxilus* species. A-B Basidiomata C. Pileal context and hymenophore showing color change on cut C. Basidiospores D. Basidium E. Pleurocystidium F. Cheilocystidia G. Pileipellis H. Stipitipellis with caulocystidia. Scale bars: A-B 10mm, C-F, H = 10 μm, G = 20 μm.

Comments: *Paxillus* species collected during this study is characterized by creamy white to ochraceous brown and rusty stained pileus without umbo, crowded, narrow, deeply decurrent and forked lamellae, yellowish to brown context, ovoid to amygdalifom basidiospores, presence of hymenial cystidia, and a stipitipellis with caulocystida. *Paxillus involutus* and present collection are having similar characters like growing around conifers, basidimoata with greyish brown pileus, and similar size and shape of cystidia. However, Kerala collection differs from *P. involutus* in having creamy white to ochraceous brown pileus that lacks an umbo, smaller basidiospores, non-gelatinous piliepellis and a stipitipellis with caulocystidia. Another similar species, *P. rubicundulus* has ixocutis type pileipellis and cutis type stipitipellis. But our collection has a cutis type of piliepellis and caulocystidia on stipitipellis. Molecular phylogenetic analysis using 28S gene region of species in Paxillaceae family revealed the independent status of Kerala collection (Figure 45). *Paxillus* species clustered independently in the *Paxillus* clade with moderate bootstrap support (74%).

4.2.2.4 Serpulaceae

Serpula (Pers.) Gray

Basidiomata resupinate to effuse-reflexed or pileate, membranaceous, soft, easily detachable. Hymenophore merulioid to poroid, orange to brownish or with olivaceous tints. Hyphal system dimitic, hyphae polymorphic, generative hyphae with clamps, skeletoid hyphae present in the context, true skeletal hyphae occur in the rhizomorphs. Cystidia absent, hyphoid cystidiols may be present. Basidia clavate, with 4-sterigmata and a basal clamp. Basidiospores ellipsoid to ovoid, smooth, thick-walled, brownish, not or weakly dextrinoid, cyanophilous.

Serpula similis (Berk. and Broome) Ginns, Mycologia 63: 231 (1971)

Figure 9

Basionym:

Merulius similis Berk. and Broome, J. Linn. Soc., Bot. 14(no. 73): 58 (1873) [1875]

Synonymy:

Gyrophana similis (Berk. and Broome) Pat., Bull. Soc. mycol. Fr. 39(1): 53 (1923)
Sesia similis (Berk. and Broome) Kuntze, Revis. gen. pl. (Leipzig) 2: 870 (1891)

Basidiomata annual, resupinate to slightly pileate, imbricate, sessile, fleshy and more or less watery when fresh, becoming brittle and light weight on drying, 60 – 80 mm × 25 – 35 mm. **Pileus** semicircular to subovoid, surface cream to bright yellow to orange in centre, uneven, thick, fleshy; margine cream, entire, thick. **Context** pale cream, soft, spongy up to 4 mm thick. **Hymenium** merulioid to reticulate folds, folds more prominent and thicker in towards the center, bright yellow to orange; pores 1 – 2 per mm, irregular, yellow.

Basidiopores 4 – 5 × 2.5 – 4 µm (Q = 1 – 1.1, Qm = 1.06), globose to subglobose, thin to thick-walled, inamyloid. **Basidia** 34 – 48 × 6 – 8 µm, cyanophilic. **Hyphal system** dimitic; generative hyphae 3 – 5 µm wide, branched, hyaline, inamyloid, thin-walled with clamp-connections; skeletal hyphae 2 – 5 µm wide, thick-walled up to 1.5 µm, inamyloid, brached.

Habitat: On decaying or living trees. Solitary or as a bunch.

Specimens examined: India, Kerala State, Kozhikode district, Civil Station, 27 September 2015, Vinjusha N., ZGCSN1; Peruvannamoozhi forest range, 28 July 2018, Salna Nanu, ZGCSN2; Malappuram district, Calicut university campus, 22 July 2021, Salna Nanu, ZGCSN76; Thiruvananthapuram district, Palode, 01 October 2021, ZGCSN102.

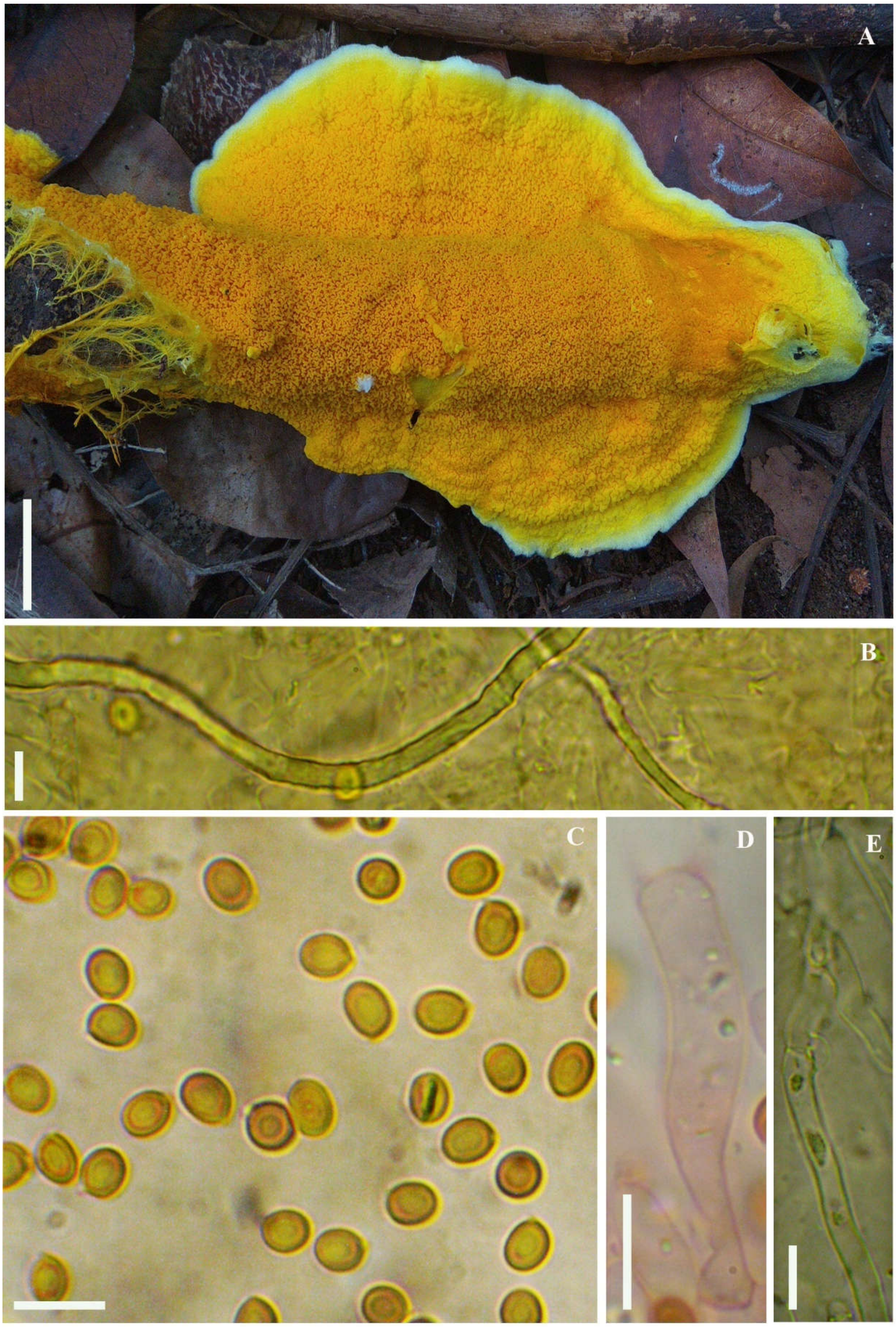


Figure 9. *Serpula similis* A. Basidiomata B. Skeletal hyphae C. Basidiospores D. Basidium E. Generative hypahe. Scale bars: A = 50 mm, B-E = 10 µm.

Comments: Characters like annual, sessile and fleshy basidiomata, context with pale cream color, dimitic hyphal system, small, globose to sub-globose bright yellow basidiospores place the specimen under *Serpula*. Silva et al. (2019) updated the original description of *Serpula similis* from Ginns (1971) and they reported this species from Brazil. All the macroscopic and microscopic features of the present collection agree with the description of *Serpula similis* given by Verma et al. (2017) and Silva et al. (2019).

4.2.2.5 Gyroporaceae

Gyroporus Quél.

Basidiomata small to middle-sized. Pileus whitish, yellowish, yellow-brown to red-brown villous or scaly. Pileal context white, unchanging or turning blue or purple on bruising. Hymenophore poroid; pores white to light yellow. Stipe chambered or completely hollow and brittle. Basidiospores short ellipsoid. Clamp-connections present.

***Gyroporus* species**

Figure 10

Basidiomata small-sized. **Pileus** 15 – 30 mm diam, hemispherical to applanate, with a depression at centre; surface yellowish brown, brownish towards the centre, subtomentose, dry; margin entire, straight. **Pileal context** up to 5 mm wide, white, without any color change on bruising or cut. **Hymenophore** poroid; pores 2 – 3 per mm, nearly angular, yellowish, unchanging when bruised; tubes up to 8 mm long, yellowish, without any color change on bruising. **Stipe** 200 – 350 mm, reddish brown, subtomentose to glabrous, solid when young, hollow when mature. **Stipe context** white, unchanging when bruised. **Basal mycelium** dull white.

Basidiospores 6 – 7 × 4 – 5 µm (Q = 1.47, Qm = 1.2–1.75), subglobose to ellipsoid, slightly thick-walled (up to 0.5 µm), smooth. **Basidia** 35 – 40 × 10 – 14 µm, 4-spored, clavate, hyaline; sterigmata up to 5.5 µm long. **Pleurocystidia** not observed. **Cheilocystidia** 18 – 26 × 6 – 9 µm, broadly fusiform to lageniform, thin-walled, hyaline. **Hymenophoral hyphae** 3 – 6 µm, thin-walled, hyaline. **Pileipellis** a trichodermium consisting of cystidioid terminal elements, 43 – 58 × 8 – 13 µm, broadly fusiform, lageniform, nearly clavate, sometimes with apical protrusion (up to 7 µm long), thin-walled, hyaline; pileal trama interwoven with thin-walled hyphae, 3 – 7 µm wide. **Stipitipellis** basically a cutis; hyphae 4 – 9 µm wide, hyaline, thin-walled. **Clamp-connections** present in all tissues.

Habitat: On soil, solitary or scattered, frequently Dalzell.

Additional material examined: INDIA, Kerala State, Thurayilkkotta, Kozhikode District, 26 October 2023, Salna Nanu, ZGCSN225; 07 November 2023, Salna Nanu, ZGCSN230,

Comments: *Gyroporus* species collected from Kerala is characterized by the presence of basidiomata having yellowish brown pileus with tomentose surface and depressed centre, whitish pileal context that unchanging when bruised, trichodermial type of pileipellis with cystidioid terminal cells, and a cutis type of stipitipellis interrupted by cylindrical hyphae. The independent status of the species is evident from phylogenetic tree (Figure 44).

Zhang et al. (2022) proposed four sections in the genus *Gyroporus* based on phylogenetic analyses using ITS-nrLSU and *atp6* datasets. ML analysis (Figure 44) in our study using ITS and LSU sequences, *Gyroporus* species belongs to the *Gyroporus* section *Castaneus* Ming Zhang and T.H. Li. Brownish pileal surface, whitish hymenophore that unchange when bruised, subtomentose stipe surface, oval to ellipsoid, thin-walled, smooth basidiospores, absence or rare presence of pleurocystidia, and trichodermium

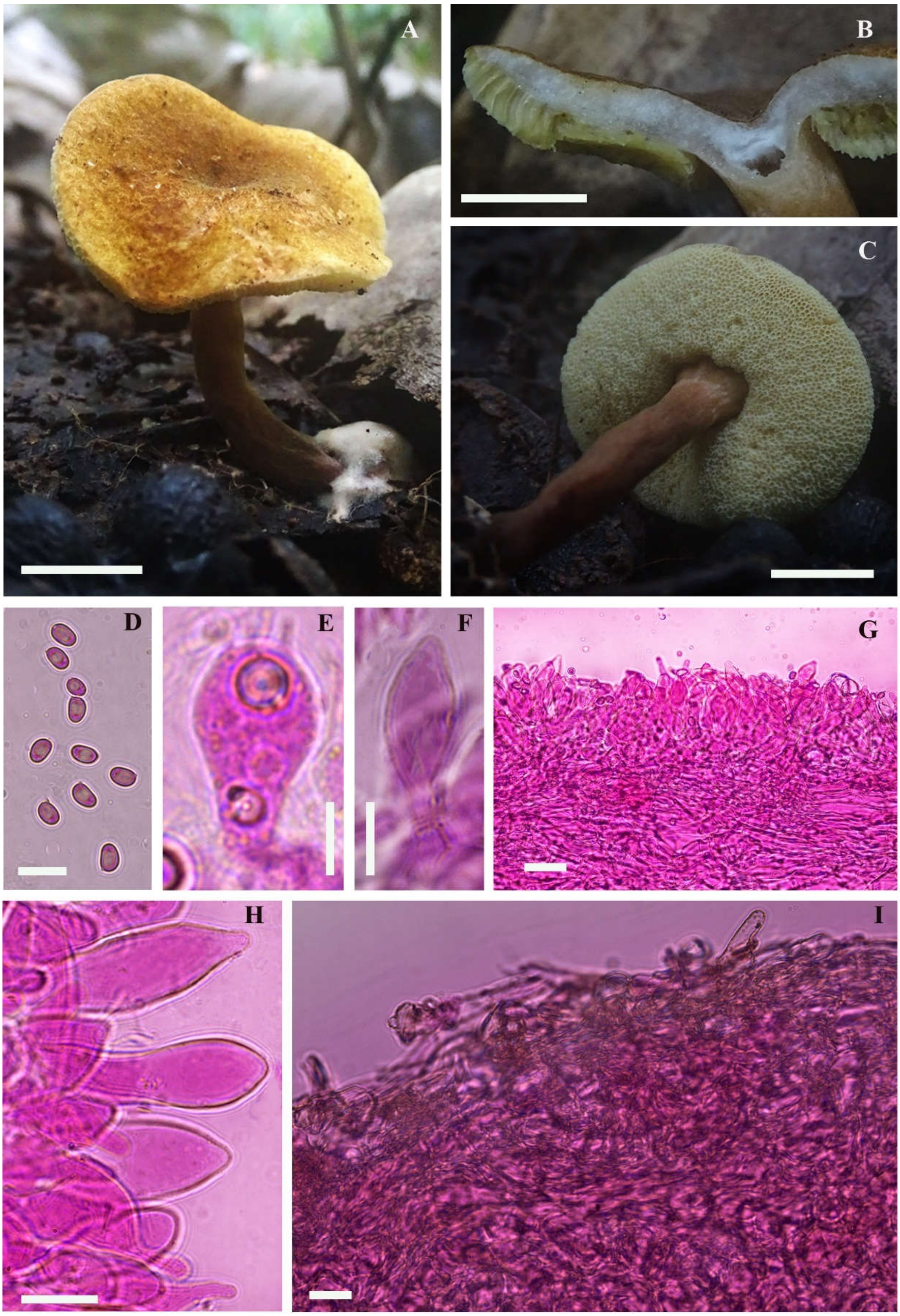


Figure 10. *Gyroporus* species. A-C. Basidiomata D. Basidiospores. E. Basidium F. Cheilocystidium. G. Pileipellis. H. Elements of pileipellis. I. Stipitipellis. S cale bars: A-C = 10 mm, D-F, H = 10 µm, G, I = 20 µm.

type of pileipellis are the morphological characters that leads to the section *Castaneus. Gyroporus* species clusters with *G. subglobosus* N.K. Zeng, H.J. Xie, L.P. Tang and M. Mu with 99% of bootstrap support in ML tree. *G. subglobosus* is a recently described species from China (Xie et al. 2022). Our *Gyroporus* species and *G. subglobosus* shows similar features like small-sized brownish pileus, whitish pore surface, subtomentose stipe surface, and a trichodermium type of pileipellis. *Gyroporus* species can be distinguished from *G. subglobosus* by tomentose pileal surface, smaller pores, smaller basidiospores (6.5 – 10 × 5 – 7 µm in *G. subglobosus*), and stipitipellis which is a cutis interrupted by hyphal patches. *Gyroporus paramjitii* K. Das, D. Chakraborty and Vizzini*, G. ammophilus* (M.L. Castro and L. Freire) M.L. Castro and L. Freire, *G. austrobrasiliensis* A.C. Magnago, *G. porphyreus* N.K. Zeng, H.J. Xie and Zhi Q. Liang are the other phylogenetically related species. *Gyroporus paramjitii*, a species first described from India (Das et al. 2017), have similar colored basidiomata, smaller pores, and trichodermium type of pileipellis. However, our *Gyroporus* species differ from *G. paramjitii* by the presence of whitish context that is unchanging on bruising, smaller basidiospores (7.5 –13 × 5 – 7 µm in *G. paramjitii*), and smaller terminal cells in pileipellis (25 – 110 × 36 – 15 µm in *G. paramjitii*). Our *Gyroporus* species is distinct from *G. paramjitii* in the phylogenetic analysis. *Gyroporus ammophilus* has pinkish to salmon colored context staining light blue when handled or bruised and they were reported from sandy calcareous pine groves (Crous et al. 2016). *Gyroporus austrobrasiliensis* reported from Brazil can be distinguish from our *Gyroporus* species by orange-brown pileus with a margin splits on aging, smaller tubes, and presence of pleurocystidia (Magnago et al. 2018). *Gyroporus porphyreus* described from China and shows distinct differences with Kerala collection such as yellow-brown pileus that turn to purple, larger basidiospores (6.5 – 11 × 3.5 – 6 µm), and presence of pleurocystidia (Xie et al. 2022).

4.2.2.6 Boletinellaceae

Boletinellus Murrill

Basidiomata small to medium-sized. Pileus brownish with fulvous or olivaceous tinge and villose pileal margin. Hymenophore arcuate-decurrent and gyrose to alveolate; olivaceous brown to dull ochraceous unchanging or staining blue very slowly. Context of pileus and stipe pale olivaceous yellow. Basidiospores smooth, shortly ellipsoid to subreniform or shortly phaseoliform. Cheilo- and pleurocystidia poorly differentiated, fusoid to ventricose. Clamp-connections present in all tissues.

Boletinellus viridianus Salna Nanu and T. K. A. Kumar, Phytotaxa 594: 227 (2023)

Figure 11

Basidiomata medium-sized. **Pileus** 40 – 100 mm diam., convex when young becoming nearly applanate on maturity, slightly depressed in the centre with age; margin incurved to nearly undulate; surface glabrous or subvelutinous, becoming viscid when wet, brownish to yellowish brown, sometimes with greyish brown or dark brownish tinge. **Pileal context** thick, 10 – 25 mm, pale yellowish, slowly changing to greenish blue slowly on bruising. **Hymenophore** deeply decurrent, poroid-lamellate, lamellae connected with many cross-veins; pores 3 – 5 mm wide, nearly angular, elongate towards the margin, yellowish, pale yellow towards the margin, becoming brownish yellow with ageing, changing to bluish green immediately on bruising; tubes up to 3 mm long, yellowish, changing to bluish green when cut. **Stipe** 30 – 60 × 8 – 30 mm, eccentric to lateral, almost cylindrical, expanding towards the base, squamulose; squamules up to 3 mm long, yellowish, denser towards the centre, sparse towards base; surface pale yellowish in centre, off white to yellowish in lower and upper parts, changing to bluish green immediately on bruising. **Stipe context** thick, firm, pale yellowish, with pinkish or reddish-brown tinges, turning bluish slowly with touch or on bruising.

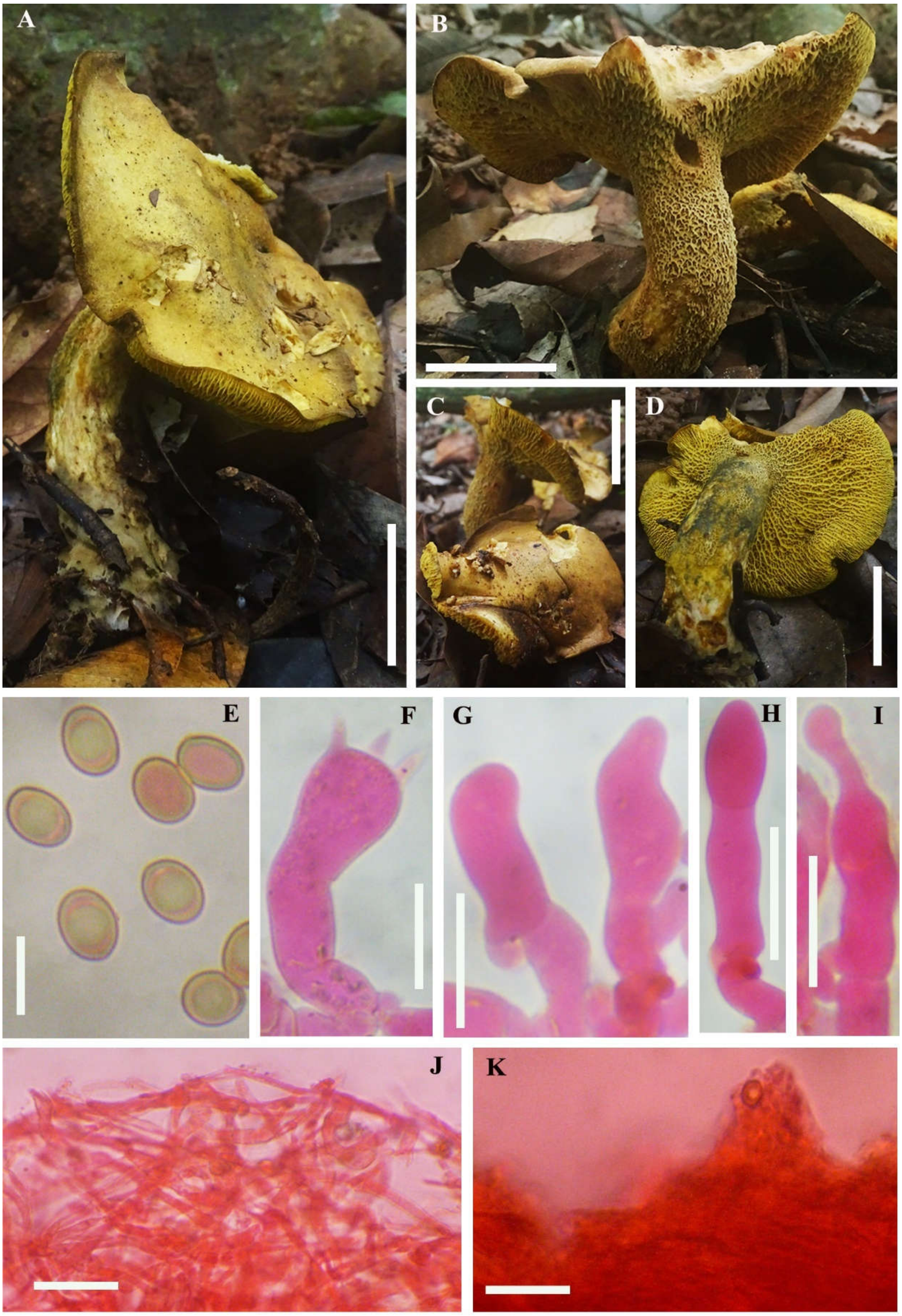


Figure 11. *Boletinellus viridianus*. A-D. Basidiomata E. Basidiospores F. Basidium G. Cheilocystidia H-I. Pleurocystidia J. Pileipellis K. Stipitipellis. Scale bars: A-D = 10 mm, E-I, J-K = 20 µm.

Basidiospores 6.5 – 7.5 × 5 – 5.5 µm (Q = 1.2 – 1.4, Qm = 1.29), oblong to shortly ellipsoid, with a large oil globule, yellowish in water, thin- to thick-walled (wall thickness up to 1 µm), inamyloid. **Basidia** 26 – 36 × 6 – 10 µm, narrowly clavate to clavate, 4- spored, rarely 2- spored, thin-walled, hyaline to pale yellow in water; sterigmata up to 5 µm long. **Pleurocystidia** 21 – 35 × 4 – 9 µm, rare, subfusiform or flexouse, septate in some, most with attenuated apex, thin- walled, pale yellow to hyaline in water. **Cheilocystidia** similar to pluerocystidia in size and shape, rare. **Hymenophoral trama** divergent sometime with cylindrical swollen hyphae; hyphae 3.5 – 21 µm wide, thin-walled, hyaline to pale yellow in water. **Pileipellis** a cutis with ascending to trichodermal patches of filamentous hyphae, 3 – 7 µm wide, thin- walled, pale yellowish in water. **Pileal trama** interwoven, hyphae 3 – 8 µm wide, thin-walled. Clamp-connections present in all hyphae.

Habitat: On soil. Scattered under *Terminalia* species.

Additional specimen examined: India, Kerala State, Palakkad district, Parambikkulam, 5 June 2022, Salna Nanu, ZGCSN163; 6 June 2022, Salna Nanu, ZGCSN186.

Comments: *Boletinellus viridianus* is a newly described species from Kerala (Salna and Kumar, 2023). *Boletinellus viridianus* possess deeply decurrent, poroid-lamellate hymenophore, eccentric to lateral stipe, rare, oblong to ellipsoid basidiospores, septate hymenial cystidia and clamp-connections on all hyphae. *B. viridianus* showed maximum similarities with *B. merulioides* in morphological and molecular study. *B. merulioides* was originally described as *Daedalea merulioides* De Schweinitz from northeastern United States (De Schweinitz 1832). *B. merulioides* is mostly found associated with ash trees (*Fraxinea* spp.) and well known as the ‘ash tree bolete’. Our species was collected around *Terminalia* species from evergreen forests of Kerala State. *B. viridianus* and *B. merulioides* have yellowish brown to reddish brown pileus, eccentric to lateral stipe and nearly ellipsoid, smooth basidiospores, trichodermal pileipellis and context unchanging or changing to bluish-green slowly on bruising or ageing (Murril 1909). However, our species differ from *B. merulioides* by having squamulose stipe surface, oblong to shortly ellipsoid, inamyloid basidiospores and presence of 2-spored and 4-spored basidia.

Boletinellus viridianus and *B. merulioides* form sister clades with 82% bootstrap support in phylogram (Figure 43). The new species also showed maximum percentage of identity (89.49%) in BLAST search with *B. merulioides* (Genbank accession number: MF161227) reported from United States of America. The phylogenetic studies revealed the presence of more than one species of *Boletinellus* in United States of America, and all are treated as *B. merulioides* (Liu *et al*. 2022). Detailed morphological study and disscussions on molecular phylogeny are given in Nanu and Kumar (2023).

Phlebopus (R. Heim) Singer

Basidiomata with typically robust stature. Stipe with a central thick, non-hollow centre. Basidiospores short, smooth, and olivaceous brown. Clamp-connections on hyphae of the basidiomata.

Phlebopus portentosus (Berk. and Broome) Boedijn, Sydowia 5: 218 (1951)

Figure 12

Basionym:

Boletus portentosus Berk. and Broome 1873

Synonymy:

Gyroporus portentosus (Berk. and Broome) G. Stev., Field Guide to Fungi: 91 (1982)
Phaeogyroporus portentosus (Berk. and Broome) McNabb, N.Z. Jl Bot. 6: 142 (1968)
Suillus portentosus (Berk. and Broome) Kuntze, Revis. gen. pl. (Leipzig) 3(3): 536 (1898)

Basidiomata large-sized. **Pileus** 140 – 200 mm in diam., hemispherical to broadly convex, yellowish brown to greyish brown when young becoming brownish to blackish on maturity, some parts with dirty white to light yellow as patches; margin slightly incurved in young specimens, becoming decurved at maturity, splitting in to many on maturation; surface dry, slightly viscid in wet weather, superficially smooth when young becoming minutely granulose on aging. **Pileal context** 15 – 30 mm thick at the centre of the pileus, fleshy, pale yellow to creamy white, becoming pale bluish and sometimes immediately changing to brown slowly on cut. **Hymenophore** poroid, depressed around apex of stipe; pores 1 – 2/ mm, round to angular, greyish yellow, turning reddish brown on bruising; tubes up to 10 mm long, concolorous with pores, slowly change the color to bluish when injured. **Stipe** 100 – 170 × 60 – 100 mm, central to slightly eccentric, greyish brown, darker in the apex, becoming reddish brown in areas when handled, almost cylindrical; context pale yellow or dirty white changing to bluish sometimes very slowly, basal mycelium yellowish.

Basidiospores 6 – 8 × 5 – 7 µm (Q = 1.1 – 1.5, Qm = 1.3), broadly ellipsoid, smooth, guttulate, thin to thick-walled (wall thickness up to 1 µm), pale yellow to yellowish in water, inamyloid. **Basidia** 13 – 18 × 6 – 7 µm, clavate, thin-walled, hyaline, inamyloid, 4- spored; sterigmata up to 6 µm long. **Hymenophoral trama** subregular, boletoid; hyphae 3 – 8 µm wide, pale yellow or hyaline, thin-walled, inamyloid. **Cystidia** not observed. **Pileipellis** a trichoderm with elongated terminal cells; terminal cells 3 – 7 µm long, narrowly clavate to cylindrical with round apex, hyaline, thin-walled, brownish yellow in Melzer’s reagent. **Pileal trama** subparallel; hyphae 6 – 13 µm, slightly thick-walled (thickness up to 0.5 µm), hyaline in water, brownish yellow in Melzer’s reagent; oleiferous hyphae present. **Stipitipellis** a cutis interrupted by trichodermal patches; terminal cells 13 – 30 × 4 – 12 µm, cystidioid, fusifom to cylindrical, thin-walled, hyaline. **Stipe trama** interwoven; hyphae 3 – 13 µm wide, thick-walled (thickness up to 1 µm), pale yellow to hyaline. **Clamp-connections** present on all hyphae.

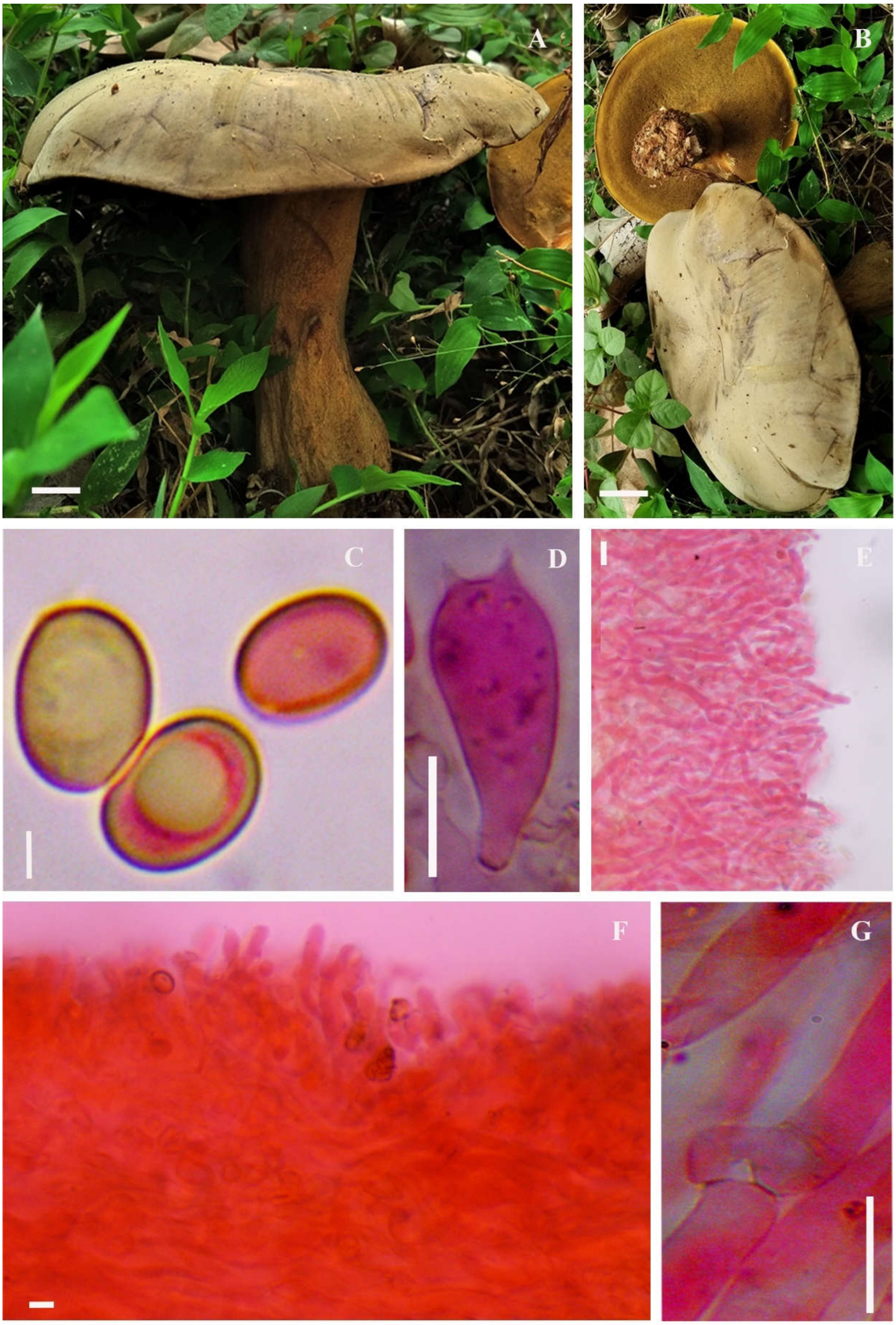


Figure 12. *Phlebopus portentosus*. A-B. Basidiomata C. Basidiospores D. Basidium E. Pileipellis F. Stipitipellis G. Clamp connection in hymenium. Scale bars: A-B = 10mm, C-D = 10 µm, F-G = 10 µm.

Habitat: On soil, solitary, near trees like *Macaranga peltata* and *Terminalia* species

Specimens examined: India, Kerala State, Kozhikode district, Pantheerankavu, 02 May 2019, Salna Nanu, ZGCSN15; 03 May 2019, Salna Nanu, ZGCSN16; Thottilpalam, 18 April 2021, Salna Nanu, ZGCSN62.

Comments: Large basidiomata, yellowish brown to greyish brown pileus when young then becoming brownish to blackish on maturity, pileal context changing to brownish on cut, absence of cystidia, broadly ellipsoid basidiospores are the distinguishing features of the present species. All these characters are similar to *Phlebopus portentosus* (Boedijn 1951; Raghoonundon et al. 2021). Raghoonundon et al. (2021) did not observe bluish color change on the pileal context, but some specimens collected from Kerala showed a pale bluish color on bruising which is changing to brown immediately. The molecular analysis with LSU data also supports the placement of Kerala collections. Our collections placed along with the collections obtained from China and Thailand with 100% bootstrap support in the phylogram (Figure 43). *Phlebopus portentosus* is using as edible by tribal people of Kannur, Wayanad and Palakkad district.

4.2.2.7 Suillaceae

Suillus Gray

Basidiomata stipitate-pileate. Pileus hemispherical to convex, yellowish brown, reddish brown, pale reddish or brownish, glabrous and viscid normally; context whitish to pale yellow, unchanging when bruised. Hymenophore poroid; pores small, round to angular, occasionally radially arranged, beaded with milky droplets when young; tubes normally concolorous with pores, unchanging when bruised. Stipe central, whitish to dirty white, solid, with scattered brownish glandular dots; context white or yellowish, unchanging when bruised. Basidiospores smooth, normally ellipsoid, thin-walled.

Pleurocystdia and cheilocystidia present, sometimes with brownish contents. Pileipellis trichoderm or ixotrichoderm. Clamp-connections absent.

Suillus granulatus (L.) Roussel, Fl. Calvados: 34 (1796)

Figure 13

Synonymy:

Agaricus granulatus (L.) Lam., Encycl. Méth. Bot. 1(1): 51 (1783)
Boletus campanulatus (J. Blum) J. Blum, Bull. trimest. Soc. mycol. Fr. 85: 43 (1969)
Boletus circinans var. *lactifluus* (With.) Pers., Syn. meth. fung. (Göttingen) 2: 506 (1801)
Boletus flavorufus Schaeff., Fung. bavar. palat. nasc. (Ratisbonae) 4: 83 (1774)
Boletus fusipes var. *pictilis* (Quél.) Bigeard and H. Guillemin, Fl. Champ. Supér. France (Chalon-sur-Saône) 2: 341 (1913)
Boletus granulatus L., Sp. pl. 2: 1177 (1753)
Boletus granulatus var. *campanulatus* J. Blum, Bull. trimest. Soc. mycol. Fr. 81: 485 (1965)
Boletus granulatus var. *flavorufus* (Schaeff.) J. Blum, Bull. trimest. Soc. mycol. Fr. 81: 484 (1965)
Boletus granulatus var. *heterosporus* J. Blum, Bull. trimest. Soc. mycol. Fr. 81: 485 (1965)
Boletus granulatus var. *lactifluus* (With.) J. Blum, Bull. trimest. Soc. mycol. Fr. 81: 484 (1965)
Boletus granulatus var. *longisporus* J. Blum and Perr.-Bertr., Bull. trimest. Soc. mycol. Fr. 81: 484 (1965)
Boletus granulatus var. *meridionalis* J. Blum, Bull. trimest. Soc. mycol. Fr. 81: 485 (1965)
Boletus granulatus var. *pictilis* (Quél.) J. Blum, Bull. trimest. Soc. mycol. Fr. 81: 485 (1965)
Boletus granulatus var. *rufopunctatus* J. Blum, Bull. trimest. Soc. mycol. Fr. 81: 485 (1965)
Boletus granulatus var. *violaceopunctatus* J. Blum and Azéma, Revue Mycol., Paris 31(5): 371 (1967) [1966]
Boletus heterosporus (J. Blum) J. Blum, Bull. trimest. Soc. mycol. Fr. 85: 43 (1969)
Boletus lactifluus (With.) J. Blum, Bull. trimest. Soc. mycol. Fr. 85(1): 43 (1969)
Boletus lactifluus Sowerby, Col. fig. Engl. Fung. Mushr., Suppl. (London)(no. 30 [no. 3 of suppl.]): tab. 420 (top) (1814)
Boletus lactifluus With., Arr. Brit. pl., Edn 3 (London) 4: 320 (1796)
Boletus longisporus (J. Blum and Perr.-Bertr.) J. Blum, Bull. trimest. Soc. mycol. Fr. 85: 42 (1969)
Boletus meridionalis (J. Blum) J. Blum, Bull. trimest. Soc. mycol. Fr. 85: 44 (1969)
Boletus pictilis (Quél.) Sacc. and Traverso, Syll. fung. (Abellini) 19: 170 (1910)
Boletus rufopunctatus (J. Blum) J. Blum, Bull. trimest. Soc. mycol. Fr. 85: 42 (1969)
Boletus violaceopunctatus (J. Blum and Azéma) J. Blum, Bull. trimest. Soc. mycol. Fr. 85: 42 (1969)
Ixocomus granulatus (L.) Quél., Fl. mycol. France (Paris): 412 (1888)
Ixocomus pictilis Quél., C. r. Assoc. Franç. Avancem. Sci. 22(2): 487 (1894)
Leccinum lactifluum (With.) Gray, Nat. Arr. Brit. Pl. (London) 1: 647 (1821)
Rostkovites granulatus (L.) P. Karst., Revue mycol., Toulouse 3(no. 9): 16 (1881)
Suillus collinitus var. *velatipes* Contu, Lavorato and Simonini, in Simonini, Fungi Non Delineati, Raro vel Haud Perspecte et Explorate Descripti aut Definite Picti 6: 26 (1998)
Suillus granulatus f. *marchandii* G. Moreno and Heykoop, Riv. Micol. 37(3): 226 (1994)
Suillus granulatus subsp. *leptopus* Singer, Farlowia 2(1): 42 (1945)
Suillus granulatus subsp. *snellii* Singer, Farlowia 2(1): 40 (1945)
Suillus granulatus var. *snellii* (Singer) Blanco-Dios, Tarrelos 20: 31 (2018)
Suillus granulatus var. *velatipes* (Contu, Lavorato and Simonini) Klofac, in Klofac and Krisai-Greilhuber, Öst. Z. Pilzk. 27: 261 (2018)
Suillus lactifluus (With.) A.H. Sm. and Thiers, Michigan Bot. 7: 16 (1968)
Viscipellis granulata (L.) Quél., Enchir. fung. (Paris): 156 (1886)

Basidiomata small-sized. Pileus 30 – 90 mm in diam, hemispherical to applanate; surface dirty white to whitish yellow, brownish orange to reddish brown in middle, glabrous, viscid; margin slightly incurved to straight. **Pileal context** up to 8 mm thick, whitish, unchanging the color when bruised. **Hymenophore** adnate to sinuate; surface pale yellow to bright yellow, creamy white towards the margin, unchanging when bruised; pores round, 2 per mm; tubes up to 4 mm long, creamy white to pale yellow, unchanging when bruised, often beaded with milky droplets when young. **Stipe** 6 – 12 × 3 – 8 mm, subcylindrical, central, tapering towards the base; surface creamy white with pale pinkish tinges, with glandular dots. **Stipe context** whitish, unchanging the color when bruised.

Basidiospores 6 – 9 × 3 – 4 µm (Q = 1.8 – 3, Qm = 2.1), ellipsoid, smooth, thin-walled, hyaline to pale yellow in water. **Basidia** 17 – 26 × 5 – 7 µm, clavate, 4- spored, thin-walled, hyaline; sterigmata up to 3 µm long. **Pleurocystidia** 20 – 52 x 3 – 8 µm, fusoid, narrowly lageniform, thin-walled, brownish yellow in water. **Cheilocystidia** 24 – 46 × 5 – 7 µm, fusiform, thin-walled, brownish yellow in water. **Pileipellis** an ixocutis, up to 110 µm wide, consist of interwoven, more or less elongated, cylindrical, pale yellowish hyphae with crystalline contents, embedded in gelatinous matrix; terminal cells subclavate with obtuse apex, 12 – 16 µm long. **Pileal trama** interwoven, hyphae 3 – 12 µm wide, thin-walled, pale yellow in water. **Stipitipellis** a cutis interrupted by bunches of caulocystidia. **Caulocystidia** 20 – 42 × 6 – 12 µm, fusoid, clavate or lanceolate, thin-walled, brownish yellow in water. **Clamp-connections** not observed.

Habitat: On soil, solitary to scattered, always found near *Pinus* species.

Specimens examined: India, Kerala State, Idukki District, Vagamon Pine valley, on soil, associated with *Pinus,* 4 July 2019, Salna Nanu, ZGCSN32; 19 July 2023, Salna Nanu, ZGCSN217.

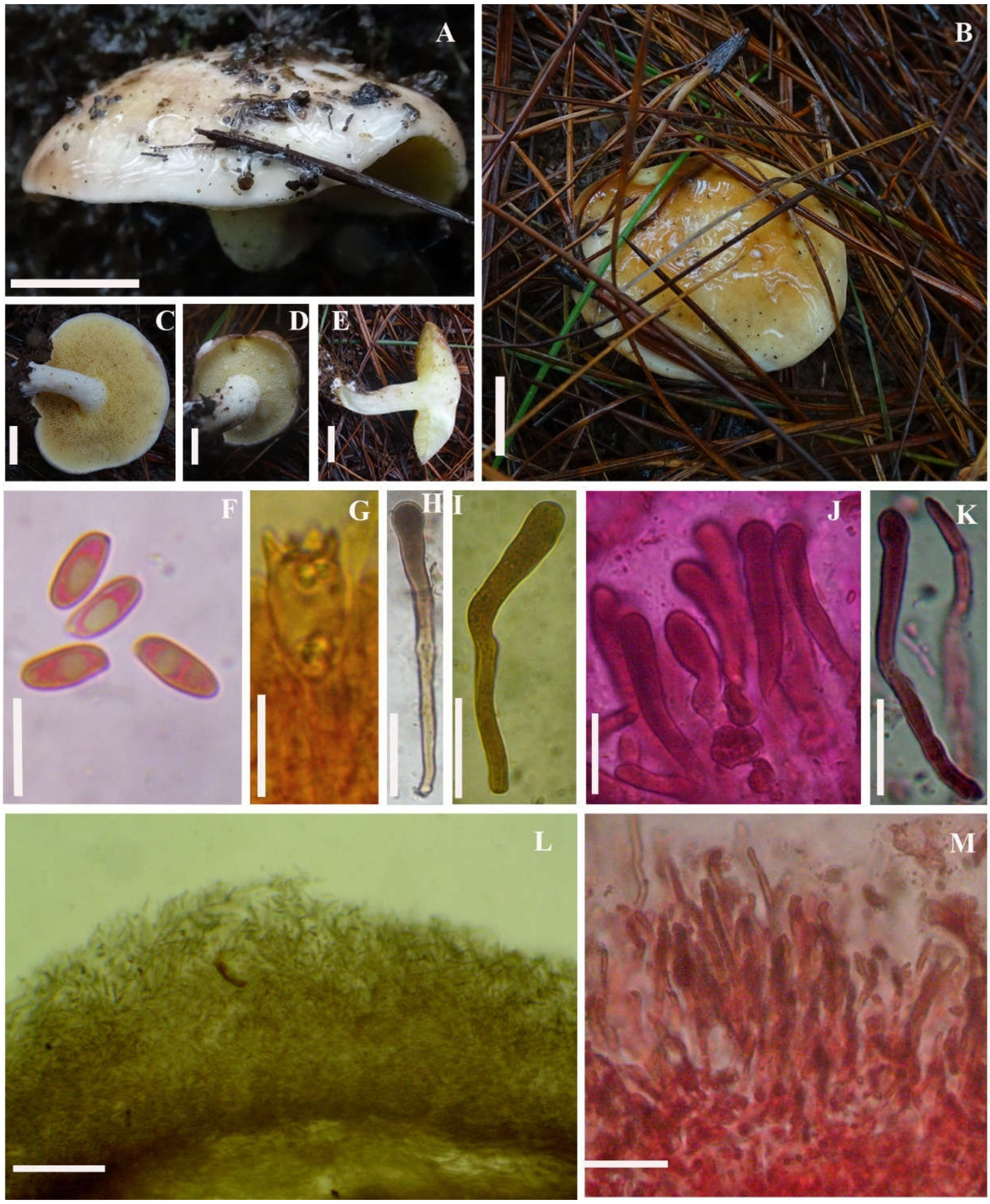


Figure 13. *Suillus granulatus*. A-C, E. Basidiomata D. Young basidiomata showing milky droplets F. Basidiospores G Basidia H-I. Pleurocystidia J. Cheilocystdia K. Caulocystidia L. Pileipellis M. Stipitipellis. Scale bars: A-C= 2 cm, D-I, L-M=10 μm, J-K=20 μm.

Comments: *Suillus granulatus* is an ectomycorrhizal species associated with *Pinus* species*. Suillus granulatus* can be considered as edible, and it is a source of nutraceutical and biologically active compounds (Reis et al. 2014). *Suillus granulatus* reported worldwide and can be distinguished from other closely related *Suillus* species by the absence of an annulus, and the secretion of droplets when young. Kerala specimens show close similarity with Malaysian collections (Horak 2011) except for size difference of caulocystidia. Molecular phylogenetic analysis also confirms the species identity (Figure 47).

4.2.2.8 Boletaceae

Phylloporus Quél.

Basidiomata stipitate-pileate. Pileus surface dry, subtomentose, normally brownish or yellowish. Pileal context yellowish, becoming dark blue on bruising. Hymenophore lamellate, lamellae subdecurrent or decurrent. Stipe central, almost equal, with glabrous or faintly striated surface. Hymenophoral trama phylloporoid. Basidiospores fusoid or ellipsoid, smooth. Plearocystidia and cheilocystidia fusoid, broadly clavate or lanceolate. Pileipellis a trichodermium. Stipitipellis a trichodermium consist of caulocystidia. Clamp-connections absent.

Phylloporus septocystidiatus C.K. Pradeep and K.B. Vrinda, in Pradeep, Vrinda, Varghese and Arun Kumar, Phytotaxa 226: 270 (2015)

Figure 14

Basidiomata small. **Pileus** 25 mm diam., plano-convex, with a shallow depression at center; surafce yellowish brown, subtomentose; margin somewhat uplifted. **Hymenophore** lamellate; lamellae decurrent, up to 4 mm wide, thick, yellowish to brownish yellow. **Stipe** 40 × 5 mm, central, cylindrical, striations present in upper half, tomentose under stereo microscope, yellowish to brownish yellow.

Basidiospores 6.5 – 8.5 × 3.5 – 4.5 µm (Q = 1.6 – 2.1, Qm = 1.83), broadly ellipsoid, thick-walled (wall thickness up to 7 µm), smooth, hyaline to pale yellow in water. **Basidia** 38 – 40 × 5.5 – 6 µm, elongate clavate, 4-spored, thin-walled, hyaline to pale yellow in water; sterigmata up to 3 µm long.

Hymenophoral trama phylloporoid, bilateral with slightly divergent hyphae; hyphae 6 – 14 µm wide, short, thin-walled, hyaline; subhymenium composed of interwoven hyphae. **Pleurocystidia** 45 – 85 × 9 – 11.5 µm, variously shaped, fusoid, narrowly clavate, 1,2, or 3 septate, thick-walled (wall thickness up to 1 µm, hyaline in water. **Cheilocystidia** 34 – 70 × 6 – 11 µm, similar to pleurocystidia in shape, hyaline in water. **Pileipellis** trichodermium composed of cylindric to cylindro-clavate elements, 25 – 55 × 7 – 11 µm, thin-walled, hyaline to pale yellow in water. **Pileal trama** interwoven; hyphae 4 – 10 µm wide, thin-walled, hyaline in water. **Stipitipellis** a trichodermium composed of interwoven hyphae with caulocystidia; hyphae 3 – 7 µm wide. **Caulocystidia** 30 – 85 × 7 – 12 µm, cylindrical, flexuose, thick-walled, with pale yellow plasmatic contents. Stipe trama parallel; hyphae 5 – 12 µm, thin-walled, hyaline in water. **Clamp-connections** absent.

Habitat: On soil, solitary to scattered on soil or on mud wall under *Hopea parviflora* Bedd. (Dipterocarpaceae) and *Xanthophyllum arnottianum* Wight (Xanthophyllaceae) trees in tropical evergreen forest.

Specimens examined (herbarium material): India, Kerala State, Thiruvananthapuram district, Palode, JNTBGRI campus, 02 May 2014, TBGT14975.

Comments: Studied with dried specimens (collection no: TBGT14975). *Phylloporus septocystidiatus* is the only species reported from Kerala State in the genus *Phylloporus*. It was reported as a new species from India. Herbarium material was received from Jawaharlal Nehru Tropical Botanic Garden and Research Institute, Thiruvananthapuram. The specimen was in good condition. All the morphological characters seem to be similar to the original description (Pradeep et al. 2015) except the size of hymenial cystidia. Specimen with collection number TBGT14975 showed larger cystidia (34 – 85 × 6 – 11 µm). However, the size of cystidia ranges 28.5 – 47.5 × 8.5 – 15 µm in original description by Pradeep et al. (2015).

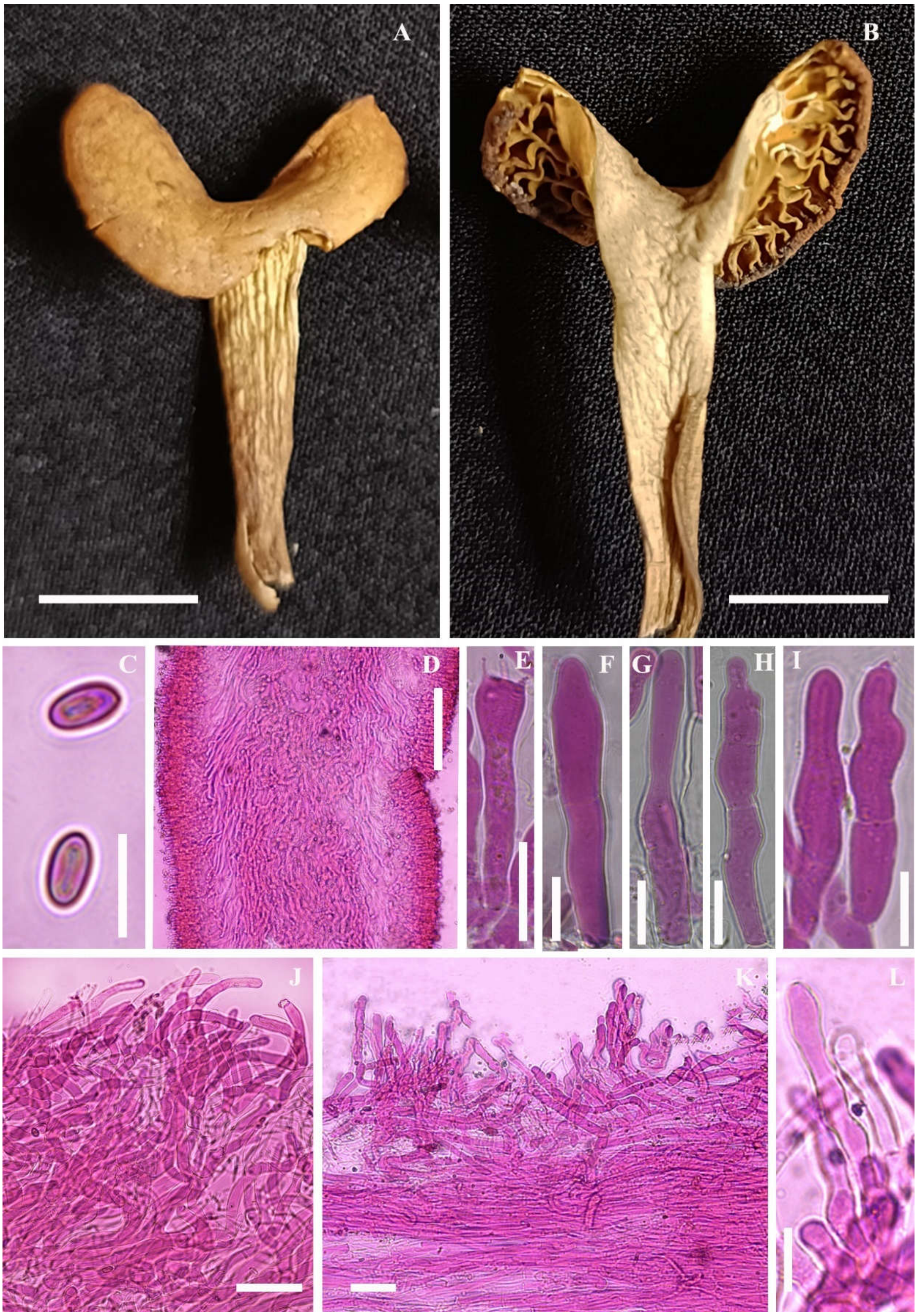


Figure 14. *Phylloporus septocystidiatus*. A-B. Basidiomata (Photos taken from herbarium materials) C. Basidiospores D. Hymenophoral trama E. Basidia. F-H. Pleurocystidia I. Cheilocystidia J. Pileipellis K. Stipitipellis. L Caulocystidia. Scale bars: A-B= 10 mm, C, E-I = 10 µm, D = 50 µm, J-L = 20 µm.

Erythrophylloporus Ming Zhang and T.H. Li

Basidiomata stipitate-pileate. Pileus subhemispheric to convex when young becoming convex to plano-convex to convex when old, dry, pruinose or velutinous, subtomentose to tomentose, yellowish-orange to red. Pileus context vivid yellow to yellowish-orange. Hymenophore lamellae, slightly thick, decurrent, deeply yellowish-orange to deep orange or reddish-orange to orange red or brownish-orange to red. Stipe central to slightly excentric, cylindrical or clavate, yellowish- to reddish-orange to yellowish red, with scattered yellowish- to reddish-orange to red squamules on surface, with bright yellow basal mycelium. Stipe context solid, yellow to reddish-yellow or yellow with olivaceous brown. Basidiospores ovoid or ellipsoid to broadly ellipsoid to subovoid, thin-walled, with non-bacillate surface. Basidia clavate to narrowly clavate. Cheilocystidia and pleurocystidia present, subcylindrical or narrowly conical to narrowly fusiform to ventricose with slightly or obtuse apex, thin-walled, sometimes thick-walled and sometimes containing yellowish-brown pigments. Pileipellis a subcutis to cutis to trichoderm to palisadoderm, composed of thin to slightly thick-walled hyphae. Clamp connection absent in all tissues.

Erythrophylloporus suthepensis Vadthanarat, Raspé and Lumyong, in Vadthanarat, Amalfi, Halling, Bandala, Lumyong and Raspé, MycoKeys 55: 48 (2019)

Figure 15

Basidiomata medium-sized, stipitate-pileate. **Pileus** 13 – 40 mm, hemispherical to convex when young, plano-convex at maturity; margin slightly incurved to straight; surface dry, glabrous, yellowish brown to brown, becoming blackish on aging. **Pileal context** bright yellow, unchanging when bruised. **Hymenophore** lamellate; lamellae subdecurrent, closely packed, thick, brownish orange with yellowish tinge, with deep yellow to orange edge. **Stipe** 18 – 80 × 5 – 10 mm, central, almost cylindrical, brownish, yellowish at the base and apex. **Stipe context** bright yellow to yellow, unchanging when bruised.

Basidiospores 5 – 7 × 4 – 5 μm (Q = 1.2 – 1.6, Qm = 1.32), broadly ellipsoid to subglobose, smooth, thin-walled, pale yellow in water. **Basidia** 32 – 40 × 4 – 7 μm, 4-spore, thin-walled, hyaline to pale yellow in water; sterigmata up to 7 μm long. **Hymenophoral trama** subregular to slightly divergent; hyphae 4 – 9 μm wide, thin-walled, hyaline. **Pleurocystidia** 75 – 130 × 9 – 16 μm, narrowly lageniform, thin-walled, hyaline to pale yellow in water. **Cheilocystidia** 40 – 82 × 10 – 12 μm, similar to pleurocystidia, lageniform, thin-walled, hyaline. **Pileipellis** a trichodermium composed of cylindrical hyphae; terminal cells 25 – 50 × 5 – 10 μm, with rouded apex, thin-walled, hyaline. **Pileal trama** interwoven; hyphae 4 – 10 μm wide, thin-walled, pale yellowish in water. **Stipitipellis** a trichodermium; terminal elements 28 – 78 × 4 – 7 μm, thin-walled, pale yellow in water. **Clamp-connections** not observed.

Habitat: On soil, solitary to scattered.

Specimens examined: India, Kerala State, Palakkad District, Silent Valley National Park, 23 October 2019, Salna Nanu, ZGCSN57.

Comments: *Erythrophylloporus suthepensis* is characterised by yellow to dull red pileus, brownish-orange lamellae with deep yellow to orange edge, pileus surface and lamellae turning blue when bruised, some pleurocystidia containing yellowish-brown to dark brown pigments in water (Vadthanarat et al. 2019). *Erythrophylloporus suthepensis* shows morphological similarity with *E. cinnabarinus* by having similar colored basidiomata and presence of yellowish brown contents in pleurocystdia. However, *E. cinnabarinus* can be distinguished from *E. suthepensis* by larger size of basidiospores (Zhang and Li 2018). Kerala collection is morphologically closely similar to the Thailand collections (holotype) of *E. suthepensis* (Vadthanarat et al. 2019).

Figure 15. *Erythrophylloporus suthepensis*. A-B. Basidiomata C. Basidiospores D-F. Pleurocystidia G. Cheilocystidia H. Lamellar section I. Pileipellis J. Stipitipellis. Scale bars: A-10 = mm, B-G, I-J = 10 µm, H = 20 µm.

Rubroboletus Kuan Zhao and Zhu L. Yang

Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical, convex or applanate, greyish, pinkish to red; context white, yellowish to lemon-yellow, bluing quickly when exposed. Hymenophore surface orange red to blood red, sometimes orange-yellow when mature, rapidly bluing when bruised; tubes yellow to olivaceous green, turning blue promptly when injured, then back to the original color slowly. Stipe central, covered with pinkish, red to brownish red reticula or spots. Pileipellis an interwoven trichoderm composed of more or less vertically arranged, sometimes gelatinized filamentous hyphae. Hymenophoral trama boletoid. Basidiospores smooth, subfusiform to ovoid-ellipsoid, slightly thick-walled. Pleuro- and cheilocystidia lageniform, thin-walled. Clamp-connections absent. Amyloid reaction not observed.

***Rubroboletus* species**

Figure 16

Basidiomata small- to medium-sized. **Pileus** 15 – 25 mm in diam., hemispherical when young becoming applanate at maturation; surface greyish red to dark red, dry, pruinose, dark immediately turning blue to dark blue on bruising. **Pileal context** 5 – 15 mm thick, cream to white, turning blue to dark blue on bruising. **Hymenophore** somewhat depressed around stipe apex; surface pinkish to reddish, fading with aging, immediately changing to blue with bruising; pores round to angular, 1 – 2 per mm; tubes up to 3.5 mm long, yellowish, rapidly changing to blue on bruising. **Stipe** 20 – 40 × 5 – 15 mm, reddish, paler towards the middle, with scattered darker pruinose patches, changing to dark blue on bruising, subcylindrical, broadening towards the base. **Stipe context** pale yellow, turning blue quickly when cut. **Basal mycelium** white.

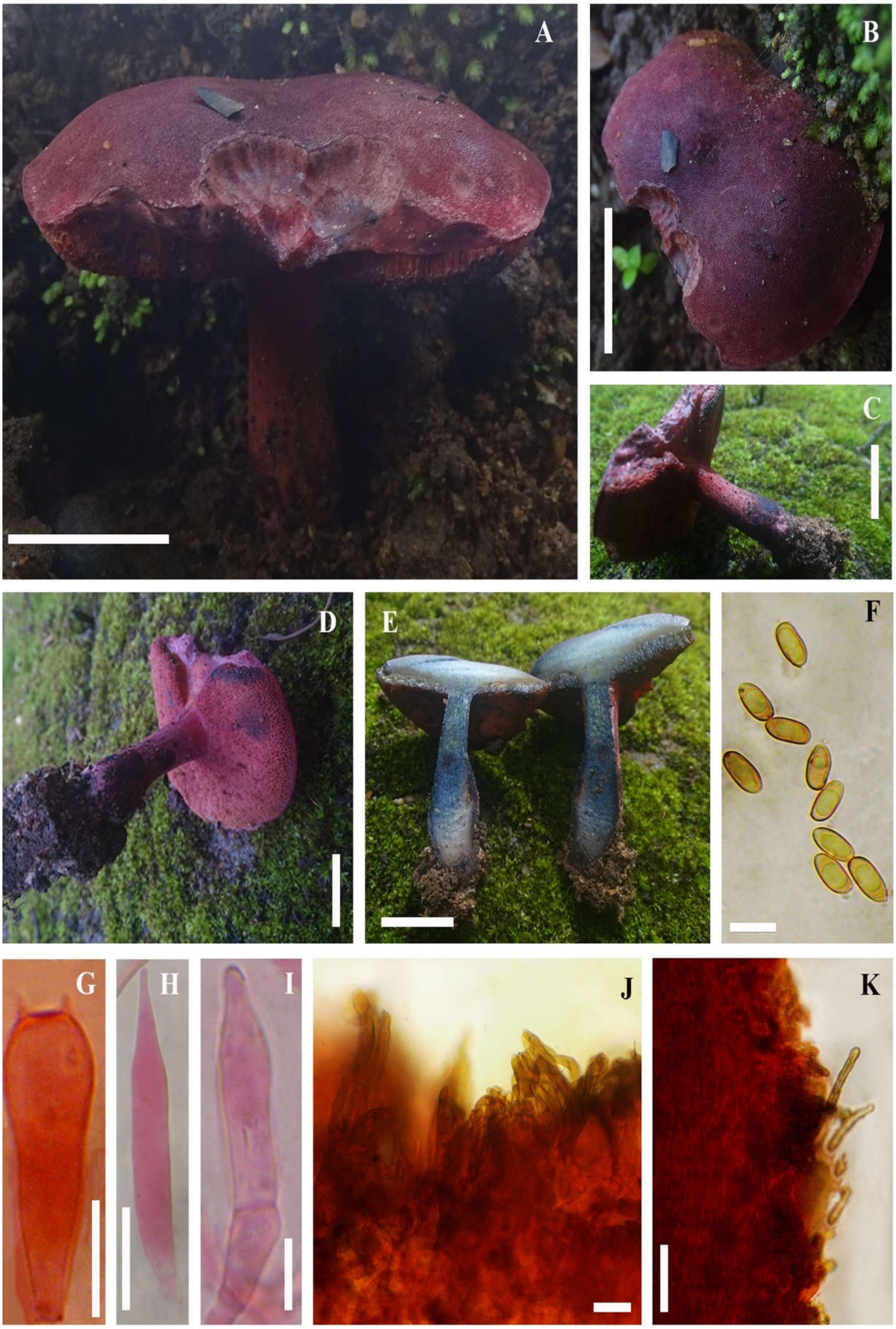


Figure 16. *Rubroboletus* species. A-E. Basidiomata. F Basidiospores G. Basidia H. Pleurocystidia I. Cheilocystidia J. Pileipellis K. Stipitipellis. Scale bars: A, B, C, D, E =10 mm, F, G, H, I =10 μm, J, K = 20 μm.

Basidiospores 8 – 10 × 4.5 – 5.5 µm (Q = 1.6 – 2 µm, Qm = 1.74 µm), broadly ellipsoid, smooth, with a large guttule, thin- to thick-walled, hyaline to pale yellow, inamyloid. **Basidia** 24 – 31 × 9 – 13 µm, clavate, thin-walled, 4-spored, hyaline, inamyloid, sterigmata up to 4 µm long. **Pleurocystidia** 28–60 × 7–9 µm, lageniform, mostly with apical protrusions up to 11 µm long, thin-walled, yellow or yellowish brown in water, inamyloid. **Cheilocystidia** 26 – 40 × 6 – 10.5 µm, lageniform, utriform, abundant, thin-walled, hyaline to pale yellow in water, inamyloid. **Pileipellis** a cutis disrupted by trichodermial patches of ascending to erect hyphae with cylindrical end cells; end cells 2 – 6 µm wide, thick-walled (wall thickness up to 1.5 µm), yellowish to bright yellow in water; hyphae 3 – 6 µm wide, thick-walled (wall thickness up to 1.5 µm), with reddish brown plasmatic pigment. **Pileal trama** interwoven; hyphae 4 – 10 µm wide, thin-walled, hyaline to pale yellow, inamyloid. **Stipitipellis** a cutis disrupted by trichodermial patches; terminal elements 2 – 4 µm wide, slightly thick-walled (wall thickness up to 0.5 µm), cylindrical, with brownish yellow plasmatic pigments. **Stipe trama** interwoven, hyphae 3 – 10 µm, hyaline, thin-walled.

Habitat: On soil. Solitary.

Specimens examined: India, Kerala State, Kollam district, near Ammayambalam temple, 10 August 2021, Salna Nanu, ZGCSN100.

Comments: Kerala collection of *Rubroboletus* is characterized by medium-sized basidiomata, greyish red to dark red pileus, pinkish to reddish pores fading with aging, stipe with pruinose surface, 4-spored basidia and cutis interrupted by trichodermial patches in pileipellis. Kerala collection shows resemblances with *Rubroboletus legaliae* in having depressed hymenial region around the stipe apex, yellowish tubes, color change of the pileal context to blue when bruised, and pleurocystidia and cheilocystidia with identical shapes and dimensions. However, *R. legaliae* differs from Kerala collection in having larger basidiomata, reticulated stipe surface, larger basidiospores (10 – 15 × 4.5 – 5 μm), pileipellis that is an intricate trichodermium and by the presence of caulocystidia. *Rubroboletus rhodosanguineus* shows similar characters with this prorposed new species like pileus color, context of the pileus and stipe changing to blue when hurt and subcylindrical stipe. But, *R. rhodosanguineus* has a smell of over-ripe fruit, yellowish pileal context, glabrous pileal surface and mostly distributed in North and Central America and Europe.

Our species is clustering as a separate taxon within *Rubroboletus* clade of the *Pulveroboletus* group in the maximum likelihood analysis (Figure 42). The species is described here as distinct based on the morphological and molecular evidences.

Chalciporus Bataille

Basidiomata stipitate-pileate with tubular hymenophore. Pileus convex to broadly convex, glabrous to obscurely subtomentose, dry, but sometimes subviscid when wet; context whitish to light yellow, unchanging or staining bluish slowly when injured. Hymenophore decurrent; hymenophoral pores and tubes concolorous, pinkish red to reddish brown, unchanging or staining bluish to dull blue slowly when cut. Pileipellis composed of trichoderm to matted interwoven hyphae. Pleuro- and cheilocystidia subfusiform-ventricose, with subacute apex or long beak. Basidiospores smooth, subfusiform, pale yellow to olive yellow. Clamp-connections absent.

Chalciporus rubrostipitatus Salna Nanu and T. K. A. Kumar, Mycologia (2024)

Figure 17

Basidiomata small. **Pileus** 15 – 30 mm in diameter, convex when young, becoming applanate with maturity, margin slightly incurved; surface dark purplish red when young, pinkish red to reddish when mature, aging with a yellowish shade especially towards the margin, glabrous when young, becoming subtomentose to rugose with the formation of cracks like spaces on the surface with age. **Pileal context** up to 7 mm wide at the centre, whitish, without color change when cut. **Hymenophore** poroid, nearly adnate to slightly depressed around the stipe apex; pores round to merulioid, 2 – 3 per mm; surface pinkish when young becoming paler with maturity, no color change when bruised; tubes up to 5 mm long, pinkish pinkish when young becoming paler with maturity. **Stipe** 10 – 30 × 3 – 10 mm, central, solid, cylindrical, becoming wider towards the apex; surface reddish orange to red with pale yellowish tinges on maturity, minutely pruinose towards the apex. **Stipe context** pale yellowish, no color change when cut. **Basal mycelium** whitish.

Basidiospores 7 – 9.5 × 3.5 – 4 µm (Q= 1.8 – 2.3, Qm = 2.16), ellipsoid to subfusiform, thin- to slightly thick-walled (up to 0.5 µm), smooth, pale yellowish in water, inamyloid. **Basidia** 25 – 31 × 6 – 9 µm, clavate, 4-spored, thin-walled, hyaline to pale yellow in water; sterigmata up to 4 µm long. **Hymenophoral trama** boletoid; hyphae 3 – 8 µm wide, pale yellow to brownish yellow in water, thin-walled. **Pleurocystidia** 31 – 50 × 6 – 8.5 µm, lageniform or utriform, thin-walled, hyaline to pale yellow in water. **Cheilocystidia** 30 – 45 × 4 – 6.5 µm, lageniform, thin-walled, hyaline to pale yellow in water. **Pileipellis** a trichodermium up to 120 – 135 µm wide; terminal cells 18 – 60 × 4 – 13 µm wide, thin- to thick-walled, cylindrical, lageniform, utriform with apical protrusions up to 15 µm, brownish in water. **Pileus trama** interwoven, hyphae 4 – 15 µm wide, thin- to slightly thick-walled. **Stipitipellis** basically a cutis interrupted by ascending hyphae towards stipe apex, that are 4 – 8 µm wide thin-walled, reddish brown in water; a cutis in middle to bottom with reddish brown, thin-walled hyphae. Stipe trama sub-parallel; hyphae 4 – 10 µm wide, thin-walled, yellowish brown in water. **Clamp-connections** not observed.

Habitat: On soil, scatterd under the *Acacia auriculiformis*.

Figure 17. *Chalciporus rubrostipitatus*. A-D. Basidiomata E. Basidiospores F. Basidium G-H. Pleurocystidia I-J. Cheilocystidia K. Pileipellis L. Element of pileipellis. Scale bars: A-D = 10 mm, E-J, L = 10 µm, K,M = 20 µm.

Specimens examined: India, Kerala State, Kozhikode District, Zamorin's Guruvayurappan College campus, 15 May 2022, Salna Nanu, ZGCSN160; 16 May 2022, Salna Nanu, ZGCSN153.

Comments: *Chalciporus rubrostipitatus* is characterized by basidiomata with a rugose pileus that is dark purplish red when young, pinkish red to reddish when mature, with cracks like spaces, whitish pileal context unchanging when cut, round to merulioid pores, minutely pruinose stipe surface at the apex, ellipsoid to subfusiform basidiospores, trichodermium type of pileipellis with hyphae having brownish contents and a stipitipellis basically a cutis, interrupted by ascending hyphal patches in the stipe apex.

Chalciporus rubrostipitatus shows morphological resemblances with *C. vulparius,* a species described from China (Xu et al. 2021). Both of the specimens possess reddish basidiomata, whitish pileal context, which is unchanging when bruised, 4-spored basidia, ellipsoid to subfusiform, slightly thick-walled basidiospores, and trichodermial type of pileipellis. But *C. vulparius* can be distinguished from *C. rubrostipitatus* by the presence of a pileus without rugose nature, stipe surface densely covered with squamules and a trichodermium type of stipitipellis. Moreover, Indian collections were always found associated with *Acacia auriculiformis* while, *C. vulparius* was collected from forests dominated by Fagaceae trees (Xu et al. 2021). *Chalciporus rubrostipitatus* clusters with other *Chalciporus* species forming a well-supported clade with maximum bootstrap (100%) value in maximum likelihhod analysis (Figure 42). Detailed Phylogenetic analysis and comparisons are presented in Nanu and Kumar (2024a).

Strobilomyces Berk.

Basidioma stipitate-pileate with tubular hymenophore, mostly dark brown to blackish. Pileus hemispherical, convex or applanate, coarsely squamose or squamulose, dry, margin oftenappendiculate; context whitish to greyish or pale greyish cream, quickly staining reddish then slowly blackish when injured. Hymenophore adnexed or adnate; hymenophoral surface whitish cream, greyish brown or vinaceous, staining reddish then blackish when injured; pores angular; tubes concolorous with hymenophoral surface, staining reddish then blackish when injured. Stipe central, ornamented with woolly or fibrillose squamules, apical or upper part usually reticulate; partial veil often present, persistent as an annulus on the stipe apex or as an appendiculate margin on the pileus; basal mycelium whitish to blackish. Basidiospores subglobose to obtusely ellipsoid, blackish brown, echinulate, reticulate or longitudinally striate. Pleuro- and cheilocystidia subfusiform, ventricose or clavate. Pileipellis often an intricated trichodermium, composed of loosely branching hyphae. Clamp-connections absent.

Strobilomyces giganteus M. Zang, Acta bot. Yunn. 7(4): 385 (1985)

Figure 18

Basidiomata medium-sized. **Pileus** 40 – 120 mm in diam., hemispherical; surface dry, hard, greyish, covered densely with greyish to black tufts of subpyramidal squamules; margin narrowly appendiculate with whitish to greyish membraneous veil. **Pileal context** whitish to grey, 6 mm thick, staining orange red immediately then to blackish slowly. **Hymenophore** adnate, surface white when young, becoming greyish on maturation, staining dark orange red to reddish immediately, then blackish when bruised; pores almost round to angular, 1 or 2/mm; tubes 7 – 10 mm long, whitish to greyish changing to copper red when bruised. **Stipe** 50 × 15 mm, cylindrical, whitish in the apex, becoming greyish to black to the bottom, with conical squamules to fluffy floss; context concolorous with pileal context, color changes similar to tubes; basal mycelium whitish black.

Basidiospores 7 – 9.5 × 7.5 – 9.5 µm (Q = 1 – 1.1, Qm = 1.04), globose to subglobose, sometimes broadly ellipsoid, with pronounced apiculus, thin to thick-walled (wall thickness up to 0.5 µm), pale yellowish brown in water, inamyloid, reticulated under light miceroscope and SEM; reticulations complete. **Basidia** 42 – 51 × 14 – 20 µm, clavate, thin-walled, pale yellowish in water, 4- sterigmate; sterigmata up to 9 µm long. **Pleurocystidia** 42 -79 × 17 – 20 µm, infrequent, nearly clavate or fusiform, with small beak in some, thin-walled, hyaline or with yellowish brown contents. **Cheilocystidia** 52 -77 × 11 – 16 µm, broadly clavate to fusiform, frequent, thin-walled, with pale yellow to brownish yellow contents. **Hymenophoral trama** boletoid; hyphae 3 – 9 µm, thin-walled, with yellowish brown crystals. **Pileipellis** a trichodermium composed of thin-walled, yellowish brown, interwoven, septate hyphae, 4 – 8 µm wide; terminal cells 3 -16 µm wide, slightly attenuate towards the apex. **Pileal trama** interwoven; hyphae 3 – 10 µm wide, thin-walled with yellowish brown pigments. **Stipitipellis** covered by a caulohymenium with caulobasidia and cystidioid elements; caulobasidia numerous, similar to hymenial basidia in size, shape, and color, thin-walled; cystidioid elements 13 – 37 × 11 – 21 µm, broadly clavate or floccose, thin-walled. **Stipe trama** parallel to interwoven; hyphae 3 – 10 µm wide, thin-walled. **Clamp-connections** not observed.

Habitat: On soil, near Dipterocarpaceae trees.

Specimens examined: India, Kerala State, Wayanad district, Kuruva Islets, 13 October 2021, Salna Nanu, ZGCSN107; Kozhikode district, Thurayil Kotta sacred grove, 20 June 2023, Salna Nanu, ZGCSN205, ZGCSN210; 26 June 2023, Salna Nanu, ZGCSN212.

Comments: *Strobilomyces giganteus* is characterized by medium-sized basidiomata, pileus with hard conical squamules, orange red color change of the pileal context when bruised, whitish stipe surface with conical squamules to fluffy floss, reticulated basidiospores, and presence of pleurocystidia and

Figure 18. *Strobilomyces giganteus*. A-C. Basidiomata D. Basidiospores E. Basidium F-G. Pleurocystidia H-I. Cheilocystidia J. Pileipellis K. Stipitipellis. Scale bars: A-C = 10mm, D-I = 10, J-K = 20 µm.

cheilocystidia. However, the type specimens showed a spore range of 8.5 – 10 × 7 – 8.5 µm (Han et al. 2020). But, Kerala collections have a spore range of 7 – 9.5 × 7.5 – 9.5 µm. Phylogenetic analysis also substantiates the species identification. Maximum likelihood analysis by using ITS gene sequences confirmed the identifation of *S. giganteus.* Kerala collection clustered with other *S. giganteus* collection with 100% bootstrap support (Figure 42).

Strobilomyces strobilaceus (Scop.) Berk., Hooker's J. Bot. Kew Gard. Misc. 3: 78 (1851)

Figure 19

Synonymy:

Boletus cinereus Pers., Syn. meth. fung. (Göttingen) 2: 504 (1801)
Boletus floccipes Spreng., Syst. veg., Edn 16 4(1): 470 (1827)
Boletus floccopus Vahl, Fl. Danic. 8: tab. 1252 (1797)
Boletus squarrosus subsp. strobilinus (Dicks.) Pers., Mycol. eur. (Erlanga) 2: 145 (1825)
Boletus strobilaceus Scop., Annus hist.-nat. 4: 148 (1770)
Boletus strobiliformis Dicks., Fasc. pl. crypt. brit. (London) 1: 17 (1785)
Boletus strobiliformis Vill., Hist. pl. Dauphiné 3(2): 1039 (1789)
Boletus strobilinus Dicks., Plantarum cryptogamicarum britanniae 1: 17, tab. 3, fig. 2 (1785)
Eriocorys strobilacea (Scop.) Quél., Enchir. fung. (Paris): 163 (1886)
Eriocorys strobilacea var. floccopus (Vahl) Quél., Enchir. fung. (Paris): 163 (1886)
Strobilomyces floccopus (Vahl) P. Karst., Bidr. Känn. Finl. Nat. Folk 37: 16 (1882)
Strobilomyces squarrosus var. floccopus (Vahl) Gillot and Lucand, Bull. soc. Hist. nat. Autun 3: 142 (1890)
Strobilomyces strobilaceus subsp. floccopus (Vahl) P. Karst., Bidr. Känn. Finl. Nat. Folk 37: 16 (1882)
Strobilomyces strobilaceus var. mexicanus R. Heim and Perr.-Bertr., Bull. trimest. Soc. mycol. Fr. 80(1): 100 (1964)
Strobilomyces strobilaceus var. zapotecorum R. Heim and Perr.-Bertr., Bull. trimest. Soc. mycol. Fr. 80(1): 100 (1964)
Strobilomyces strobiliformis Beck, Z. Pilzk. 2(7): 148 (1923)
Suillus cinereus (Pers.) Poiret, in Lamarck, Encycl. Méth. Bot. (Paris) 7: 496 (1806)

Basidiomata medium-sized. **Pileus** 50 – 60 mm in diam., surface smoky grey to blackish on maturity, rugose towards the margin, covered with brownish black appressed squamules, mainly in the center; margin somewhat wavy, thin veil remnants present along the margin. **Pileal context** off white to greyish, slightly changes to dark copper reddish, but no changes in over matured specimens. **Hymenophore** adnate to adnexed; surface greyish when young, becoming greyish black, unchanging or changes to darker on bruising; pores angular, 1/mm; tubes up to 10 mm long, concolorous to pore surface. **Stipe** 60 – 70 × 10 – 15 mm, central subcylindrical, greyish with white fluffy floss at upper and lower halves, covered with small blackish spots all-over.

Basidiospores 8 – 11 × 8 – 10 µm (Q = 1 – 1.2, Qm = 1.14), subglobose, brownish yellow, reticulated; reticulations incomplete. **Basidia** 22 – 44 × 7 – 14 µm, clavate to narrowly clavate, thin-walled, 4-spored, pale yellowish; sterigmata up to 5 µm long. **Pleurocystidia** 38 – 60 × 12 – 16 µm, fusiform or broadly lageniform with sub-acute apex, slightly thick-walled (up to 0.5 µm) with yellowish brown pigments. **Cheilocystidia** abundant, 31 – 50 × 10 – 15 µm, tin-walled, fusiform to narrowly lageniform or conical, usually containing yellowish brown pigments. **Hymenophoral trama** boletoid; hyphae 3 – 12 µm, thin-walled, yellowish to yellowish brown. **Pileipellis** an irregular trichodermium; hyphae 4 – 15 µm, thin- to thick-walled, with yellowish brown pigments. **Pileal trama** interwoven; hyphae 3 – 10 µm, thin- to thick-walled, pale yellowish to yellow. **Stipitipellis** a cutis interrupted by trichodermial patches with caulocystidia; terminal cells subglobose, clavate or flexouse, 15 – 35 × 3 – 6 µm; hyphae 3 – 6 µm wide, thin-walled, many of them have brownish yellow encrustations. **Caulocystidia** 17 – 28 × 3 – 6 µm, broadly clavate or nearly fusiform with sub-acute apex, thin-walled. **Stipe trama** parallel to interwoven; hyphae 3 – 10 µm, thick-walled, pale yellow. **Clamp-connections** not observed.

Habit: on soil, single or scattered, near Dipterocarpaceae trees.

Specimens examined: India, Kerala State, Thiruvananthapuram district, Palode, 28 April 2022, Salna N., ZGCSN157.

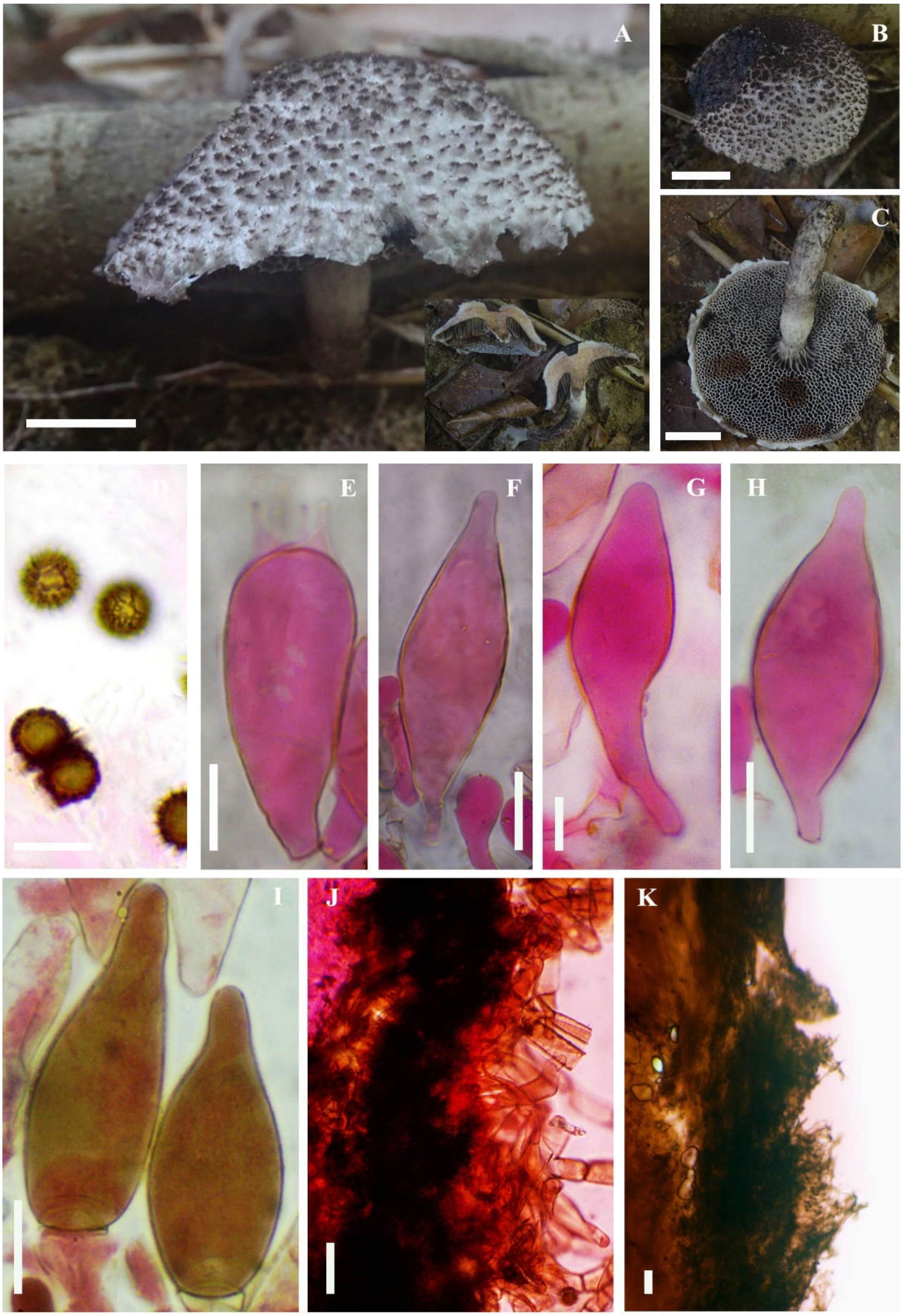


Figure 19. *Strobilomyces strobilaceous*. A-C. Basidiomata D. Basidiospores E. Basidia F-H. Pleurocystidia I. Cheilocystidia J. Pileipellis K. Stipitipellis Scale bars: A-C = 10 mm, D-I = 10 µm, J-K = 20 µm.

Comments: *Strobilomyces strobilaceus* is characterized by its medium-sized to large basidiomatas (60 – 120 mm diam), pileus with black-brown to grey-black, large, more or less erect conical to pyramidal squamules or patch-like to appressed squamules, large hymenophoral pores (1 – 1.5 mm diam), rusty red discoloration of the context on exposure and medium-sized reticulate basidiospores (9 – 11 × 8 – 9.5 µm) (Han et al. 2020). *Strobilomyces strobilaceus* shares morphological similarities with *S. glabriceps* or *S. parvirimosus* with regard to their pileal squamules. But, *S. glabriceps* differs from *S. strobilaceus* by its grey to dirty white stipe with grey-black thin fluffy floss on the upper and bottom half, the context's discoloration turning grey-black upon exposure, and its subtropical range. *Strobilomyces parvirimosus* has smaller basidiomatas (30 – 70 mm in diameter), a pileus with medium-sized black-brown squamules (3 – 5 mm in diameter), a stipe with thin black-brown floss and no annulus, smaller hymenophoral pores (0.5 – 1 mm in diameter), and smaller basidiospores.

Austroboletus (Corner) Wolfe

Basidiomata stipitate-pileate. Pileus dry to viscid or mucilaginous. Pileal context pink, pinkish vinaceous, purplish brown. Hymenophore tubular, whitish or pale cream becoming flesh-pink to vinaceous pink when young, brownish pink at maturity. Stipe surface smooth, furfuraceous-fibrillose to reticulate-alveolate, lacerate or lacunose. The tissues unchanging the color in general. Spore print rust brown to chocolate brown. Basidiospores variously ornamented, amygdaliform to ellipsoid-fusiform. Hymenophoral trama bilateral-divergent hymenophoral trama of the "*Boletus*-type". Pileipellis a trichoderm or ixotrichoderm type. Species shows ectomycorrhizal association with several plant families including Fagaceae, Pinaceae, Dipterocarpaceae, Myrtaceae, and caesalpinoid legumes.

Austroboletus fusisporus (Imazeki and Hongo) Wolfe, Biblthca Mycol. 69: 96 (1980)

Figure 20

Synonymy:

Porphyrellus fusisporus Kawam. ex Imazeki and Hongo, Couloured Illustrations of Fungi of Japan: 89 (1957)
Porphyrellus fusisporus Kawam. ex Imazeki and Hongo, Acta phytotax. geobot., Kyoto 18(4): 110 (1960)
Strobilomyces fusisporus Kawam., Icones of Japanese fungi 2: 282 (1954)

Basidiomata medium-sized. **Pileus** 20 – 30 mm broad, conical to convex; surface slightly viscid, reddish brown to salmon brown, paler towards the margin, covered with reddish brown tomentose squamules, unchanging when bruised; margin extending and covering the stipe when young, then broken in to pieces and hanging on the pileal margin. **Pileal context** whitish, unchanging when bruised. **Hymenophore** depressed around the stipe apex; surface pinkish, unchanging when bruised; pores angular; tubes short, up to 5 mm long, concolorous with the pore surface, no color change when bruised. **Stipe** 50 – 60 × 5 – 7 mm, broadening towards the base; surface whitish from apex to middle, becoming reddish brown towards the base, covered by reticulate meshes up to 2 mm height.

Basidiospores 12 – 15 × 4 – 6 µm (Q = 1.8 – 3.25, Qm = 2.36), elongate amygdaliform, ornamented with large tuberculations, 0.5–1.5 µm in diam., about 1–1.5 lm deep, yellowish to brownish yellow in water. **Basidia** 27 – 38 × 12 – 15 µm, clavate, 4-spored, thin-walled, inamyloid, hyaline in water; sterigmata up to 4 µm long. **Hymenophoral trama** boletoid; hyphae 3 – 10 µm wide thin-walled. **Pleurocystidia** 52 – 80 × 12 – 16 µm, thin-walled, pale yellow to hyaline in water, inamyloid, and with two cells; the lower cell nearly clavate, upper cell narrower and long. **Cheilocystidia** 40 – 46 × 12 – 13 µm, morphologically similar pleurocystidia, thin-walled, hyaline to pale yellow in

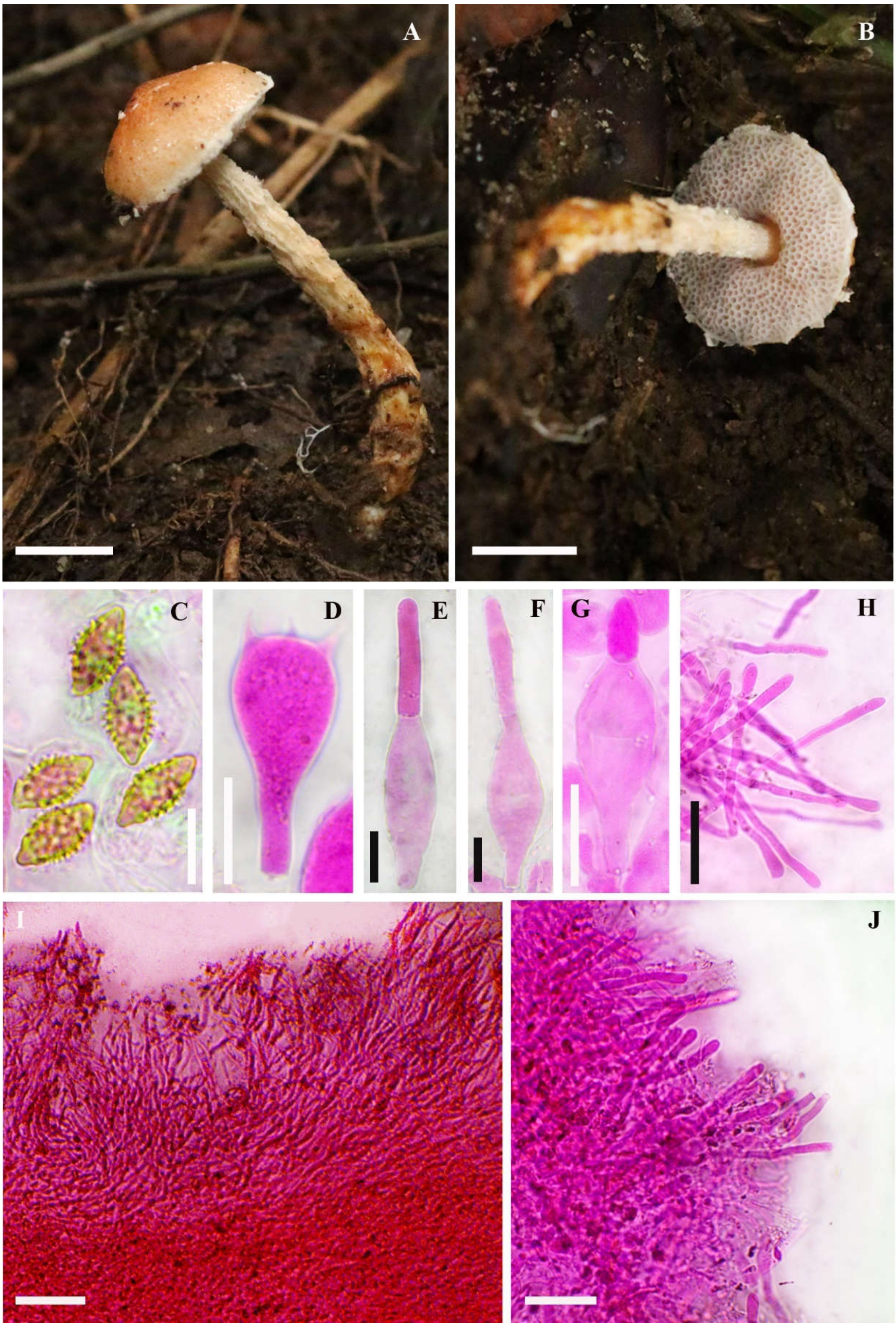


Figure 20. *Austroboletus fusiporus*. A-B. Basidiomata C. Basidiospores D. Basidia E-F. Pleurocystidia G. Cheilocystidia H. Elements of stipitipellis I. Pileipellis J. Stipitipellis. Scale bars: A-B = 10 mm, C-H = 10 µm, I-J = 20 µm.

water. **Pileipellis** a trichodermium, composed of slender, frequently septate hyphae having crystalline contents; hyphae 3 – 7 µm wide, thin-walled, pale brownish in water; terminal elements 25 – 70 × 3 – 5 µm slender, bulbous at apex, thin-walled. **Pileal trama** interwoven, made up of 4 – 10 µm wide, gelatinous hyphae which are pale yellow in water. **Stipitipellis** a trichodermium; terminal elements 32 – 62 × 3 – 5 µm, with bulbous apex, some contains oil globules, brownish yellow in water, inamyloid.; globose hyphae, 3 – 8 µm wide, also present in pellis. **Stipe trama** interwoven consisted of 3 – 8 µm wide, gelatinous hyphae. **Clamp-connections** not observed.

Habitat: On soil, solitary to scattered, near Dipterocarpaceae trees.

Specimens examined: India, Kerala State, Thiruvananthapuram district, Palode, 12 July 2022, Salna Nanu, ZGCSN177.

Comments: *Austroboletus fusisporus* is characterized by the reddish brown to salmon brown viscid basidiomata, whitish pileal context, pinkish hymenophore, stipe surface with reticulate meshes, ornamented basidiospores, presence of pleurocystidia and cheilocystidia, and a trichodermial type of pileipellis. *Austroboletus fusisporus* shows similarities with *A. mucosus* (Corner) Wolfe, but differs in spore size and ornamentations of spores. Our collection is closely similar to Chinese collection of *A. fusisporus*, except in the smaller size of cheilocystidia (Wu et al. 2016a).

Tylopilus P. Karst.

Basidioma stipitate-pileate with tubular hymenophore. Pileus hemispherical to subhemispherical or applanate; surface subtomentose or glabrous, dry to gelatinous; context white, without color change when injured, mostly with a bitter taste. Hymenophore depressed around apex of stipe; hymenophoral surface white when young, and becoming pinkish when mature; pores angular or roundish; tubes concolorous with hymenophoral surface, unchanging in color when injured. Stipe central, glabrous or distinctly reticulate; basal mycelium white. Basidiospores ellipsoid to oblong. Pleuro- and cheilocystidia abundant, subfusiform. Pileipellis a subcutis to trichodermium. Clamp-connections absent.

Tylopilus glutinosus Iqbal Hosen, Nordic Jl Bot. 39: e03338, 3 (2021)

Figure 21

Basidiomata small to medium-sized. **Pileus** 40 – 120 mm, subhemispherical to hemispherical when young, becoming broadly convex on maturity; surface purplish grey with pink tinges, becoming brownish when mature, without color change when bruised, dry, slightly viscid when wet, pruinose when young, glabrous on maturity; margin slightly incurved when young, straight to uplifting when mature, splitting in some. **Pileal context** white, no color change on bruising. **Hymenophore** adnexed to adnate; surface pale purplish grey with pinkish shade, without color change on bruising; pores 2 – 4 per mm, nearly angular; tubes up to 8 mm long, concolorous with surface, no color change on bruising. **Stipe** 50 – 90 × 25 – 35 mm, almost central, cylindrical to obclavate; surface purplish in apex, purplish grey to whitish towards base, without color change on bruising, minutely pruinose with longitudinal striations. **Stipe context** whitish, no color change on bruising. **Basal mycelium** white.

Basidiospores 7 – 10 × 4 – 5 μm (Q = 1.8 – 2.3, Qm = 2.03), broadly ellipsoid to narrowly ellipsoid, thin-walled, smooth, hyaline to pale yellow in water. **Basidia** 19 – 32 × 7 – 9 μm, clavate, 4- spored, hyaline in water. **Hymenophoral trama** boletoid; hyphae 3 – 7 μm wide, thin-walled, hyaline to yellowish in water. **Pleurocystidia** 32 – 65 × 7 – 10 μm, lageniform, fusiform, with apical beak up to 10 μm long, thin-walled, hyaline to pale yellow in water. **Cheilocystidia** 25 – 58 × 6 – 9 μm, lageniform, some with oil globules, thin-walled, hyaline to pale yellow in water. **Pileipellis** an ixotrichoderm, composed of erect, interwoven, brownish hyphae; terminal elements 25 – 52 × 5 – 8 μm, subcylindrical to fusoid, thin-walled, brownish in water. **Pileal trama** interwoven, hyphae 3 – 7 μm wide, thin-walled. **Stipitipellis** a cutis interrupted by bunches of caulocystidia. **Stipe trama** parallel to interwoven; hyphae 4 – 12 μm wide, thin-walled, brownish in water. **Caulocystidia** 25 – 70 × 8 – 12 μm, fusoid, with oil globules, thin-walled, pale yellow to brownish in water. **Clamp-connections** not observed.

Habitat: On soil, solitary to scattered, under *Acacia* trees or other evergreen trees.

Specimens examined: India, Kerala State, Kozhikode district, Zamorin' Guruvayurappan College campus, 26 June 2019, Salna Nanu, ZGCSN26; 21 May 2022, Salna Nanu, ZGCSN161; 25 June 2022, Salna Nanu, ZGCSN168; 16 June 2023, Salna Nanu, ZGCSN204; Thiruvananthapuram district, Palode, 20 April 2022, Salna Nanu, ZGCSN149.

Comments: *Tylopilus glutinosus* was originally described from Bangladesh (Iqbal Hosen 2021) and recently reported from India by Chakraborty et al. (2022). Morphologiacal and molecular characters of Kerala collections agree with the descriptions of Iqbal Hosen (2021) and Chakraborty et al. (2022). The original description stated that pleurocystidia were smaller (30 – 45 μm), but larger cystidia were found in Bengal collections. Kerala collections also show larger pleurocystidia. Caulocystidia of our specimens observed as larger than in the previous reports. Kerala collections placed in *Tylopilus* clade with 100% bootstrap support in the molecular phylogenetic analysis (Figure 42).

Figure 21. *Tylopilus glutinosus*. A-B Basidiomata C. Basidiospores D. Basidia E. Pleurocystidia F-H. Cheilocystidia I. Pileipellis J. Stipitipellis. Scale bars: A-B = 10mm, C-H = 10 µm, I-J = 20 µm.

Tylopilus griseipurpureus (Corner) E. Horak, Malayan Forest Records 51: 132 (2011)

Figure 22

Synonymy:

Boletus griseipurpureus Corner, Boletus in Malaysia (Singapore): 168 (1972)

Basidiomata small to medium-sized. **Pileus** 30 – 40 mm broad, subhemispherical when young, becoming applanate on maturity; surface purplish to purplish grey, paler on aging, glabrous when mature, dry, slightly viscid when wet, without color change when bruised; margin staright. **Pileal context** up to 5 mm wide, white, unchanging when bruised. **Hymenophore** adnate; surface whitish with pinkish tinge, without color change on bruising; pores small, 2 – 3 per mm, angular; tubes up to 4 mm long, concolorous with pore surface, unchanging when bruised. **Stipe** 40 – 70 × 3 – 5 mm, cylindrical, broadening towards base; surface minutely pruinose, whitish with greyish purple tinge, without color change on bruising. **Stipe context** white, non-discoloring when bruised. **Basal mycelium** white.

Basidiospores 8 – 10 × 3.5 – 4 µm (Q = 2 – 2.5, Qm = 1.89), subfusiform, smooth, thin-walled, hyaline to pale yellow in water. **Basidia** 18 – 23 × 6 – 8 µm, clavate, 4-spored, rare, thin-walled, pale yellow in water. **Hymenophoral trama** boletoid; hyphae 5 – 49 µm wide. **Pleurocystidia** 25 – 36 × 6 – 8 µm, fusiform, with apical beak up to 6 µm long, brownish yellow in water. **Cheilocystidia** 17 – 22 × 5 – 8 µm, fusoid-ventricose, with small apical beak up to 3 µm long, thin-walled, pale brownish yellow in water. **Pileipellis** a trichodermium, composed of interwoven filamentous hyphae, 3 – 6 µm wide; terminal cells 16 – 32 × 5 – 8 µm, arise from semiglobose cells, thin-walled, brownish yellow pigments present along with crystalline contents. **Pileus trama** interwoven; hyphae 3 – 6 µm wide, thin-walled, hyaline. **Stipitipellis** a

Figure 22. *Tylopilus griseipurpureus*. A-B. Basidiomata C. Hymenophore D. Stipe surface E. Basidiospores F. Basidium G-I. Pleurocystidia J-K. Cheilocytidia L. Pileipellis M. Stipitipellis N, P. Elements in pileipellis O. Element in stipitipellis. Scale bars: A-D= 10 mm, E-K,N-P = 10 μm, L-M = 20 μm.

cutis interrupted by cystidioid hyphal patches; cystidioid elements 16 – 45 × 6 – 18, rare, thin-walled, pale brownish yellow in water. **Stipe trama** parallel to interwoven. Hyphae 3 – 8 µm wide, thin-walled, hyaline in water. **Clamp-connections** not observed.

Habitat: On soil, solitary.

Specimens examined: India, Kerala State, Thiruvananthapuram district, Palode, 10 July 2022, Salna Nanu, ZGCSN181.

Comments: *Tylopilus griseipurpureus* is characterized by greyish purple or purple-fuscous pileus, the white and non-discoloring context when bruised, and the white to pinkish hymenophore. This species is originally described as *Boletus griseipurpureus* from Singapore by Corner (1972). Horak (2011) transferred it to the genus *Tylopilus* based on its hymenophoral color. *Tylopilus griseipurpureus* reported from southern China by Wu et al. (2016a). Kerala collections show smaller-sized pleurocystidia with brownish yellow pigments when compared to Malaysian and Chinese collections.

***Tylopilus* species**

Figure 23

Basidiomata small to medium-sized. Pileus 28 – 80 mm in diam., hemispherical when young, becoming broadly convex on maturity; surface dark purplish to purplish when young, becoming paler on maturation with pinkish tinge, glabrous, dry, with a depressed centre in some; margin straight or slightly incurved. **Pileal context** whitish, changing to pale brownish on bruising very slowly. **Hymenophore** adnate; slightly depressed around the stipe apex; surface pinkish when young becoming brownish on maturity, slightly changing to pale brown when bruised; tubes up to 15 mm long, pinkish to pale brownish, unchanging or slightly changing to pale brown when bruised. **Stipe** 30 – 60 × 5

– 20 mm, central, subcylindrical; surface whitish with yellowish and pinkish tinges, glabrous to pruinose. **Stipe context** whitish, changing to pale brownish on bruising slowly. **Basal mycelium** white.

Basidiospores 7 – 12 × 4 – 5 µm (Q = 2 – 2.6, Qm = 2.75), ellipsoid, thin-walled, guttulate, hyaline to pale yellow in water. **Basidia** 16 – 25 × 7 – 8 µm, clavate, 4-spored, thin-walled, hyaline in water; sterigmata up to 4 µm long. **Hymenophoral trama** boletoid; hyphae 3 – 9 µm wide, thin-walled. **Pleurocystidia** 45 – 70 × 10 – 15 µm, lageniform, with long apical protrusons (up to 10 µm long), thin- to thick-walled, brownish yellow in water, brownish contents present as globules in some. **Cheilocystidia** 40 – 65 × 6 – 9 µm, lageniform, thin- to thick-walled, brownish yellow in water, brownish contents present as globules in some. **Pileipellis** a trichodermium with caulocystidia like elements; terminal elements 25 – 38 × 6 – 12 µm, thin-walled; hyphae 3 – 8 µm wide. **Pileal trama** interwoven, hyphae 3 – 6 µm wide, thin-walled. **Stipitipellis** a cutis to trichodermium with tightly interwoven hyphae; hyphae 3 – 6 µm wide, thin-walled, brownish yellow in water. **Stipe trama** parallel to interwoven; hyphae 3 – 8 µm wide, thin-walled, hyaline to pale yellow in water. **Clamp-connections** not observed.

Habitat: On soil, solitary to scattered, near Dipterocarpaceae trees.

Specimens examined: India, Kerala State, Kozhikode district, Thurayilkotta sacred grove, 15 June 2023, Salna Nanu, ZGCSN203; 20 June 2023, Salna Nanu, ZGCSN206; 20 June 2023, Salna Nanu, ZGCSN208.

Comments: *Tylopilus* species is characterized by dark purplish basidiomata when young, whitish pileal context that changes to pale brownish, pinkish hymenophore, ellipsoid basidiospores, cystidia with brownish yellow contents, and a trichodermium type of pileipellis. All these characters lead to the genus *Tylopilus*. Morphological features of this collection differ from other related

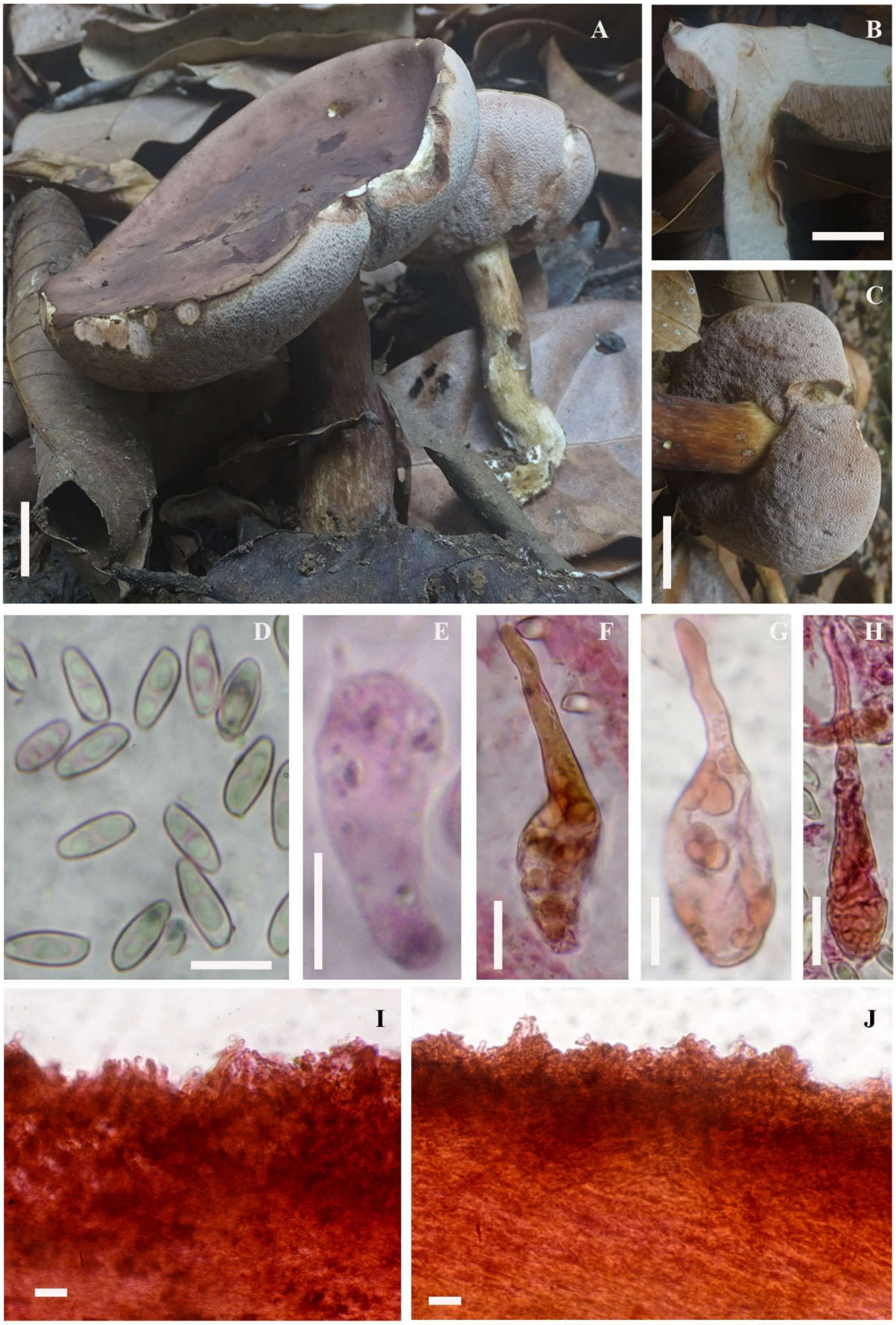


Figure 23. *Tylopilus* species. A-C. Basidiomata D. Basidiospores E. Basidium F-G. Pleurocystidia H. Cheilocytidium I. Pileipellis J. Stipitipellis. Scale bars: A-C= 10 mm, D-H = 10 μm, I-J = 20 μm.

Tylopilus species. Based on morphological and molecular data, the specimen is hitherto undescribed *Tylopilus* species. The closely similar species is *T. purpureus* S. Nanu and T. K. A. Kumar, possess similar colored pileus and stipe, a pinkish hymenophore, and trichodermium type of pileipellis (Nanu and Kumar 2024a). However, the newly proposed *Tylopilus* species can be distinguished from *T. purpureus* by smaller basidiospores, larger cystidia, and absence of cystidioid elements in stipitipellis. In the multigene phylogenetic analysis, the undescribed species is forming an independent clade related to *T. purpureus* (Figure 42).

Tylopilus purpureus Salna Nanu and T. K. A. Kumar, Mycologia (2024)

Figure 24

Basidiomata 30–60 mm broad, at first convex, becoming plano-convex to applanate on maturity with slightly curved margin; surface dry, finely tomentose, purple to vinaceous purple pileus when young, becoming paler when mature. **Pileus context** thick, firm, 10 – 15 mm broad, white when young, then creamy white, unchanging or changing to pale reddish on bruising. **Hymenophore** adnate to adnexed, depressed around the apex of stipe, pore 2 – 3 per mm, angular; pore surface whitish when young, becoming pale pink to pink at maturity, changing to pale reddish brown on bruising; tubes up to 10 mm long, concolorous to the pores, changing to pale reddish brown on bruising very slowly. **Stipe** 40–120 × 5 – 20 mm, central, stubby, subcylindrical, enlarges downwards, pale purplish when young, becoming darker shades of purple when mature, except towards base and apex, in the middle, white towards the apex and base, minutely pubescent towards centre; context spongy, white to cream. **Basal mycelium** white. Spore print not obtained. **Odour** not distinct.

Basidiospores 9.5 – 13 × 4 – 6 µm (Q = 2.1–3.0, Qm = 2.40), subcylindrical to ellipsoid, with a distinct apiculum, smooth, thin-walled, pale yellow to hyaline in water. **Basidia** 13 – 26 × 8 – 12 µm, clavate, mostly 4-spored, rarely 2-spored, guttulate, hyaline in water, thin-walled; sterigmata up to 3 µm long. Hymenophoral trama boletoid; hyphae 3.5 – 10 µm wide, cylindrical, thin-walled, hyaline. **Pleurocystidia** 27 – 48 × 7 – 9 µm, lageniform, with apical protrusion up to 16 µm, usually containing brownish yellow pigments in water, thin-walled. **Cheilocystidia** 24 – 40 × 7 – 9 µm, lageniform, with brownish yellow pigments and distinct globular contents, thin-walled. **Pileipellis** a trichodermium composed of interwoven hyphae that 3.5 – 6 in diam., brownish yellow in water; terminal elements clavate or cylindrical, 18 –46 × 3 – 5 µm, thin-walled. **Pileal trama** parallel to interwoven, made up of 3 – 9 µm wide, thin-walled hyphae. **Stipitipellis** an irregular trichodermium composed of interwoven parallel to ascending hyphae with scattered cystidioid elements; hyphae 3 – 8 µm wide, thin-walled; cystidioid elements 4 – 16 × 2 – 4 µm wide, clavate, utriform or cylindrical, thin-walled, brownish yellow in water. **Clamp-connections** not observed.

Habitat: On soil, scattered under *Hopea glabra.*

Specimens examined: India, Kerala State, Wayanad district, Kuruva Islets, 04 April 2022, Salna Nanu, ZGCSN130; 26 April 2022, Salna Nanu ZGCSN142; 26 April 2022, Salna Nanu ZGCSN143; 20 April 2022, Salna Nanu, ZGCSN145; 20 April 2022, Salna Nanu, ZGCSN147.

Comments: *Tylopilus purpureus* is characterized by a basidiomata having purple to vinaceous purple pileus when young, becoming darker when mature, whitish pore surface changing to reddish brown on bruising, minutely pubescent stipe centre, cheilocystidia with brownish yellow pigments and distinct globular contents, and a trichodermial pileipellis composed of brownish yellow hyphae.

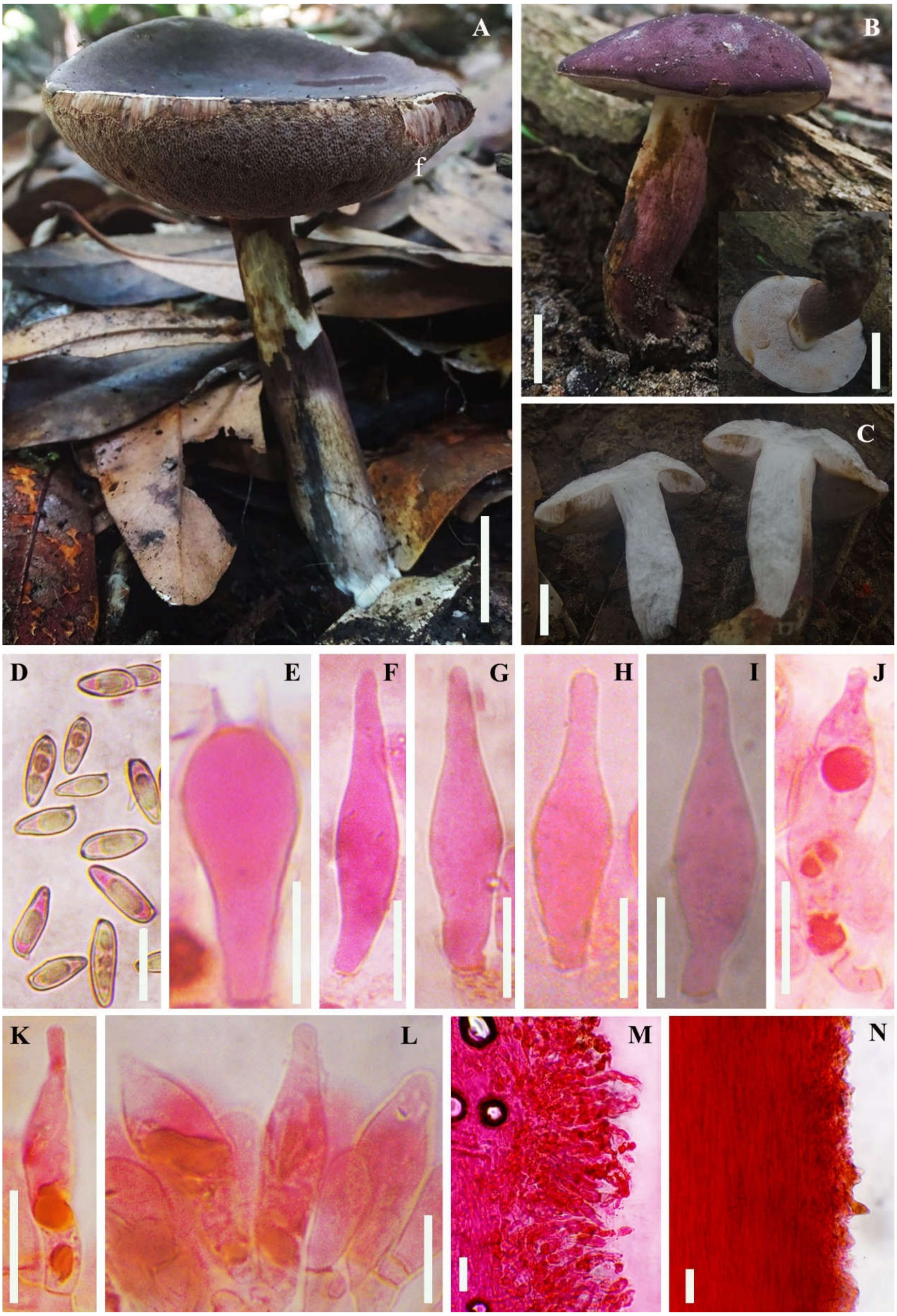


Figure 24. *Tylopilus purpureus*. A-C Basidiomata D. Basidiospores E. Basidium F-I. Pleurocystidia J-L. Cheilocystidia M. Pileipellis N. Stipitipellis. Scale bars: A-C = 10 mm, D-I, L-M = 10 μm, J-K = 20 μm.

The morphological features of *Tylopilus purpureus* are similar to that of *T. atroviolaceobrunneus* in having almost similar colored pileus, white to pinkish hymenophore that changes to reddish brown on bruising, similar shape and size of basidia and presence of brownish yellow cystidia. However, *T. atroviolaceobrunneus* differs from *T. purpureus* by the presence of narrower basidiospores, larger pleurocystidia, cheilocystidia without globular contents, and a trichodermial pileipellis composed of brownish to yellowish brown inflated cells. Moreover, *T. atroviolaceobrunneus* has been reported from the tropical forests dominated by plants of the family Fagaceae in China. The detailed comparisons and phylogenetic analysis of the genus *Tylopilus* is presented in Nanu and Kumar (2024).

Leccinum Gray

Basidiomata stipitate-pileate. Pileus hemispherical, convex or applanate, glabrous to fibrillose, dry, sometimes subviscid when wet; context whitish, always staining brownish, pinkish, reddish, or occasionally bluish when cut. Hymenophore adnexed, surface concolorous with tubes, whitish; tubes and pores staining yellowish, brownish, brown, vinaceous to blackish when hurt. Stipe central, whitish to dirty white, covered with brown to blackish dots or squamules and sometimes additionally with longitudinal ridges; context same to that of pileus; basal mycelium whitish to white. Basidiospores smooth, subfusiform, pale olive-brownish. Pleurocystidia and cheilocystidia subfusiform-ventricose. Pileipellis an interwoven trichodermium or interwoven subcutis, rarely ixosubcutis. Clamp-connections absent.

Leccinum intusrubens (Corner) Høil., in Høiland and Schumacher, Nordic Jl Bot. 2: 270 (1982)

Figure 25

Basidiomata small to medium-sized. **Pileus** 35 – 55 mm in diam., hemispherical to convex becoming applanate; surface dry, densely tomentose squamulose, hair greyish to black, arranged in close patches in the center, small patches in the outer showing whitish to greyish ground; margin somewhat wavy without membranous veil. **Context** whitish to greyish, 4 – 8 mm thick, staining light orange-red slowly, then blackish on bruising. **Hymenophore** adnate to sinuate, surface whitish to greyish, grey when mature, staining light orange-red slowly, becoming copper red to blackish on bruising; pores angular, 2 – 3/ mm, whitish to grey, color changes like context; tubes concolorous with the pores. **Stipe** 30 – 50 × 10 – 20 mm, cylindrical; surface whitish to grey, covered with greyish to black squamulose squamules, reticulate with elongate meshes, apex almost greyish with less squamules; context concolorous with that of pileus, color changes similar to pores; basal mycelium whitish to grey.

Basidiospores 10 – 13 × 4 – 5 µm (Q = 2.5 – 3.25, Qm = 2.67), elongate ellipsoid, thin- to thick-walled (wall thickness up to 0.5 – 0.7 µm), with one or more oil guttules, pale yellowish brown in water. **Basidia** 28 – 35 × 8 – 10 µm, clavate, thin-walled, pale yellowish, 4- sterigmate; sterigmata up to 6 µm long. **Pleurocystidia** 42 – 54 × 10 – 13 µm, scattered, fusoid with long beak, thin to thick-walled towards the bottom, pale yellow, dark brownish yellow pigment in some. **Cheilocystidia** 37 – 55 × 9 – 13 µm, numerous, subfusoid, some with small beak in the apex, thin-walled, pale yellow to brownish yellow in water. **Pileipellis** a trichodermium of 80 **–** 170 µm wide, composed of brownish yellow interwoven encrusted (encrustations in z pattern) septate hyphae, 5 – 16 µm wide; terminal cells 3 – 8 × 3 – 6 µm, thin-walled, cylindrical. **Pileal trama** interwoven; hyphae 3 – 10 µm wide, pale yellow in water. **Stipitipellis** a cutis, 90 – 140 µm wide, composed of cylindrical, parallel, thin-walled hyphae with brownish pigments, interrupted by groups of caulocystidia; hyphae 4 – 10 µm wide. **Caulocystidia** 19 – 64 × 5 – 15 µm, subfusoid, cylindrical, broadly clavate, with rounded apex, slightly thick-walled, brownish in water. Stipe trama parallel to interwoven; hyphae 4 – 8 µm wide, thin-walled, pale yellow. **Clamp-connections** not observed.

Figure 25. *Leccinum intusrubens*. A-C Basidiomata D. Basidiospores E. Basidium F-G. Pleurocystidia H. Cheilocystidia I. Caulocystidia J. Pileipellis K. Stipitipellis Scale bars: A-C = 10mm, D-I = 10 µm, J-K = 20 µm.

Habitat: On soil, scattered, among trees of Dipterocarpaceae.

Specimens examined: India, Kerala State, Wayanad district, Kuruva Islets, 13 October 2021, Salna Nanu, ZGCSN109.

Comments: *Leccinum intusrubens* initially described from Malaysia as *Boletus intusrubens* (Corner 1972). The species is characterised by dark colored pileal surface with squamules, pileal context changing to reddish on bruising, whitish to greyish hymenophore that changing to reddish brown to black on bruising, pale yellowish brown, ellipsoid basidiospores, and cystidia with brownish pigment. Kerala collection is closely similar to the described Malaysian species. But, Kerala collection shows smaller pleurocystidia and larger caulocystidia.

Indoporus A. Parihar, K. Das, Hembrom and Vizzini

Basidiomata epigeous. Pileus grey with black squamules, non-glutinous. Pileal context yellowish white, quickly becoming dull red to greyish red then slowly becoming black to charcoal black. Hymenophore tubulose, depressed at the juncture of stipe, reddish grey or paler brownish orange on bruising, finally black, pores angular. Stipe cylindrical to clavate, becoming narrow towards base, smooth, greyish violet at upper half, then grey to blackish brown. Stipe context greyish violet to dark violet in upper half and dark blackish brown on lower half, slowly becoming black to charcoal black on exposure. Basidiospores greyish brown in deposit, smooth, inamyloid. Pleurocystidia rare, lanceolate to ventricose, hyaline. Cheilocystidia frequent, narrowly lanceolate with rounded to capitate apex, hyaline. Pileipellis a trichoderm, with irregular and inflated terminal cells with brownish-black intracellular pigmentations. Clamp-connections absent.

***Indoporus* species**

Figure 26

Basidiomata medium-sized. **Pileus** 20 – 30 mm broad, convex when young, becoming applanate on maturity; surface dry, squamulose, whitish to greyish with black squamules, becoming blackinsh on aging; margin entire, slightly wavy. **Pileal context** up to mm thick, whitish, changing to dull red to greyish red slowly when bruised, becoming blackish slowly. **Hymenophore** adnate to sinuate; surface whitish to greyish, becoming reddish on bruising initially, then to blackish; pores angular, two to three per mm; tubes up to 5 mm long, pinkish white, changing to reddish on bruising. **Stipe** 30 – 50 × 4 – 7 mm, almost cylindrical, whitish to grey, squamulose, with appressed small black squamules, faint striations present. **Stipe context** whitish to grey, changing to pale reddish slowly. **Basal mycelium** white.

Basidiospores 8.5 – 11 × 3.5 – 4.5 μm (Q = 2.25 – 3.25, Qm = 2.6), ellipsoid to cylindrical, smooth, guttulate, thin- to thick-walled (wall thickness up to 1 μm), pale yellowish in water. **Basidia** 27 – 38 × 7 – 9 μm, clavate, broadly clavate, 4-spored, thin-walled, hyaline to pale yellow in water; sterigmata up to 6 μm long. **Hymenophoral trama** boletoid; hyphae 3.5 – 13 μm wide, thin-walled, pale yellow in water. **Pleurocystidia** 31 – 55 × 9 – 11 μm, fusiform, with long apical protrusion, thin-walled, pale yellow to dark brownish in water. **Cheilocystidia** 28 – 50 × 7 – 10 μm, fusiform, with small apical protrusion, thin-walled, brownish yellow in water. **Pileipellis** an irregular trichodermium, consist of cylindrical terminal cells, 10 – 15 × 3 – 7 μm wide, thin-walled, brownish yellow in water. **Pileal trama** interwoven; hyphae 3 – 9 μm wide, thin-walled, hyaline. **Stipitipellis** a cutis interrupted by caulohymenium; caulobasidia similar to hymenial basidia, pale yellowish in water; caulocystidia 15 – 27 × 5 – 8 μm, nearly clavate, thin-walled, brownish yellow in water. **Clamp-connections** not observed.

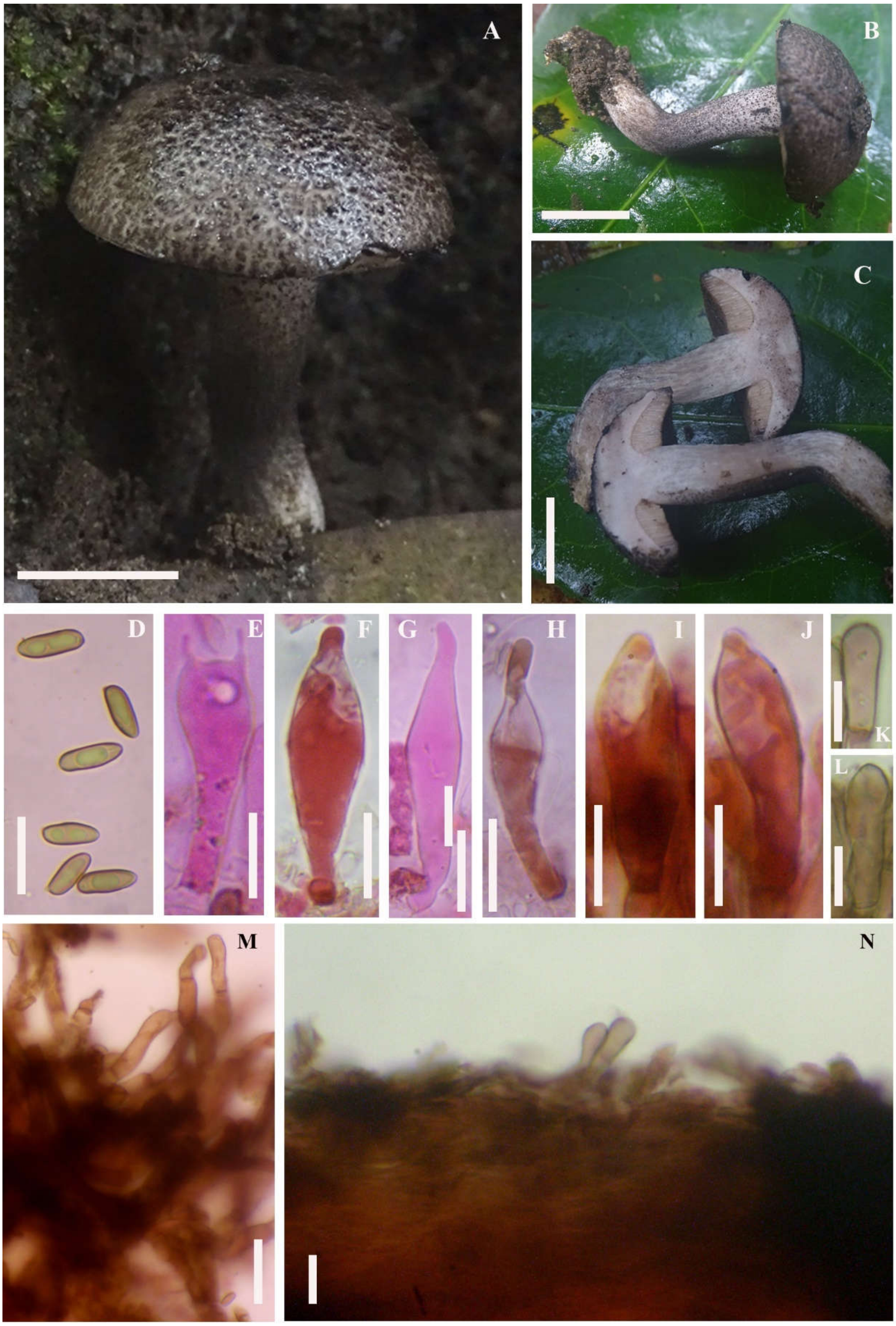


Figure 26. *Indoporus* species. A-C. Basidiomata D. Basidiospores E. Basidium F-H. Pleurocystidia I-J. Cheilocystidia K-L. Caulocystidia M. Pileipellis N. Stipitipellis. Scale bars: A-C = 10mm, D-L = 10 µm, M-N = 20 µm.

Habitat: On soil, solitary.

Specimens examined: India, Kerala State, Wayanad district, Kuruva isletes, 13 October 2021, Salna Nanu, ZGCSN108.

Comments: *Indoporus* is a recently described genus from India (Parihar et al. 2018). Two species are included in this genus, *Indoporus shoreae* A. Parihar, K. Das, Hembrom and Vizzini and *I. squamulosus* Yan C. Li and Zhu L. Yang (Parihar et al. 2018, Li and Yang 2021). Squamulose pileal surface, reddening of the pileal and stipe context, smooth basidiospores, presence of brownish contents in cystidia, trichodermial pileipellis, and presence of caulohymenium in stipitipellis of Kerala collection indicate a placement in the genus *Indoporus.* Current species is morphologically similar to *I. shoreae* by possessing squamulose pileus, reddening of the context and hymenophore, shape of cystidia, trichodermial pileipellis, and presence of caulohymenium in the stipitipellis. But, Kerala collection differs from *Indoporus shoreae* by the presence of slow color change of context and hymenophore, squamulose stipe surface, smaller basidiospores, narrower pleurocystidia, and absence of inflated cells in pileipellis. *Indoporus squamulosus*, described from China, shows similar morphological characters with the Kerala collection such as greyish squamulose pileal surface, whitish to greyish white hymenophore, and cystidia with yellowish contents. However, *I. squamulosus* differs from the present collection by smooth stipe surface, larger cystidia, and a palisadoderm type of pileipellis. Morphological and molecular data of more collections are needed for the further analyses.

Anthracoporus Yan C. Li and Zhu L. Yang

Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical to applanate, surface tomentose, usually rugose, dry; context solid, white to greyish white, becoming reddish then blackish when injured.

Hymenophore adnate or depressed around apex of stipe; hymenophoral surface black to greyish black when young, greyish white to greyish pink when mature; tubes concolorous with hymenophoral surface; pores angular; staining reddish firstly then blackish finally when injured. Stipe central, glabrous or reticulate, concolorous with pileus, becoming reddish then blackish when injured; context white to cream, becoming reddish then blackish when bruised; basal mycelia cream, becoming reddish then blackish when bruised. Basidiospores smooth, subfusiform, yellow to brownish yellow. Pleuro- and cheilocystidia fusiform to subfusoid-ventricose. Pileipellis often a trichoderm or epithelium. Clamp-connections absent.

Anthracoporus nigropurpureus (Hongo) Yan C. Li and Zhu L. Yang

Figure 27

Basidiomata small- to medium-sized. **Pileus** 70 mm broad; surface whitish to greyish, with blackish brown thin, soft, scattered, repent or lying, squamules throughout, more squamules present in the centre; margin somewhat wavy. **Pileal context** whitish, turning blackish on bruising. **Hymenophore** tubular, whitish to greyish, turning black on bruising; tubes up to 3 mm long, whitish, changing to black on bruising; pores nearly angular, greyish, 1 – 2 per mm. **Stipe** 50 × 15 mm, longitudinally striped, pale greyish near the hymenophore, becoming blackish towards bottom; surface covered by small scattered grey to black flocci rising in fluffy tufts; context whitish, changing to blackish on bruising. **Basal mycelium** whitish.

Basidiospores 11 – 13.5 × 4 – 5 μm (Q = 2.5 – 3.25, Qm = 2.95), ellipsoid to subcylindrical, thin- to thick-walled, normally with one oil guttule, smooth, pale yellowish in water. **Basidia** 26 – 32 × 10.5 – 12 μm, clavate, 4-sterigamte, thin-walled, hyaline to pale yellow; sterigmata up to 5 μm long. **Hymenophoral trama** boletoid; hyphae 4 – 13 μm, thin-walled, hyaline. **Pleurocystidia**

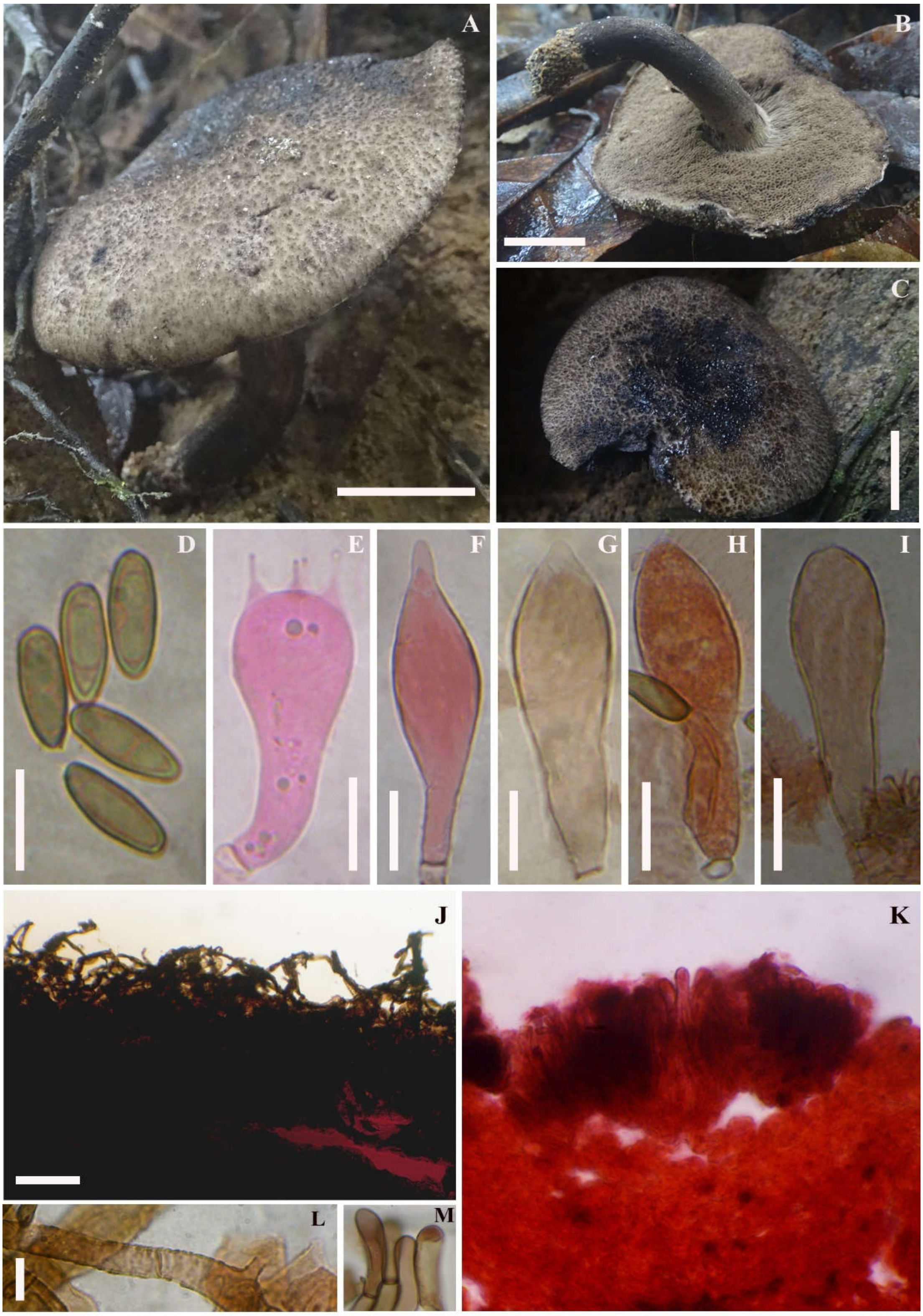


Figure 27. *Anthracoporus nigropurpureus*. A-C Basidiomata D. Basidiospores E. Basidium F-G. Pleurocystidia H-I. Cheilocystidia J. Pileipellis K. Stipitipellis L. Encrusted hyphae in piliepellis M. Elements in stipitipellis. Scale bars: A-C = 10 mm, D-I, L-M = 10 µm, J-K = 20 µm.

30– 50 × 11 – 19 µm, fusiform, subfusiform, lageniform, normally with long apical protrusion, thin- to slightly thick-walled, with yellowish contents. **Cheilocystidia** 38 – 46 × 13 – 17 µm, fusiform or subfusiform, thin-walled, pale yellow to brownish yellow in water. **Pileipellis** a trichodermium with ascending hyphal clusters; terminal cells 33 – 70 × 8 – 17 µm, cylindrical, subcylindrical or fusiform with rounded apex, thick-walled (up to 1 µm thick), with pale brownish yellow encrustations in zebroid pattern; subterminal cells also encrusted. **Pileal trama** interwoven; hyphae 3 – 12 µm, thin-walled. **Stipitipellis** basically a cutis interrupted by trichodermial patches of stipe covering flocci or hairs; terminal cells cylindrical, smooth or minutely encrusted, thin- to slightly thick-walled, pale yellowish in water. **Stipe trama** interwoven; hyphae 3 – 8 µm wide, minutely encrusted, thin-walled, pale yellow in water. **Clamp-connections** absent.

Habitat: Solitary, on ground, near Dipterocarpaceae members.

Materials examined: India, Kerala State, Wayanad District, Kuruva islets, 12 October 2021, Salna Nanu, ZGCSN104.

Comments: *Anthracoporus nigropurpureus* is characterized by dark purplish to greyish black pileus, white to greyish pileal context, becoming reddish to black on bruising, ellipsoid, smooth, slightly thick-walled basidiospores, presence of pleurocystidia and cheilocystidia and trichodermium type of pileipellis with terminal cells having encrustations. Morphologically, Kerala collections shows similarities with other reported *A. nigropurpureus* collections except in larger basidiospore measurement. Molecular analysis also supports the species identification (Figure 42).

Anthracoporus holophaeus (Corner) Yan C. Li & Zhu L. Yang, The Boletes of China: *Tylopilus* s. l. (Singapore): 53 (2021)

Figure 28

Basidiomata medium- to large-sized. **Pileus** 70 – 130 mm broad, hemispherical to applanate; surface minutely pruinose, greyish to greyish black, becoming blackish on age. **Pileal context** up to 25 mm wide, whitish, changing to reddish first then to blackish when bruised or cut. **Hymenophore** poroid, adnate to depressed around apex of stipe; surface whitish to dirty pink or greyish pink, becoming reddish first then to blackish when bruised; pores nearly angular, 1 per mm or 1 per 2 mm; tubes up to 15 mm long, concolorous to hymenophoral surface, changing to reddish on cut. **Stipe** 65 – 80 × 15 – 25 mm, broad in the middle; surface greyish in upper, becoming greyish black towards the bottom, reticulated, distinct reticulations present on apex to middle, faintly reticulated or nearly glabrous towards the bottom. **Stipe context** greyish to blackish, changing to reddish on bruising. **Basal mycelium** whitish.

Basidiospores 9 – 13 × 5.5 – 7 µm (Q = 1.6 – 2, Qm = 1.91), ellipsoid to somewhat oblong, smooth, slightly thick-walled (0.5–1 µm in thickness), nearly hyaline to pale yellowish in water. **Basidia** 35 – 45 × 8 – 10.5 µm, clavate, 4-sterigamte, thin-walled, hyaline to pale yellow; sterigmata up to 5.5 µm long. **Hymenophoral trama** boletoid; hyphae 3 – 8 µm wide, thin-walled, pale yellow with crystalline contents in water. **Pleurocystidia** 45 – 66 × 12 – 13 µm, subfusiform to ventricose, thin-walled, hyaline to pale brownish yellow in water. **Cheilocystidia** 35 – 40 × 9 – 15 µm, fusiform, thin-walled, hyaline to pale brownish yellow in water. **Pileipellis** a trichodermium, composed of cylindrical hyphae with cystidioid terminal cells; hyphae 3 – 8 µm wide, thin-walled; terminal cells 22 – 42 × 4 – 10 µm, clavate, fusiform or lanceolate, pale yellow in water. **Pileal trama** interwoven; hyphae 3 – 8 µm, thin-walled, pale yellow in water. **Stipitipellis** a trichodermium of tightly packed interwoven hyphae; terminal cells 10 – 35 × 4 – 8 µm, nearly clavate, thin-walled, pale yellow in water. **Stipe trama** interwoven; hyphae 3 – 9 µm wide, thin-walled, pale yellow to brownish yellow in water. **Clamp-connections** absent.

Habitat: Solitary or scattered, on soil, near *Diospyros paniculata.*

Materials examined: INDIA. Kerala State: Kozhikode District, Thurayil Kotta sacred grove, 26 Oct 2023, Salna N., ZGCSN224; ZGCSN231; ZGCSN236.

Comments: *Anthracoporus holophaeus* is characterized by greyish to greyish black pileal surface, whitish hymenophore changing to reddish on bruising, reticulated stipe surface, and trichodermium type of pileipellis. *Boletus holophaeus* Corner was transferred to recently erected *Anthracoporus* based on molecular phylogenetic data (Li and Yang 2021). Kerala collections closely resemble Chinese collections (Li and Yang 2021) in morphology. However, our specimens differ from Malyasian collections (Horak 2011) by larger pores and basidia. The species identity proved by phylogenetic analysis of Boletaceae family (Figure 42). *Anthracoporus holophaeus* is distinct in the phylogenetic analysis also (Figure 42).

Boletellus Murrill

Basidiomata small- to medium-sized. Pileus subhemispherical when young, becoming convex, dry, tomentose; context yellowish, turning blue on bruising. Hymenophore adnate to slightly depressed around the apex of stipe, yellowish; pores angular, yellowish, changing to blue on bruising; tubes concolorous to the pore surface, changing to blue on bruising. Stipe central, subcylindrical, solid; surface dry, fibrous, concolorous with the pileus or brownish. Basal mycelium white. Basidiospores fusiform, with longitudinal or oblique ridges. Pleurocystidia and cheilocystidia abundant, large, fusiform or subfusiform. Pileipellis a trichoderm or intricate trichoderm. Clamp-connections absent in all tissues.

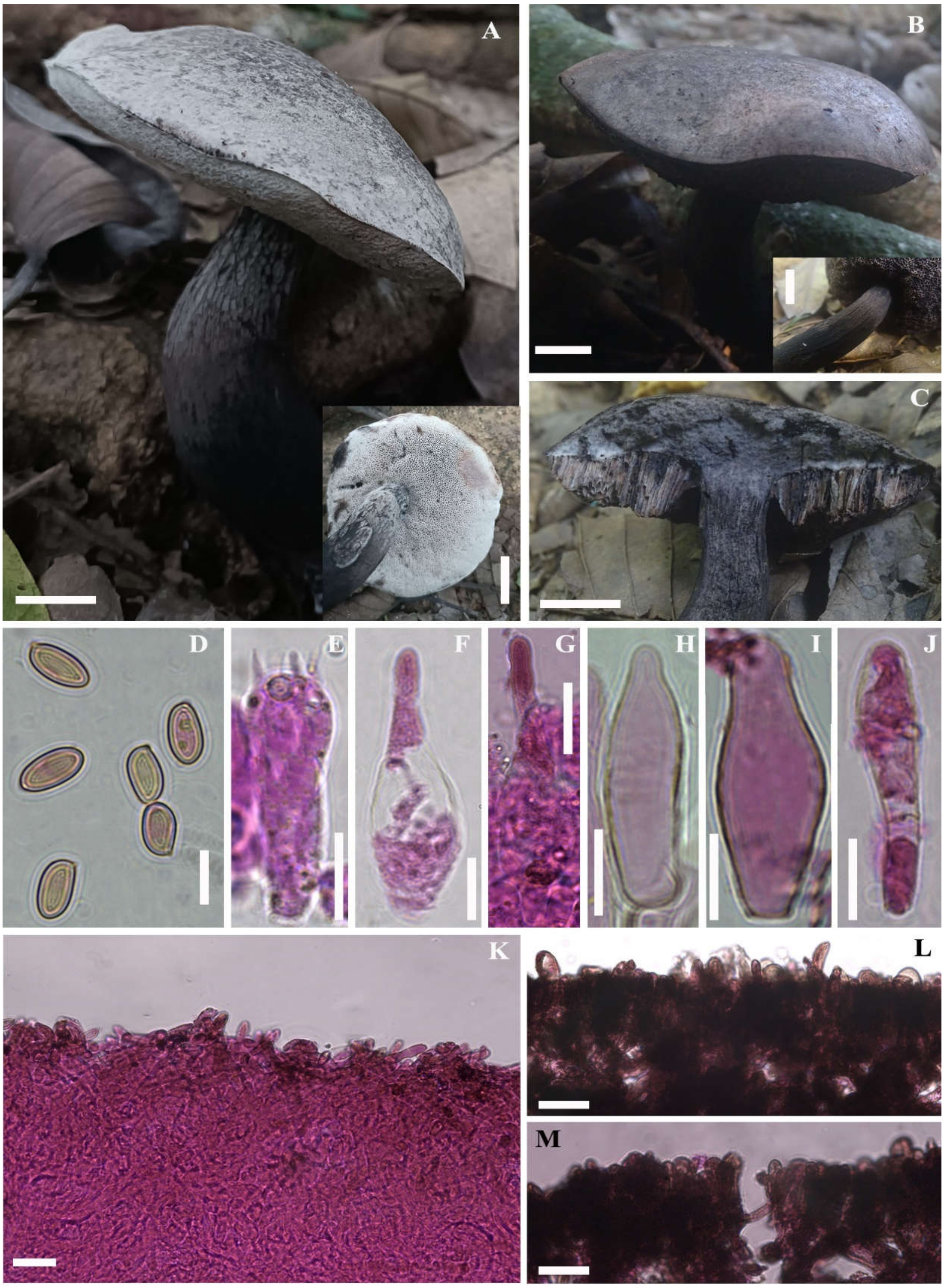


Figure 28. *Anthracoporus holophaeus*. A-B Basidiomata (Inset: A-hymenophore surface, B-stipe surafce) C. Pileal context and hymenophore showing color change on cut D. Basidiospores E. Basidium F-G. Pleurocystidia H-I. Cheilocystidia J. Element of pileipellis K. Pileipellis L-M. Stipitipellis. Scale bars: A-C 10mm, D-J = 10 µm, K-M = 20 µm.

Boletellus emodensis (Berk.) Singer, Annls mycol. 40(1/2): 19 (1942)

Figure 29

Basidiomata small- to medium-sized. **Pileus** 40 – 60 mm in diam., convex when young, becoming applanate on maturity; surface dry, squamulose, purple to crimson red; squamules darker, present as small patches when young, becoming large by cracking on maturation; margin at first extended to a false veil and covers the pores, then splitting radially, appendiculate with veil remnants. **Pileal context** up to 10 mm thick at the centre, yellowish, rapidly changing to blue on bruising. **Hymenophore** poroid; surface yellow, changing to blue on bruising, depressed around the apex of the stipe; pores 1-2/mm, angular; tubes up to 10 mm long, concolorous to that of pore surface, changing to blue on bruising**. Stipe** 40 – 70 x 5 – 10 mm, cylindrical, solid; surface dry, fibrous, concolorous with pileus, yellowish at the apex; base bulbous. **Stipe context** yellowish. **Basal mycelium** white.

Basidiospores 13.5 – 20 × 6 – 8.5 µm µm (Q = 2.2 – 3.3, Qm = 2.79), elongate ellipsoid with longitudinal ridges, 6 – 7 ridges visible in lateral view, thick-walled (up to 1 µm thick), with many guttules, yellowish to brownish yellow in water. **Basidia** 38 – 60 × 9.5 – 16 µm, clavate, thin-walled, 4-spored, hyaline to pale yellow in water; sterigmata up to 6 µm long. **Hymenophoral trama** boletoid; hyphae 3 – 7 µm wide, thin-walled, pale yellow. **Pleurocystidia** 45 – 85 × 9 – 14 µm, fusiform, some with long beak (up to 11 µm), hyaline to pale yellow with crystalline contents. **Cheilocystidia** 35 – 61 × 8 – 12 µm, numerous, fusoid, thin-walled, hyaline to pale yellow in water, with crystalline contents. **Pileipellis** an intricate trichodermium composed of interwoven, thin-walled hyphae, 3 – 7 µm wide; terminal cells 20 – 52 × 3 – 8 µm, thin-walled, with obtuse tip, brownish yellow in water. **Pileal trama** interwoven; hyphae thin-walled, 3 – 10 µm wide, pale yellow to hyaline. **Stipitipellis** a cutis

Figure 29. *Boletellus emodensis*. A-D. Basidiomata E-F. Basidiospores G. Basidium H-I. Pleurocystidia J. Cheilocystidium K. Pileipellis L. Stipitipellis. Scale bars: A-D = 10 mm, E-J = 10 µm, K - L = 20 µm.

disrupted by cystidioid hyphal elements in clusters; elements 41 – 60 × 6 – 9 µm, thin-walled, pale yellow to brownish yellow. Stipe trama parallel to interwoven, hyphae 3 – 12 µm wide, thin-walled, pale yellow to brownish yellow. Clamp-connections absent.

Habitat: Solitary or gregarious on decaying tree stumps or on dying *Terminalia paniculata* or on soil. Always found near Dipterocarpaceae members.

Specimens examined: INDIA, Kerala State, Thiruvananthapuram district, on dying *Terminalia paniculata*, 15 September 2021, Salna Nanu, ZGCSN113; Thiruvananthapuram district, Palode, on dying *Terminalia paniculata*, 20 April 2022, Salna Nanu, ZGCSN150; 15 July 2022, Salna Nanu, ZGCSN174.

Comments: *Boletellus emodensis* is characterized by purple to dull crimson pileus, a yellow context in both pileus and stipe that is strongly and rapidly cyanescent in both when injured, longitudinally ridged basidiospores with fine cross-striations on the ridges. Our collection shows close similarities with the specimens described by Corner (1972) and Zeng and Yang (2011). However, Chinese collections showed larger spores (16 – 23 × 7 – 10 µm) than our collections (Zeng and Yang 2011).

Boletellus aurocontextus Hirot. Sato, in Sato and Hattori, PLoS ONE 10: e0128184, 6 (2015)

Figure 30

Basidiomata medium-sized. **Pileus** 40 – 70 mm broad, convex at first, becoming plano-convex; surface dry, lemon yellow to pale yellowish, covered with rose-red squamulose to verruculose squamules; margin widely appendiculate with a membranous veil concolorous with pileus surface. **Pileal context** up to 20 mm wide, yellowish, changing to blue on bruising. **Hymenophore** poroid; pores up to 1.5 mm wide, yellow, changing to dark blue immediately; tubes up to 10 mm long, concolorous with pores, changing to pale blue on bruising. **Stipe** 50 – 120 × 3 – 8 mm, subcylindrical, broadening towards the base; surface wine red to pale greyish red, longitudinally fibrillose, pale yellow in apex. **Stipe context** pale yellow, turning to pale blue on bruising. **Basal mycelium** white.

Basidiospores 17 – 20 × 7 – 9 µm µm (Q = 2 – 2.5, Qm = 2.20), ellipsoid, with longitudinally winged ornamentations, 6 – 8 ridges in lateral view, ridges up to 1 µm high. **Basidia** 35 – 40 × 8 – 18 µm, clavate, broadly clavate, 4-spored, thin-walled, inamyloid, hyaline in water; sterigmata up to 6 µm long. **Hymenophoral trama** boletoid; hyphae 3 – 12 µm wide thin-walled, hyaline to pale yellow in water. **Pleurocystidia** 40 – 85 × 12 – 16 µm, utriform, narrowly utriform, hyaline to pale yellow in water, thin- to thick-walled. **Cheilocystidia** 45 – 60 × 8 – 16 µm, utriform or narrowly utriform, hyaline to pale yellow in water, thin- to thick-walled. **Pileipellis** an irregular trichodermium, made up of slender, thin-walled, pale yellow hyphae, 3 – 10 µm wide. **Pileal trama** interwoven; hyphae 3 – 12 µm wide, thin-walled, pale yellow in water. **Stipitipellis** a cutis interrupted by caulocystidia like elements; terminal elements 30 – 70 × 8 – 12 µm, nearly clavate, pale yellow in water, thin- to thick-walled. **Stipe trama** subparallel, hyphae 3 – 13 µm, pale yellow to yellow in water, thin-walled. **Clamp-connections** not observed.

Habitat: On soil, solitary to scattered, near Dipterocarpaceae trees.

Specimens examined: India, Kerala State, Thiruvananthapuram district, Palode, on soil, 15 July 2022, Salna N., ZGCSN174; ZGCSN175.

Comments: *Boletellus aurocontextus* is characterized by a pileus with bright yellow to lemon yellow pileus, relatively large and elongated basidiospores, a trichodermial pileipellis, and stipitipellis with caulocystidia like elements. *B. aurocontextus* was originally described from Japan (Sato and Hattori 2015).

Figure 30. *Boletellus aurocontextus*. A-B. Basidiomata C. Basidiospores D. Basidia E-F, H. Pleurocystidia G. Pileipellis I. Cheilocystidium. Scale bars: A-C= 10 mm, D-H = 10 µm, I-J = 20 µm.

Kerala collections agree with the description of Sato and Hattori (2015) in all morphological characters except slight difference in the spore range and larger cystidia. The phylogenetic analysis of Boletaceae family indicates the position of *B. aurocontextus* (Figure 42) along with other *Boletellus* species.

Lanmaoa G. Wu and Zhu L. Yang

Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical, convex or applanate, subtomentose, dry, slightly incurved at the margin when young; context off-white to cream yellow, slowly staining pale blue to blue when injured. Hymenophore adnexed or sinuate, hymenophoral surface yellow or cream yellow to lemon yellow, staining dull blue when injured; pores angular or nearly round; tubes concolorous with hymenophoral surface or light red, staining dark blue when injured. Stipe central, cream yellow, light yellow to lemon yellow at the apex and light to dark purple red towards the base; basal mycelia yellowish white to white. Pileipellis often an interwoven trichodermium to subcutis, rarely ixosubcutis. Pleuro- and cheilocystidia subfusiform-ventricose or clavate. Basidiospores smooth, narrowly suboblong to subfusoid, light yellow to brownish yellow. Clamp-connections absent.

***Lanmaoa* species**

Figure 31

Basidiomata medium-sized. **Pileus** 45 – 70 mm broad; hemispherical to convex; surface tomentose, pinkish brown to rose brown with dark colored spots and small ridges and groves; margin staright to wavy. **Pileal context** whitish to pale yellowish, changing to pale blue slowly. **Hymenophore** adnate to adnexed; surface bright yellow, changing to dark blue immediately on bruising; pores nearly angular, 1 to 2 per mm; tubes up to 10 mm long, concolorous with the pores, changing to dark blue on bruising. **Stipe** 40 – 50 ×

15 – 20 mm, subcylindrical; surface glabrous, whitish with yellowish tinge, unchanging or changing to bright orange in some areas. **Stipe context** up to 50 mm wide, bright golden yellow to orange, unchanging when bruised.

Basidiospores 5.5 – 7 × 3 – 4 µm µm (Q = 1.7 – 2, Qm = 1.78), elongated subfusiform, smooth, thin-walled, golden yellow in water. **Basidia** 23 – 35 × 6 – 8 µm, elongate clavate, 4-spored, thin-walled, inamyloid, pale yellow in water; sterigmata up to 3 µm long. **Hymenophoral trama** boletoid; hyphae 3 – 15 µm wide thin-walled. **Pleurocystidia** 33 – 45 × 12 – 18 µm, fusoid, broadly fusoid, some with narrow beak, thin-walled, hyaline to pale yellow in water. **Cheilocystidia** 32 – 35 × 7.5 – 11.5 µm, fusoid, numerous, hyaline to yellowish, thin-walled. **Pileipellis** an irregular trichodermium, composed of cylindrical hyphae; hyphae 4 – 7 µm wide, mostly encrusted, thin to thick-walled, hyaline in water. **Pileal trama** interwoven, made up of 3 – 5 µm wide, thin-walled hyphae. **Clamp-connections** not observed.

Habitat: On soil, solitary, near Dipetrocarpaceae trees.

Specimens examined: India, Kerala State, Thiruvananthapuram district, Palode, on soil, 28 April 2022, Salna Nanu, ZGCSN156; 15 July 2022, Salna Nanu, ZGCSN171.

Comments: Basidiomata with pinkish brown to rose brown pileus, whitish to pale yellowish pileal context that changing to pale blue slowly, bright yellow hymenophore that changing to dark blue immediately on bruising, and a trichodermial type of pileipellis indicative of the genus *Lanmaoa.* Our specimens morphologically resemble *L. pseudosensibilis* (A.H. Sm. and Thiers) G. Wu, Halling and Zhu L. Yang in having pinkish colored pileus surface and yellowish hymenophore. However, *L. pseudosensibilis* differs from our species by the presence of short tubes and subcutis type of pileipellis.

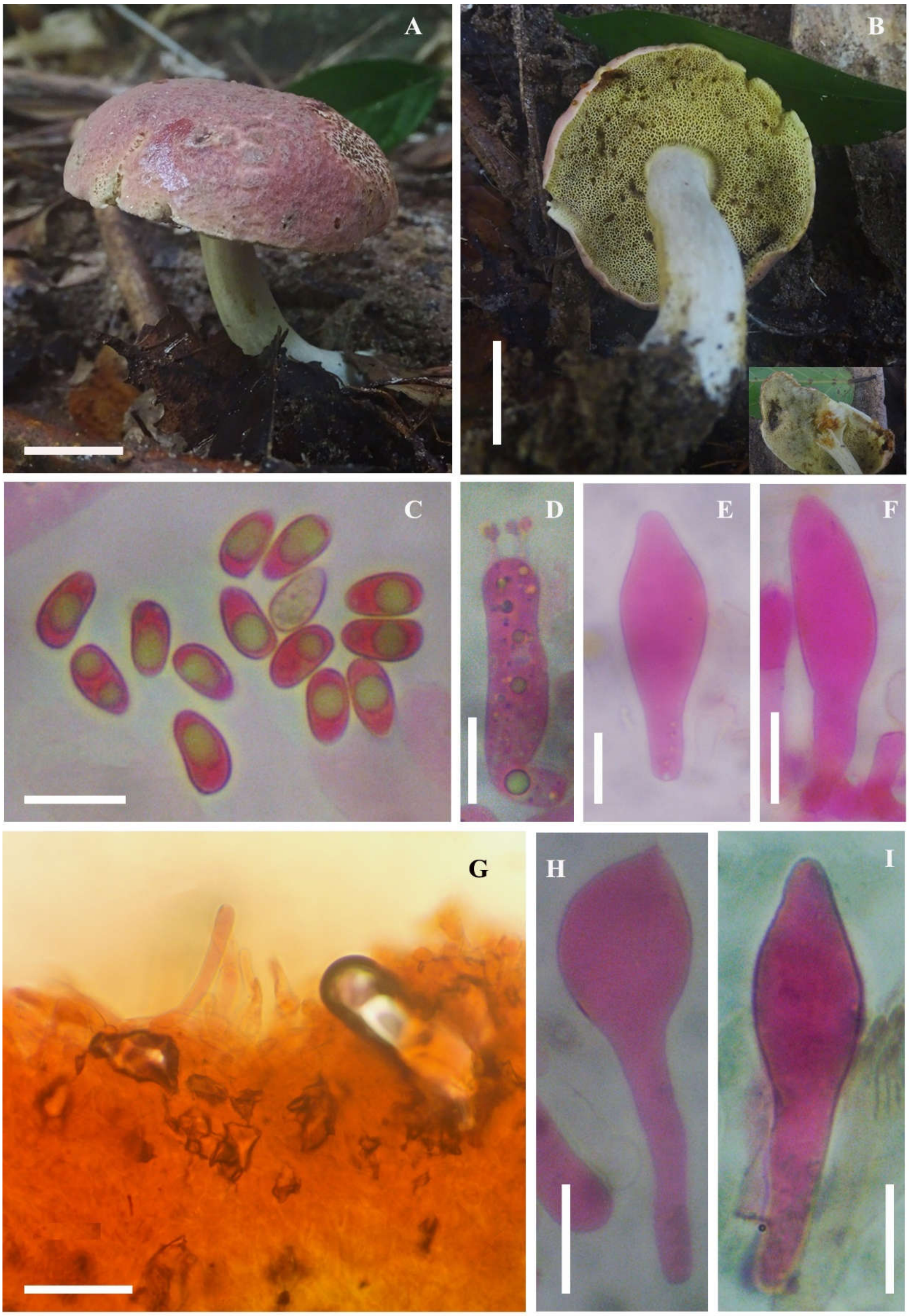


Figure 31. *Lanmaoa* species. A-B. Basidiomata (inset: showing bluish color change on bruising) C. Basidiospores D. Basidia E-F, H. Pleurocystidia G. Pileipellis I. Cheilocystidium. Scale bars: A-B= 2 cm, C-F, H-I=10 μm, G=20 μm.

Specimens are closely related to a species of the genus *Baorangia*, *B. bicolor*, which is thought to be a species complex in North America (Bessette et al. 2017). *Baorangia* and *Lanmaoa* are closely similar genera in the *Pulveroboletus* clade. Our specimens show similar characters like medium-sized basidiomata, dark red to rose red pileus with ridges, pale yellowish pileal context that changing to pale blue slowly, bright yellow hymenophore that changing to dark blue immediately on bruising, tubes up to 10 mm long, golden colored stipe context, and narrower cheilocystidia. However, Kerala collection differs from *B. bicolor* by the presence of whitish stipe surface, and smaller basidiospores. *B. bicolor* is reported only from North America and it is very common there during summer and fall under oaks. The Kerala collection is consistently found near evergreen trees belongs to Dipterocarpaceae. In phylogenetic analysis (Figure 3) using 28S gene sequences, our species clustered together with other *Lanmaoa* species (Figure 42).

Buchwaldoboletus Pilát

Basidioma stipitate-pileate with tubular hymenophore. Pileus convex or applanate; surface subtomentose to tomentose or pulverulent, dry, usually incurved at the margin; context light yellow to yellow, staining bluish when injured. Hymenophore slightly decurrent to sinuate; hymenophoral pores and tubes concolorous, light yellow to ochraceous yellow, staining bluish to dark blue when injured. Stipe central, subcylindrical. Basidiospores smooth, subfusiform, pale yellow to brownish-yellowish. Pleuro- and cheilocystidia subfusiform-ventricose or clavate, with subacute apex or long beak. Pileipellis subcutis or ixocutis. Clamp-connections absent.

Buchwaldoboletus xylophilus (Petch) Both and B. Ortiz, Ortiz-Santana and Both, Bull. Buffalo Soc. nat. Sci. 40: 3 (2011)

Figure 32

Synonymy:

Boletus xylophilus Petch, Ann. R. bot. Gdns Peradeniya 7(4): 283 (1922)
Gyrodon xylophilus (Petch) Heinem. and Rammeloo, Bull. Jard. Bot. natn. Belg. 53(1/2): 295 (1983)
Pulveroboletus xylophilus (Petch) Singer, in Singer, Araujo and Ivory, Beih. Nova Hedwigia 77: 98 (1983)

Basidiomata medium to large-sized. **Pileus** 60 – 100 mm in diam., convex to applante; surface golden yellow to greyish orange, subtomentose, dry. **Context** light yellow to yellow, up to 30 mm thick in mature specimens, staining light blue to bluish black on touch or bruising. **Hymenophore** adnate to slightly decurrent; pores and tubes concolorous, pale yellow, yellow or olive yellow, staining dark blue when cut or bruised; pores small, 2 – 3/mm, oblong, nearly radially arranged; tubes 6 – 12 mm long. **Stipe** 35 – 60 × 6 – 10 mm, central, subcylindrical, broader to bottom, surface yellowish to olive yellow or brownish yellow, nearly glabrous; context concolorous with that of pileus, tinged with brownish yellow color, staining bluish when cut. **Basal mycelium** pale yellow to bright yellow.

Basidiospores 4.5 – 5.5 × 3 – 3.5 µm µm (Q = 1.2 – 1.5, Qm = 1.4), globose to subglobose, thin-walled, with one guttule normally, pale yellow in water. **Basidia** 13 – 18 × 5 – 7 µm, clavate, 4-spored, thin-walled, hyaline; sterigmata up to 4.5 µm long. **Hymenophoral trama** boletoid; hyphae 2.5 – 10 µm wide, thin-walled. **Pleurocystidia** 17 – 48 × 6 – 11 µm, fusoid ventricose with long beak, thin-walled, hyaline**. Cheilocystidia** 17 – 30 × 4 – 6.5 µm, numerous, fusoid with long beak in many, clavate with acute tip in some, thin-walled, hyaline. **Piliepellis** an ixocutis of interwoven hyphae, 100 – 205 µm thick; outer pellis consist of 2.5 – 5 µm wide frequently septate hyphae arranged as interwoven; inner layer composed of interwoven thin-walled, loosely packed filamentous hyphae, 3 – 6 μm wide. **Pileal trama** parallel to interwoven, hyphae 4 – 15 μm wide, thin-walled. **Stipitipellis** a cutis interrupted by caulohymenium; caulobasidia same as hymenial basidia in size and shape. **Stipe trama** parallel to interwoven; hyphae 3 – 8 μm wide, thin-walled, hyaline. **Caulocystidia** 15 – 25 × 4 – 7 μm, clavate to broadly clavate, thin-walled, pale yellow. **Clamp-connections** not observed.

Habitat: Solitary to scattered on soil, under bamboo plants *Bambusa* species.

Specimens examined: India, Kerala State, Thiruvananthapuram district, Palode, on soil, 24 September 2021, Salna Nanu; ZGCSN110; 1 October 2021, Salna Nanu, ZGCSN111.

Comments: The distinguishing characters of *Buchwaldoboletus xylophilus* are the dry to subviscid, minutely velvety, ferruginous-brown pileus, yellowish context, very small pores that change to bluish on bruising, reddish brown stipe with sulphur yellow mycelium at the base, small basidiospores (4.5 – 5.5 × 3.2 – 4 μm) and trichodermial type of pileipellis. The species originally described as *Boletus xylophilus* from Sri Lanka. The holotype was collected from decaying stumps and rotting logs of dicotyledonous trees. *B. xylophilus* look like *B. lignicola* in yellowish brown pileus and bluing of the pileal context when cut. However, *B. lignicola* have large basidiospores (6 – 9 (–12) × 3 – 4 μm) and cystidia (29 – 80 × 4 – 9 μm). *B. brachyspermus*, originally described from Central America as *Pulveroboletus brachyspermus* and it closely resembles *B. xylophilus* except very small pores, russet-colored stipe, and large-sized cystidia (40 – 55 × 11 – 14 μm). The present collection from India was obtained from soil around *Bambusa bambos*, and represents a new record from India. Results of molecular phylogenetic analysis and detailed comparisons are presented in Nanu and Kumar (2022).

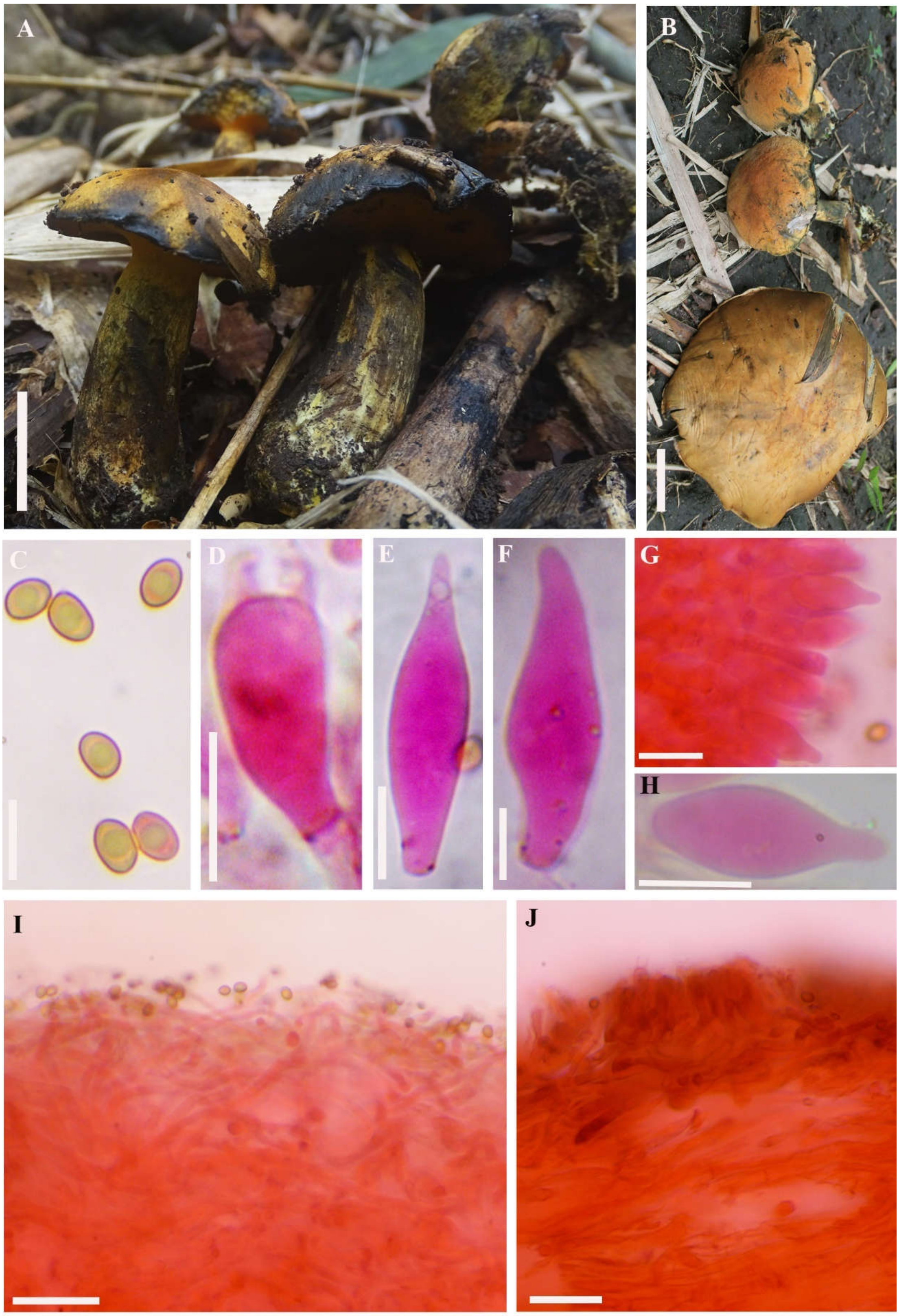


Figure 32. *Buchwaldoboletus xylophilus*. A-B. Basidiomata C. Basidiospores B. Basidia D. Basidium E-F. Pleurocystidia G-H. Cheilocystidia I. Pileipellis J. Stipitipellis. Scale bars: A-B = 10 mm, C-H = 10 μm, I-J = 20 μm.

Buchwaldoboletus pseudolignicola (Neda) Both and B. Ortiz

Figure 33

Synonymy:

Gyrodon pseudolignicola (Neda) Har. Takah., MSJ News, Nippon Kingakkai Nyūsu (no. 19): 28 (1992)
Pulveroboletus pseudolignicola Neda, in Neda, Yokoyama and Furukawa, Trans. Mycol. Soc. Japan 28(3): 319 (1987)

Basidiomata medium- to large-sized. **Pileus** 30 – 140 mm in diam., convex to applanate; surface yellowish to rownish yellow, dry, viscid when wet, subtomentose. **Pileal context** up to 40 mm thick in the center, pale yellow to greenish yellow, changing to pale blue to bluish on bruising; margin somewhat incurved and wavy in mature specimens. **Hymenophore** adnate to slightly decurrent; pores small, 2 – 3 per mm, nearly round, yellowish to greenish yellow, changes to blue on bruising; tubes up to 12 mm long, yellowish, changes to blue on bruising. **Stipe** 30 – 80 × 4 – 20 mm, central, sub cylindrical, broadening to the base; surface yellowish on the apex, yellowish brown to reddish brown in other area, slightly pruinose. **Stipe context** yellowish, tinged with brown, staining to blue when bruised. **Basal mycelium** pale yellow.

Basidiospores 5 – 6.5 × 4 – 4.5 µm µm (Q = 1.25 – 1.6, Qm = 1.46), subglobose to ellipsoid, normally with a large oil guttule, thin- to thick-walled, pale yellowish in water**. Basidia** not observed. Basidiole 8 – 14 × 4 – 7 µm, thin-walled. **Pleurocystidia** 32 – 52 × 7 – 12 µm, fusiform, lageniform, thin-walled, pale yellow to brownish yellow in water. **Cheilocystidia** 22 – 37 × 6 – 7 µm, numerous, narrowly clavate to fusiform, thin-walled, pale yellow to brownish yellow in water. **Pileipellis** a trichodermium; outer layer made up of tightly interwoven hyphae, 3 – 8 µm wide, thin-walled, hyaline to pale yellow in water; inner layer made up of loosely packed interwoven hyphae, 3 – 6 µm wide, thin-walled, hyaline to pale yellow in water. **Pileus trama** interwoven; hyphae 4 – 15 µm wide, thin- walled. **Stipitipellis** a cutis interrupted by caulocystidial clusters.

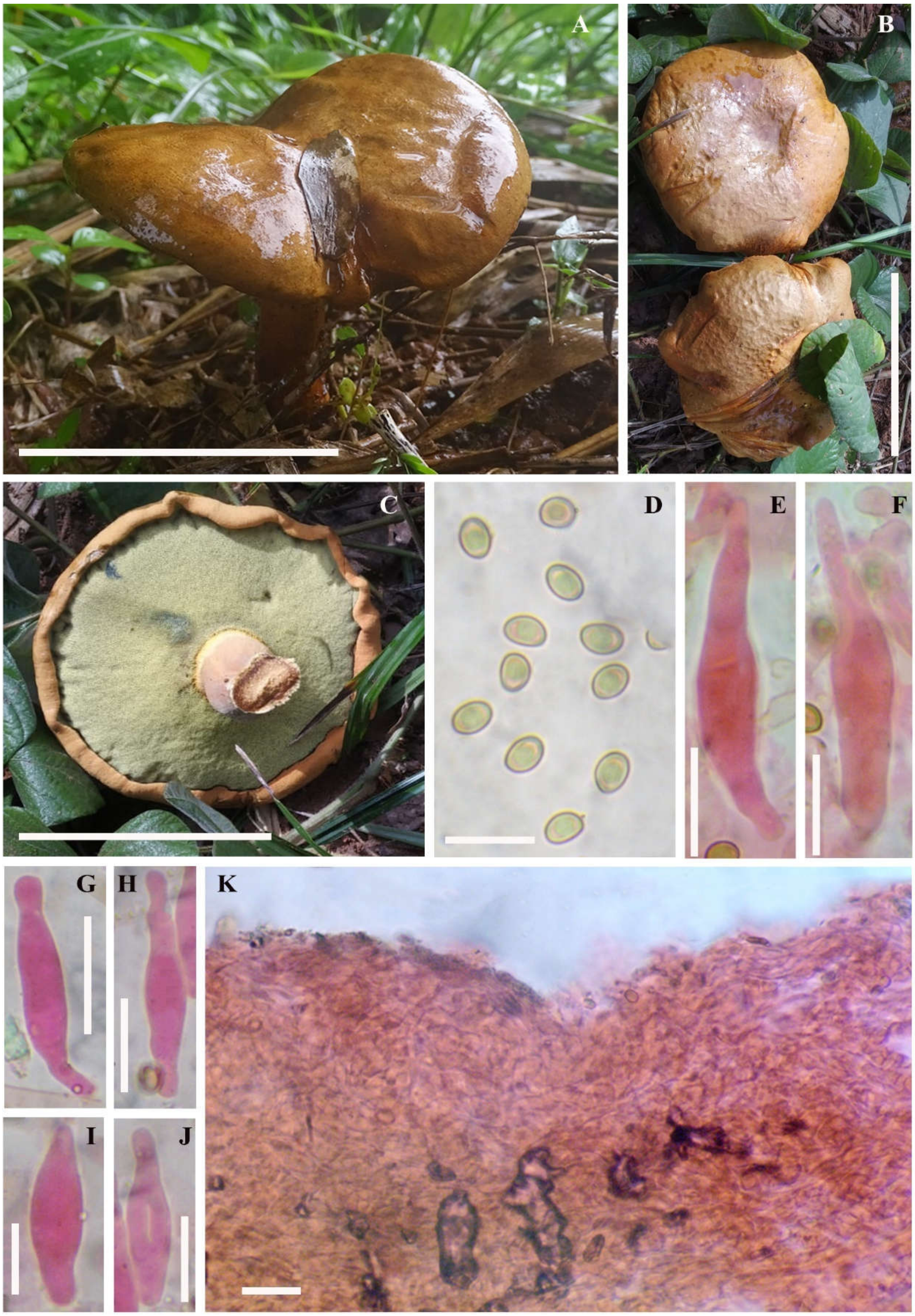


Figure 33. *Buchwaldoboletus pseudolignicola*. A-C Basidiomata D. Basidiospores E-F. Pleurocystidia G-J. Cheilocystidia K. Pileipellis. Scale bars: A-C = 10cm, D-J = 10 µm, K = 20 µm.

Caulocystidia 12 – 20 × 5 – 7 µm, nearly clavate, thin-walled, pale yellow to brownish yellow in water. **Stipe trama** interwoven; hyphae 3 – 6 µm, thin-walled, hyaline. **Clamp-connections** not observed.

Habitat: Solitary to scattered on soil, in tropical evergreen forest of Kerala State, near *Bambusa bambos* (L.) Voss.

Specimens examined: India, Kerala State, Kannur District, Maloor, on soil, 10 June 2023, Salna Nanu; ZGCSN193; 16 June 2023, Salna Nanu, ZGCSN194.

Comments: *Buchwaldoboletus pseudolignicola* is characterized by basidiomata with yellowish pileus, yellow to greenish yellow pores and tubes that changes blue on bruising, smaller basidiospores, presence of numerous cheilocystidia, and a trichodermium type of pileipellis (Ortize and Both 2011, Jo et al. 2019). The closely related species is *B. lignicola,* that differs from *B. pseudolignicola* by having reddish brown pileus, and larger basidiospores.

Xerocomellus Šutara

Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical, convex or applanate; surface velvety, dry; context white to yellowish, slowly staining bluish when injured. Hymenophore adnate to sinuate, sometimes depressed around the stipe; surface olive yellow to brownish yellow, becoming ochraceous with age, staining blue immediately when bruised; pores compound, angular, comparatively large (1 – 2.5 mm in diam.); tubes concolorous with hymenophoral surface, staining blue when injured. Stipe comparatively slender, red to brownish red, longitudinally fibrillose; basal mycelium dirty white. Basidiospores subfusiform to slender amygdaliform in side view with poor suprahilar depression, subfusoid in ventral view, brownish yellow, smooth (under SEM), rarely with indistinctly longitudinal ridges. Pleuro- and cheilocystidia fusoid to lageniform, thin-walled. Pileipellis a palisadoderm consisting of vertically arranged, yellowish brown, more or less broadened and often incrusted hyphal elements, terminal cells of which reach almost at the same level. Clamp-connections absent.

Xerocomellus corneri Xue T. Zhu and Zhu L. Yang, in Wu, Li, Zhu, Zhao, Han, Cui, Li, Xu and Yang, Fungal Diversity 81: 171 (2016)

Figure 34

Basidiomata small. **Pileus** 10 – 15 mm in diam., subhemispherical to convex; surface dry, velvety, red-brown to dull red-brown. **Pileal context** yellowish, staining blue quickly. **Hymenophore** adnate to adnexed, sometimes depressed around the stipe; surface golden yellow to yellow, bluing immediately when bruised; pores angular; tubes concolorous with the hymenophiral surface, bluing on injury. **Stipe** 20 – 25 mm long, subcylidrical to cylindrical, apical part yellow, basal part dirty white to pale yellow, middle part red to brownish red, slightly fibrillose; context yellow, unchanging or changing to pale blue when bruised.

Basidiospores 8 – 10 × 4 – 5 µm µm (Q = 2 – 2.5, Qm = 2.12), subfusiform to ellipsoid, thin-walled, smooth, hyaline in water. **Basidia** 26 – 35 × 6 – 9 µm, clavate, 4-sterigmate, thin-walled, hyaline; sterigmata up to 4 µm long. **Hymenophoral trama** boletoid; hyphae 4 – 7.5 µm, thin-walled. **Pleurocystidia** 37 – 47 × 5 – 10 µm, fusiform, thin-walled, yellowish in water. **Cheilocystidia** 30 – 40 × 5 – 8 µm, fusiform, thin-walled, pale yellow in water. **Pileipellis** a palisadoderm consisting of vertically arranged terminal elements; terminal elements 25 – 45 × 5 – 10 µm, cylindrical, closely septate, thin-walled, with pale brownish contents or hyaline. **Stipitipellis** basically a cutis, interrupated by hyphal patches; hyphae 3 – 7 µm, thin-walled. **Stipe trama** interwoven; hyphae 4 – 12 µm wide, thin- to thick-walled. **Clamp-connections** not observed.

Habitat: solitary to scattered on soil.

Figure 34. *Xerocomellus corneri*. A-D Basidiomata E. Basidiospores f. basidia G-I. Pleurocystidia J. Cheilocystidia K. Pileipellis L. Stipitipellis. Scale bars: A-D = 10cm, E-J = 10 µm, K-L = 20 µm.

Specimens examined: India, Kerala State, Kozhikode district, Peruvannamoozhi, 15 October 2019, Salna N., ZGCSN54.

Comments: *Xerocomellus corneri* is characterized by velvety, red-brown to dull brown pileal surface, and subfusiform to slender amygdaliform basidiospores (Corner 1972). *Xerocomellus corneri* was originally described as *B. pseudochrysenteron* from Malaysia (Corner 1972). Kerala collection is closely similar to *Xe. corneri* in all characters described by Wu et al. (2016a) except for smaller basidiospores and cystidia in Kerala collection.

Parvixerocomus G. Wu and Zhu L. Yang

Basidiomata small, stipitate-pileate with tubular hymenophore. Pileus convex to applanate, subtomentose, dry; context yellowish to yellow, staining blue immediately when injured. Hymenophore subdecurrent, often with teeth on the apex of stipe; surface yellowish to yellow, staining blue immediately when injured; pores irregular, angular to round, often compound; tubes concolorous with hymenophoral surface, staining blue immediately when injured. Stipe central, light brown, brownish red to reddish brown, surface often pruinose; basal mycelia cream to greyish yellowish. Pileipellis an epithelium composed of submoniliform to moniliform hyphae with cystidioid terminal cells. Pleuro- and cheilocystidia subfusiform-ventricose or clavate, with subacute apex or with long beak. Basidiospores smooth, ovoid to ellipsoid, yellowish to brownish yellow. Clamp-connections absent.

Parvixerocomus matheranensis P.B. Patil, Senthil., S.K. Singh and S.A. Vaidya, Mycoscience 62: 245 (2021)

Figure 35

Basidiomata small-sized. **Pileus** 6 – 12 mm in diam., hemispherical to convex; surface dry, subtomentose, bright red or ruby red to brownish red;

margin straight. **Context** up to 3 mm thick, pale yellowish, turning blue immediately when injured. **Hymenophore** poroid, adnate to subdecurrent; pores angular, 2 – 3/mm, yellow to bright yellow, turning bluish when injured; tubes 1 – 2 mm long, pale yellow to yellow, turning bluish when injured. **Stipe** 10 – 15 × 2 – 3 mm, central, subcylindrical, solid; surface pruinose, reddish in the bottom, yellowish in the apex, staining blue when bruised; annulus absent.

Basidiospores 8 – 10 × 4 – 5.5 µm µm (Q = 1.75 – 2.5, Qm = 1.4), elongate ellipsoid with indistinct superhilar depression, smooth, thin to thick-walled, pale yellow in water. **Basidia** 27 – 37 × 8 – 11 µm, clavate, hyaline to pale yellow, thin-walled, 4-spored. **Pleurocystdia** 22 – 52 × 5 – 8 µm, fusoid-ventricose with long beak, thin-walled, hyaline. **Cheilocystidia** 23 – 42 × 5 – 7 µm, fusoid ventricose or clavate with subacute apex, thin-walled, hyaline. **Pileipellis** an epithelium consists of submoniliform to cylindrical cells, 23 – 62 × 3 – 14 µm, some terminal cells with acute apex. **Pileal trama** interwoven, thin-walled, 3 – 10 µm wide, hyaline. **Stipe trama** consist of parallel hyphae, 6 – 10 µm wide, thin-walled, hyaline. **Clamp-connections** not observed.

Habitat: On soil, between the roots of *Terminalia* species.

Specimens examined: India, Kerala State, Kozhikode district, Janaki forest, 01 June 2021, Salna Nanu, ZGCSN74; Palakkad district, Parambikkulam Tiger Reserve, 24 June 2022, Salna Nanu, ZGCSN165.

Comments: *Parvixerocomus matheranensis* is characterized by small-sized basidiomata, bright red or ruby red to brownish red pileal surface, pale yellowish context that immediately changes to blue on bruising, elongate ellipsoid basidiospores and an epithelium type of pileipellis. The species was originally described from Maharashtra, India (Patil et al. 2021). Kerala collection differs from the holotype specimen differs from by the presence broader spore range, whitish pileal context and larger pleurocystidia. Molecular phylogenetic analysis using 28S gene sequences confirmed the identity (Figure 42).

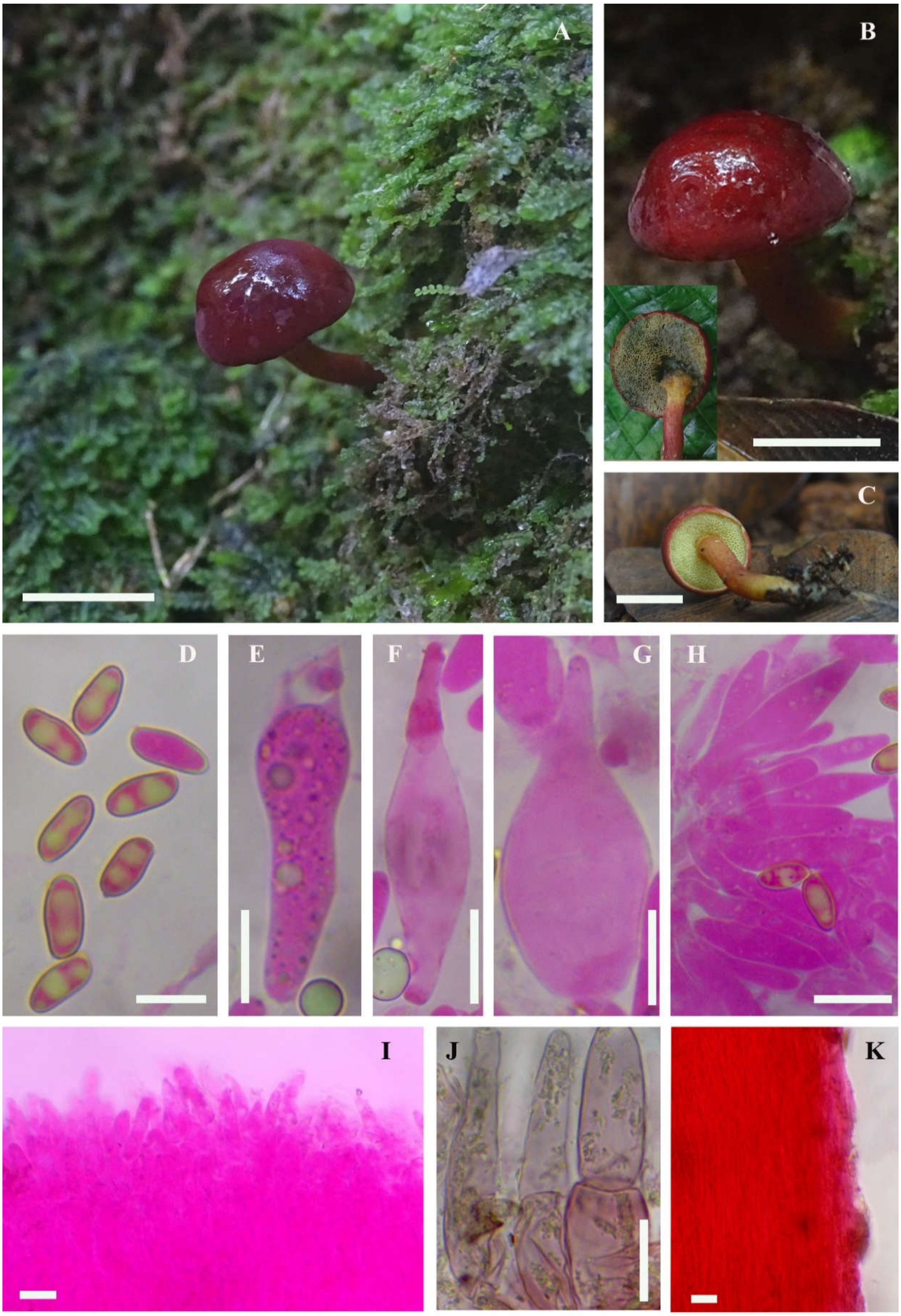


Figure 35. *Parvixerocomus matheranensis*. A-B. Basidiomata D. Basidiospores E. BasidiUM F-G. Pleurocystidia H. Cheilocystidia I. Pileipellis J. Pileal elements K. Stipitipellis. Scale bars: A-C = 10 mm, D-H, J = 10 µm, I,K = 20 µm.

Baorangia G. Wu and Zhu L. Yang

Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical, convex or applanate, subtomentose, dry, usually incurved at the margin when young; context pale yellow to yellow, slowly staining pale blue when cut. Hymenophore relatively thin (thickness of hymenophore 1/3 – 1/5 times that of pileal context at the position halfway to the pileus center), usually decurrent; hymenophoral surface and tubes yellow, immediately staining light blue to greenish blue when injured or without any change; pores angular, or sometimes nearly round; tubes short. Stipe smooth or occasionally with reticulations at the upper part; context pale yellow to yellow, staining pale blue; basal mycelia white to pale yellow. Pileipellis a trichodermium. Pleuro- and cheilocystidia present. Basidiospores smooth, subfusiform to elongated subfusiform, light yellow to brownish-yellowish or golden yellow. Clamp-connections absent.

Baorangia albostipitata Salna Nanu and T. K. A. Kumar, Nordic Journal of Botany, 2024: e04357

Figure 36

Basidiomata medium to large-sized. **Pileus** 55 – 100 mm in diam., hemispherical at first, becoming convex to applanate; margin somewhat wavy, slightly uplifted when mature; surface dry, indistinctly pruinose, pinkish, with yellowish edges and center. **Pileal context** up to 20 mm thick, whitish, changing to pale blue very slowly on cut or bruising. **Hymenophore** poroid, adnate; pores angular, 1 – 2 per mm, yellowish, unchanging the color when bruised or cut, becoming brownish yellow on age; tubes up to 8 mm long, yellowish, unchanging the color when bruised or cut. **Stipe** 50 – 70 × 10 – 15 mm, central, almost cylindrical, solid; surface dry, glabrous, whitish, slowly changing to bright orange when bruised. **Stipe context** whitish, unchanging, or changing to pale blue slowly when cut or bruised. **Basal mycelium** white.

Basidiospores 5 – 7 × 3 – 4 μm (Q = 1 – 1.75, Qm = 2.24), subglobose to ellipsoid, smooth, thin-walled, guttulate, hyaline to pale yellow in water. **Basidia** 25 – 38 × 6 – 8 μm, clavate, thin-walled, 4-spored, hyaline in water. **Pleurocystidia** 32 – 60 × 8 – 12 μm, fusiform, some with long apical beaks (up to 10 μm long), brownish yellow in water. **Cheilocystidia** 34 – 40 × 6 – 8 μm, fusiform, thin-walled, pale brownish yellow in water. **Pileipellis** an irregular trichodermium; hyphae 3 –12 μm wide, cylindrical, thin-walled, some are faintly encrusted, pale yellow to brownish yellow in water. **Pileal trama** interwoven; hyphae 3 – 10 μm wide, thin-walled, pale yellow in water. Stipitipellis a cutis of tightly interwoven hyphae; hyphae 3 – 8 μm wide, thin-walled, with encrustation, pale yellow to brownish yellow in water. **Clamp-connections** not observed on all hyphae.

Habitat: Solitary or in group containing 2 – 3 specimens, under *Diospyros paniculata* (Ebenaceae).

Specimens examined: India, Kerala State, Kozhikode district, Thurayil Kotta sacred grove, 20 June 2023, ZGCSN211 (holotype); 26 Oct 2023, Salna Nanu, ZGCSN228.

Comments: Narrow hymenophore (1/3 – 1/5 times narrower than that of pileal context), yellowish pores and tubes, pale yellow pileal context that slowly changes to pale blue when cut or bruised, and a trichodermium type of pileipellis of the new specimen are the characteristics of the genus *Baorangia.* According to Wu et al. (2016b), the genus consists of a pale yellowish hymenophore surface which changes to blue immediately on cut or bruising. However, our specimen did not exhibit a color change at hymenophore surface on bruising or cut.

Figure 36. *Baorangia albostipitata*. A. Basidiomata B. Context of pileus and stipe immediately after cut C. Basidiomata showing hymenophore D. Color change of pileal context to pale blue after some time E. Basidiospores F. Basidium G. Pleurocystidium H. Pileipellis. Scale bars: A-D = 10mm, E-G = 10 μm, H = 20 μm.

Morphologically and phylogenetically *B. albostipitata* is similar to *B. alexandri* by having a pinkish pileal surface, yellowish pileal context that slowly changing to blue on bruising, yellowish hymenophore surface, small pores (1 – 2 per mm), fusiform shaped cystidia and a trichodermial pileipellis. However, *B. alexandri* differs from *B. albostipitata* by having a pileus with velutinous to glabrous surface and involute margin, yellowish hymenophore that changes to dark blue when bruised, a stipe surface with yellow at the apex and carmine red to the bottom, and larger basidiospores. *B. alexandri* was found in deciduous forests with *Quercus mongolica* Fisch. ex Ledeb., *Corylus heterophilla* Fisch. ex Trautv. and *Lespedeza bicolor* Turcz. (Crous et al. 2018). Morphological comparisons and phylogenetic analysis of *B. albostipitata* is presented in Nanu and Kumar (2024).

Hiranmaya indica Salna Nanu and T. K. A. Kumar, gen. et. sp. nov

Figure 37

Basidiomata small-sized. **Pileus** 15 – 60 mm in diam., plano-convex to applanate; surface reddish brown with yellowish tinge towards the periphery, becomes darker with age, turning to pale vinaceous brown on bruising, sub-tomentose, with scattered irregular depressions, dry or viscid when wet. **Pileal context** up to 5 mm thick, pale yellow to yellow, changes to vinaceous brown on cut or bruising. **Hymenophore** poroid, adnate to adnexed; pores angular, 1 – 2 mm, pale yellow to greenish yellow, unchanging when cut or bruised; tubes 4 – 10 mm long, concolorous with the pores, unchanging when cut or bruised. **Stipe** 25 – 60 × 3 – 5 mm, subcylindrical central, solid, pruinose with whitish powder like squamules all over the surface, reddish brown to dark brown when mature, turning in to blackish with age, unchanging when bruised. **Stipe context** pale yellow, changing to vinaceous brown very fast when cut or bruised. Basal mycelium white.

Basidiospores 8.5 – 11 × 4 – 5.5 µm, subfusiform with distinct hilar depression, some with a guttule, smooth under light microscope, smooth to irregularly warted to under SEM, thin-walled, pale yellow to brownish yellow in water. **Basidia** 23 – 30 × 8 – 12 µm, clavate, broadly clavate, 4-spored, hyaline to pale yellow, thin-walled; sterigmata up to 5 µm long. **Hymenophoral trama** boletoid; hyphae 3 – 8 wide, thin-walled. **Pleurocystidia** 18 – 57 × 7 – 18 µm, scattered, sub-fusiform or fusiform, with long beak in some, thin to slightly thick-walled, yellow or golden yellow at first, immediately changes to pale yellow then hyaline in 5% KOH. **Cheilocystidia** 23 – 41 × 8 – 13 µm, numerous, fusiform, thin-walled, hyaline to pale yellow. **Pileipellis** an epithelium, 70 – 105 µm thick, composed of globose to ovoid inflated or cylindrical cells; cylindrical terminal cells 11 – 18 µm wide, thin-walled; narrowly cylindrical terminal cells 12 – 36 × 8 – 12 µm wide. **Pileal trama** interwoven to parallel, hyphae 4 – 16 wide, thin-walled. **Stipitipellis** an intermittent trichodermium with caulobasidia nad caulocystidia; caulobasidia same as hymenial, 26 – 30 × 9.5 – 12 µm; caulocystidia 15 – 25 × 4 – 7 µm, fusoid, thin-walled. **Stipe trama** parallel to interwoven, hyphae 3 – 8 µm wide, hyaline. **Clamp-connections** not observed.

Habit: On soil, solitary to gregarious, under Dipterocarpaceae trees like *Hopea ponga*.

Specimens examined: India, Kerala State, Wayanad district, Kuruva isletes, 26 May 2022, Salna Nanu, ZGCSN139; 14 October 2022, Salna Nanu, ZGCSN190; Kozhikode district, Thurayilkotta sacredgrove,12 October 2023, Salna Nanu, ZGCSN221; 26 October 2023, Salna Nanu, ZGCSN226; 13 November 2023, Salna Nanu, ZGCSN235.

Comments: The collections are characterized by sub-tomentose, reddish brown pileal surface with yellowish tinge and ridges and groves that turn to vinaceous brown on bruising, pale yellow to yellow pileal context that changes to vinaceous brown on bruising, yellowish to greenish yellow hymenophore

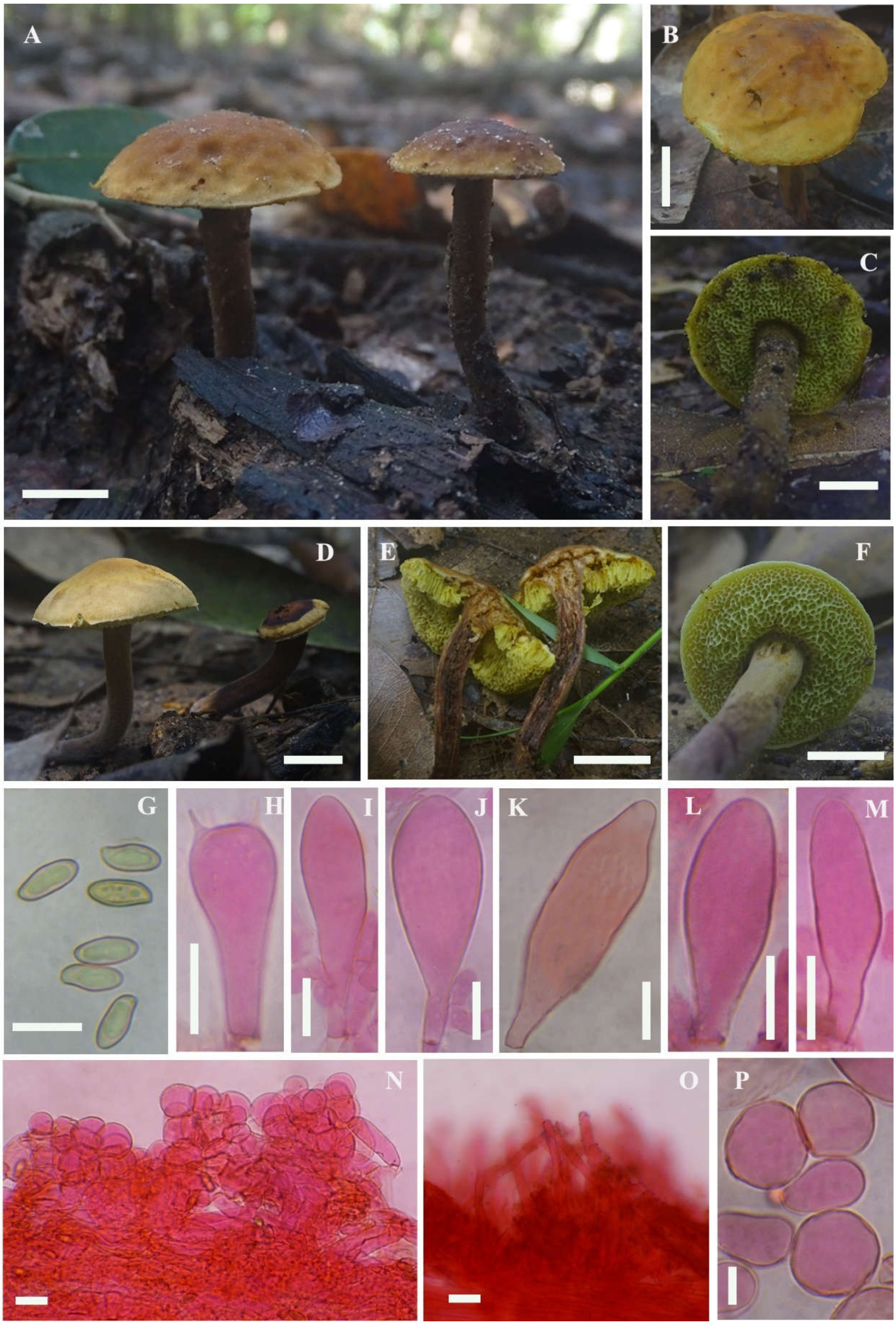


Figure 37. *Hiranmaya indica*. A-F. Basidiomata G. Basidiospores H. Basidium I-K. Pleurocystidia L-M. Cheilocystidia N. Pileipellis O. Stipitipellis P. Terminal cells of pileipellis. Scale bars: A-F = 10 mm, G-M, P = 10 μm, N-O = 20 μm.

unchanging when bruised or cut, pruinose stipe surface, subfusiform basidiospores which are smooth under light microscope, smooth to rugged under SEM, and an epithelioid type of pileipellis. Molecular phylogenetic analysis based on ITS, 28S and *RPB2* gene sequences placed all collections of *Hiranmaya* in Boletoideae clade of Boletaceae with 100% boot strap support (Figure 42).

Phylogenetically, the current species is closely related to *Xanthoconium* included in Boletoideae clade of Boletaceae (Figure 42). *Xanthoconium* species have morphological similarities such as yellowish hymenophore, fusiform cystidia, and an epithelium to a trichodermium type of pileipellis. However, unchanging context when bruised, glabrous or faintly striated stipe surface, and smooth basidiospores under SEM are the distinguishing characters of *Xanthoconium* species from the Kerala collections.

Kerala collections are morphologically similar to the other genera present in Xerocomoideae clade of Boletaceae. *Aureoboletus* is a widely distributed bolete genus with 35 known species (Ayala-Vásquez et al. 2023). Kerala collections shares similar characters with *Aureoboletus* in the yellowish hymenophore surface, round to angular pores, yellowish basidiospores, and fusiform shaped cystidia. However, *Aureoboletus* can be distinguished from the Kerala collections by its viscid pileus, yellowish pileal context without any color change on bruising or cut, usually smooth, rarely longitudinally striate basidiospores, and ixotrichodermium or trichodermium type of pileipellis (Wu et al. 2016a).

Kerala collections and *Boletellus* have yellow hymenophore surface, yellowish basidiospores, and fusiform cystidia with or without long neck. *Boletellus* is comprised of mostly tropical species and morphologically distinct from other genera by the presence of longitudinally ridged basidiospores (Magnago et al. 2019). *Boletellus* can be differentiated from Kerala collections by the presence of glabrous, tomentose, fibrillose, or velvety pileal surface, yellowish pileal context changing to bluish, blue to dark blue or unchanging when bruised or cut, longitudinally striate basidiospores, and trichodermium to an intricated trichoderm type of pileipellis.

The combination of vinaceous color change of the context, yellowish to greenish yellow pore surface, pruinose stipe surface, smooth to rugged basidiospores under SEM, and epithelioid type of pileipellis are indicative of a yet undescribed genus in the clade Boleoideae. The single new species in this genus is morphologically and phylogenetically (Figure 42) distinct from all other species of Boletaceae family.

Retiboletus Manfr. Binder and Bresinsky

Basidiomata stipitate-pileate with tubular hymenophore. Pileus hemispherical to subhemispherical; surface tomentose or subtomentose, dry; context white to pallid or yellow, unchanging or becoming brownish in color when injured. Hymenophore adnate or depressed around apex of stipe; hymenophoral surface pallid to off white, greyish pink or yellow; pores angular or roundish; tubes concolorous with hymenophoral surface, unchanging or brownish or reddish brown in color when bruised. Stipe central, wholly reticulate, rarely non-reticulate; basal mycelium white to yellow. Basidiospores smooth, subfusoid. Pleuro- and cheilocystidia abundant, subfusiform to fusoid-ventricose. Pileipellis subrepent to trichodermium composed of filamentous interwoven hyphae. Clamp-connections absent.

***Retiboletus* species**

Figure 38

Basidiomata medium-sized. **Pileus** 60 – 80 mm in diam., convex to applanate, slightly depressed in the center; surface dry, hard, greyish brown to blackish, densely covered with appressed fibrillose sqamules; margin slightly uplifted, nearly straight. **Pileal context** up to 10 mm wide, whitish, changing to brownish on cut. **Hymenophore** adnate to adnexed; surface greyish white when young, becoming blackish on maturity, changing to brownish on bruising slowly; pores angular 1 or 2 /mm; tubes up to 8 mm long, whitish when young, changing to brownish on bruising, becoming black on aging. **Stipe** 50 – 65 × 15 – 20 mm, central, thick, almost cylindrical; surface greyish with black squamules, narrow elongated reticulations present. **Stipe context** off white, changing to brownish on cut. **Basal mycelium** whitish to blackish.

Basidiospores 10 – 13 × 3 – 4 µm (Q = 2.25 – 3.5, Qm = 2.7), ellipsoid, smooth, guttulate, thin- to thick-walled (wall thickness up to 0.5 µm), pale yellow in water. **Basidia** 26 – 38 × 8 – 10 µm, clavate, 4-spored, thin-walled, pale yellow in water; sterigmata up to 4.5 µm long. **Pleurocystidia** 41 – 72 × 10 – 14 µm, fusiform with or without apical protrusion, pale brownish yellow in water. **Cheilocystidia** 27 – 52 × 8 – 12 µm, fusiform, thin-walled, pale brownish yellow in water. **Hymenophoral trama** boletoid; hyphae 3 – 10 µm wide, thin-walled, hyaline to pale brownish yellow in water. **Pileipellis** an irregular trichodermium, composed of interwoven hyphae, 4 –12 µm wide, thin- to thick-walled, some are encrusted, brownish in water.; terminal elements cylindrical, 15 – 45 × 3 – 6 µm, thin- to thick-walled, brownish yellow in water. **Pileal trama** interwoven, hyphae 3–6 µm, thin-walled, yellowish in water. **Stipitipellis** a cutis interrupted by bunches of caulocystidia. **Caulocystidia** 25 – 37 × 5 – 9 µm, flexuous, narrowly clavate, thin-walled, brownish yellow in water. **Clamp-connections** not observed.

Habitat: Solitary, on soil, near *Hopea parviflora.*

Specimens examined: India, Kerala State, Wayanad district, Kuruva islets, 20 April 2022, Salna Nanu, ZGCSN126; 15 Oct 2022, Salna Nanu, ZGCSN187.

Figure 38. *Retiboletus* species. A-B. Basidiomata C. Context changing to copper red to black on cut D. Basidiospores E. Basidium F-H. Pleurocystidia I-J. Cheilocystidia K. Pileipellis L. Stipitipellis Scale bars: A-C= 10 mm, D-J = 10 μm, K-L = 20 μm.

Comments: Kerala collections are characterized by fibrillose pileus, whitish pileal context tturns brownish when bruised, greyish white hymenophore turns brownish on bruising, reticulate stipe surface, and trichodermium type of pileipellis. These are characteristics of the genus *Retiboletus.* Kerala collection are and closely similar to *Retiboletus brunneolus* Yan C. Li and Zhu L. Yang. Greyish brown pileus, greyish white pileal context, greyish yellow stipe apex, reticulated stipe surface, similar basidiospores, and trichodermial pileipellis are the similar morphological characters. However, *R. brunneolus* differs from Kerala collections by the presence of tomentose squamules on pileipellis, absence of color change on pileal and stipe context after bruising, absence of color change on the hymenophore surface after bruising, and yellowish tinge at the base of stipe context. Our species forms a clade with other *Retiboletus* species 100% bootstrap support in phylogenetic analysis (Figure 42).

Aureoboletus Pouzar

Basidiomata stipitate-pileate with tubular hymenophore. Pileus convex to applanate; surface usually glabrous and viscid. Pileal context yellowish to yellow, without color change on bruising. Hymenophore adnate to sinuate; surface bright yellow to yellowish, without color change on bruising; pores angular to nearly round; tubes concolorous with pores, unchanging in color on bruising. Stipe central, without color change when injured; basal mycelium usually white. Basidiospores usually smooth, rarely longitudinally striate, subfusiform, yellowish. Pleurocystidia and cheilocystidia fusiform-ventricose or clavate, sometimes with protrusions, yellowish to yellow in KOH, but soon dissolving in the medium. Pileipellis ixotrichodermium or trichodermium. Clamp-connections absent.

***Aureoboletus* species**

Figure 39

Basidiomata medium-sized. **Pileus** 50 – 80 mm broad, hemispherical to applanate; surface finely fibrillose with greyish squamules scattered, dry, cracking in to many on aging, pale grey to dark grey with whitish tinges, becoming yellowish on drying, without any color changes on bruising. **Context** up to 25 mm wide in centre, whitish, no color change on bruising. **Hymenophore** poroid, adnate when young, becoming depressed around the stipe when mature; surface yellowish to olive yellow, without color changes on bruising, becoming reddish brown on drying; pores 1 – 2 per mm, nearly angular; tubes up to 12 mm long, concolorous to pore surface, changes to pale brown to reddish brown on drying. **Stipe** 50 – 70 × 30 – 40 mm, central, subcylindrical, enlarging downwards; surface minutely pubescent in apex, from apex to near bottom covered with distinct yellowish fibrils, whitish to yellowish, without any color change on bruising. **Basal mycelium** whitish.

Basidiospores 7 – 8 × 4.5 – 5.5 µm (Q = 1.2 – 1.7, Qm = 1.46), subovoid to subfusiform with superhilar depression, pale yellowish, smooth, thin- to slightly thick-walled. **Basidia** 22 – 31 × 10 – 12 µm, clavate, thin-walled, hyaline in water; sterigmata up to 4.5 µm long. **Pleurocystidia** 25 – 48 × 6 – 13 µm, fusoid ventricose, with subacute apex in many, thin-walled, hyaline in water. **Cheilocystidia** 40 – 56 × 6.5 – 8.5 µm, abundant, fusoid ventricose with long beak up to 12 µm, thin-walled, hyaline in water. **Pileipellis** an ixotrichodermium, up to 350 µm wide, composed of filamentous hyphae, 4 – 10 µm wide, thin-walled, hyaline in water; terminal elements 25 – 60 × 6 – 11 µm. **Pileal trama** interwoven, tightly packed; hyphae 3 – 7 µm wide, thin-walled. **Stipitipellis** hymeniform, with caulobasidia and caulocystidia; caulobasidia similar to hymenial basidia in size and shape, 2- and 4-spored; caulocystidia 22 – 50 × 7 – 9 µm, clavate to obclavate, sometimes with acute apex, thin-walled.

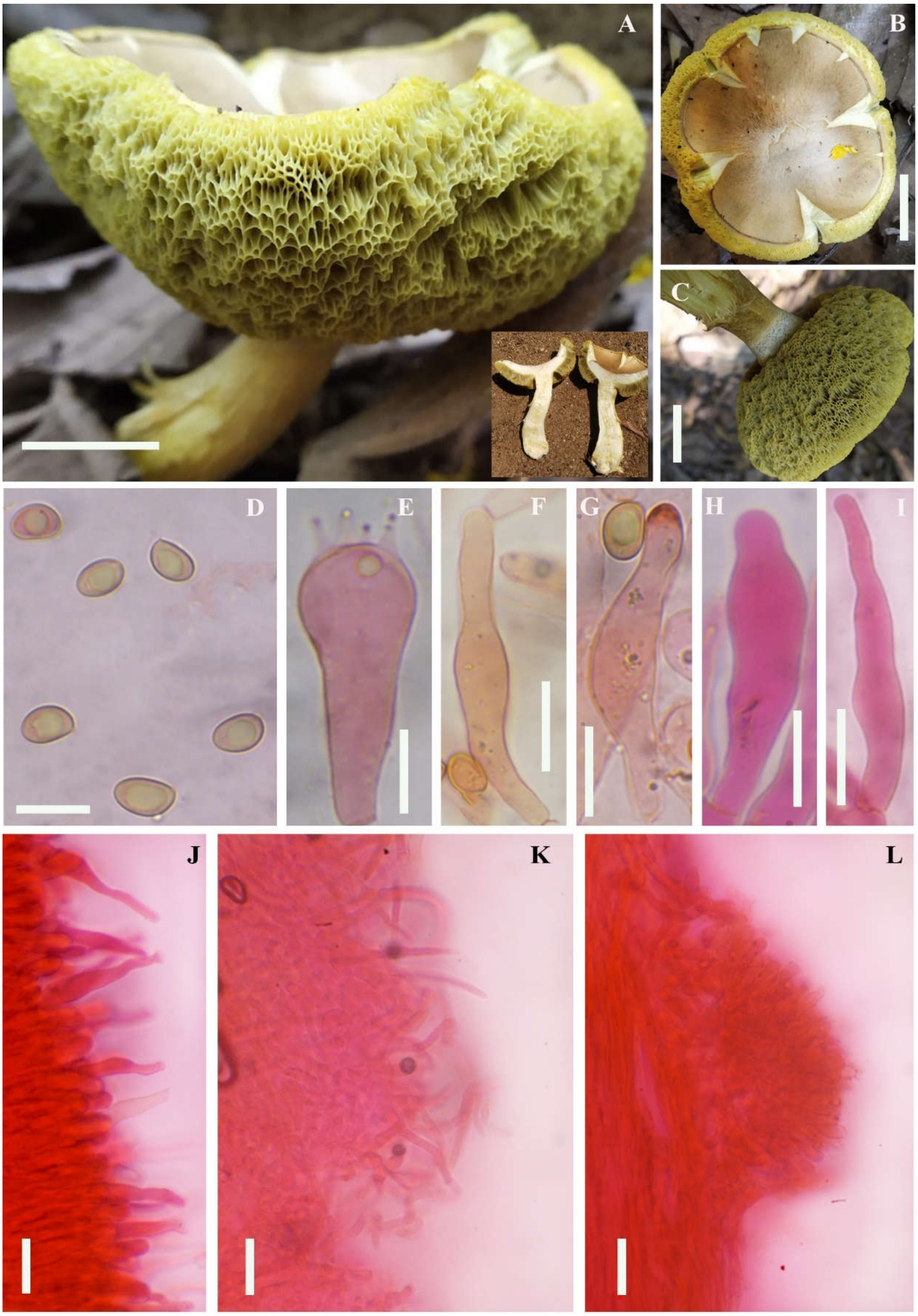


Figure 39. *Aureoboletus* species. A-C Basidiomata D. Basidiospores E. Basidium F-G. Pleurocystidia H-J. Cheilocystidia K. Pileipellis L. Stipitipellis. Scale bars: A-C = 10 mm, D-J = 10 µm, K-L = 20 µm.

Stipe trama parallel; hyphae 3 – 10 µm wide, thin- to slightly thick-walled, hyaline in water. **Clamp-connections** not observed.

Habitat: On soil, solitary to scattered.

Specimens examined: India, Kerala State, Kannur District, Kelakam, on soil, 27 February 2022, Salna N., ZGCSN120.

Comments: The *Aureoboletus* collection from Kerala resemble with *Aureoboletus yunnanensis* morphologically in the presence of similarly colored basidiomata, pores and tubes, and ixotrichodermium type of stipitipellis. However, Kerala collection differs from *A. yunnanensis* in having longer tubes (20 – 80 mm), minutely pubescent stipe apex, smaller basidiospores, larger cheilocystidia, and a trichodermial type of pileipellis. Additional collections and molecular data are needed to confirm the identity of the collection.

Rostrupomyces

Basidiomata stipitate-pileate. Pileus convex becoming applanate; surface at first rugulose then subrugulose with age, finely tomentose to tomentose, brownish becoming greyish orange, unchanging when bruised; context off-white becoming yellowish to dull pale orange in age, unchanging when cut. Stipe central, cylindrical; surface scabrous, yellowish white to pale yellow, with scattered brown to dark brown to reddish brown granulose squamules, unchanging when bruised; basal mycelium white. Hymenophore tubulate, slightly depressed to depressed around the stipe; tubes pale yellow then greyish yellow, separable from the pileus context, unchanging when cut; pores roundish to angular; white when young becoming yellowish white to greyish yellow, unchanging when touched. Spore print yellowish brown. Basidiospores ellipsoid to broadly ellipsoid, thin-walled, smooth under light microscope and SEM. Basidia 4-spored, clavate without basal clamp connection. Cheilocystidia and pleurocystidia narrowly fusiform to fusiform or narrowly utriform, thin-walled. Pileipellis an intricate trichoderm, made of moderately interwoven to loosely interwoven, thin-walled hyphae. Clamp-connections absent.

Rostrupomyces sisongkhramensis (Khamsuntorn, Pinruan and Luangsa-ard) Vadthanarat, Raghoonundon and Raspé, MycoKeys 103: 145 (2024)

Figure 40

Basidiomata medium-sized. **Pileus** 70 mm in diam., subhemispherical to applanate; surface dry, glabrous, brownish yellow. **Pileal context** 30 mm wide, whitish**,** without any color change on bruising. **Hymenophore** adnate to adnexed; surface yellowish, unchanging when bruised, becoming ochraceous on aging; pores 1 – 2/ mm, round to angular; tubes up to 4 mm long, yellowish, unchanging when bruised. **Stipe** 60 × 20 mm, subcylindrical, yellowish, pruinose, finely striated; context yellow, unchanging when bruised. **Basal mycelium** white.

Basidiospores 8 – 10 × 4 – 5 µm (Q = 1.2 – 1.6, Qm = 1.73), obovoid to ellipsoid, thin-walled, pale yellow in water. **Basidia** 32 – 35 × 6 – 9 µm, clavate, 4-spored, thin-wallled, hyaline in water. **Pleurocystidia** 30 – 455× 6 – 8 µm, fusiform, narrowly fusiform, thin-walled, hyaline in water. **Cheilocystidia** not observed. Pileipellis an intricate trichoderm; terminal cells 3 – 6 µm wide, cylindrical, thin-walled, hyaline in water. **Pileal trama** interwoven; hyphae 3 – 5 µm wide, thin-walled, hyaline. **Stipitipellis** basically a cutis interrupted by bunches of terminal caulocystidia like hyphae; terminal cells 20 – 50 × 3 – 10 µm, cylindrical to fusiform, thin-walled, hyaline. **Stipe trama** interwoven; hyphae 4 – 14 µm wide, thin- to thick-walled. **Clamp-connections** not observed.

Habitat: solitary on soil.

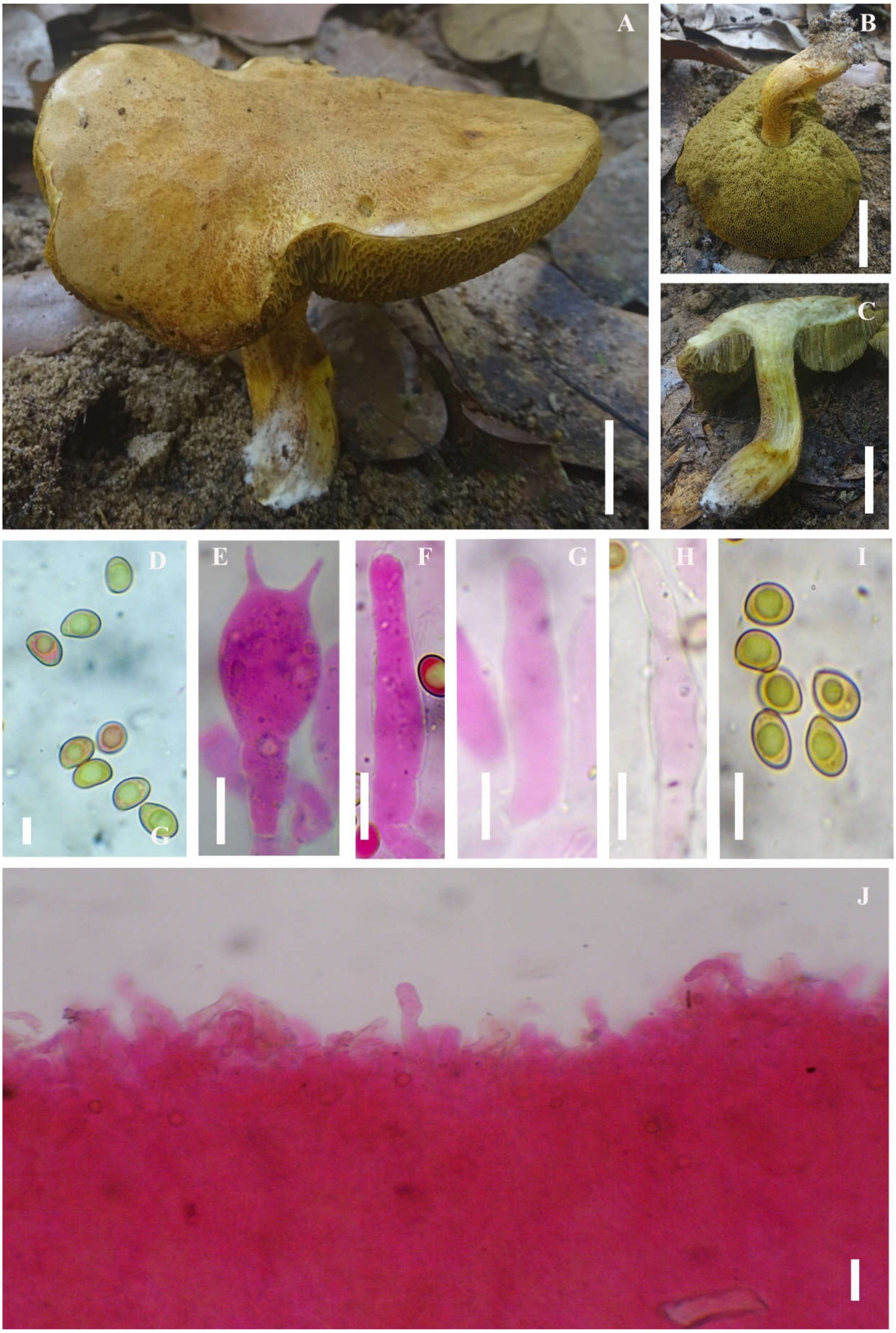


Figure 40. *Rostrupomyces sisongkhramensis*. A-B. Basidiomata C. Context changing to copper red to black on cut D. Basidiospores E. Basidium F-H. Pleurocystidia I. Basidiospores J. Pileipellis. Scale bars: A-C= 10 mm, D-I = 10 μm, J = 20 μm.

Specimens examined: India, Kerala State, Wayanad district, Kuruva isletes, 20 May 2022, Salna N., ZGCSN124.

Comments: *Rostrupomyces sisongkhramensis* was originally described as *Xerocomus sisongkhramensis* Khamsuntorn, Pinruan and Luangsa-ard (Tan et al. 2022). Later, the species was transferred in to a new genus *Rostrupomyces* based on morphological and molecular analyses (Vadthanarat et al. 2024). Present collection shows morphological similarities with the description of the holotype specimen in having yellowish brown basidiomata, yellowish hymenophore, pruinose stipe surface, similar size of basidiospores and pleurocystidia, and in presence of caulocystidia. Description of Tan et al. (2022) indicates the absence of cheilocystidia and presence of large caulocystidia. Vadthanarat et al. (2024) indicated the presence of cheilocystidia and caulocystidia described as undifferentiated terminal cells Phylogenetic analysis of Kerala collection (Figure 42) by using 28S sequence confirms the identity of the Kerala collection as *R. sisongkhramensis.*

Neotropicomus

Basidiomata epigeous. Pileus smooth to rugulose. Pileal context pale yellowish or white, unchanging on bruising. Hymenophore tubulose-poroid, pale olivaceous yellow; pores 1 –2 mm wide, isodiametric to subangular. Stipe smooth to minutely pruinose. Basidiospores olivaceous in deposit, subfusoid to fusoid, smooth.

Neotropicomus indicus Salna Nanu and T. K. A. Kumar, Cryptogamie Mycologie 45 (5): 47-52

Figure 41

Basidiomata small-sized. **Pileus** 20 – 30 mm broad, convex when young, becoming plano-convex on maturity; surface viscid when wet, smooth to minutely pruinose, reddish brown to greyish brown towards the centre; margin straight. **Pileal context** whitish to pale yellowish, unchanging when cut. **Hymenophore** adnate, depressed around the apex of stipe; surface pale yellow to olive yellow; pores 1–2 per mm, angular, unchanging on bruising; tubes 2 – 4 mm long, concolorous to the hymenophore surface, unchanging when cut. **Stipe** 20 – 40 × 3 – 4 mm, central, almost equal; surface finely pruinose in the apex to middle with small reddish brown squamules, whitish to pale yellowish in apex, reddish brown in middle to bottom in a cream background. **Stipe context** whitish, unchanging on bruising. **Basal mycelium** white.

Basidiospores 9–11 × 4–5 μm (Q = 1.8–2.75, Qm = 2.2), subfusoid to fusoid, thin- to slightly thick-walled (up to 0.5 μm), smooth, yellowish in water, inamyloid. **Basidia** 20–27× 7–10 μm, clavate, thin-walled, 4-spored; sterigmata up to 3 μm long, hyaline with many oil droplets. **Pleurocystidia** 42–62 × 6–12 μm, narrowly fusiform to fusiform, thin-walled, hyaline, inamyloid. **Cheilocystidia** 28–50 × 7–10 μm, narrowly utriform, nearly fusiform, broadly clavate or nearly cylindrical, hyaline, inamyloid. Hymenophoral trama phylloporoid; hyphae 3–15 μm wide, thin-walled, hyaline. **Pileipellis** a trichodermium, made up of densely packed chains of terminal elements formed on subglobose cells; terminal elements 16–31 × 4–13 μm, nearly cylindrical or broadly clavate, some of them having subacute apex, thin-walled, inamyloid. **Pileus trama** tightly interwoven; hyphae 3–12 μm wide, thin-walled, hyaline, inamyloid. **Stipitipellis** a cutis interrupted by caulocystidia clusters; caulocystidia 13–28 × 4–7 narrowly clavate to clavate, rarely with subacute apex, thin-walled, inamyloid. **Stipe trama** parallel to interwoven; hyphae 3–12 μm wide, thin-walled. **Clamp-connections** absent.

Habitat: On soil, solitary, in forest dominated by Dipterocarpaceae members.

Figure 41. *Neotropicomus indicus*. A-C. Basidiomata D. Basidiospores E. Basidium F-G. Pleurocystidia H. Cheilocystidia I. Pileipellis J. Stipitipellis K. Terminal cells of pileipellis L. Caulocystidium Scale bars: A-C = 20 mm, D-H, K-L = 10 µm, I-J = 20 µm.

Comments: Morphologically and phylogenetically, the new species can be comfortably placed in the recently described genus *Neotropicomus*. Morphologically *N. indicus* shows more resemblance with *N. australis* by having small basidiomata, reddish brown pileus which is viscid when wet, depressed hymenophore around the stipe apex, pruinose stipe surface, absence of color change in pileal and stipe context, subfusoid to fusoid basidiospores and trichodermial type of pileipellis. However, *N. australis* differs from *N. indicus* in having larger basidiospores, ventricose pleurocystidia with long neck, smaller cheilocystidia, and a stipitipellis, which is a palisade of erect clusters of caulocystidia. *Neotropicomus indicus* shows resemblances with *N. parvogracilis* by having basidiomta with a pileus which is viscid when wet, unchanging pileal and stipe context and a trichodermial type of pileipellis. But, *N. parvogracilis* differs from *N. indicus* by the presence of finely rugulose pileal surface, larger basidiospores, 2- to 4- spored basidia, absence of cheilocystidia and stitpitipellis is a trichodermial palisade.

Phylogenetic analysis based on ITS and 28S sequences placed the new species in *Neotropicomus* with maximum bootstrap support. However, *N. indicus* undoubtedly formed a separate lineage in the *Neotropicomus* clade. Taxonomic description, morphological comparison and molecular phylogenetic analysis are presented in Nanu and Kumar (2024).

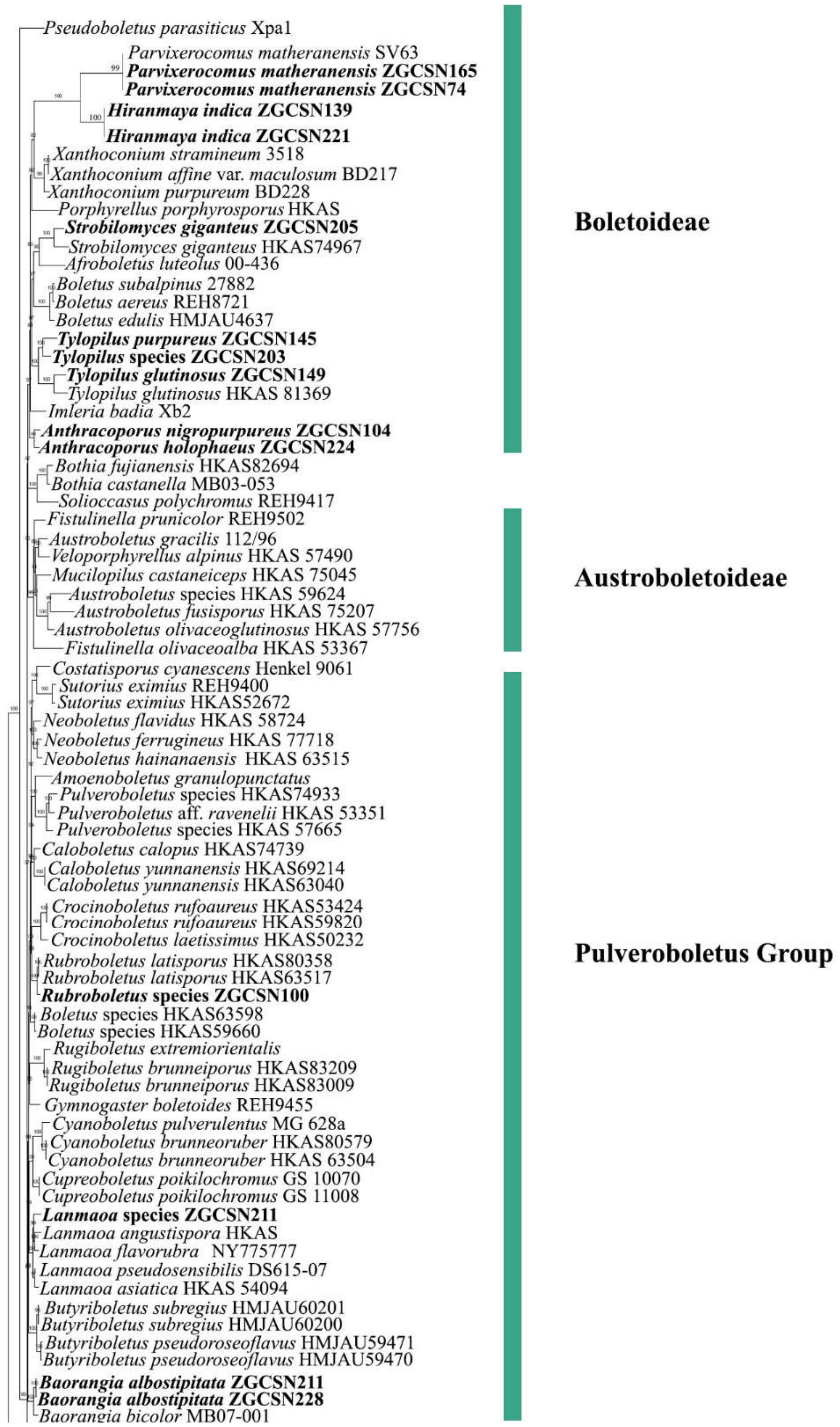


Figure 42 (Part 1). Maximum Likelihood tree of Boletaceae generated from a combined dataset using ITS, 28S and *RPB2* sequences. Bootstrap values (>60 %) are indicated above/below branches. Kerala collections are indicated in bold.

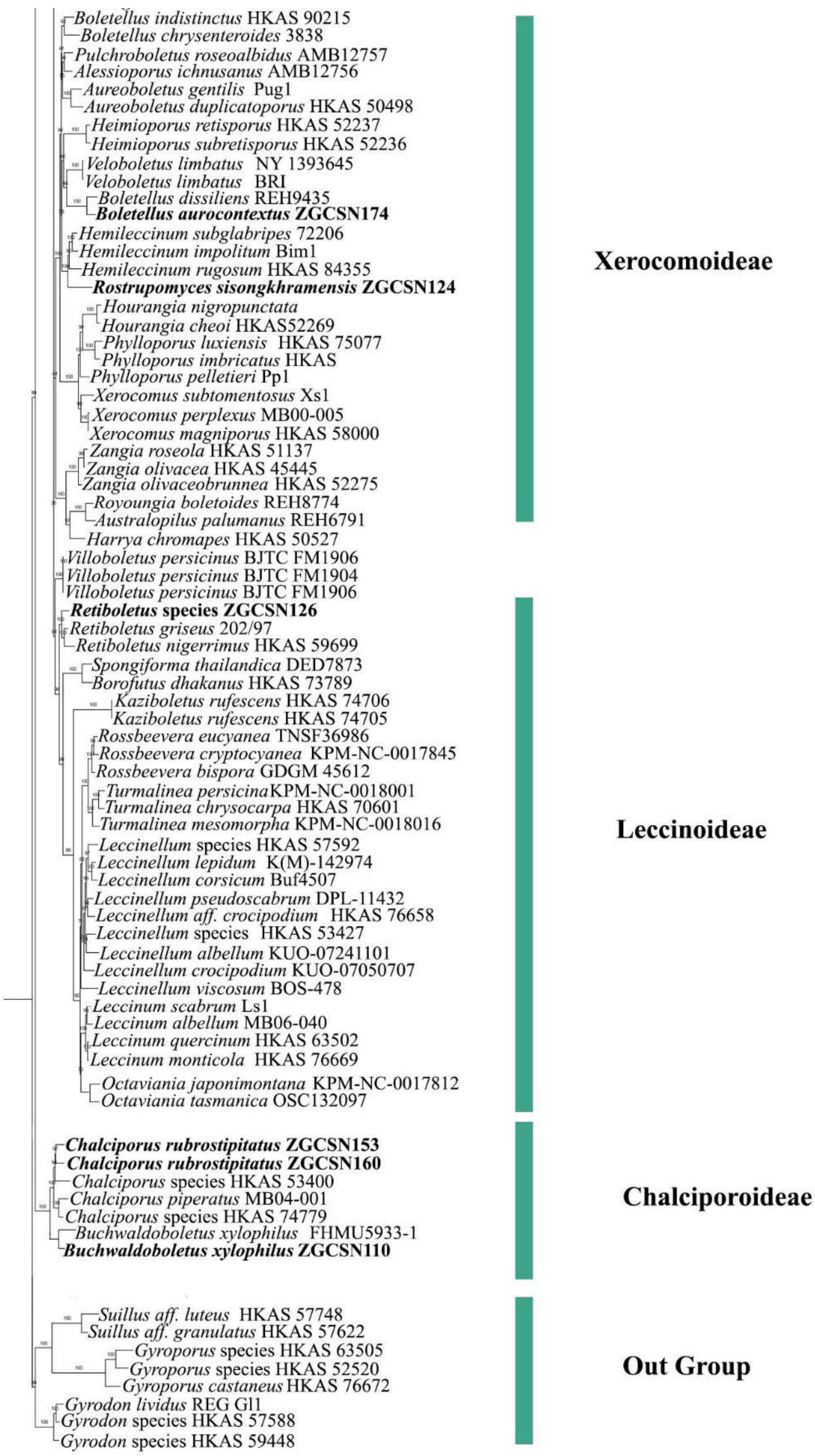


Figure 42 (Part 2). Maximum Likelihood tree of Boletaceae generated from a combined dataset using ITS, 28S and *RPB2* sequences. Bootstrap values (>60 %) are indicated above/below branches. Kerala collections are indicated in bold.

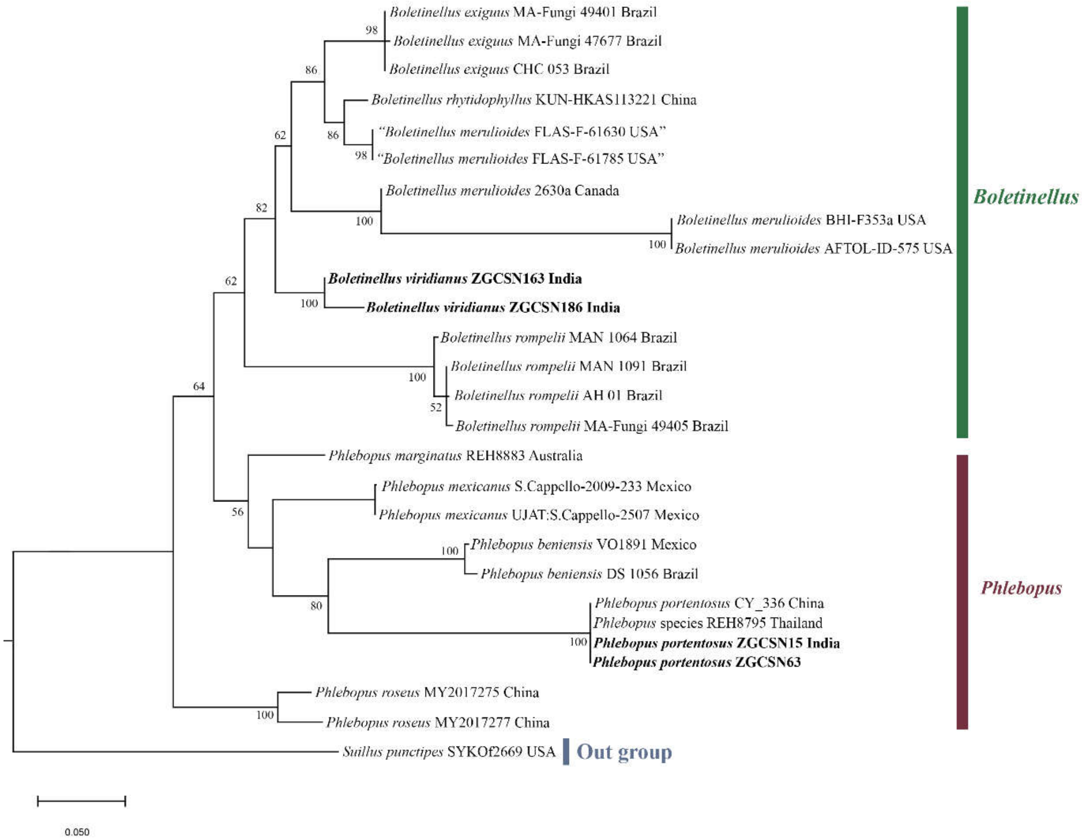


Figure 43. Maximum Likelihood tree of Boletinellaceae generated from a combined dataset using ITS and 28S sequences. Bootstrap values (>50 %) are indicated above/below branches. Kerala collections are indicated in bold.

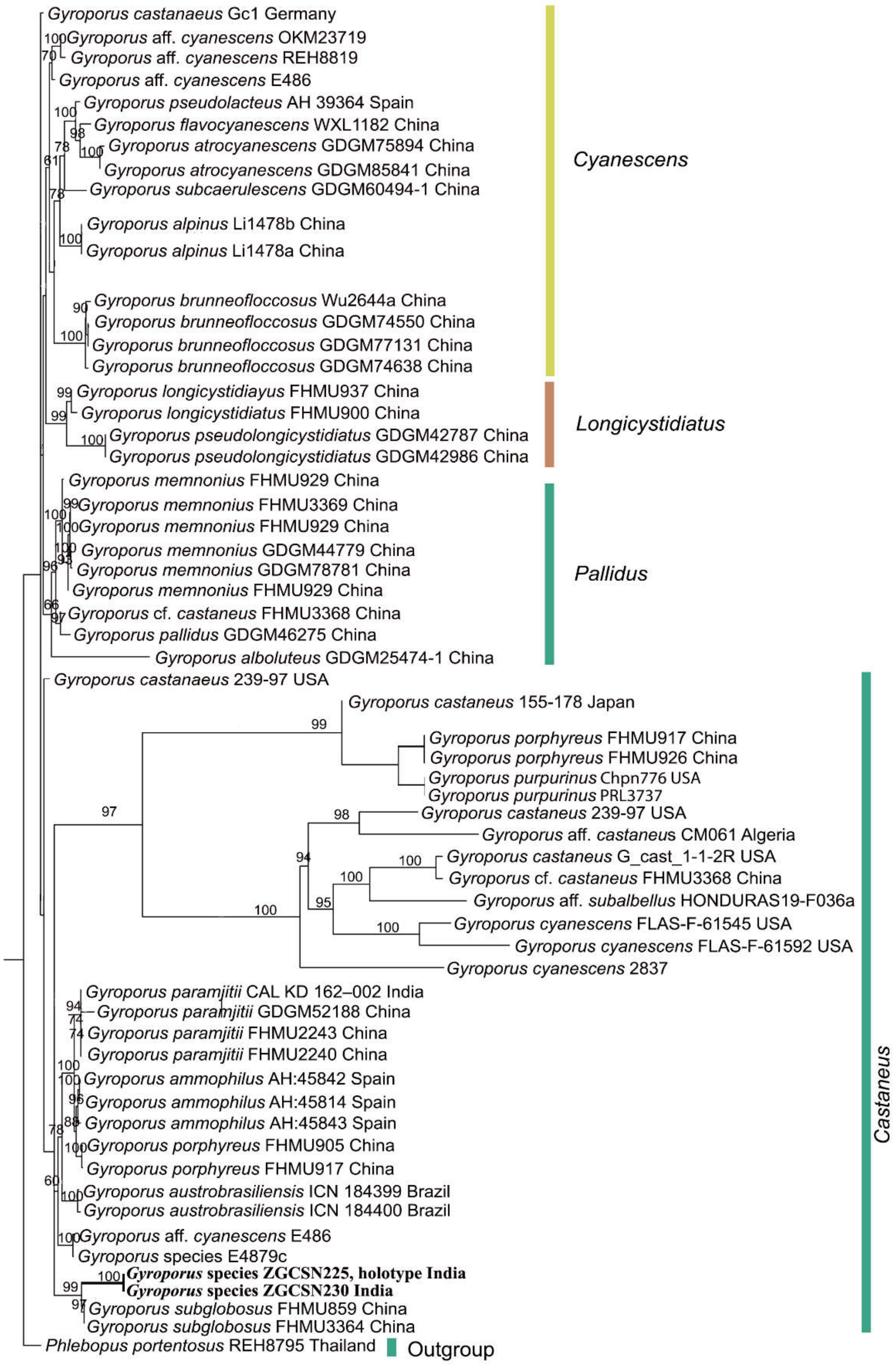


Figure 44. Maximum Likelihood tree of *Gyroporus* generated from a combined dataset using ITS and 28S sequences. Bootstrap values (>60 %) are indicated above/below branches. The new species is indicated in bold.

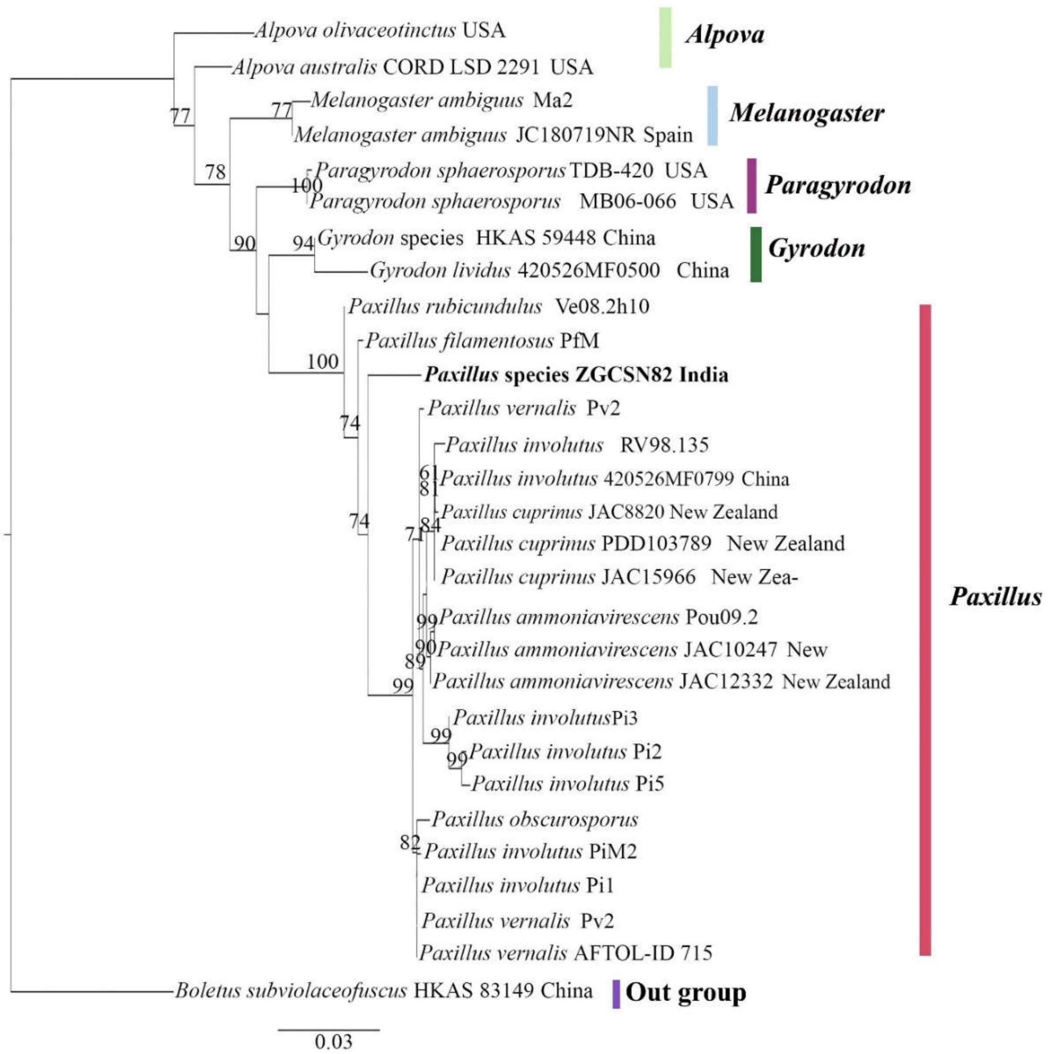


Figure 45. Maximum Likelihood tree of Paxillaceae generated from a combined dataset using 28S sequences. Bootstrap values (>60 %) are indicated above/below branches. The new species is indicated in bold.

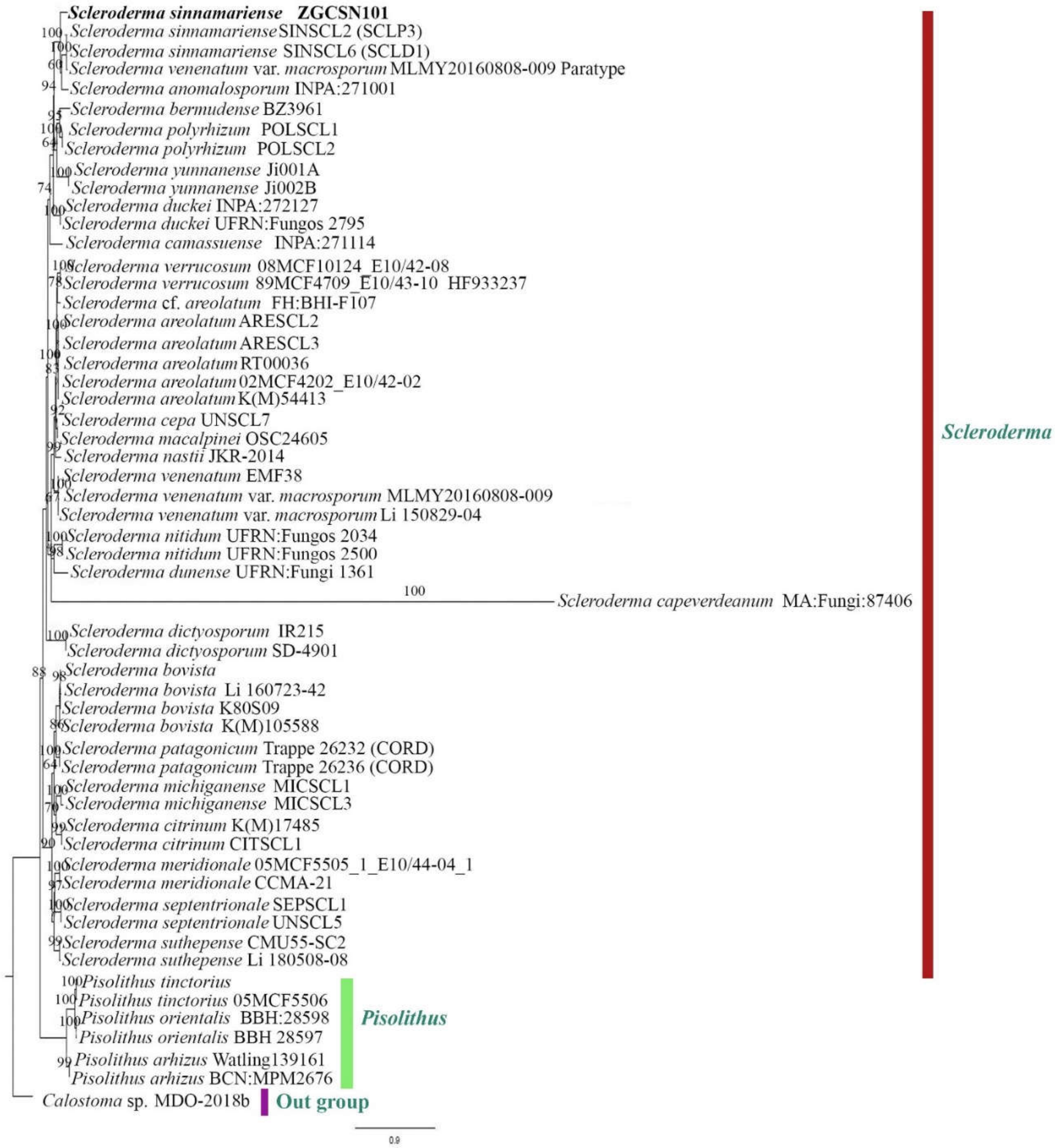


Figure 46. Maximum Likelihood tree of Sclerodermataceae generated from a combined dataset using ITS sequences. Bootstrap values (>60 %) are indicated above/below branches. Kerala collection is indicated in bold.

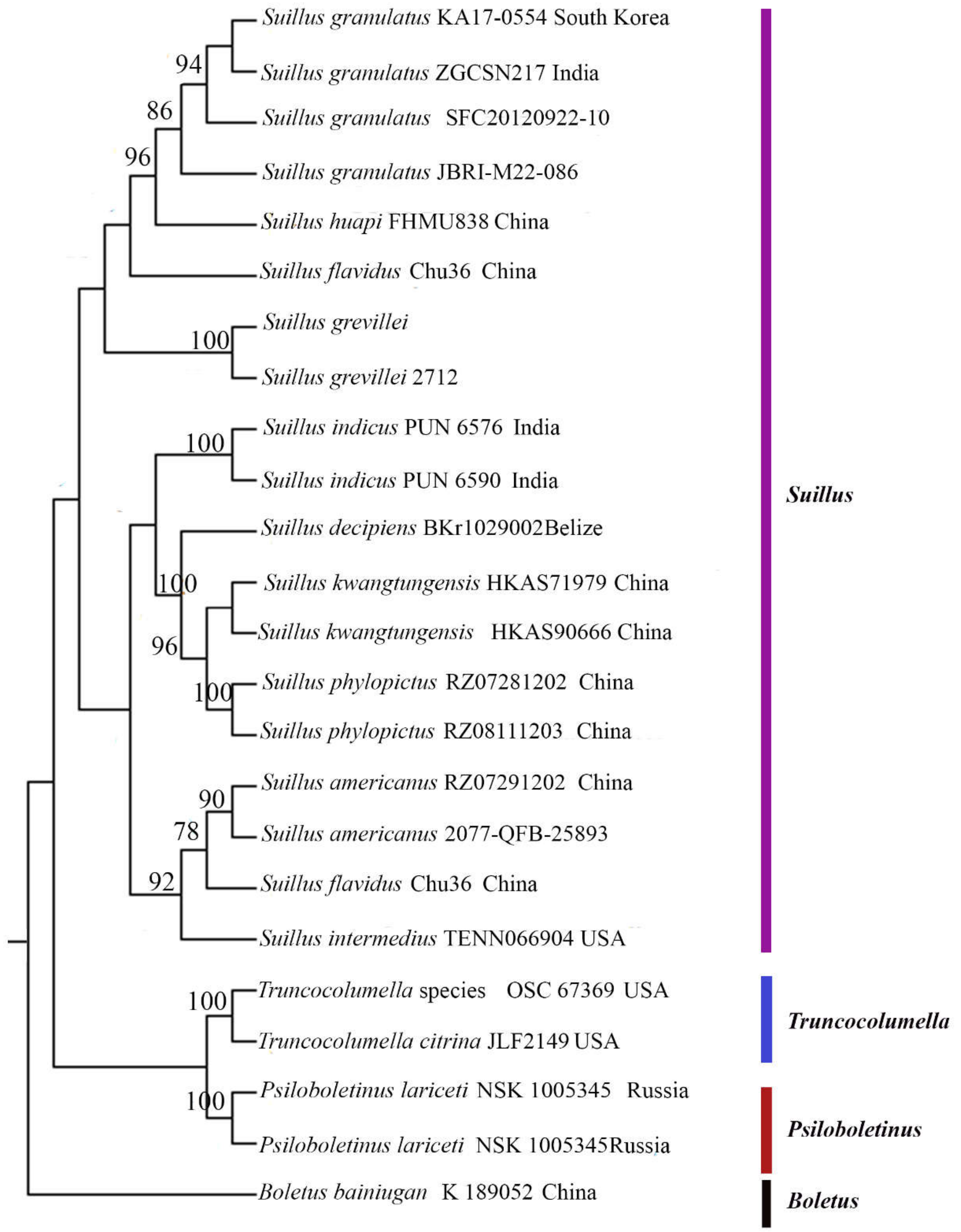


Figure 47. Maximum Likelihood tree of Suillaceae generated from a combined dataset using ITS sequences. Bootstrap values (>60%) are indicated above/below branches. Kerala collection is indicated in bold.

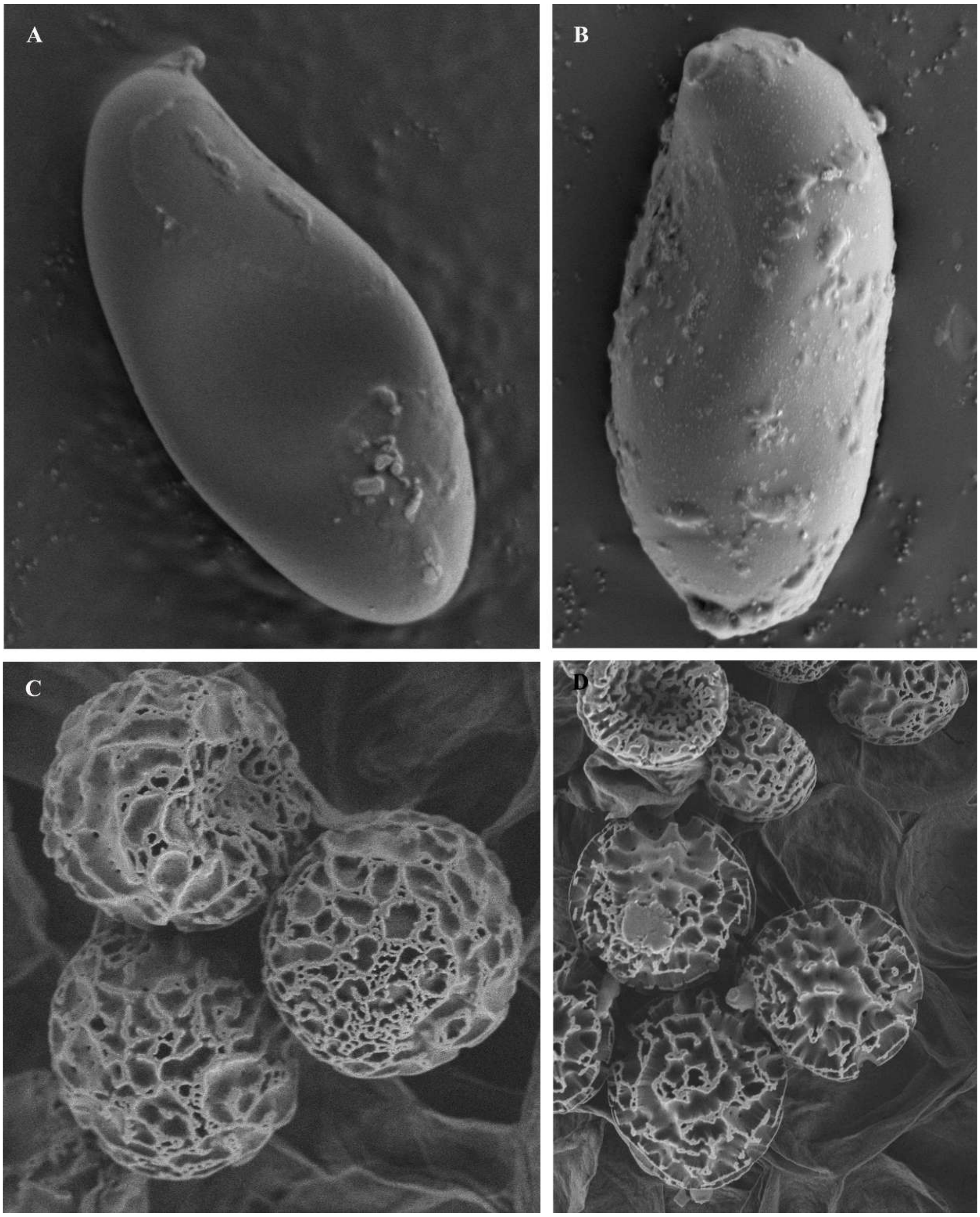


Figure 48. SEM (Scanning Electron Microscope) images of basidiospores. A-B. *Hiranmaya indica* C-D. *Strobilomyces giganteus*.

5. SUMMARY

Boletoid fungi are included under the monophyletic order Boletales (Agaricomycetes, Basidiomata). Boletoid fungi are usually fleshy, stipitate-pileate with poroid or lamellate hymenophore. Many boletes show ectomycorrhizal associations with higher plants and some are edible. Recently, boletoid fungi are used as model organisms to study the biogeographic aspects of fungi. But one issue with evaluating the biogeography and molecular reconstruction of boletes is the lack of specimens from tropical regions, particularly the Indian subcontinent. Most of the Indian records of boletoid fungi are from northern states. There are no comprehensive studies on Boletales of South India. Hence, a study of documentation of the diversity of boletoid fungi of Kerala was conducted during the period 2018-2024.

Morphological characterisation along with molecular phylogenetic analyses of the collected specimens were conducted. During the study, 40 bolete species belonging to 29 genera of eight families (Boletaceae, Boletinellaceae, Gyroporaceae, Paxillaceae, Pisolithaceae, Serpulaceae, Sclerodermataceae, Suillaceae) were recorded. Significant number of bolete collections was obtained from Kuruva Islets and the Thurayilkotta Sacred Grove. Both these areas are having plant species belonging to the Dipterocarpaceae family and a sandy soil preferable for the growth of boletes. Of the fourteen species proposed as new to science in this study, five were formally published and other formally undescribed species are in the process of publication. Out of the total taxa documented, nine were new records to India and 18 were new records to Kerala. All the specimens including holotypes are maintained at Zamorin's Guruvayurappan College Herbarium (ZGC). A total of 50 gene sequences were generated from the collections made during the study and used for the molecular phylogenetic analyses. Molecular phylogeny

is also used to study a large number of taxa, and the gene sequences that are generated deposited in open repositories. Six phylogenetic trees are presented in this study, representing five families and one genus. This taxonomic treatment provides descriptions, comparisons, and taxonomic keys of boletes along with macroscopic and microscopic photographs. The present monographic treatment forms the first largest comprehensive study of the diversity and phylogeny of boletoid fungi from South India.

6. RECOMMENDATIONS

Boletoid fungi are an ecologically and economically significant group. Boletoid fungi form ectomycorrhizal relationships, which promote plant growth. Boletales also includes species that are highly nutritious and commercially cultivated. Boletoid fungi is a least studied fungal group in South India. The present study was focused on documenting the diversity and phylogeny of boletes of Kerala State. Collections were conducted during the five-year period in the study. Some boletoid species may have gone unnoticed during the five-year collection period because to their lack of seasonal fruiting in their habitats. Hence, more diversity documentation spanning larger periods with better detection techniques are required to bring out the real diversity that exists.

Ectomycorrhizal boletes affect the growth of higher plants significantly. More studies on mycorrhizal associations of boletes may provide better knowledge about plant-fungal relationships and their role in ecosystem. Destruction of ecosystems and deforestation may lead to the extinction of bolete species. So, new strategies should be formalized to conserve bolete diversity *in vitro* and *in vivo*. Some edible bolete species like *Phlebopus portentosus* has been proved to be cultivable without its host plant. The cultivation and marketing of such species make a scope for getting better income to farmers. Biogeographical analyses will lead to the evolutionary reconstruction and diverisification pattern of organisms. Boletes can be used as better model organisms for the biogeographic analysis. More research on biogeographical aspects using boletoid fungi will shed light on long-distance dispersal of fungi. Boletes contain different types of bioactive compounds like terpenoids, ergosterol, lectins, pulvinic acid derivatives, and triterpenoids. Many of them possess anti-inflammatory, antimicrobial, and anticancer properties. To find and use bio-active chemicals from these fungi, extensive mycochemical screening is necessary. Future research scope on this topic include whole genome analyses, biogeographic analyses, chemical screening, study of plant-fungus relationships, and bioprospecting of boletoid fungi.

REFERENCES

Adamčík S, Cai L, Chakraborty D, Chen XH, Cotter HV, Dai DQ, Dai YC, Das K, Deng C, Ghobad–Nejhad M, Hyde KD. Fungal biodiversity profiles 1–10. 2015. Cryptogamie, Mycologie 36: 121–166.

Adarsh CK, Vidyasagaran K, Ganesh PN. 2018. A Checklist of polypores of Kerala State, India. Studies in fungi 3: 202–226.

Agerer R. 1987. Studies on Ectomycorrhizae. V: Mycorrhizae formed by Dermocybe cinnamomea and Dermocybe sanguinea on spruce. Nova Hedwigia 44: 69–89.

Agerer R. 1999. Never change a functionally successful principle: The evolution of Boletales s. l. (Hymenomycetes, Basidiomycota) as seen from below–ground features. Sendtnera 6: 5–91.

Agerer R. Characterization of Ectomycorrhiza. 1991. Methods in microbiology 23: 25–73.

Agerer R. 2006. Fungal relationships and structural identity of their ectomycorrhizae. Mycological Progress 5: 67–107.

Ahmed A, Taj M, Yongliang Z, Taj I, Hassani MT, Sajıd M, Ahmed Z, Ullah AU, Menga MA, Liping S. 2015. Chemical composition and antioxidant properties of eight wild edible Boletaceae mushrooms growing in Yunnan province of China. Jökull Journal 65: 146–167.

Alexopoulos CJ, Mims CW, Blackwell M. 1996. Introductory Mycology, 4th edition, New York: Wiley.

Alvarado P, Cabero J, Moreno–Mateos D, Vizzini A, Alonso J, Lebeuf R, Siquier JL, Vidal JM. 2021. Phylogenetic relationships among false truffle genera of Paxillaceae—*Alpova*, *Melanogaster*, *Neoalpova*, and *Paralpova*, gen. nov. Mycologia 113: 828–841.

Ammirati JF. 1985. Poisonous mushrooms of the northern United States and Canada. University of Minnesota Press. 396 pp.

Amtoft A, Halling RE, Mueller GM. 2002. *Tylopilus alkalixanthus*, a new species of Boletaceae from Costa Rica and Japan. Brittonia 54: 262–265.

Anderson IC, Chambers SM, Cairney JWG. 2001. ITS–RFLP and ITS sequence diversity in *Pisolithus* from central and eastern Australia sclerophyll forests. Mycological Research 105: 1304–1312.

Aravindakshan DM, Manimohan P. 2015. Mycenas of Kerala. Spore Print Books, Calicut. 213 pp.

Arora D, Frank JL. 2014. Clarifying the butter Boletes: a new genus, *Butyriboletus*, is established to accommodate Boletus sect. *Appendiculati*, and six new species are described. Mycologia 106: 464–480.

Arzù, R, Yu F–Q. (Eds.), Mushrooms, Humans and Nature in a Changing World – Perspectives from Ecological, Agricultural and Social Sciences. Cham: Springer Nature. 480 pp.

Ayala–Vásquez O, Pérez–Moreno J, Pinzón JP, Garibay–Orijel R, García–Jiménez J, de la Fuente JI, Venegas–Barrera CS, Martínez–Reyes M, Montoya L, Bandala V, Aguirre–Acosta CE. 2023. Broadening the Knowledge of Mexican Boletes: Addition of a New Genus, Seven New Species, and Three New Combinations. Journal of Fungi 9: 1126.

Badou SA, Furneaux B, De Kesel A, Khan FK, Houdanon RD, Ryberg M, Yorou NS. 2022. *Paxilloboletus* gen. nov., a new lamellate bolete genus from tropical Africa. Mycological Progress 21: 243–56.

Banasiak Ł, Pietras M, Wrzosek M, Okrasińska A, Gorczak M, Kolanowska M, Pawłowska J. 2019. *Aureoboletus projectellus* (Fungi, Boletales)–An American bolete rapidly spreading in Europe as a new model species for studying expansion of macrofungi. Fungal Ecology 39: 94–99.

Baroni TJ, Cifuentes J, Santana BO, Cappello S. 2015. A new species of *Phlebopus* (Boletales, Basidiomycota) from Mexico. North American Fungi 10: 1–3.

Barroetaveña C, Toledo CV. 2020. Diversity and ecology of edible mushrooms from Patagonia native forests, Argentina. Mushrooms, humans and nature in a changing world: Perspectives from ecological, agricultural and social sciences. 297–318 pp.

Baseia IG, Silva BD, Ishikawa NK, Soares JV, França IF, Ushijima S, Maekawa N, Martín MP. 2016. Discovery or extinction of new Scleroderma species in Amazonia?. Plos One 11: e0167879.

Bataille F. 1908. Quelques champignons intéressants des environs de Besançon. Bulletin de la Société d' Histoire Naturelle du Doubs. 15.

Bau T, Bao HY, Li Y. 2014. A revised checklist of poisonous mushrooms in China. Mycosystema 33: 517–548.

Becerra A, Nouhra E, Daniele G, Domínguez L, McKay D. 2005. Ectomycorrhizas of *Cortinarius* helodes and *Gyrodon monticola* with *Alnus acuminata* from Argentina. Mycorrhiza 15: 7–15.

Berkeley MJ. 1851. Decades of fungi. Decades XXXIV. Sikkim Himalaya fungi, collected by Dr. J.D. Hooker. Hooker's Journal of Botany Kew Garden Miscellany 3: 77–84.

Bernicchia A, Gorjón SP. 2010. Fungi Europaei 12: Corticiaceae s. l. Alassio: Edizioni Candusso. Lomazzo 12: 1008.

Besl H, Bresinsky A, Kämmerer A. 1986. Chemosystematik der Coniophoraceae. Zeitschrift für Mykologie 52: 277.

Besl H, Bresinsky A. 1997. Chemosystematics of Suillaceae and Gomphidiaceae (suborder Suillineae). Plant Systematics and Evolution 206: 223–242.

Bessette AE, Roody WC, Bessette AR. 2000. North American Boletes: A Color Guide to the Fleshy Pored Mushrooms. Syracuse: Syracuse University Press. 396 pp.

Bessette AE, Roody WC, Bessette AR. 2017. Boletes of Eastern North America. Syracuse University Press, Syracuse. 536 pp.

Binder M, Besl H. 2000. 28S rDNA sequence data and chemotaxonomical analyses on the generic concept of Leccinum (Boletales). Mycologia 2000: 71–82

Binder M, Bresinsky A. 2002. Derivation of a polymorphic lineage of Gasteromycetes from boletoid ancestors. Mycologia 94: 85–98.

Binder M, Hibbett DS, Larsson KH, Larsson E, Langer E, Langer G. 2005. The phylogenetic distribution of resupinate forms across the major clades of mushroom-forming fungi (Homobasidiomycetes). Systematics and Biodiversity 3: 113–157.

Binder M, Hibbett DS. 2002. Higher–level phylogenetic relationships of homobasidiomycetes (mushroom–forming fungi) inferred from four rDNA regions. Molecular Phylogenetics and Evolution 22: 76–90.

Binder M, Hibbett DS. 2006. Molecular systematics and biological diversification of Boletales. Mycologia 98: 971–81.

Boedijn KB. 1951. Some mycological notes. Sydowia 5: 211–229.

Bon M. 1977. Macromycètes de la zone maritime picarde (4ème supplément).

Both E. 1993. The Boletes of North America, a Compendium. Buffalo Museum of Science: Buffalo, NY, USA: 1–436.

Bottomley AM. 1948. Gasteromycetes of South Africa. Bothalia 4: 473–810.

Bougher NL. Diversity of ectomycorrhizal fungi associated with eucalypts in Australia. 1994. Mycorrhizas for Plantation Forestry in Asia 62: 8–15.

Bozok F, Assyov B, Taşkın H, Büyükalaca S. 2019. A New Macrofungi Record for Turkey and Asia with Molecular Characterization: *Xerocomellus redeuilhii* (Boletales, Basidiomycota). Mantar Dergisi 10: 1–9.

Bresinsky A, Besl H. 2003. Beiträge zu einer Mykoflora Deutschlands Schlüssel zur Gattungsbestimmung der Blätter, Leistenund Röhrenpilze mit Literaturhinweisen zur Artbestimmung. Regensburger Mykologische Schriften 11: 5–236.

Bresinsky A, Jarosch M, Fischer M, Schönberger I, Wittmann–Bresinsky B. 1999. Phylogenetic relationships within Paxillus s. l. (Basidiomycetes, Boletales): Separation of a Southern hemisphere genus. Plant Biology 1: 327–33.

Bresinsky A. 1974. Zur Frage der taxonomischen Relevanz chemischer Merkmale bei höheren Pilzen. Bulletin mensuel de la Société Linnéenne de Lyon–numero special: 61–84.

Brundrett M, Bougher N, Dell B,Grove T, Malajczuk N.1996. Working with Mycorrhizas in forestry and agriculture. ACIAR Monograph. 374 pp.

Brundrett MC, Kendrick B. 1987. The relationship between the Ash Bolete (*Boletinellus merulioides*) and an Aphid Parasitic on Ash Tree Roots. Symbiosis 3: 315–320.

Bruns TD, Fogel R, White TJ, Palmer JD. 1989. Accelerated evolution of a false–truffle from a mushroom ancestor. Nature 339: 140–142.

Caiafa MV, Smith ME. 2022. Polyphyly, asexual reproduction and dual trophic mode in *Buchwaldoboletus*. Fungal Ecology 56: 101141.

Carlson J. 2019. Adobe Photoshop Elements 2020 Classroom in a Book. Adobe Press.

Castro ML, Freire L. 1995. *Gyroporus ammophilus* a new poisonous bolete from the Iberian Peninsula. Persoonia 16: 123–126.

Chai H, Liang ZQ, Jiang S, Fu XL, Zeng NK. 2018. *Lanmaoa rubriceps*, a new bolete from tropical China. Phytotaxa. 347: 71–80.

Chakraborty D, Das K, Baghela A, Singh SK, Dentinger BT. 2015. Boletus recapitulatus (Boletaceae), a new species from India with peculiar mushroom–shaped cells. Phytotaxa 236:150–160.

Chakraborty D, Gelardi M, Hembrom ME, Ghosh A. 2022. First records of Tylopilus glutinosus Iqbal Hosen (Boletaceae) from Shorea robusta–dominated forests in tropical India: morphological description and phylogenetic estimation. Check List 18: 553–562.

Chakraborty D, Semwal KC, Adhikari S, Mukherjee SK, Das K. 2017. Morphology and phylogeny reveal two new records of boletoid mushrooms for the Indian mycobiota. Tropical Plant Research 4: 62–70.

Chakraborty D, Vizzini A, Das K. 2018. Two new species and one new record of the genus *Tylopilus* (Boletaceae) from Indian Himalaya with morphological details and phylogenetic estimations. MycoKeys 33:103.

Chambers SM, Cairney JW. *Pisolithus.* 1999. In Ectomycorrhizal Fungi Key Genera in Profile. Springer. 31 pp.

Champion HG, Seth SK. 1968. A revised survey of the forest types of India. Manager of publications. 404 pp.

Chen CM, Yeh KW, Hsu HK. 1998. The boletes of Taiwan (X). Taiwania 43: 140–149.

Chen CM, Yeh KW. 2000. The boletes of Taiwan (XI). Taiwania 45: 201–206.

Chen ZH, Yang Z, Tolgor B, Li TH. 2016. Poisonous Mushrooms: Recognition and Poisoning Treatment. Beijing: Science Press. 308 pp.

Chiu WF. 1948. The Boletes of Yunnan. Mycologia 40: 199–231.

Chiu WF. 1957. Atlas of the Yunnan Bolets. Science Press.

Chuankid B, Vadthanarat S, Hyde KD, Thongklang N, Zhao R, Lumyong S, Raspé O. 2019. Three new *Phylloporus* species from tropical China and Thailand. Mycological Progress. 18: 603–14.

Chuankid B, Vadthanarat S, Thongbai B, Stadler M, Lumyong S, Hyde KD, Raspé O. 2021. *Retiboletus* (Boletaceae) in northern Thailand: one novel species and two first records. Mycoscience. 2021 Sep 20;62(5):297–306.

Coker WC, Couch N. 1928. The Gasteromycetes of the Eastern United States and Canada, Chapel Hill: University of North Carolina Press. 201 pp.

Corner EJH. 1972. *Boletus* in Malaysia. Singapore Botanic Gardens, Singapore. 263 pp.

Cortés–Pérez A. 2011. Diversidad del género Scleroderma Pers. emend. Fr. (Fungi, Basidiomycotina, Sclerodermatales) en Veracruz. Profesional thesis, Facultad de Biología, Universidad Veracruzana, Xalapa. 78 pp.

Crous PW, Wingfield MJ, Burgess TI, Hardy GS, Gené J, Guarro J, Baseia IG, García D, Gusmao LF, Souza–Motta CM, Thangavel R. 2018. Fungal Planet description sheets: 716–784. Persoonia: Molecular Phylogeny and Evolution of Fungi 40: 240.

Crous PW, Wingfield MJ, Richardson DM, Leroux JJ, Strasberg D, Edwards J, Roets F, Hubka V, Taylor PW, Heykoop M, Martín MP. 2016. Fungal Planet description sheets: 400–468. Persoonia–Molecular Phylogeny and Evolution of Fungi 36: 316–458.

Cui YY, Feng B, Wu G, Xu J, Yang ZL. 2015. Porcini mushrooms (Boletus sect. Boletus) from China. Fungal Diversity 81: 189–212.

Cunningham GH. 1942. The Gasteromycetes of Australia and New Zealand. Dunedin: Privately published. 236 pp.

Dahlberg A, Finlay RD. 1999. *Suillus*. Ectomycorrhizal fungi key genera in profile. 1999: 33–64.

Das K, Chakraborty D, Vizzini A. 2017. Morphological and phylogenetic evidences unveil a novel species of *Gyroporus* (Gyroporaceae, Boletales) from Indian Himalaya. Nordic Journal of Botany 356: 669–75.

Das K, Dentinger BT. 2015. *Austroboletus olivaceoglutinosus*, a new mushroom species from Sikkim, India with a distinctive green, glutinous pileus. Kew Bulletin 70: 15.

Das K, Ghosh A, Chakraborty D, Datta S, Bera I, Layola MR R, Banu F, Vizzini A, Wisitrassameewong K. 2023. Four novel species and two new records of boletes from India. Journal of Fungi 9: 754.

Das K, Ghosh A, Datta S, Singh U, Chakraborty D, Tudu D, Vizzini A. 2024. Concordance of multigene genealogy along with morphological evidence unveils five novel species and two new records of boletoid mushrooms (fungi) from India. Scientific Reports 14: 9298.

Das K, Sharma JR, Mishra D. 2012. *Tylopilus pseudoscaber*–an addition to Indian mycoflora. Nelumbo 54: 269–272.

De Schweinitz LD. 1832. Synopsis Fungorum in America Boreali media degentium. Secundum Observationes. Transactions of the American Philosophical Society 4: 160.

Degreef J, Kesel AD. 2008. *Chalciporus africanus*, a new bolete species from Africa. Mycotaxon 103: 329–335

Demoulin V. 1968. Gasteromycetes de Belgique: Sclerodermatales, Tulostomatales, Lycoperdales. Bulletin du Jardin Botaniquede l'Etat Ii Bruxulles 38: 1–101.

den Bakker HC, Gravendeel B, Kuyper TW. 2004. An ITS phylogeny of *Leccinum* and an analysis of the evolution of minisatellite–like sequences within ITS1. Mycologia 96: 102–118

den Bakker HC, Noordeloos ME. 2005. A revision of European species of *Leccinum* Gray and notes on extralimital species. Persoonia 18: 511–587

Dentinger BT, Ammirati JF, Both EE, Desjardin DE, Halling RE, Henkel TW, Moreau PA, Nagasawa E, Soytong K, Taylor AF, Watling R. 2010. Molecular phylogenetics of porcini mushrooms (*Boletus* section *Boletus*). Molecular Phylogenetics and Evolution 57: 1276–1292.

Desjardin DE, Binder M, Roekring S, Flegel T. 2009. *Spongiforma*, a new genus of gasteroid boletes from Thailand. Fungal Diversity 37: 1–8.

Drehmel D, James T, Vilgalys R. 2008. Molecular phylogeny and biodiversity of the boletes. Fungi 1: 17–23.

Duchesne LC. 1989. Protein synthesis in *Pinus resinosa* and the ectomycorrhizal fungus *Paxillus involutus* prior to ectomycorrhiza formation. Trees 3: 73–7.

Eastwood DC, Floudas D, Binder M, Majcherczyk A, Schneider P, Aerts A, Asiegbu FO, Baker SE, Barry K, Bendiksby M, Blumentritt M. 2011. The plant cell wall–decomposing machinery underlies the functional diversity of forest fungi. Science. 333: 762–765.

Farid A, Bessette AE, Bessette AR, Bolin JA, Kudzma LV, Franck AR, Garey JR. Investigations in the boletes (Boletaceae) of southeastern USA: four novel species, and three novel combinations. Mycosphere 12: 1038–1076.

Farmer DJ, Sylvia DM. 1998. Variation in the ribosomal DNA internal transcribed spacer of a diverse collection of ectomycorrhizal fungi. Mycological Research 102: 859–865.

Farook VA, Khan SS, Manimohan P. 2013. A checklist of agarics (gilled mushrooms) of Kerala State, India. Mycosphere 4: 97–131.

Fechner N, Bonito G, Bougher NL, Lebel T, Halling RE. 2017. New species of Austroboletus (Boletaceae) in Australia. Mycological Progress. 16: 769–775.

Feng B, Xu J, Wu G, Hosen MI, Zeng NK, Li YC, Tolgor B, Kost GW, Yang ZL. 2012. DNA sequence analyses reveal abundant diversity, endemism and evidence for Asian origin ofthe porcini mushrooms. PLoS One 7: e37567.

Fischer E. 1900. Gasteromycetes in Engler and Prantl. Die Natiirlichen Pfianzenfamilien 1: 334–338.

Frank JL. 2015. Nomenclatural novelties. *Index Fungorum* 248: 1

Frank JL, Siegel N, Schwarz CF, Araki B, Vellinga EC. 2020. *Xerocomellus* (boletaceae) in western north America. Fungal systematics and Evolution 6: 265–288.

Fries E. 1829. Systema Mycologicum 3: 524 pp.

Fries EM. 1821. Systema Mycologicum. Greifswald: Ernest Mauritius.

Fulgenzi TD, Halling RE, Henkel TW. 2010. Fistulinella cinereoalba sp. nov. and new distribution records for Austroboletus from Guyana. Mycologia 102: 224–232.

Fulgenzi TD, Henkel TW, Halling RE. 2007. *Tylopilus orsonianus* sp. nov. and *Tylopilus eximius* from Guyana. Mycologia 99: 622–627.

Fulgenzi TD, Mayor JR, Henkel TW, Halling RE. 2008. New species of *Boletellus* from Guyana. Mycologia 100: 490–495.

Garbaye J, Delwaulle JC, Diangana D. 1988. Growth response of eucalyptus in the Congo to ectomycorrhizal inoculation. Forest Ecology and Management 24: 151–157.

García–Jiménez J, Garza–Ocañas F, de la Fuente JI, Saldivar ÁE, Ayala–Vásquez O. 2019. Three new records of *Aureoboletus Pouzar* (Boletaceae, Boletales) from Mexico. Check List 15: 759–765.

Gargano ML, Maisano S, Venturella G. *Pisolithus albus*, a new record for Italy. 2018. Field mycology 19: 86–89.

Garza–Ocañas F, García Jiménez J, Guevara–Guerrero G, Martínez–González CR, Ayala–Vásquez O. 2022. *Xerocomellus carmeniae* (Boletales, Basidiomycota), a new fungus from northeastern Mexico. Acta botánica Mexicana: 129.

Gelardi M, Simonini G, Ercole E, Vizzini A. 2014. *Alessioporus* and *Pulchroboletus* gen. nov. (Boletaceae, Boletineae), two novel genera to accommodate *Xerocomus* *ichnusanus* and *X. roseoalbidus* from European Mediterranean basin: molecular and morphological evidence. Mycologia 106: 1168–1187.

Gelardi M, Vizzini A, Ercole E, Voyron S, Wu G, Liu XZ. *Strobilomyces echinocephalus* sp. nov. (Boletales) from south-western China, and a key to the genus *Strobilomyces* worldwide. Mycological Progress 12: 575–588.

Gelardi M. 2020. Diversity, biogeographic distribution, ecology, and ectomycorrhizal relationships of the edible Porcini Mushrooms (*Boletus* s. str., Boletaceae) worldwide: state of the art and an annotated checklist. Mushrooms, humans and nature in a changing world: Perspectives from ecological, agricultural and social sciences: 223–271.

Gelardi M. 2021. Boletales. Zaragoza, O. (ed) Encyclopedia of Mycology. Oxford: Elsevier. 329–360 pp.

Gilbert EJ. 1931. Les bolets. Librairie E. Le Franc¸ois, Paris.

Ginns J. 1971. The genus Merulius IV. species proposed by Berkeley, by Berkeley & Curtis, and by Berkeley & Broome. Mycologia 63: 219–236.

Ginns JH. 1998. Genera of the North American Corticiaceae sensu lato. Mycologia 90: 1–35.

Grand LF. 1976. Distribution, plant associates and variation in basidiocarps of *Pisolithus tinctorius* in the United States. Mycologia 68: 672–678.

Gray SF. 1821. A natural arrangement of British plants. London.

Guzmán G, Cortés–Pérez A, Guzmán–Dávalos L, Ramírez–Guillén F, del Refugio Sánchez–Jácome M. 2013. An emendation of *Scleroderma*, new records, and review of the known species in Mexico. Revista mexicana de biodiversidad 84: 173–191.

Guzmán G, Ovrebo CL. 2000. New observations on sclerodermataceous fungi. Mycologia 92:174–179.

Guzmán G. A new delimitation and probable phylogeny of the family sclerodermataceae. Transactions of the British Mycological Society. 56: 195–199.

Halama M. 2015. *Rubroboletus legaliae* (Boletales, Basidiomycota), a species new for Poland. Acta Mycologica 50: 1066.

Hall IR, Stephenson S, Buchanan P, Wang Y, Cole ALJ. 2003. Edible and Poisonous Mushrooms of the World. Portland: Timber Press.

Halling RE, Fechner N, Nuhn M, Osmundson T, Soytong K, Arora D, Binder M, Hibbett D. 2015. Evolutionary relationships of *Heimioporus* and *Boletellus* (Boletales), with an emphasis on Australian taxa including new species and new combinations in

Aureoboletus, *Hemileccinum* and *Xerocomus*. Australian Systematic Botany 8: 1–22.

Halling RE, Ortiz–Santana B. 2009. A revision of *Boletellus* sect. *Ixocephali*. Mycological Progress 8: 237–244.

Halling RE, Osmundson TW, Neves MA. 2007. Pacific boletes: Implications for biogeographic relationships. Mycological Research 112: 437–447.

Halling RE. 2001. Ectomycorrhizae: co–evolution, significance, and biogeography. Annals of the Missouri Botanical Garden 1: 5–13.

Halling RE, Mueller GM. 2005. Common Mushrooms of the Talamanca Mountains, Costa Rica. New York Botanical Garden. 197 pp.

Halling RE, Mueller GM. 2003. *Leccinum* (Boletaceae) in Costa Rica. Mycologia 95: 488–499.

Han LH, Buyck B, Yorou NS, Halling RE, Yang ZL. 2017. *Afroboletus sequestratus* (Boletales), the first species with sequestrate basidioma in the genus. Phytotaxa 305: 11–20.

Han LH, Feng B, Wu G, Halling RE, Buyck B, Yorou NS, Ebika ST, Yang ZL. 2018. African origin and global distribution patterns: Evidence inferred from phylogenetic and biogeographical analyses of ectomycorrhizal fungal genus *Strobilomyces*. Journal of Biogeography 45: 201–12.

Han LH, Wu G, Horak E, Halling RE, Xu J, Ndolo ES, Sato H, Fechner N, Sharma YP, Yang ZL. Phylogeny and species delimitation of *Strobilomyces* (Boletaceae), with an emphasis on the Asian species. Persoonia–Molecular Phylogeny and Evolution of Fungi 44: 113–139.

Harsh NSK, Bisht NS. 1982. Boletaceae of Kumaon Hills–III. Current Science 52: 641–644.

Hawksworth DL. 1995. Biodiversity: measurement and estimation. Springer Science & Business Media.

He MQ, Zhao RL, Hyde KD, Begerow D, Kemler M, Yurkov A, McKenzie EH, Raspé O, Kakishima M, Sánchez–Ramírez S, Vellinga EC. 2019. Notes, outline and divergence times of Basidiomycota. Fungal diversity 99: 105–367.

Hedh J, Samson P, Erland S, Tunlid A. 2008. Multiple gene genealogies and species recognition in the ectomycorrhizal fungus *Paxillus involutus*. Mycological research 112: 965–975.

Heim R. 1936. Observations sur la flore mycologique malgache, III. Trois bolets gigantesques d’Afrique et de Madagascar. Revue de mycologie 1: 3–18.

Heinemann P, Goossens–Fontana M. 1954. Fascicle 3. Boletineae. Jardin Botanique de l’Etat.

Heinemann P, Rammeloo J. 1982. Observations sur le genre *Phlebopus* (Boletineae). Mycotaxon: 384–404.

Heinemann P, Rammeloo J. 1987. Novitates generis *Phyllopori* (Boletineae). Bulletin du Jardin botanique national de Belgique/Bulletin van de National Plantentuin van België 57: 272–274.

Heinemann P. 1954: Boletineae. Flore Iconographique des Champignons du Congo 3: 49–80.

Henrici A, Kibby G. 2014. *Paxillus* – An End to Confusion? Field Mycology 15: 121–127.

Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, Eriksson OE, Huhndorf S, James T, Kirk PM, Lücking R, Lumbsch HT. 2007. A higher–level phylogenetic classification of the Fungi. Mycological research 111: 509–547.

Hibbett DS, Binder M. 2002. Evolution of complex fruiting–body morphologies in homobasidiomycetes. Proceedings of the Royal Society of London, Series B: Biological Sciences 269:1963–1969.

Hibbett DS, Pine EM, Langer E, Langer G, Donoghue MJ. 1997. Evolution of lamellate mushrooms and puffballs inferred from ribosomal DNA sequences. Proceedings of the national academy of sciences. 94: 12002–12006.

Hibbett DS, Thorn RG. 2001. Basidiomycota: Homobasidiomycetes. Systematics and Evolution. The Mycota 7B. Springer. 121–168 pp.

Hibbett D, Matheny P.B. 2009. The relative ages of ectomycorrhizal mushrooms and their plant hosts estimated using Bayesian relaxed molecular clock analyses. BMC biology 7: 1–3.

Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS. 2018. UFBoot2: improving the ultrafast bootstrap approximation. Molecular biology and evolution 35: 518–522.

Høiland K. 1987. A new approach to the phylogeny of the order Boletales (Basidiomycotina). Nordic journal of botany 7: 705–718.

Hongo T. 1960. The Agaricales of Japan 1–2: Rhodophyllaceae, Paxillaceae, Gomphidiaceae, Boletaceae and Strobilomycetaceae. Acta Phytotaxonomica et Geobotanica 18: 97–112.

Horak E. 1983. Mycogeography in the South Pacific region: Agaricales, Boletales. Australian Journal of Botany 10: 1–41.

Horak E. 2011. Revision of Malaysian species of Boletales s. l. (Basidiomycota) described by E. J. H. Corner (1972, 1974). Malayan Forest Records 51. 283 pp.

HorakE. 1968. Synopsis generum Agaricalium (Die Gattungstypen der Agaricales). Kommissions verlag Druckerei Büchler. Waber–Bern.

Hosen MI, Li TH. 2015. *Phylloporus gajari*, a new species of the family Boletaceae from B angladesh. Mycoscience 56: 584–589.

Husbands DR, Henkel TW, Bonito G, Vilgalys R, Smith ME. 2013. New species of *Xerocomus* (Boletales) from the Guiana Shield, with notes on their mycorrhizal status and fruiting occurrence. Mycologia 105: 422–435.

Izumitsu K, Hatoh K, Sumita T, Kitade Y, Morita A, Gafur A, Ohta A, Kawai M, Yamanaka T, Neda H, Ota Y. 2012. Rapid and simple preparation of mushroom DNA directly from colonies and fruiting bodies for PCR. Mycoscience 53: 396–401.

Jargeat P, Chaumeton JP, Navaud O, Vizzini A, Gryta H. 2014. The *Paxillus involutus* (Boletales, Paxillaceae) complex in Europe: genetic diversity and morphological description of the new species *Paxillus cuprinus*, typification of *P. involutus* s. str., and synthesis of species boundaries. Fungal biology 118: 12–31.

Jargeat P, Moreau PA, Gryta H, Chaumeton JP, Gardes M. 2016. *Paxillus rubicundulus* (Boletales, Paxillaceae) and two new alder–specific ectomycorrhizal species, *Paxillus olivellus* and *Paxillus adelphus*, from Europe and North Africa. Fungal biology 120: 711–28.

Jarosch M. 2001. Zur molekularen Systematik der Boletales: –Coniophorineae, Paxillineae und Suillineae. Cramer in der Gebr.-Borntraeger-Verl.-Buchh.

Jenkinson TS, Celio GJ, Padamsee M, Dentinger BT, Meyer ML, McLaughlin DJ. 2008. Conservation of cytoplasmic organization in the cystidia of *Suillus* species. Mycologia. 100: 539–547.

Jiang L, Yang D, Cao Y, Wang P, Zhang Y, Zhang KQ, Xu J, Zhang Y. 2017. The complete mitochondrial genome of the edible Basidiomycete mushroom *Phlebopus portentosus*. Mitochondrial DNA Part B 2: 696–697.

Jo JW, Kwag YN, Cho SE, Han SK, Han JG, et al. 2019. First report of Buchwaldoboletus lignicola (Boletaceae), a potentially endangered Basidiomycete species, in South Korea. Mycobiology 47: 521−26

Justus K, Herrmann R, Klamann JD, Gruber G, Hellwig V, Ingerl A, Polborn K, Steffan B, Steglich W. 2007. Retipolides–Unusual Spiromacrolactones from the Mushrooms *Retiboletus retipes* and *R. ornatipes*. Europian Journal of Organic Chemistry 33: 5560−5572.

Kanchanaprayudh J, Zhou Z, Yomyart S, Sihanonth P, Hogetsu T. 2003. Molecular phylogeny of ectomycorrhizal Pisolithus fungi associated with pine, dipterocarp, and eucalyptus trees in Thailand. Mycoscience 44: 287–294.

Karsten PA. 1881. Enumeratio Boletinearum et Polyporearum Fennicarum, systemate novo dispositarum. Revue Mycologique 3: 16–19.

Kasuya MC, Coelho ID, Campos DT, Araújo EF, Tamai Y, Miyamoto T. Morphological and molecular characterization of Pisolithus in soil under eucalyptus plantations in Brazil. Revista Brasileira de Ciencia do Solo 34: 1891–1898.

Kasuya TG, Guzmán F, Ramírez–Guillén, Kato T. 2002. *Scleroderma laeve* (Gasteromycetes, Sclerodermatales), new to Japan. Mycoscience 4: 475–476.

Kennedy PG, Matheny PB, Ryberg KM, Henkel TW, Uehling JK, Smith ME. 2012. Scaling up: examining the macroecology of ectomycorrhizal fungi. Molecular ecology. 21: 4151–4154.

Kim S, So HM, Roh HS, Kim J, Yu JS, Lee S, Seok S, Pang C, Baek KH, Kim KH. 2017. Vulpinic acid contributes to the cytotoxicity of *Pulveroboletus ravenelii* to human cancer cells by inducing apoptosis. RSC advances 7: 35297–35304.

Kirk PM, Cannon PF, David JC, Stalpers JA. 2001. Ainsworth and Bisby's Dictionary of the Fungi. CABI publishing.

Kirk PM, Cannon PF, Minter DW, Stalpers JA. 2008. Dictionary of the Fungi (10th edition). Wallingford, UK. 771 pp.

Klofac W, Krisai–Greilhuber I. 2020. *Chalciporus pseudopiperatus*, a new taxon in the *Chalciporus piperatus* species complex. Öst Z Pilzk 28: 75–78.

Klofac W. 2007. Schlüssel zur Bestimmung von Frischfunden der europäischen Arten der Boletales mit röhrigem Hymenophor. Österreichische Zeitschrift für Pilzkunde 16: 187–279.

Klofac W. 2010. The genus *Aureoboletus*, a world–wide survey. A contribution to a monographic treatment. Österr. Z. Pilzk 19: 133–174.

Knudsen H, Taylor AFS. 2012. *Paxillus* Fr. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera. Nordsvamp, Copenhagen. 214–215 pp.

Knudsen H, Taylor AFS. 2008. Boletales E.–J. Gilbert. Funga Nordica – Agaricoid, Boletoid and Cyphelloid Genera. Nordsvamp, Copenhagen.

Kope HH, Fortin JA. 1990. Germination and comparative morphology of basidiospores of *Pisolithus arhizus*. Mycologia 82: 350–357.

Kour H, Kumar S, Sharma YP. 2013. Two species of *Strobilomyces* from Jammu and Kashmir, India. Mycosphere 4: 1006–10013.

Kretz O, Creppy E, Dirheimer G. 1991. Characterization of bolesatine, a toxic protein from the mushroom Boletus satanas Lenz and it's effects on kidney cells. Toxicology 66: 213–224.

Kretzer A, Li Y, Szaro T, Bruns TD. 1996. Internal transcribed spacer sequences from 38 recognized species of *Suillus* sensu lato: phylogenetic and taxonomic implications. Mycologia 88: 776–85.

Krishnakumar PK, Bhat GS. 2009. Seasonal and interannual variations of oceanographic conditions off Mangalore coast (Karnataka, India) in the Malabar upwelling system during 1995–2004 and their influences on the pelagic fishery. Fisheries Oceanography 17: 45–60.

Kühner R, Romagnesi H. 1953. Analytical flora of the higher fungi (Agarics, Boleti, Chanterelles). 558 pp.

Kühner R. 1977. Les grandes lignes de la classification des Agaricales Asterosporales et Boletales. Survol historique et critique. Bulletin de la Société Linneenee de Lyon. 81–108 pp.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. Molecular biology and evolution 35: 1547–1549.

Kumar TKA, Thomas A, Kuniyil K, Nanu S, Nellipunath V. 2019. A checklist of the non–lamellate fleshy fungi (Basidiomycota) of Kerala State, India. Mycotaxon 134: 221.

Kumla J, Danell E, Bussaban B, Lumyong S. 2012. Suitable growth conditions and nutrition factors on in vitro culture of Phlebopus portentosus (Boletales). Chiang Mai Journal of Science 38:156–159.

Ladurner H, Simonini G. 2003. *Xerocomus* s. l. Fungi Europaei 8. Alassio: Edizioni Candusso. 528 pp.

Lakhanpal TN. 1996. Mushrooms of India, Boletaceae. APH Public Corporation. 170 pp.

Larsson KH. Re-thinking the classification of corticioid fungi. 2007. Mycological research 111: 1040–1063.

Larsson KH, Larsson E, Kõljalg U. 2004. High phylogenetic diversity among corticioid homobasidiomycetes. Mycological Research 108: 983–1002.

Lebel T, Pennycook S, Barrett M. 2018. Two new species of *Pisolithus* (Sclerodermataceae) from Australasia, and an assessment of the confused nomenclature of *P. tinctorius*. Phytotaxa 348:163–186.

Lebel T, Syme A. 2012. Sequestrate species of *Agaricus* and *Macrolepiota* from Australia: New combinations and species, and their position in a calibrated phylogeny. Mycologia 104: 496–520.

Li YC, Feng B, Yang ZL. 2011. *Zangia*, a new genus of Boletaceae supported by molecular and morphological evidence. Fungal Diversity 49: 125–143.

Li YC, Yang ZL. 2021. The boletes of China: *Tylopilus* s. l. Singapore: Springer.

Li TH, Song B. 2000. Chinese boletes: A comparison of boreal and tropical elements. Tropical Mycology Liverpool: Liverpool John Moores University, B.M.S., The Millenium Meeting on Tropical Mycology (Main Meeting 2000). 1–10 pp.

Li YC, Yang ZL. 2011. Notes on tropical boletes from China. Journal of Fungal Research 9: 204–211.

Linzenkirchner J, Besl H. 1993. Regensburger Pilzflora: Boletaceae sensu lato, Gomphidiaceae und Paxillaceae. Regensburgische Botanische Gesellschaft.

Liu HY, Li YC, Bau T. 2020. New species of *Retiboletus* (Boletales, Boletaceae) from China based on morphological and molecular data. MycoKeys 67: 33.

Liu B. 1984. Chinese Medicinal Fungi. Taiyuan: Shanxi People's Press. 1-228 pp.

Liu JK. 2007. Secondary metabolites from higher fungi in China and their biological activity. Drug Discoveries and Therapeutics 1: 94–103.

Liu LR, Wang GS, Jia LK, Kang JQ, Yang ZL, Li YC. 2022. Type studies on two *Paxillus* species (Paxillaceae, Boletales) described from China. Phytotaxa 530: 177–188.

Lloyd CG. 1925. Mycological Notes 74. Mycological Writings 7: 1333–1348.

Lumbsch HT, Buchanan PK, May TW, Mueller GM. 2008. Phylogeography and biogeography of fungi. Mycological Research 112: 423–424.

Ma J, Xia J, Li HJ, Su LJ, Xue R, Jiang S, Yu TJ, Liu Y, Tang LP. 2023. Four cases of reported adverse effects from black boletoi, *Anthracoporus nigropurpureus* (Boletaceae) mushroom ingestion. Toxicon 230: 107155.

Madhosingh C. 1966. Pigmented bacteriostatic substances and amino acids produced by *Phlebopus sulphureus* and *Phlebopus lignicola*. Applied Microbiology 14: 331–336.

Magnago AC, Alves–Silva G, Henkel TW, da Silveira RM. 2022. New genera, species, and combinations of Boletaceae from Brazil and Guyana. Mycologia 114: 607–625.

Magnago AC, Alves–Silva G, Neves MA, Silveira RM. 2018. A new species of *Gyroporus* (Gyroporaceae, Boletales) from Atlantic forest in southern Brazil. Nova Hedwigia 107: 291–301.

Magnago AC, Neves MA, Silveira RM. 2019. *Boletellus nordestinus* (Boletaceae, Boletales), a new species from Northeastern Atlantic Forest, Brazil. Studies in Fungi 4: 47–53.

Magnago AC, Neves MA. 2014. New record of *Austroboletus festivus* (Boletaceae) from Santa Catarina, Brazil. Brazilian Journal of Botany 37: 197–200.

Magnago AC, Reck MA, Dentinger BT, Moncalvo JM, Neves MA, Silveira RM. 2017. Two new *Tylopilus* species (Boletaceae) from Northeastern Atlantic Forest, Brazil. Phytotaxa 316: 250–260.

Maire R. 1902. Recherches cytologiques et taxonomiques sur les Basidiomycètes. Bulletin trimestriel de la Société mycologique de France, 18 (Supplement). 212 pp.

Malinowska E, Szefer P, Falandysz JJ. 2004. Metals bioaccumulation by bay bolete, *Xerocomus badius*, from selected sites in Poland. Food Chemistry 84: 405–16.

Malloch D, Kuja AL. 1979. Occurrence of the ectomycorrhizal fungus *Pisolithus tinctorius* in Ontario. Canadian Journal of Botany 57: 1848–1849.

Manjula B. 1983. A revised list of the agaricoid and boletoid basidiomycetes from India and Nepal. Proceedings: Plant Sciences 92: 81.

Mao N, Zhao TY, Xu YY, Fan L. 2023. *Villoboletus persicinus*, gen. et sp. nov. (Boletaceae), a bolete with flocculent–covered stipe from northern China. Mycologia 115: 255–262.

Martin F, Díez J, Dell D, Delaruelle C. 2002. Phylogeography of the ectomycorrhizal *Pisolithus* species as inferred from nuclear ribosomal DNA ITS sequences. New Phytologist 153: 345–357.

Martinez–Reyes M, Carrera–Martinez A, de la Fuente JI, Rios–Garcia U, Ortiz–Lopez I, Ayala–Vasquez O. 2023. *Xerocomellus perezmorenoi* (Boletaceae, Boletales), a new edible species from Mexico. Phytotaxa 584: 104–114.

Marx DH, Bryan WC, Cordell CE. 1977. Survival and growth of pine seedlings with *Pisolithus* ectomycorrhizae after two years on reforestation sites in North Carolina and Florida. For. Sci., 16: 363–373.

Matheny PB, Curtis JM, Hofstetter V, Aime MC, Moncalvo JM, Ge ZW, Yang ZL, Slot JC, Ammirati JF, Baroni TJ, Bougher NL. 2007. Major clades of Agaricales: a multilocus phylogenetic overview. Mycologia 98: 982–995.

McNabb RF. 1967. The Strobilomycetaceae of New Zealand. New Zealand Journal of Botany 5: 532–547.

McNabb RF. 1968. The Boletaceae of New Zealand. New Zealand journal of botany 6: 137–176.

McNabb RF. 1969. The Paxillaceae of New Zealand. New Zealand journal of botany 7: 349–362.

Mei Y, Liu CY, Li SH, Guerin–Laguette, A, Xiao YJ, Tang P, Wan SP, Bonito G, Wang Y. 2020. *Phlebopus roseus*, a new edible bolete from China, is associated with insects and plants. Mycologia 113: 33–42.

Mei Y, Liu CY, Li SH. 2021. *Phlebopus roseus*, a new edible bolete from China, is associated with insects and plants. Mycologia 113: 33–42.

Mello A. 2012. State of the art of the research on *Boletus edulis*. Edible Ectomycorrhizal Mushrooms: Current Knowledge and Future Prospects 17: 73–81.

Meng X, Wang GS, Wu G, Wang PM, Yang ZL, Li YC (2021) The genus *Leccinum* (Boletaceae, Boletales) from China based on morphological and molecular data. J Fungi 7(9):732

Migliorini D, Capretti P, Santini A. 2012. Carattezizzazione morfo–fisiologica ed analisi di alcuni aspetti ecologici di Buchwaldoboletus lignicola. Micologia Italiana 41: 45–52.

Miller OKM, Lodge DJ and Baroni TJ. 2000. New and interesting ectomycorrhizal fungi from Puerto Rico, Mona, and Guana Islands. Mycologia 92: 558–570.

Min YJ, Park MS, Fong JJ, Seok SJ, Han S–K, Lim YW. 2014. Molecular taxonomical re–classification of the genus Suillus Micheli ex S. F. Gray in South Korea. Mycobiology 42: 221–228.

Mohanan C. 2011. Kerala Forest Research Institute. Macrofungi of Kerala. Kerala Forest Research Institute. 597 pp.

Momoh ZO, Gbadegesin RA. 1980. Field performance of *Pisolithus tinctorius* as a mycorrhizal fungus of pines in Nigeria. Tropical mycorrhiza research, Oxford University Press. 72–79 pp.

Montoya L, Bandala VM. 2011. A new *Phylloporus* from two relict Fagus grandifolia var. mexicana populations in a montane cloud forest. Mycotaxon 117: 9–18.

Moreau PA, Welti S, Perić B, Jargeat P, Manzi S, Vizzini A. 2013. *Alpova komoviana* (Boletales, Paxillaceae), a new sequestrate fungus from Montenegro, with a revised phylogeny of the genus in Europe. Mycological Progress 12: 109–119.

Moser M, Kibby G. 1983. Keys to agarics and boleti: Polyporales, Boletales, Agaricales, Russulales. Mad River Press publishes. 535 pp.

Moyersoen B, Beever RE, Martin F. 2003. Genetic diversity of *Pisolithus* in New Zealand indicates multiple long–distance dispersal from Australia. New Phytologist 160: 569–579.

Muñoz JA. 2005. *Boletus* s. l. (excluding *Xerocomus*). Fungi Europaei 2. Alassio: Edizioni Candusso. 952 pp.

Murrill WA. 1909. Boleti from Western North Carolina. Torreya 8: 209–217.

Nair SSC. 2011. The changing landscape of Kerala, Birds of Kerala, Status and distribution. DC books, Koattayam. 835 pp.

Nanu S, Kumar TA. 2024a. New species of *Chalciporus* and *Tylopilus* from India, with keys to the known species. Mycologia: 1–5.

Nanu S, Kumar TA. 2024b. A new species of *Baorangia* (Boletaceae, Boletales) from a sacred grove in India. Nordic Journal of Botany: e04357.

Nanu S, Kumar TA. 2023. A new species of *Boletinellus* (Boletinellaceae, Boletales) from India. Phytotaxa 594: 223–231.

Nanu S, Kumar TA. 2022. *Buchwaldoboletus xylophilus*, a boletoid fungus new to India. Studies in Fungi 7: 1–4.

Nanu S, Kumar TA. 2024c. Paleotropical distribution of the genus *Neotropicomus* AC Magnago, Alves-Silva & TW Henkel: a new species from India. Cryptogamie, Mycologie 45: 47–52.

Natarajan K, Senthilarasu G, Kumaresan V, Riviere T. 2005. Diversity in ectomycorrhizal fungi of a dipterocarp forest in Western Ghats. Current Science. 88: 1893–1895.

Natarajan K. On some ectomycorrhizal fungi occurring in Southern India. 1988. Kavaka: 16.

Nelsen SF. 2010. Bluing components and other pigments of boletes. Fungi 3: 11–4.

Neves MA, Binder M, Halling R, Hibbett D, Soytong K. 2012. The phylogeny of selected *Phylloporus* species, inferred from NUC–LSU and ITS sequences, and descriptions of new species from the Old World. Fungal Diversity 55: 109–123.

Newman EI, Reddell P. 1987. The distribution of mycorrhizas among families of vascular plants. New Phytologist 106: 745–751.

Nguyen LT, Schmidt HA, Von Haeseler A, Minh BQ. 2015. IQ–TREE: a fast and effective stochastic algorithm for estimating maximum–likelihood phylogenies. Molecular biology and evolution. 32: 268–274.

Nguyen NH, Vellinga EC, Bruns TD, Kennedy PG. 2016. Phylogenetic assessment of global Suillus ITS sequences supports morphologically defined species and reveals synonymous and undescribed taxa. Mycologia. 108: 1216–1228.

Noordeloos ME, Kuyper TW, Vellinga EC. 1999. Flora Agaricina Neerlandica. CRC Press. 200 pp.

Nuhn ME, Binder M, Taylor AFS, Halling RE, Hibbett DS. 2013. Phylogenetic overview of the Boletineae. Fungal Biology 117: 479–511.

Olsson PA, Münzenberger B, Mahmood S, Erland S. 2000. Molecular and anatomical evidence for a three–way association between *Pinus sylvestris* and the ectomycorrhizal fungi *Suillus bovinus* and *Gomphidius roseus*. Mycological Research 104: 1372–1378.

Orihara T, Smith M, Shimomura N, Iwase K, Maekawa N. 2012. Diversity and systematics of the sequestrate genus *Octaviania* in Japan: two new subgenera and eleven new species. Persoonia 28: 85–112.

Ortiz–Santana B, Both EE. 2011. A preliminary survey of the genus *Buchwaldoboletus*. Bulletin of the Buffalo Society of Natural Sciences 40: 1–4.

Orton PD. 1969. Notes on British Agarics III. Notes from the Royal Botanical Garden Edinburgh 29: 75–127.

Osmundson TW, Halling RE, Den Bakker HC. 2007. Morphological and molecular evidence supporting an arbutoid mycorrhizal relationship in the Costa Ricanpáramo. Mycorrhiza. 17: 217–222.

Osmundson TW, Halling RE. 2010. *Tylopilus oradivensis* sp. nov.: a newly described member of the *Tylopilus balloui* complex from Costa Rica. Mycotaxon 113: 475–483.

Parihar A, Hembrom ME, Vizzini A, Das K. 2018. *Indoporus shoreae* gen. nov. (Boletaceae) from tropical India. Cryptogamies, Mycologie 39: 447–466.

Patil PB, Gunasekaran S, Singh SK, Vaidya S. 2021. *Parvixerocomus matheranensis* (Boletaceae), a new species from India. Mycoscience 62: 244–249.

Patocka J. 2018. Bolesatine, a toxic protein from the mushroom *Rubroboletus satanas*. Military Medical Science Letters 87: 14–20.

Pegler D, Young T. 1981. A natural arrangement of the Boletales, with reference to spore morphology. Transactions of British Mycological Society 76: 103–146.

Pegler DN. 1982. Agaricoid and Boletoid Fungi (Basidiomycota) from Malaŵi and Zambia. Kew Bulletin: 255–271.

Peintner U, Schwarz S, Mešić A, Moreau PA, Moreno G, Saviuc P. 2013. Mycophilic or mycophobic? Legislation and guidelines on wild mushroom commerce reveal different consumption behaviour in European countries. PloS one 8: e63926.

Pérez-Moreno J, Guerin-Laguette A, Arzú RF, Yu FQ. 2020. Mushrooms, humans and nature in a changing world: Perspectives from ecological, agricultural and social sciences. Springer. 480 pp.

Persoon CH. 1801. Synopsis methodica fungorum: sistens enumerationem omnium huc usque detectarum specierum, cum brevibvs descriptionibus nec non synonymis et observationibus selectis. Dieterich.

Petri L. 1909. Flora Italica Cryptogama, Pars I: Fungi. Gasterales, Secotiaceae, Lycoperdaceae, Sclerodermataceae 5, Società Botanica Italiana, Stabilimento Tipografico Cappelli, Rocca S, Casciano. 104–109 pp.

Pham NDH, Takahashi H, Fukiharu T, Shimizu K, Le BD, Suzuki A. 2012. "*Phlebopus spongiosus* sp. Nov. (Boletales, Boletinellaceae) with a Sponge–Like Tissue." Mycotaxon 119: 27–34.

Phookamsak R, Hyde KD, Jeewon R, Bhat DJ, Jones EG, Maharachchikumbura SS, Raspé O, Karunarathna SC, Wanasinghe DN, Hongsanan S, Doilom M. 2019. Fungal diversity notes 929–1035: taxonomic and phylogenetic contributions on genera and species of fungi. Fungal diversity. 95: 1–273.

Pilát A, Dermek A. 1974. Hríbovité huby: československé hríbovité a sliziakovité huby [boletaceae–gomphidiaceae]. Veda, Bratislava. 207 pp.

Pilát A. 1969. *Buchwaldoboletus*, genus novum Boletacearum. Friesia 9: 217−18.

Poinar Jr G. 2014. Evolutionary history of terrestrial pathogens and endoparasites as revealed in fossils and subfossils. Advances in Biology 2014: 181353.

Power RC, Salazar-García DC, Straus LG, Morales MR, Henry AG. 2015. Microremains from El Mirón Cave human dental calculus suggest a mixed plant–animal subsistence economy during the Magdalenian in Northern Iberia. Journal of archaeological science. 60: 39‒46.

Pradeep CK, Vrinda KB, Varghese SP, Kumar TK. 2015. A new species of *Phylloporus* (Agaricales, Boletaceae) from India. Phytotaxa 226: 269–274.

Pradhan P, Dutta AK, Roy A, Acharya K. 2011. Boletales of West Bengal, India. I. Sclerodermataceae: Pisolithus and Scleroderma. Researcher 3: 21–26.

Putzke J, Maria L, Pereira AB. 1994. Os fungos da família Boletaceae conhecidos do Rio Grande do Sul (Fungi, Basidiomycota). Caderno de Pesquisa, Série Botânica 6: 75–100.

Verma RK, Tiwari CK, Jagrati Parihar, Shailendra Kumar. 2017. Diversity of macro–fungi in central India–III: *Serpula* spp. Van Sangyan 4: 50–54.

Raghoonundon B, Raspé O, Thongklang N, Hyde KD. 2021. *Phlebopus* (Boletales, Boletinellaceae), a peculiar bolete genus with widely consumed edible species and potential for economic development in tropical countries. Food Bioscience 41: 100962.

Rambaut A. 2018. FigTree. Tree figure drawing tool. http://tree. bio. ed. ac. uk/software/figtree/.

Reddy MS, Singla S, Natarajan K, Senthilarasu G. 2005. *Pisolithus indicus*, a new species of ectomycorrhizal fungus associated with dipterocarps in India. Mycologia 97: 838–843.

Reis FS, Stojković D, Barros L, Glamočlija J, Ćirić A, Soković M, Martins A, Vasconcelos MH, Morales P, Ferreira IC. 2014. Can *Suillus granulatus* (L.) Roussel be classified as a functional food?. Food & function. 5: 2861–2869.

Robinson R, Gates G. 2020. *Buchwaldoboletus hemichrysus* in Tasmania: A golden dilemma. The Tasmanian Naturalist 142: 67–72.

Rogerson CT, Samuels GJ. 1989. *Boleticolous* species of *Hypomyces*. Mycologia 81: 413–432.

Roy N, Jha DK, Dutta AK. 2022. A checklist of the macrofungi of North East India. Studies in Fungi 7: 1–24.

Sahr T, Ammer H, Besl H, Fischer M. 1999. Infrageneric classification of the boleticolous genus Sepedonium: Species delimitation and phylogenetic relationships. Mycologia 91: 935-943.

Sanchez–Zabala J, Majada J, Martín–Rodrigues N, Gonzalez–Murua C, Ortega U, Alonso–Graña M, Arana O, Duñabeitia MK. 2013. Physiological aspects underlying the improved out planting performance of *Pinus pinaster* Ait. seedlings associated with ectomycorrhizal inoculation. Mycorrhiza 23: 627–640.

Sanon KB, Bâ AM, Delaruelle C, Duponnois R, Martin F. 2009. Morphological and molecular analyses in *Scleroderma* species associated with some Caesalpinioid legumes, Dipterocarpaceae and Phyllanthaceae trees in southern Burkina Faso. Mycorrhiza. 19: 571–584.

Sarc L, Jurca T, Planinc NS. 2013. Poisoning by *Boletus satanas* causes hyperprocalcitoninemia: Case report. Clinical Toxicology 51: 264.

Sarwar S, Khalid AN. 2014. Addition to the boletes: *Boletus pakistanicus* sp. nov. from the coniferous forests of Pakistan. International Journal of Agriculture and Biology: 16.

Sarwar S, Siddique ZE, Bashir A, Khalid AN. 2021. *Rubroboletus himalayensis* sarwar & khalid–a new mushroom from pakistan. Bangladesh Journal of Plant Taxonomy: 28.

Sasek V, Musilek V. 1967. Cultivation and antibiotic activity of mycorrhizal basidiomycetes. Folia Microbiologica 12: 515–523.

Sasidharan N. 2012. Flowering Plants of Kerala–Version 2.0. Kerala Forest Research Institute, Peechi.

Sato H, Hattori T, Lee S–S, Murakami N .2011. Two species of *Strobilomyces* (Boletaceae, Boletales), *S. seminudus* and *S. hongoi* sp. nov. from Japan. Mycologia 103: 598–609.

Sato H, Hattori T. 2015. New Species of *Boletellus* Section *Boletellus* (Boletaceae, Boletales) from Japan, *B. aurocontextus* sp. nov. and *B. areolatus* sp. nov. PLoS One 10: e0128184.

Sato H, Yumoto T, Murakami N. 2007. Cryptic species and host specificity in the ectomycorrhizal genus *Strobilomyces* (Strobilomycetaceae). American Jornal of Botany 94: 1630–1641.

Sato H, Toju H. 2019. Timing of evolutionary innovation: scenarios of evolutionary diversification in a species-rich fungal clade, Boletales. New Phytologist 222: 1924–1935.

Schmidt J, Hartmann W Würstlin A, Deicher H. 1971. Akutes Nierenversagen durch immunhämolytischesbAnämie nach Genuß des Kahlen Kremplings (*Paxillus involutus*). Dtsch. Wiener Medizinische Wochenschrift 28: 1188–1191.

Šebek S. 1953. Monograph of the Central European species of the genus *Scleroderma* Pers. Sydowia 7: 158–190.

Silva JM, Nascimento SPGG, Massahud RTR, Santos TMC, Lima GSA. 2019. Atributos químicos e biológicos do solo: Um estudo no Semiárido Alagoano. Ensaios interdisciplinares em ciências agrárias no Nordeste do Brasil, Ananindeua: Itacaiúnas. 42–80 pp.

Sims KP, Watling R, de La Cruz R, Jeffries P. 1997. Ectomycorrhizal fungi of the Phillipines: a preliminary survey and notes on the geographic biodiversity of the Sclerodermatales. Biodiversity and Conservation 6: 45–58.

Sims KP, Watling R, Jeffries P. 1995. A revised key of the genus *Scleroderma*. Mycotaxon 56: 40–420.

Singer R. 1938. Sur les genres *Ixocomus*, *Boletinus*, *Phylloporus*, *Gyrodon* et *Gomphidius*. Revue de Mycologie 3: 157e177.

Singer R. 1962. The Agaricales in modern taxonomy, 2nd edition J. Cramer, Weinheim.

Singer R, Araujo I, Ivory MH. 1983. The ectotrophically mycorrhizal fungi of the neotropical lowlands, especially central Amazonia (Litter decomposition and ectomycorrhiza in Amazonian forests). Beihefte zur Nova hedwigia.

Singer R, Digilio APL. 1960. The Boletaceae of tropical South America. Lilloa 30: 141–164.

Singer R. 1936. Studien zur Systematik der Basidiomyceten. Beihefte zum Botanischen Centralblatt 56: 137–156.

Singer R. 1942. Das System der Agaricales 2. Annals of Mycology 40: 1–132.

Singer R. 1945. New Boletaceae from Florida (a preliminary communication). Mycologia 37: 797–799.

Singer R. 1965. Die Röhrlinge. Teil I. Boletaceae (ohne Boletoideae). Die Pilze Mitteleuropas 5. Bad Heilbrunn: Verlag Julius Klinkhardt. 131 pp.

Singer R. 1967. Die Röhrlinge. Teil II. Die Boletoideaea und Strobilomycetaceae. Die Pilze Mitteleuropas 6. Bad Heilbrunn: Verlag Julius.

Singer R. 1986. The Agaricales in modern taxonomy, 4th edn. Koeltz Scientific Books, Koenigstein.

Singer R. 1951. New genera of fungi. V. Mycologia 43: 598–604.

Singer R. 1947. The Boletoideae of Florida with notes on extralimital species III. The American Midland Naturalist 37: 1–35.

Singer R., Digilio APL. 1957. Las boletáceas austrosudamericanas. Lilloa 7: 246–68.

Singer R, García J, Gómez LD. 1992. The Boletineae of Mexico and Central America IV. Beihefte zur Nova Hedwigia 105: 1–62.

Singla S, Reddya MS, Marmeisse R, Gay G. 2004. Genetic variability and taxonomic position of ectomycorrhizal fungus *Pisolithus* from India. Microbiology Research 159: 203–210.

Sitta N, Davoli P. 2012. Edible ectomycorrhizal mushrooms: international markets and regulations. Edible ectomycorrhizal mushrooms: Current knowledge and future prospects 17: 355–380.

Sitta N, Floriani M. 2008. Nationalization and globalization trends in the wild mushroom commerce of Italy with emphasis on porcini (*Boletus edulis* and allied species). Economic Botany 62: 307–322.

Sitta N, Angelini C, Balma M, Berna C, Bertocchi C, Bragalli A, Cipollone R, Corrias S, Donini M, Giananneschi L, Gioffi D, Golzio F, Granati P, Panata M, Tani O, Tursi A, Suriano E. 2020. I funghi che causano intossicazioni in Italia. Analisi dei dati provenienti da Centri micologici di differenti Regionie valutazioni complessive sulle intossicazioni da specie commestibili. Pagine di Micologia 41: 23–80.

Skrede I, Engh IB, Binder M, Carlsen T, Kauserud H, Bendiksby M. 2011. Evolutionary history of Serpulaceae (Basidiomycota): molecular phylogeny, historical biogeography and evidence for a single transition of nutritional mode. BMC Evolutionary Biology 11: 1–3.

Smith AH, Thiers HD, Walting R. 1967. A preliminary account of the North American species of *Leccinum*, sections *Luteoscabra* and *Scabra*. Michigan Botanist 6: 107–154

Smith AH, Thiers HD. 1971. The boletes of Michigan. University of Michigan Press, Ann Arbor. 372 pp.

Smith AH, Thiers HD. 1964. Contributions Toward a Monograph of North American Species. Lubrecht and Cramer. 116 pp.

Snell WH, Dick EA. 1941. Notes on boletes. VI. Mycologia 33: 23–37.

Snell WH, Dick EA. 1970. The boleti of northeastern North America. Lehre, Germany: Cramer. 115 pp.

Sun Z, Hu M, Sun Z, Zhu N, Yang J, Ma G, Xu X. 2018. Pyrrole alkaloids from the edible mushroom *Phlebopus portentosus* with their bioactive activities. Molecules 23: 1198.

Tan YP, Bishop–Hurley SL, Shivas RG, Cowan DA, Maggs–Kölling G, Maharachchikumbura SS, Pinruan U, Bransgrove KL, De la Peña–Lastra S, Larsson E, Lebel T. 2022. Fungal Planet description sheets: 1436–1477. Persoonia–Molecular Phylogeny and Evolution of Fungi 49: 261–350.

Taylor JW, Jacobson DJ, Kroken S, Kasuga T, Geiser DM, Hibbett DS, Fisher MC. 2000. Phylogenetic species recognition and species concepts in fungi. Fungal Genetic Biology 31:21–32.

Tedersoo L, May TW, Smith ME. 2010. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. Mycorrhiza 20: 217–63.

Thiers HD, Halling RE. California Boletes V. 1976. Two new species of boletus. Mycologia 68: 976–983.

Thomas KJ. 1979. The extent of *Salvinia* infestation in Kerala (South India): its impact and suggested methods of control. Environmental Conservation 6: 63–69.

Trappe JM, Castellano MA, Halling RE, Osmundson TW, Binder M, Fechner N, Malajczuk N. 2013. Australasian sequestrate fungi. 18: *Solioccasus polychromus* gen. and sp. nov., a richly colored, tropical to subtropical, hypogeous fungus. Mycologia 105: 888–895.

Tremble K, Henkel T, Bradshaw A, Domnauer C, Brown L, Tham LX, Furci G, Aime C, Moncalvo JM, Dentinger B. 2023. Phylogenomics, biogeography, and trait evolution of the Boletaceae (Boletales, Agaricomycetes, Basidiomycota). bioRxiv 21: 2023–2010.

Tremble K, Henkel T, Bradshaw A, Domnauer C, Brown LM, Thám LX, Furci G, Aime MC, Moncalvo JM, Dentinger B. 2024. A revised phylogeny of Boletaceae using whole genome sequences. Mycologia 116: 392–408.

Tsai SY, Tsai HL, Mau JL. 2007. Antioxidant properties of *Agaricus blazei*, *Agrocybe cylindracea*, and *Boletus edulis*. Food Science and Technology 40: 1392–1402.

Vadthanarat S, Amalfi M, Halling RE, Bandala V, Lumyong S, Raspe O. 2019. Two new *Erythrophylloporus* species (Boletaceae) from Thailand, with two new combinations of American species. Mycokeys 55: 29.

Vadthanarat S, Raghoonundon B, Lumyong S, Raspé O. 2024. *Rostrupomyces*, a new genus to accommodate *Xerocomus sisongkhramensis*, and a new *Hemileccinum* species (Xerocomoideae, Boletaceae) from Thailand. MycoKeys 103: 129.

Varga T, Krizsán K, Földi C, Dima B, Sánchez–García M, Sánchez–Ramírez S, Szöllősi GJ, Szarkándi JG, Papp V, Albert L, Andreopoulos W. 2019. Megaphylogeny resolves global patterns of mushroom evolution. Nature ecology and evolution 3: 668–78.

Varghese SP, Pradeep CK, Vrinda KB. 2010. Mushrooms of tribal importance in Wayanad area of Kerala. Journal of Mycopathological Research 48: 311–320.

Venturella G, Saitta A. 2003. The traditional use of fungi in Sicily, Italy. Delpinoa 45: 105–108.

Verma B, Reddy MS. 2015. *Suillus indicus* sp. nov. (Boletales, Basidiomycota), a new boletoid fungus from northwestern Himalayas, India. Mycology 6: 35–41.

Verma RK, Pandro V. 2018. Distribution of Boleteceous mushrooms in India, some new records from Sal forest of central India. International Journal of Current Microbiology and Applied Science 7: 1694–1713.

Vilgalys R, Hester M. 1990. Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of bacteriology 172: 4238–4246.

Vinod PG. 2017. Development of topographic position index based on Jenness algorithm for precision agriculture at Kerala, India. Spatial Information Research 25: 381–388.

Vizzini A, Angelini C, Ercole E. 2015. Molecular confirmation of *Gyroporus lacteus* and typification of *Boletus cyanescens*. Phytotaxa 226: 27–38.

Vizzini A. 2014a. *Caloboletus*. *Index Fungorum* 146:1.

Vizzini A. 2014b. *Imleria*. *Index Fungorum* 147:1.

Vizzini A. 2015. Nomenclatural novelties. *Index Fungorum* 244, 1.

Wang QB, Yao YJ. 2005. *Boletus reticuloceps*, a new combination for *Aureoboletus reticuloceps*. Sydowia 57: 131–136.

Wang XH, Das K, Bera I, Chen YH, Bhatt RP, Ghosh A, Hembrom ME, Hofstetter V, Parihar A, Vizzini A, Xu TM. 2019. Fungal biodiversity profiles 81–90. Cryptogamie, Mycologie 40: 57–95.

Wang Y, Wang LY, Dai D, Qi ZX, Zhang ZH, Liu YJ, Hu JJ, Zhang P, Li Y, Zhang B. 2023. Boletaceae in China: Taxonomy and phylogeny reveal a new genus, two new species, and a new record. Frontiers in Microbiology 13: 1052948.

Wang Y, Yu FQ, Zhang C, Liu C, Yang M, Li S. 2020. Edible ectomycorrhizal fungi and their cultivation in China. Mushrooms, humans and nature in a changing world: Perspectives from ecological, agricultural and social sciences: 31-60.

Watkinson SC, Eastwood DC. 2012. *Serpula lacrymans*, wood and buildings. Advances in applied microbiology 78: 121–149.

Watling R, Hills AE. 2005. British Fungus Flora: Agarics and Boleti. Boletes and Their Allies, Boletaceae: Strobilomycetaceae: Gyroporaceae: Paxillaceae: Coniophoraceae: Gomphidiaceae. Royal Botanic Garden Edinburgh. 200 pp.

Watling R, Sims KP. 2004. Taxonomic and oristic notes on some larger Malaysian fungi IV (*Scleroderma*). Fungi in forest ecosystems, systematics, diversity and ecology, CL Crips (edition). Memoirs of the New York Botanical Garden 89: 9–96.

Watling R, Taylor A, See LS, Sims K, Alexander I. 1995. A rainforest *Pisolithus*, its taxonomy and ecology. Nova Hedwigia 61: 417–429.

Watling R. 1970. British Fungus Flora – Agarics and Boleti, I: Boletaceae, Gomphidiaceae, Paxillaceae. Her Majesty's Stationery Office, Royal Botanical Garden, Edinburgh. 108 pp.

Watling R. 2001. The relationships and possible distributional patterns of boletes in south–east Asia. Mycological Research. 105: 1440–1448.

Watling R, De Meijer AR. 1997. Macromycetes from the state of Paraná, Brazil: 5. Poroid and lamellate boletes. Edinburgh Journal of Botany 54: 231–251.

Watling R, Gregory NM. 1988. Observations on the boletes of the Cooloola Sandmass, Queensland and notes on their distribution in Australia. Part 2B. Smoothspored taxa of the family Gyrodontaceae and the genus *Pulveroboletus*. Proceedings of the Royal Society of Queensland 99: 65–76.

Watling R. 2008. A manual and source book on the boletes and their allies. Synopsis Fungorum 24. Oslo: Fungiflora. 250 pp.

Watling R, Li TH. 1999. Australian boletes. A preliminary survey. Edinburgh: Royal Botanic Garden Edinburgh.

Watling R, Turnbull E. 1992. Boletes from south and east central Africa – I. Edinburgh Journal of Botany 49: 343–361.

Wendland J, Kothe E. 1997. Isolation of tef1 encoding translation elongation factor EF1α from the homobasidiomycete Schizophyllum commune. Mycological Research 101: 798–802.

White TJ, Bruns T, Lee SJ, Taylor J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. PCR protocols: a guide to methods and applications 18: 315–322.

Wilf P, Nixon KC, Gandolfo MA, Cúneo NR. 2019. Eocene Fagaceae from Patagonia and Gondwanan legacy in Asian rainforests. Science 364: eaaw5139.

Wilson AW, Binder M, Hibbett DS. 2012. Effects of gasteroid fruiting body morphology on diversification rates in three independent clades of fungi estimated using binary states peciation and extinction analysis. Evolution 65: 1305–1322

Winner M, Giménez A, Schmidt H, Sontag B, Steffan B, Steglich W. 2004. Unusual pulvinic acid dimers from the common fungi *Scleroderma citrinum* (common earthball) and *Chalciporus piperatus* (Peppery Bolete). Angew Chemie 43: 1883–1886.

Wolfe Jr. CB, Bougher NL. 1993. Systematics, mycogeography, and evolutionary history of *Tylopilus* subg. *Roseoscabra* in Australia elucidated by comparison with Asian and American species. Australian Systematic Botany 6: 187–213.

Wolfe CB. 1980. *Austroboletus* and *Tylopilus* subg. *Porphyrellus*, with emphasis on North American taxa. Bibliotheca Mycologica, 69. Berlin Stuttgart: J. Cramer.

Wu G, Feng B, Xu J, Zhu XT, Li YC, Zeng NK, Hosen MI, Yang ZL. 2014. Molecular phylogenetic analyses redefine seven major clades and reveal 22 new generic clades in the fungal family Boletaceae. Fungal Diversity 69: 93–115.

Wu G, Li YC, Zhu XT, Zhao K, Han LH, Cui YY, Li F, Xu JP, Yang ZL. 2016a. One hundred noteworthy boletes from China. Fungal Diversity 81: 25–188.

Wu G, Zhao K, Li YC, Zeng NK, Feng B, Halling RE, Yang ZL. 2016b. Four new genera of the fungal family Boletaceae. Fungal Diversity 81: 1–24.

Wu F, Zhou LW, Yang ZL, Bau T, Li TH, Dai YC. 2019. Resource diversity of Chinese macrofungi: edible, medicinal and poisonous species. Fungal diversity 98: 1–76.

Wu G, Wu K, Qi LL, Morozova OV, Alexandrova AV, Gorbunova IA, Li Y, Liu JW, Yang ZL. 2020. *Psiloboletinus* is an independent genus sister to *Suillus*. Mycologia 112: 185–196.

Xie HJ, Tang LP, Mu M, Fan YG, Jiang S, Su MS, Liang ZQ, Zeng NK. 2022. A contribution to knowledge of *Gyroporus* (Gyroporaceae, Boletales) in China: three new taxa, two previous species, and one ambiguous taxon. Mycological Progress 21: 71–92.

Xie HJ, Zhang CX, He MX, Liang ZQ, Deng XH, Zeng NK. *Buchwaldoboletus xylophilus* and *Phlebopus portentosus*, two non–ectomycorrhizal boletes from tropical China. Phytotaxa 520: 137–154.

Xu C, Liang ZQ, Xie HJ, Jiang S, Fu XH, Zeng NK. 2021. Two new species of *Chalciporus* (Boletaceae, Boletales) from tropical China. Mycological Progress 20: 1573–1582.

Yang ZL. 2011. Molecular techniques revolutionize knowledge of basidiomycete evolution. Fungal Diversity 50: 47–58.

Zang M. 1985. Notes on the Boletales from eastern Himalayas and adjacent of China. Acta Botanica Yunnanica 7: 383–401.

Zang M. 2006. Boletaceae (I). Flora Fungorum Sinicorum 22. Beijing: Science Press.

Zang M, Li XJ, He YS. 2013. Boletaceae (II). Flora Fungorum Sinicorum 44. Beijing: Science Press.

Zeller SM. 1948. Notes on certain Gasteromycetes, including two new orders. Mycologia 40: 639–668.

Zeng NK, Chai H, Liang ZQ, Tang LP, Xue R, Yang ZL. 2018. The genus *Heimioporus* in China. Mycologia 110:1110–1126.

Zeng NK, Liang ZQ, Wu G, Li YC, Yang ZL, Liang ZQ. 2016. The genus *Retiboletus* in China. Mycologia 108: 363–380.

Zeng NK, Tang LP, Li YC, Tolgor B, Zhu XT, Zhao Q, Yang ZL. 2013. The genus *Phylloporus* (Boletaceae, Boletales) from China: morphological and multilocus DNA sequence analyses. Fungal Diversity 58: 73–101.

Zeng NK, Wu G, Li YC, Liang ZQ, Yang ZL. 2014. *Crocinoboletus*, a new genus of Boletaceae (Boletales) with unusual polyene pigments boletocrocins. Phytotaxa 175: 133–140.

Zhang C, He M, Liu J, Xu X, Cao Y, Gao F, Fang Y, Wang W, Wang Y. 2017. Brief introduction to a unique edible Bolete–*Phlebopus portentosus* in Southern China. Journal of Agricultural Science and Technology 7: 386–394.

Zhang M, Li TH, Wang CQ, Zeng NK, Deng WQ. 2019. Phylogenetic overview of *Aureoboletus* (Boletaceae, Boletales), with descriptions of six new species from China. MycoKeys 61: 111.

Zhang M, Li TH. 2018. *Erythrophylloporus* (Boletaceae, Boletales), a new genus inferred from morphological and molecular data from subtropical and tropical China. Mycosystema 37: 1111–1126.

Zhang M, Xie DC, Wang CQ, Deng WQ, Li TH. 2022. New insights into the genus *Gyroporus* (Gyroporaceae, Boletales), with establishment of four new sections and description of five new species from China. Mycology 13: 223–242.

Zhang X, Qin WQ, Liang ZQ, Tian R, Zeng NK. 2022. *Rubroboletus flammeus* (Boletaceae, Boletales), a novel species unveiled from subtropical China based on morphological and phylogenetic evidences. Archives of Microbiology 204: 379.

Zhao K, Shao HM. 2017. A new edible bolete, *Rubroboletus esculentus*, from southwestern China. Phytotaxa 303: 243–252.

Zhao K, Wu G, Feng B, Yang ZL. 2014. Molecular phylogeny of *Caloboletus* (Boletaceae) and a new species in East Asia. Mycological Progress 13: 1127–1136.

Zhao K, Wu G, Yang Z. 2014. A new genus, *Rubroboletus*, to accommodate Boletus sinicus and its allies. Phytotaxa 188: 61–77.

Zheng YT, Chen LL, Zhao K. 2023. Complete mitochondrial genome sequence of *Lanmaoa macrocarpa* (Boletales, Basidiomycota). Mitochondrial DNA Part B. 8:1067–1070.

Zheng CJ, Sohn MJ, Kim WG. 2006. Atromentin and leucomelone, the first inhibitors specific to enoyl-ACP reductase (FabK) of *Streptococcus pneumoniae*. The Journal of antibiotics 59: 808–812.

Zhou F, Gao Y, Song HY, Hu HJ, Li SX, Liu JH, Hu DM. 2022. *Retiboletus Huanggangensis*, A New Species of *Retiboletus* From China. Preprint.

Zhou X, Zhu H, Liu L, Lin J, Tang K. 2010. A review: recent advances and future prospects of taxol–producing endophytic fungi. Applied microbiology and biotechnology 86: 1707–1717.

Zhu XT, Li YC, Wu G, Feng B, Zhao K, Gelardi M, Kost GW, Yang ZL. 2014. The genus *Imleria* (Boletaceae) in East Asia. Phytotaxa 191: 81–98.

Zmitrovich IV, Spirin WA. 2002. A contribution to the taxonomy of corticioid fungi. II. The genera *Serpula*, *Serpulomyces* gen. nov., *Amylocorticiellum* gen. nov. Mikologiya i Fitopatologiya 36: 11–26.

APPENDICES

Appendix 1. List of figures

Appendix 2. List of tables