

# TAXONOMY AND PHYLOGENY OF GOMPHACEAE AND OTHER CLAVARIOID FUNGI

XINYU ZHU

DOCTER OF PHILOSOPHY
IN
BIOLOGICAL SCIENCE

SCHOOL OF SCIENCE

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XINYU ZHU

# THIS DISSERTATION IS A PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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#### **ABSTRACT**

The clavarioid fungi are very important both economically and ecologically, characterized by coralloid, simple, or branched basidiome. They include 30 genera with about 800 species, distributed in worldwide. In this study, taxonomic and phylogenetic studies were done based on 790 collections of clavarioid fungi, including 666 from China, 88 from Thailand, and 36 collections from other areas. The family containing the largest number of clavarioid fungi is the Gomphaceae.

In the Gomphaceae family, the most representative genus is *Phaeoclavulina*. However, *Phaeoclavulina* species are poorly understood due to insufficient morphological descriptions and a lack of DNA sequence data. In addition, the misidentification of Phaeoclavulina specimens has added to the confusion regarding the taxonomy of Phaeoclavulina species. In this study, taxonomic and phylogenetic studies were done based on 79 collections of *Phaeoclavulina*, including 50 from China, 6 from Thailand, and 23 collections from other areas. The diversity of *Phaeoclavulina* in China and Thailand was evaluated by employing both morphological and phylogenetic analyses. A multi-locus phylogenetic analysis was performed using the internal transcribed spacer (ITS) region, the mitochondrial rDNA small subunit (mtSSU), partial nuclear ribosomal large subunit (nrLSU), translation elongation factor 1-alpha (tef1) and mitochondrial ATPase subunit 6 (ATP6). A total of 461 sequences were used in the phylogenetic analyses, of which 224 were newly generated in this study, including 70 sequences of ITS, 70 sequences of nrLSU, 14 sequences of mtSSU, 26 sequences of ATP6, 44 sequence of tef1. Fifteen species of Phaeoclavulina were treated in this study, including 6 new species and 9 known taxa. The 6 new Phaeoclavulina species found in China are Phaeoclavulina subabietina, P. qilianensis,

*P. sterigmata, P. jilongensis, P. subcarovinacea and P. subminutispora.* Molecular phylogenies, a summary of species diversity, descriptions and illustrate are provided.

Two new Gomphoid fungi species (*Turbinellus sp1* and *Gloeocantharellus sp1*) and three known species (*Gomphus orientalis*, *Gomphus clavatus* and *Turbinellus szechwanensis*) based on morphology and phylogenetic analysis. 336 sequences derived from three loci (ITS, nrLSU, tef1) were used to reconstruct phylogenetic trees of Gomphoid fungi, including 121 for ITS, 131 for nrLSU and 84 for tef1 representing 41 species from Gomphoid fungi. Newly generated 94 sequences, including 31 for ITS, 36 for nrLSU and 27 for tef1 representing 5 species from Gomphoid fungi. The combined three-gene dataset (ITS+nrLSU+ tef1) included sequences from 146 specimens representing 41 species from Gomphoid fungi.

Nineteen new *Ramaria* species and seven known species based on morphology and phylogenetic analysis. 376 sequences derived from three loci (ITS, nrLSU, mtSSU) were used to reconstruct phylogenetic trees of *Ramaria*, including 273 for ITS, 75 for nrLSU and 28 for mtSSU representing 134 species from *Ramaria*. Newly generated 177 sequences, including 75 for ITS, 75 for nrLSU and 28 for mtSSU representing 26 species from *Ramaria*. The ITS included sequences from 282 specimens representing 134 species from *Ramaria*.

Three new *Clavulinopsis* species, *C. sp1, sp2* and *C. sp3* collected from China and Thailand are described and illustrated, based on morphological characteristics and molecular analyses. A total of 352 sequences were used in the phylogenetic analyses, of which 43 were newly generated in this study, including 23 sequences of ITS, 10 sequences of nrLSU, 10 sequences of ATP6. Twelve species of *Clavulinopsis* were treated in this study, including 2 new species and 10 known taxa. The 2 new *Clavulinopsis* species found in China and Thailand are *C. sp1* nom. prov., *C. sp2* nom. prov. Molecular phylogenies, a summary of species diversity, descriptions and illustrate are provided.

Two new *Clavariadelphus* species and five known species based on morphology and phylogenetic analysis. 100 sequences derived from two loci (ITS, nrLSU) were used to reconstruct phylogenetic trees of *Clavariadelphus*, including 73 for ITS and 27 for nrLSU representing 26 species from *Clavariadelphus*. Newly generated 54 sequences, including 27 for ITS and 27 for nrLSU representing 7 species from *Clavariadelphus*. The ITS dataset included sequences from 73 specimens representing 26 species from *Clavariadelphus*.

Three known *Lentaria* species based on morphology and phylogenetic analysis. 64 sequences derived from ITS were used to reconstruct phylogenetic trees of *Lentaria*, including 64 for ITS representing 21 species from Lentaria. Newly generated 5 sequences, including 5 for ITS representing 3 species from *Lentaria*. The ITS dataset included sequences from 64 specimens representing 21 species from *Lentaria* 

Keywords: Fungi, New Fungi Species, Phylogeny, Taxonomy



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# ABBREVIATION AND SYMBOL

av. average

comb. combination

diam. diameter

e.g. for example

et al. and others

hr. hour

gen. genus/genera

i.e. that is

mg milligram

min minute

mm millimetre

nm nanometre

nom. prov. nomen provisorium (Latin for provisional name)

nov. novum (Latin for new)

s second

sp. species

spp. species (plural)

μm micrometer

μl microliter

% percent

#### **CHAPTER 1**

#### INTRODUCTION

# 1.1 The History of Clavarioid Fungi

The clavarioid fungi are a macro-morphologically distinct group of taxa, characterized by coralloid, simple, or branched basidiomata (Corner, 1970). They include 30 genera with about 800 species, distributed in Agaricales, Cantharellales, Gomphales, Hymenochaetales, and Russulales (Corner, 1970; Kirk et al., 2008; Petersen, 1981). Some genera, such as *Ramaria* and *Phaeoclavulina*, are edible and have ecological and economic value (De Toledo & Petersen, 1989; Henkel et al., 2005, 2011). Most clavarioid fungi are saprobic, but some can be ectomycorrhizal, lichen-forming, or parasitic on plants (Corner, 1950, 1970; Nelsen et al., 2007). Clavarioid fungi are distributed worldwide, mostly in forests (Corner, 1950, 1970; De Toledo & Petersen, 1989; Henkel et al., 2012).

The family containing the largest number of clavarioid fungi is the Gomphaceae, which was introduced by Donk (1961), with *Gomphus* Pers. as the type genus (Donk, 1961). There are four genera (*Araeocoryne* Corner, *Phaeoclavulina* Brinkmann and *Ramaria* Fr. ex Bonord., *Ramaricium* J. Erikss.) and approximately 297 species of clavarioid fungi in the Gomphaceae. Additionally, Gomphaceae encompasses nine non-clavarioid genera (*Delentaria* Corner, *Destuntzia* Fogel & Trappe, *Gautieria* Vittad., *Gloeocantharellus* Singer, *Gomphus*, *Protogautieria* A.H. Sm., *Pseudogomphus* R. Heim, *Terenodon* Maas Geest., *Turbinellus* Earle) and approximately 77 species (Corner, 1950; He, 2019).

Ramaria, the genus with the largest number of species within the Gomphaceae approximately 230, was originally described by Holmsk in 1781. The type species of this genus is *R. botrytis* (Pers.). Historically, *Ramaria* was classified under *Clavaria* (Fries, 1829); however, recent studies recognize *Ramaria* and *Clavaria* as distinct genera (Corner, 1970). Some taxonomists have even elevated *Ramaria* to its own family, Ramariaceae (Corner, 1950). According to Index Fungorum, out of 635 taxon names listed for *Ramaria*, about 230 are considered legitimate (Kirk et al., 2008).

Morphologically, *Ramaria* is known for its branching basidiomes (Holmskjöld, 1790), spores color (Donk, 1933), and the unique reaction of basidiome layers turning orchid green when exposed to iron sulphate (Doty, 1948). Spore wall ornamentation is another distinctive feature (Marr, 1968). There are four subgenera in *Ramaria*: subgenus *Ramaria*, *Laeticolora*, *Echinoramaria*, and *Lentoramaria* (Marr, 1968).

Distributed across every continent except Antarctica, *Ramaria* is predominantly found in tropical and subtropical regions. It typically grows on forest ground or decaying wood in various types of forests, including coniferous, broad-leaved, and mixed, but is seldom found in sparsely wooded areas. Ecologically, some species of *Ramaria* are saprobic, thriving on humus or decomposing wood, while others establish mycorrhizal symbioses with trees (Corner, 1950).

Taxonomic classification within the genus *Ramaria* remains challenging due to its large number of species and specific growth form, which provide fewer characters for species delimitation compared to other fungi. This has historically made taxonomic identification difficult. Molecular studies have shown that *Ramaria* is a paraphyletic genus, complicating its classification further (Exeter et al., 2006; Giachini et al., 2010; González et al., 2023; Humpert et al., 2001; Marr, 1968). Phylogenetic relationships within *Ramaria* and related taxa have been explored using mitochondrial small subunit ribosomal DNA (mit-12S-rDNA) and nuclear large subunit ribosomal DNA (nuc-25S-rDNA) sequence data (Humpert et al., 2001). Additionally, studies examining the relationships between *Ramaria* and other taxa within the Gomphaceae have employed a combination of nuc-25S-rDNA, mit-12S-rDNA, and mitochondrial atp6 DNA (mit-atp6-DNA) markers (Giachini et al., 2010). The integration of multiple gene analyses represents a crucial direction for future research in molecular systematics, aiming to resolve these complex taxonomic issues.

Phaeoclavulina, first described by Brinkmann in 1897 as having coral-like branched structures with ochraceous spores, was initially placed within the Clavariaceae family, which also includes genera Clavaria, Clavariella, Clavulina, and Typhula (Brinkmann, 1897). Overeem in 1923 recognized Phaeoclavulina as a valid genus, notably reclassifying Phaeoclavulina zippelii (Lév.), formerly a Clavaria species, under this genus (Overeem, 1923). However, acceptance of this genus among mycologists was initially limited, as noted by Petersen in 1981, who mentioned that its

species were often grouped with other ramarioid fungi in the genus *Ramaria* due to similar spore characteristics (Petersen, 1981). In 1970, Corner reclassified the ramarioid species of *Phaeoclavulina* into *Ramaria* subgenus Echinoramaria, a classification later supported by Marr & Stuntz in 1973 and Petersen in 1981.

Subsequent research by Giachini in 2004, Giachini et al. in 2010, and Giachini & Castellano in 2011, re-established *Phaeoclavulina* as a valid genus based on morphological, molecular, and phylogenetic evidence. They expanded the genus to include some gomphoid species characterized by spiny, verrucose, subreticulate, or reticulate spores, which inhabit terrestrial and lignicolous substrates (Giachini, 2004; Giachini et al., 2010; Giachini & Castellano, 2011).

Phaeoclavulina is defined as a monophyletic group with diverse characteristics including ramarioid, unipileate, or merismatoid basidiomata. Its basidiomes vary in color. The structures can be glabrous or subtomentose, adopting shapes. The hymenium ranges in color from yellow to violet (Giachini & Castellano, 2011).

Currently, *Phaeoclavulina* includes 57 species listed in Index Fungorum (www.indexfungorum.org) and is predominantly found in tropical and subtropical ecosystems, reflecting its cosmopolitan distribution (Giachini & Castellano, 2011). Recent years have seen the description of several additional ramarioid species and new combinations within the genus (González-Ávila et al., 2020; Wannathes et al., 2018).

In 1797, Persoon initially proposed the genus *Gomphus*, distinguishing it from the genera *Clavaria*, *Geoglossum*, *Mitrula*, and *Spathularia*. He described the genus as having a thickened, truncate, smooth, laterally plicate-venose structure with a weakly developed pileus. Initially, no species were assigned to this genus upon its description. The genus *Gomphus* was first associated with a specific species in 1821 when Gray described *G. clavatus* (Pers.) Gray, originating from Merulius *clavatus* Pers. This species, known for its merismatoid basidiomata and distinctive orangish-brown to violet pilei, violet hymenia, and verrucose, non-anastomosed ornamented spores, marked the beginning of complex nomenclatural shifts.

The taxonomic history of *Gomphus* has been convoluted, with species historically reclassified into several different genera including *Cantharellus* (Fries, 1821), *Craterellus* (Fries, 1838), and *Nevrophyllum* (Doassans & Patouillard, 1886). The lack of distinct morphological features and molecular data has further contributed

to this confusion. Despite these challenges, critical insights from taxonomists have significantly advanced the understanding of this group's evolution and systematics.

Giachini (2012), which included over 320 collections from *Gomphus* sensu lato and related genera, has been pivotal. He emphasized that *Gomphus* sensu stricto, distinct for its violet, lavender-brown, or milky-coffee colored hymenia, as opposed to the orange, brown, or green-olive hues typical of *Gloeocantharellus*, *Phaeoclavulina*, and *Turbinellus*, remains a unique genus within the Gomphaceae. The genus, characterized by its verrucose spores and clamp connections, currently includes three described species: *G. brunneus*, with somewhat funnel-shaped pilei, and *G. clavatus* and *G. crassipes*, both featuring fan- to funnel-shaped pilei.

Gomphus clavatus, widely distributed in the northern hemisphere, is noted for its potential to form ectomycorrhizae with species of Abies (Pantidou, 1980) and Picea (Agerer et al., 1998). Recognized for its size and color, G. clavatus has been deemed rare and possibly limited to the old-growth forests of the Pacific Northwest, necessitating surveys on all federal and state lands prior to management activities, as mandated by the Northwest Forest Plan. Gomphus brunneus and G. crassipes, however, are known from only a few collections in Africa, with G. brunneus reported in Cameroon, the Democratic Republic of Congo, and Uganda, and G. crassipes in Algeria, Morocco, and Spain.

In 1909, Earle established the genus *Turbinellus* to include *Cantharellus floccosus*, initially described by Schweinitz in 1831. Earle identified three North American species within this genus, though he only named *T. floccosus*, noting their closer resemblance to the club-shaped species of *Craterellus* than to those of *Cantharellus*. Over the years, species within *Turbinellus* underwent multiple reclassifications, moving to *Gomphus* (Singer, 1945), then to *Cantharellus* (Smith & Morse, 1947), *Nevrophyllum* (Heim, 1954), and eventually reverting to *Gomphus* (Corner, 1966). *Turbinellus* species are known for producing terrestrial, single to caespitose basidiomata that are typically large. Their pilei range from cinnamon to red and are shaped like funnels or fans, with hymenia that are yellow to pale orange and sometimes bruise vinaceous. These species feature a robust, tall stipe, strongly decurrent and deeply wrinkled hymenial folds, generally oriented longitudinally. The hyphae in these species lack clamp connections, and the spores exhibit verrucose ornamentation.

Turbinellus is recognized as one of the most common and widespread 'cantharelloid-gomphoid' genera across North America and possibly the world. In-depth studies of this genus, particularly those species found in the western U.S., were conducted by Smith and Morse (1947), Corner (1950), and Petersen (1971a). They identified a variety of forms under *T. floccosus* and *C. bonarii*, which were later consolidated under the *Gomphus* sensu lato by Corner (1966) and Petersen (1971a) following the acceptance of species delineations proposed by Smith and Morse.

During the 1900s, numerous taxonomists including Maire, Singer, Corner, Heim, Heinemann, and Donk speculated on the evolutionary relationships within the Gomphaceae, classified at the time in the Aphyllophorales. Despite their efforts, the precise limits between species remained unclear, as described by Corner in his extensive works and by Petersen. The reliance on morphological characteristics alone frequently led to the problematic classification of forms and subspecies, often based solely on a few plastic features, as demonstrated by the variety *Gomphus floccosus* f. *olivaceous*, distinguished only by its 'ecru olive' pileus.

Giachini, in his recent work, applied both morphological and molecular data from three genomic loci to reassign several species from *Gomphus* sensu lato back to *Turbinellus*, synonymizing *G. floccosus*, *G. bonarii*, and all related forms and varieties under *T. floccosus*. This restructuring was crucial for defining species boundaries within *Turbinellus*, facilitating ongoing ecological and taxonomic studies. Currently, five species are recognized in *Turbinellus*: *T. flabellatus*, *T. floccosus*, *T. fujisanensis*, *T. kauffmanii*, and *T. stereoides*, encompassing what was previously twenty-one distinct species and varieties.

The genera *Gloeocantharellus* and *Gomphus* sensu lato have historically been differentiated by the presence or absence of gleocystidia, with *Gomphus* sensu lato often exhibiting larger basidiomata and fan-shaped to funnel-shaped pilei characterized by longitudinally wrinkled hymenia. In contrast, *Gloeocantharellus*, synonymous with *Linderomyces*, is noted for its 'paxilloid' structure but is distinguished from the Paxillaceae by having gleoplerous cystidia and ornamented spores. While not all *Gloeocantharellus* species possess gleocystidia, they all feature a significant presence of gleoplerous hyphae, more so than those found in *Gomphus* sensu lato. Moreover, *Gloeocantharellus* differs from *Gomphus* sensu lato in its more agaricoid habit and in displaying species with lamellate hymenia.

The reclassification of *Cantharellus purpurascens* to *Gloeocantharellus* by Singer in 1945 was based on the presence of gleocystidia. This distinction was underscored by the presence of coscinocystidia in *Linderomyces*, which are cystidia that project as pseudocystidia. In a discussion with Petersen, Singer acknowledged that *Gloeocantharellus lateritius*, *G. purpurascens*, and *Linderomyces corneri* (synonymized as *Gloeocantharellus corneri*) all possessed coscinocystidia. However, *L. corneri* was initially thought to be differentiated by a bilateral hymenophoral trama—a feature that was not described in the original description of *Linderomyces*. Petersen, after examining the holotype of *L. lateritius* (which served as the type for *Linderomyces*), proposed reclassifying these species under *Gloeocantharellus*, despite not observing the bilateral hymenophoral trama noted by Singer.

Gloeocantharellus species are widely distributed across South America, the South Pacific, and Southeast Asia, with occurrences in diverse environments from Bolivia and Brazil to Malaysia and Sri Lanka, and extending to Japan, New Zealand, Russia, and the USA. These species are terrestrial and generally found in areas where ectomycorrhizal tree species prevail. Notably, Gloeocantharellus pallidus in Japan associates ectotrophically with fagaceous trees, while in Hawaii, it is found exclusively with Psidium of the Myrtaceae. Other species like G. dingleyae and G. novae-zelandiae are present in New Zealand's podocarp-broadleaf forests, and G. papuanus fruits near ectomycorrhizal trees in the Castanopsis-Lithocarpus forests of Papua New Guinea. Despite their association with ectomycorrhizal trees, direct evidence confirming the mycorrhizal status of Gloeocantharellus species remains elusive.

Giachini has demonstrated through molecular phylogeny that *Gloeocantharellus* is monophyletic, consisting of ten species, and occupies a basal position in the phylogenetic tree of the Gomphales. This ancestral placement underscores the importance of understanding the unique characteristics of *Gloeocantharellus* to better comprehend the evolutionary pathways of other members within the order.

Clavulinopsis, first described by Overeem in 1923 with Clavulinopsis sulcata Overeem as its type species, belongs to the family Clavariaceae under the order Agaricales within the class Agaricomycetes of the Basidiomycota phylum (He, 2019). This genus currently comprises about 40 species (He, 2019; Yan et al., 2023). Clavulinopsis has 171 taxon names listed in Index Fungorum, with approximately 81 considered legitimate. The species are characterized by their clavarioid, simple or branched basidiomata, which are

typically colored white, yellow, orange, or red. The basidiospores are usually smooth, hyaline or slightly yellow, globose or ellipsoid, and can be echinulate in some species. Both tramal hyphae and basidia possess clamp connections (Corner, 1950, 1970; Petersen, 1978).

Species of *Clavulinopsis* are distributed worldwide, displaying solitary, gregarious, or caespitose growth forms. They are predominantly terrestrial, though some species are lignicolous (Birkebak et al., 2016; He, 2019; Hyde et al., 2016). Historically, species identification within *Clavulinopsis* was primarily based on morphological characteristics. However, recent molecular phylogenetic studies have led to the proposal of ten new species: *C. aurantiaca* Araujo-Neta, G.A. Silva & Gibertoni, *C. dimorphica* A.N.M. Furtado & M.A. Neves, *C. imperata* A.N.M. Furtado & M.A. Neves, *C. trigonospora* Franchi & M. Marchetti, *C. aspersa* P. Zhang & Jun Yan, *C. bicolor* P. Zhang & Jun Yan, *C. bispora* P. Zhang & Jun Yan, *C. incarnata* P. Zhang & Jun Yan, and *C. tropicalis* P. Zhang & Jun Yan, primarily through analysis of the internal transcribed spacer region (ITS, including the 5.8S gene) and nuclear large subunit ribosomal DNA (nuc-LSU-rDNA). Notably, these studies did not include protein-coding genes, which could provide additional insights into the phylogeny and taxonomy of the genus.

Recent advancements in the molecular phylogenetics of clavarioid fungi reveal that most studies have relied predominantly on only two genetic markers: the internal transcribed spacer region (ITS) and the nuclear large subunit ribosomal DNA (nuc-LSUrDNA). It has become increasingly evident that while ITS is commonly employed for species identification, this approach often lacks the support of crucial protein-coding genes, which are essential for a more robust phylogenetic framework. Meanwhile many important species lack good illustrations and detailed descriptions. Molecular phylogeny of clavarioid fungi in Europe has been extensively studied using various genetic markers. Initial studies by Kautmanová utilized the internal transcribed spacer region (ITS, including the 5.8S gene) and nuclear large subunit ribosomal DNA (nuc-LSU-rDNA) (Kautmanová et al., 2012). Subsequent research expanded the genetic markers used to include nuclear small subunit ribosomal DNA (nuc-SSU-rDNA), as detailed by Birkebak and Halama (Birkebak et al., 2016; Halama et al., 2017). More advanced studies by Stadler and Vidović incorporated additional loci such as parts of the translation elongation factor 1α (EF-1α) and DNA-directed RNA polymerase II subunit 2 (RPB2) genes, enhancing the resolution and accuracy of phylogenetic assessments, but only the protein genes of Clavaria hypoxylon, which is not enough for the clavarioid fungi. (Stadler et al., 2014; Vidović et al., 2014).

Clavariadelphus Donk, a genus within the Clavariadelphaceae family of the Gomphales order in the Basidiomycota phylum, is defined by its erect, simple, club-shaped basidiomes that feature rhizomorphs at the stipe base. Characteristic features include a hymenium composed of (2–) 4-spored basidia, clavate leptocystidia, and ellipsoid to amygdaliform, thin-walled, inamyloid basidiospores, along with clamp connections at the septa of the hyphae. Originally described by Methven in 1990, the genus is prevalent across temperate regions of the Northern Hemisphere.

Taxonomic research on *Clavariadelphus* has been extensive in Europe and North America, highlighted by significant contributions from researchers such as Corner (1950, 1970), Welden (1966), Smith and Corner (1967), Petersen (1967, 1972), Smith (1971), Petersen et al. (1974), Methven (1989), and Methven and Guzmán (1989). In contrast, the genus has been less studied in Asia, although recent work has led to the description of novel species in Pakistan (Hanif et al., 2014; Sher et al., 2018) and China (Lu & Li, 2020).

To date, seven *Clavariadelphus* species have been documented in China: *C. griseoclavus* L. Fan & L. Xia, *C. ligula* (Schaeff.) Donk, *C. pallido-incarnatus* Methven, *C. pistillaris*, *C. sachalinensis* (S. Imai) Corner, *C. truncatus* Donk, and *C. yunnanensis* Methven. These findings stem from a variety of studies, many of which primarily focused on morphological characteristics for species identification (Methven, 1989, 1990; Mao et al., 1993; Yuan & Sun, 1995; Zang, 1996; Bau et al., 2003; Mao, 2009; Tang & Yang, 2014; Tang, 2015; Lu & Li, 2020). Despite its distinct characteristics, *Clavariadelphus* species can be challenging to differentiate due to subtle morphological variations and growth patterns.

Recent advancements in molecular techniques have proven invaluable for species delimitation in systematic fungal studies, as seen in other macrofungal groups (Hibbett, 2007; Yang, 2011). These techniques, alongside chemical reactions and scanning electron microscopy (SEM) have been employed to distinguish species within groups like *Agaricus*, *Boletopsis*, *Chroogomphus*, *Cortinarius*, *Hygrophorus*, *Leucoagaricus*, and *Leratiomyces*. However, SEM analysis of *Clavariadelphus* structures has not yet been reported.

The genus *Lentaria*, established by Corner in 1950, serves as the type of genus of the Lentariaceae family. As of 2024, it includes 19 recognized species (Kirk et al., 2008).

Lentaria species are predominantly lignicolous and play vital roles in forest ecosystems due to their wood-decaying capabilities. In China, the presence of Lentaria species has been recorded with L. byssiseda Corner and L. surculus (Berk.) Corner identified in earlier studies (Teng, 1963; Tai, 1979). Despite these records, comprehensive taxonomic research focusing specifically on Lentaria within China had not been conducted until recently.

# 1.2 Research Objective

- 1.2.1 To study the diversity and taxonomy of clavarioid Basidiomycota from China and Thailand including new taxa.
- 1.2.2 To revise the taxonomic system of Gomphaceae based on multi-gene phylogenetic analyses.

## 1.3 The Importance of Research

- 1.3.1 In China and Thailand, systematic research on Gomphaceae and other clavarioid fungi like *Clavulinopsis*, *Clavariadelphus* and *Lentaria* is notably lacking. Most existing studies on *Clavulinopsis*, *Clavariadelphus* and *Lentaria* are limited to nuclear large subunit ribosomal DNA (nuc-LSU-rDNA) and nuclear ITS ribosomal DNA (nuc-ITS-rDNA), with a significant gap in the analysis involving protein-coding genes. This lack of comprehensive genetic profiling impedes a deeper understanding of their biodiversity and evolutionary relationships.
- 1.3.2 Species within the *Ramaria* spp. and *Phaeoclavulina* spp. are recognized as edible, contributing to their economic importance. Research into these species helps in understanding their nutritional and medicinal values.
- 1.3.3 A substantial number of clavarioid species have been unidentified from China and Thailand, highlighting the rich fungal biodiversity in these regions. Enhanced research efforts are crucial for documenting these species, which are vital for ecological studies and conservation efforts.

## 1.4 Research Hypothesis

- 1.4.1 Gomphaceae and other clavarioid Basidiomycota species diversity is high in China and Thailand.
- 1.4.2 Gomphaceae and other clavarioid Basidiomycota species from tropical or subtropical Asia are different from the European clavarioid species.

## 1.5 Scope of Research

- 1.5.1 Research specimens of Gomphaceae and other clavarioid Basidiomycota collected in China and Thailand.
- 1.5.2 Research herbarium specimens of *Ramaria*, *Phaeoclavulina* and *Clavulinopsis* from Europe.
- 1.5.3 Research morphology and molecular systematics of Gomphaceae and other clavarioid Basidiomycota.

#### 1.6 Research Limitations

- 1.6.1 The holotypes of some species of Gomphaceae and other clavarioid Basidiomycota have been lost, and therefore cannot be compared with our specimens.
- 1.6.2 The collection sites are only in China and Thailand, which is expected to give an incomplete picture of the diversity of Gomphaceae and other clavarioid Basidiomycota in Asia.

# 1.7 Terminology Definition

Phenotypic: This term refers to the observable characteristics or traits of fungi, including physical features, growth patterns, reproduction methods, and other visible attributes of fungal organisms.

Monophyletic: A monophyletic group, also known as a clade, includes a common ancestor and all its descendants.

Polymorphism: This term refers to genetic variations or differences observable among sequences, individuals, populations, etc., of living organisms. Polymorphisms can occur at various levels, including the genome, gene, or phenotypic traits.

Sporophores: Formerly called "fruiting bodies," sporocarps, or carpophores, sporophores are reproductive structures produced by certain types of fungi. These structures are responsible for the production and dispersal of spores, facilitating fungal reproduction and spread.

Mutualistic: This term describes a type of symbiotic relationship in which fungi form mutually beneficial associations with other organisms. In mutualistic interactions, both the fungi and their partner organisms derive benefits. Several types of fungal mutualistic relationships exist.

Ectomycorrhizal: This term refers to a type of mycorrhizal symbiosis between certain fungi and the roots of plants, predominantly trees. Ectomycorrhizal fungi form mutualistic associations with plant roots, from which both the fungus and the plant benefit.

#### **CHAPTER 2**

#### LITERATURE REVIEW

# 2.1 The History of Clavarioid Fungi

Clavarioid fungi comprise a macro-morphologically distinct group of 29 genera with around 800 species distributed across various orders including Agaricales, Cantharellales, Dacrymycetes, Gomphales, Hymenochaetales, Russulales, Trechisporales (Corner, 1950, 1970; Kirk et al., 2008; Petersen, 1981). This group is characterized by coralloid, simple, or branched basidiomata, and is well represented by genera Clavaria and Ramaria (Corner, 1950). Notably, some genera like Ramaria and Phaeoclavulina are not only edible but also hold economic significance, for example, species such as Phaeoclavulina flaccida, Ramaria aurea, R. flava, R. formosa, R. fumigata, R. pallida, and R. rufescens contain various toxins, which are of significant economic value for drug development (De Toledo & Petersen, 1989; Henkel et al., 2005, 2011). While most clavarioid fungi are saprobic, some species engage in ectomycorrhizal, lichen-forming, or parasitic interactions with plants (Corner, 1950, 1970; Nelsen et al., 2007). Clavarioid fungi are distributed worldwide, mostly in forests (Corner, 1950, 1970; De Toledo & Petersen, 1989; Henkel et al., 2012).

Clavarioid genera include *Actiniceps* Berk. & Broome 1876, type species *A. thwaitesii* Berk. & Broome; *Amylaria* Corner 1955, type species *A. himalayensis* Corner; *Aphelaria* Corner 1950, type species *A. dendroides* (Jungh.) Corner; *Araeocoryne* Corner 1950, type species *A. elegans* Corner; Artomyces Julich 1982, type species *A. pyxidatus* (Pers.) Julich; *Artomyces* Julich 1982, type species *A. pyxidatus* (Pers.) Julich; *Calocera* (Fr.) Fr. 1828, type species *C. viscosa* (Pers.) Fr.; *Caripia* Kuntze 1898, type species *C. montagnei* (Berk.) Kuntze; *Ceratellopsis* Konrad & Maubl. 1937, type species *C. queletii* (Pat.) Konrad & Maubl.; *Chaetotyphula* Corner 1950, type species *C. hyalina* (Jungh.) Corner; *Clavaria* Vaill. ex L. 1753, type species *C. fragilis* Holmsk.; *Clavariachaete* Corner 1950, type species *C. rubiginosa* (Berk. & M.A. Curtis ex Cooke) Corner; *Clavariadelphus* Donk 1933, type species *C. pistillaris* (L.) Donk; *Clavicorona* Doty 1947,

type species *C. taxophila* (Thom) Doty; *Clavulina* J. Schrot. 1888, type species *C. cristata* (Holmsk.) J. Schrot.; *Clavulinopsis* Overeem 1923, type species *C. sulcata* Overeem; *Deflexula* Corner 1950, type species *D. fascicularis* (Bres. & Pat.) Corner; *Lachnocladium* Lev. 1846, type species *L. brasiliense* (Lev.) Pat.; *Lentaria* Corner 1950, type species *L. surculus* (Berk.) Corner; *Mucronella* Fr. 1874, type species *M. calva* (Alb. & Schwein.) Fr.; *Multiclavula* R.H. Petersen 1967, type species *M. corynoides* (Peck) R.H. Petersen; *Phaeoclavulina* Brinkmann 1897, type species *P. macrospora* Brinkmann; *Physalacria* Peck 1882, type species *P. inflata* (Schwein.) Peck; *Pterula* Fr. 1825, type species *P. plumosa* (Schwein.) Fr.; *Pterulicium* Corner 1950, type species *P. xylogenum* (Berk. & Broome) Corner; *Ramaria* Fr. ex Bonord. 1851, type species *R. botrytis* (Pers.) Ricken; *Ramaricium* J. Erikss. 1954, type species *R. occultum* J. Erikss.; *Ramariopsis* (Donk) Corner 1950, type species *R. kunzei* (Fr.) Corner; *Scytinopogon* Singer 1945, type species *S. pallescens* (Bres.) Singer; *Typhula* (Pers.) Fr. 1818, type species *T. phaccorrhiza* (Reichard) Fr. (Corner, 1950; He, 2019).

# 2.2 The Literature Review of Gomphaceae

The family containing the largest number of clavarioid fungi is the Gomphaceae, which was introduced by Donk (1961), with *Gomphus* Pers. as the type genus (Donk, 1961). The Gomphaceae have 13 genera in the present taxonomic system. Four of those (*Araeocoryne*, *Phaeoclavulina*, *Ramaria*, *Ramaricium*) contain clavarioid fungi, for a total of approximately 297 species. The other nine, non-clavarioid genera (*Delentaria*, *Destuntzia*, *Gautieria*, *Gloeocantharellus*, *Gomphus*, *Protogautieria*, *Pseudogomphus*, *Terenodon* Maas, *Turbinellus*) comprise approximately 77 species (Corner, 1950; He, 2019). During the initial micromorphological studies, species with a spore wall absorbing Cotton Blue (cyanophilus spores) were placed in *Ramaria*, *Kavinia* and *Ramaricium*. Later Donk (Donk, 1961) redefined the clavarioid genus under the name *Ramaria* (Fr.) Bonord, and because *Ramaria*, *Kavinia* and *Ramaricium*, all in the Ramariae, had the same spore characteristics, Donk promoted Ramariae to the family Gomphaceae (Donk, 1961).

#### 2.3 The Literature Review of Ramaria

The genus *Ramaria*, significant in the taxonomic history of clavarioid fungi, has garnered substantial attention from mycologists over the centuries. Holmskjöld (1790) was the first to use the name *Ramaria* to describe clavarioid fungi with a branching habit, although it was initially categorized under *Clavaria* (Holmskjöld, 1790). It was not until Gray (1821) that *Ramaria* was distinctly recognized as a separate genus, a classification later formalized by the Eleventh International Botanical Congress as *Ramaria* Fries ex Bonorden. Despite its early reports in Europe by Fries (1829), the first systematic study of *Ramaria* in the United States was conducted by Coker (1923), who compared North American species with those previously identified in Europe.

A pivotal figure in the taxonomy of *Ramaria* was the British mycologist E.J.H. Corner. He authored "A Monograph of *Clavaria* and Allied Genera" (Corner, 1950), documenting nearly 100 species of *Ramaria*, and later revised his monograph (Corner, 1970). Meanwhile, research on *Ramaria* continued in North America. Doty (1944) published "*Ramaria* in Oregon," and Marr and Stuntz (1973) reported on more than 50 species in Western Washington, including over 20 new species. Their study was notable for emphasizing the importance of macroscopic chemical reactions. Although the stability of chemical reactions was later deemed limited, their work was a significant and interesting attempt. R.H. Petersen also made substantial contributions to the study of *Ramaria*. He started with type specimens, redescribed some important species, clarified aspects of their taxonomic history, and traveled extensively, including to China, to collect fresh specimens. Petersen published of articles on the subject and monographs on two subgenera (De Toledo & Petersen, 1989; Petersen, 1981).

The framework for classical taxonomic studies of *Ramaria* in Europe and North America was largely established by the 1970s. In Europe, Schild continued to study *Ramaria*, identifying a number of new species (Schild, 1998). One of the main reasons for the relative scarcity of *Ramaria* research in Asia, Africa, and South America, compared to Europe and the United States, is the lack of local research expertise. However, these regions are rich in *Ramaria* species, presenting significant potential for future studies.

In India, Thind reported 19 species and nine varieties of *Ramaria* as early as 1959 (Thind, 1959). Subsequently, Thind collaborated with Corner on several occasions to further study *Ramaria* in India and the Himalayas. Khurana and Thind (1979) identified five species of *Ramaria* in India. In Japan, Yokoyama and Sagara conducted studies on *Ramaria*, which were documented in 1974 (Yokoyama & Tubaki, 1974).

The history of *Ramaria* research in China is relatively recent. Initially, it was mentioned several times in large fungal atlases and referenced in various studies. The most recent significant publication was in 2005, when Zhang et al. introduced two new species of *Ramaria*. This suggests that there are still many areas for improvement in the study of clavarioid fungi in China. (Zhang et al., 2005).

There are two primary issues with *Ramaria* research in China. First, no systematic and comprehensive studies have been conducted; most research has taken the form of resource surveys with very little specific research work being carried out. Second, the studies lack depth. Although 115 taxonomic units of *Ramaria* have been reported in China, most were named after similar species from Europe and North America, leading to widespread misidentification.

Morphologically, *Ramaria* is distinguished by its branching basidiomes (Holmskjöld, 1790), spores color, light yellow or brown yellow (Donk, 1933), and a unique reaction when basidiome context turn orchid green upon exposure to iron sulphate (Doty, 1948). Spore wall ornamentation is another notable feature (Marr, 1968).

Basidiomes shape and size: *Ramaria* exhibits a wide variety of branching morphologies. Both genetic and environmental factors influence the formation of the basidiomes, making its shape unstable but useful for identifying certain unusually shaped species. Adverse conditions such as low temperatures and drought can cause the basidiomes to produce a bloated meristem, resembling a deformed cotyledon (Corner, 1950).

Basidiomes colours: The basic colors of *Ramaria* substrates include yellow, white, red, pink, purple, orange, and brown, with possible variations in between. Describing the colors of the stipe, branches, and branch tips of a *Ramaria* is crucial. The discoloration reaction of the basidiome surface or flesh after injury is taxonomically significant. For instance, species like *Ramaria abietina* or *R. luteoaeruginea* exhibit a greenish reaction naturally or when injured at the stipe and lower branches. *R. sanguinipes* and *R. rubri-attenuipes* 

show a distinct burgundy or reddish brown discoloration at the basidiome base upon abrasion. The color of *Ramaria* basidiomes varies with developmental stage and environmental conditions, which can sometimes lead to pronounced changes. For example, the branches of *R. botrytoides* var. *micrispora* are bright red but quickly fade when exposed to sunlight (Corner, 1950).

Some years before, the development and widespread adoption of PCR technology and nucleic acid sequencing have significantly advanced molecular systematics. This field has rapidly emerged as a critical tool in the systematic and taxonomic study of various organisms, including fungi. Molecular systematics has resolved many challenges that traditional methods could not address. The genus *Ramaria*, notable for its numerous species and the unique shape of its basidiomes, presents fewer macroscopic features and exhibits more intraspecific variation than most other Basidiomycota, complicating taxonomic identification. However, the molecular phylogeny of *Ramaria* and its related taxa has considerably improved our understanding of their systematics and evolution. For instance, Humpert et al. (2001) conducted a preliminary phylogeny of *Ramaria* using ribosomal large subunit rDNA and mitochondrial DNA sequences. Dentinger and McLaughlin (2006) explored the phylogeny of the closely related genus *Clavaria* also using ribosomal large subunit rDNA as a marker gene. Additionally, research has explored the relationships between *Ramaria* and other taxa within the Gomphales (Giachini et al., 2010).

The classification of coralloid fungi saw further advancements through the efforts of several mycologists. Notably, Coker (1923) work significantly influenced understanding of *Ramaria*, and Corner (1950) monograph expanded the concept of clavarioid fungi. Corner work was particularly revolutionary as it included nearly 30 tropical ramarioid taxa, broadening the scope of recognized species within this fungal group (Corner, 1950).

Doty's publications in 1944 and 1948 on clavarioid fungi in Oregon created a key like Corner's work, which sparked a renewed global interest in clavarioid, coralloid, and ramarioid fungi, with a particular focus on *Ramaria*. In response to this growing interest, Corner (1970) proposed subdividing *Ramaria* into three subgenera: *Ramaria*, *Echinoramaria*, and *Lentoramaria*. This classification was later expanded by Marr and Stuntz in 1973 with the addition of the subgenus *Laeticolora* (Corner, 1970; Doty, 1944, 1948).

Significant contributions to the taxonomy of these fungi have also been made by several researchers focusing on various geographic regions. Marr, Olexia, Dodd, and McAfee have been prominent in North America, while Parmasto and Schild have contributed to European studies. Scandinavian fungal taxonomy has been advanced by researchers like Singh and Rattan, and Yokoyama and Sagara have made notable contributions in Japan. Additionally, Khurana has focused on Indian taxa, enhancing the understanding of *Ramaria* in diverse ecological zones (Corner, 1970; Doty, 1944, 1948; Marr & Stuntz, 1973).

In the late 20th century, Petersen made significant contributions to the taxonomy of *Ramaria*. He authored detailed monographs on the subgenera *Lentoramaria* in 1975 and *Echinoramaria*, which he identified as a synonym for *Phaeoclavulina*, in 1981. Additionally, his extensive publications covered *Ramaria* species globally, including a comprehensive study in 1988 on New Zealand's clavarioid fungi. Despite these considerable efforts, Petersen acknowledged in 1981 that the complexity of the group persisted, highlighting substantial gaps in detailed study and modern phylogenetic analysis of many taxa within the Gomphales (Petersen, 1981).

Recent taxonomic studies using molecular methods have demonstrated that *Ramaria* is non-monophyletic. Giachini's research, which analyzed morphology and molecular sequences from three genomic regions, showed that certain pileate species of *Gomphus* sensu lato are monophyletic with the coralloid species of *Ramaria* subgenus Echinoramaria. This discovery led to the resurrection of the genus *Phaeoclavulina* from its former synonymy under *Ramaria* subgenus *Echinoramaria* section *Dendrocladium*. Currently, *Phaeoclavulina* includes species with two main basidiomata shapes: pileate, formerly classified under *Gomphus* sensu lato, and ramarioid, previously part of *Ramaria* subgenus *Echinoramaria* (Giachini, 2004; Humpert et al., 2001).

#### 2.4 The Literature Review of *Phaeoclavulina*

*Phaeoclavulina*, first described by Brinkmann in 1897, is known for its corallike branched basidiomes, that some have pileate-stipitate basidiomes and ochraceous spores. Originally, it was classified within the Clavariaceae family, which also includes the genera *Clavaria*, *Clavariella*, *Clavulina*, and *Typhula* (Brinkmann, 1897).

The nomenclatural history of *Phaeoclavulina*, especially the pileate species, has been notably complex. Initially, *Nevrophyllum clavatum* and *N. viride* were grouped together by Patouillard due to their fan-shaped pilei. However, they were later differentiated based on spore morphology and distribution, which led to several reclassifications. These species were transferred to the genera *Chlorophyllum* and *Chloroneuron* by Murrill, before finally being placed under *Gomphus* (Giachini et al., 2010; Murrill, 1911).

The history of the ramarioid *Phaeoclavulina* species predates that of the pileate ones. Persoon first described *Clavaria abietina* (= *Phaeoclavulina abietina* (Pers.) Giachini) in 1794. Unfortunately, the name was later misapplied by Fries (Petersen, 1981).

Following Fries, significant taxonomic developments occurred when Junghuhn introduced *Clavaria ochraceo-virens* in 1830 as a substitute for *Clavaria abietina*. This was a precursor to further classifications, culminating in Brinkmann's 1897 establishment of the genus *Phaeoclavulina* within the Clavariaceae family. This genus initially grouped species that were previously scattered across various classifications (Brinkmann, 1897; Petersen, 1981).

Later taxonomists, including Cotton and Wakefield, contributed to the evolving taxonomy by creating newcombinations and reassigning *Phaeoclavulina* species to different genera such as *Clavaria*, *Ramaria*, and *Thelephora*, reflecting the ongoing debates and discoveries in fungal classification (Petersen, 1981).

In 2004, Giachini introduced *Phaeoclavulina* as a genus comprising 41 species characterized by monomitic hyphae, clamp connections, and echinulate to reticulate spores. Macroscopically, these species exhibit greenish violaceous, brown, or orangered basidiomata, with hymenia that vary from wrinkled to smooth. Several species have

been transferred from *Gomphus* and *Ramaria* subgenus *Echinoramaria*, noted for their funnel- to fan-shaped basidiomata. These species are distributed across tropical to temperate regions, with some displaying a pantropical distribution, including a refugium in the Appalachian Mountains. While many species are wood-inhabiting, suggesting a possible saprotrophic nature, their ecological roles are still uncertain, necessitating further research to clarify their ecological and evolutionary significance. (Giachini, 2004).

Further integrating morphological characteristics and DNA sequences, Giachini et al. (2011) revisited the taxonomy of the Gomphales to achieve a natural classification. This revision exposed the non-monophyly of *Gomphus* sensu lato, leading to the reclassification of its species into four distinct genera: *Gomphus* sensu stricto (3 species), *Gloeocantharellus* (11 species), *Phaeoclavulina* (41 species), and *Turbinellus* (5 species). The expansion of these genera now includes gomphoid species characterized by spiny, verrucose, subreticulate, or reticulate spores, inhabiting terrestrial and lignicolous substrates (Giachini, 2004; Giachini et al., 2010; Giachini & Castellano, 2011).

Phaeoclavulina is monophyletic and have diverse basidiomata forms, which include ramarioid, unipileate, and merismatoid types. The basidiomes of *Phaeoclavulina* vary in color, ranging from white and brown-green to pale or dark orange-yellow. These structures can adopt shapes such as infundibuliform or flabelliform and may be glabrous or subtomentose (Giachini & Castellano, 2011).

The hymenium of these fungi varies in color from yellow to violet and can present as smooth or irregularly wrinkled, adding to their distinctive appearance. On a microscopic level, *Phaeoclavulina* is distinguished by its clamped hyphae and basidia, which can bear one to four sterigmata. The spores are notable for their golden yellow to ferruginous color and exhibit cyanophilic ornamentation when stained with cotton blue (Giachini & Castellano, 2011).

Additionally, *Phaeoclavulina* may possess rhizomorphic strands. These strands are usually parallel, comprised of hyphae that tend to break easily when dry. Interspersed within these strands are polymorphic crystalloid elements, which further distinguish this genus (Giachini & Castellano, 2011).

## 2.5 The Literature Review of Gomphus

The genus *Gomphus*, part of the order Gomphales, represents a group of fungi distinguished by their complex taxonomic history and ecological significance. Characterized by their distinctive fruit body morphology and ecological roles as ectomycorrhizal fungi, species within this genus exhibit a broad array of evolutionary adaptations that have been the subject of significant scientific interest (Fan et al., 2023; Giachini & Castellano, 2011).

Research on *Gomphus* has revealed intriguing aspects of its evolutionary biology. Studies have shown that the fruit body size, spore size, and spore shape in Gomphoid fungi have remained relatively consistent through ancient periods, particularly during the Mesozoic era. It is posited that these fungi maintained their morphological traits to adapt to ecological niches and survive through various extinction events. The Cenozoic era, however, marked a period of significant morphological evolution, with these fungi developing larger and more spherical spores, an adaptation likely driven by intense climatic shifts and the resulting ecological pressures (Fan et al., 2023; Giachini & Castellano, 2011).

The reconstructed phylogenetic trees indicate that while early Gomphoid fungi exhibited smaller spores and fruit bodies, modern representatives show an increase in size, suggesting an evolutionary response to competitive and environmental pressures. These traits likely facilitated better spore dispersal and survival, enhancing reproductive success in diverse and changing environments (Fan et al., 2023; Giachini & Castellano, 2011).

Gomphus sensu stricto, as redefined through modern taxonomic efforts, includes specific species such as G. clavatus, G. brunneus, and G. crassipes. Each species is differentiated by unique morphological characteristics that are vital for accurate identification: Gomphus clavatus is widespread across the northern hemisphere and forms ectomycorrhizal associations with tree species like pines and firs. It is recognized by its fan-shaped, often violet-tinged fruit bodies and wrinkled hymenium, which are adaptations to its symbiotic lifestyle, Gomphus brunneus and G. crassipes are more regionally confined, found in Africa and the Mediterranean

region, respectively. *G. brunneus* is noted for its funnel-shaped pileus and milky-coffee colored hymenium, while *G. crassipes* is characterized by its larger fruit bodies and finely verrucose spores, features that are critical for surviving in specific microhabitats (Fan et al., 2023; Giachini & Castellano, 2011).

Molecular data have been instrumental in resolving the phylogenetic relationships within *Gomphus*, distinguishing between species that were previously conflated under broader taxonomic categorizations. DNA analyses have supported the monophyly of certain clades within the genus and have helped clarify the relationships between geographically and morphologically distinct species. These studies have also highlighted the importance of molecular tools in understanding the evolutionary dynamics and speciation processes in Gomphoid fungi (Fan et al., 2023; Giachini & Castellano, 2011).

The genus *Gomphus*, with its complex taxonomy and significant ecological roles, exemplifies the dynamic nature of fungal evolution and adaptation. Through a combination of morphological and molecular studies, mycologists have gained a deeper understanding of the evolutionary trajectories and ecological strategies of *Gomphus* species. This comprehensive approach not only enriches our taxonomic knowledge but also enhances our understanding of fungal biodiversity and its implications for forest ecosystems globally. Future research, focusing on the ecological interactions and genetic bases of adaptive traits in *Gomphus*, promises to further elucidate the evolutionary history and conservation priorities of these ecologically pivotal fungal species (Fan et al., 2023; Giachini & Castellano, 2011).

#### 2.6 The Literature Review of *Turbinellus*

The genus *Turbinellus*, initially proposed by Earle to house species like *Cantharellus floccosus*, has undergone numerous reclassifications, reflecting its complex phylogenetic relationships within the Gomphales. Characterized by scaly orange-red or brown pilei and strongly wrinkled, generally pale yellow to yellow-orange hymenia, *Turbinellus* species lack clamp connections and exhibit verrucose, ellipsoid to obovoid spores. These morphological traits, along with molecular data, have been pivotal in

differentiating *Turbinellus* from related genera such as *Gomphus* and *Cantharellus* (Fan et al., 2023; Giachini & Castellano, 2011).

Recent molecular analyses have significantly refined our understanding of *Turbinellus* taxonomy. This genus, along with *Gomphus*, forms a monophyletic clade within the Gomphales, distinctly separate from other related groups. This separation underscores the importance of both morphological and genetic data in resolving historical taxonomic ambiguities. The genus comprises several species including *Turbinellus floccosus*, which is known for its large, terrestrial basidiomata and ectomycorrhizal relationships with Pinaceae (Fan et al., 2023; Giachini & Castellano, 2011).

Turbinellus species exhibit a range of evolutionary adaptations that are crucial for their ecological roles, particularly their presumed symbiotic relationships with forest trees. The morphological diversity, from the scaly pileus to the distinct spore characteristics, likely represents adaptations to various ecological niches across different continents. These adaptations not only facilitate spore dispersal and survival but also enhance the fungi's ability to form symbiotic relationships with a wide variety of host trees, thereby playing a critical role in forest ecosystems (Fan et al., 2023; Giachini & Castellano, 2011).

The ecological significance of *Turbinellus* is highlighted by its widespread distribution and diversity in forest ecosystems globally. Some species are considered rare or threatened, such as *T. kauffmanii* in the Pacific northwestern USA, emphasizing the need for conservation efforts tailored to protect these ecologically vital fungi. The mycorrhizal associations of *Turbinellus* with conifers underscore their role in nutrient cycling and forest health, further supporting the need for understanding their phylogenetic relationships and ecological dynamics (Fan et al., 2023; Giachini & Castellano, 2011).

Turbinellus represents a fascinating example of fungal evolution, with its complex taxonomic history and significant ecological roles underscoring the dynamic interplay between morphological adaptation and environmental interactions. Ongoing research into its phylogeny and taxonomy continues to reveal the intricate relationships within the Gomphales, contributing to a deeper understanding of fungal biodiversity and its conservation implications (Fan et al., 2023; Giachini & Castellano, 2011).

## 2.7 The Literature Review of Gloeocantharellus

The genus *Gloeocantharellus*, recognized for its agaricoid-gomphoid basidiomata, primarily inhabits tropical and subtropical regions, extending to areas in Japan, New Zealand, Russia, and the USA. This genus is characterized by small basidiomata, a wrinkled to lamellate hymenium, and a notable presence of gleoplerous hyphae. Distinctive traits such as spore size and ornamentation, clamp connections, and gleocystidia presence vary across species, aiding in their identification and classification (Fan et al., 2023; Giachini & Castellano, 2011).

Gloeocantharellus presents multiple derived lineages that potentially indicate distinct subgenera, each consisting of one to several species. This phylogenetic diversity reflects significant evolutionary divergence within the genus, which is crucial for understanding the evolutionary pathways of gomphoid fungi (Fan et al., 2023; Giachini & Castellano, 2011).

The species of *Gloeocantharellus* are primarily terrestrial and are often found in proximity to well-known ectomycorrhizal tree species. While direct evidence of their mycorrhizal relationships is scant, the ecological associations suggest a potential symbiotic role with these trees, impacting forest health and nutrient cycles. The widespread distribution and ecological adaptability highlight the genus's role in various forest ecosystems, from South America to the South Pacific and Southeast Asia (Fan et al., 2023; Giachini & Castellano, 2011).

The conservation of *Gloeocantharellus* is underscored by its presence in diverse ecological zones and its interactions with significant tree species. Understanding the habitat specificity and ecological dynamics of these fungi is vital for conservation strategies, especially in regions where these fungi are associated with endangered or economically important tree species (Fan et al., 2023; Giachini & Castellano, 2011).

Gloeocantharellus exemplifies a complex group within the Gomphales, with significant implications for fungal taxonomy, phylogeny, and ecology. The genus's detailed study reveals intricate relationships and evolutionary adaptations that are crucial for understanding the broader ecological roles of fungi in forest ecosystems. Future research should focus on the detailed ecological functions of Gloeocantharellus, including its

potential mycorrhizal relationships, to further elucidate its role in sustaining forest biodiversity and health (Fan et al., 2023; Giachini & Castellano, 2011).

# 2.8 The Literature Review of Clavulinopsis

Clavulinopsis was first described by Overeem in 1923, with Clavulinopsis sulcata Overeem designated as its type species. This genus is classified within the family Clavariaceae, which falls under the order Agaricales within the class Agaricomycetes of the Basidiomycota phylum. According to He (2019) and recent updates by Yan et al. (2023), Clavulinopsis currently comprises about 40 species. These species are noted for their unique structural characteristics within the fungi (He, 2019; Yan et al., 2023).

Corner categorized *Clavaria* with several defining characteristics: white spores, clamped and thin-walled hyphae that are not secondarily septate. He centered this group around species such as *C. corniculata*, *C. fusiformis*, and *C. subtilis*, forming the largest group of white-spored Clavarias. This group is distinct from *Clavaria vermicularis*, which serves as the type species for *Clavaria* sensu stricto, thereby necessitating the establishment of a new genus (Corner, 1950).

Although the name *Cornicularia* Bon. (1851) was initially given to this group, it became a later homonym and thus ineligible for use. Technically, the name *Ramaria* S. F. Gray (1821) should have precedence. However, defining *Ramaria* in this context would lead to confusion due to the subtle differences in spore characteristics among species, their variability in fruit-body shape, size, and color, and the limited microscopic details available for many species. Key distinguishing features of these fungi include spore shape (ellipsoid or globose), size (ranging from 3–5 μm to 5–8 μm), and basidiome color. The species typically feature clavarioid basidiomata that are simple or branched and vary in color from white and yellow to orange and red. The basidiospores are usually smooth, hyaline or slightly yellow, either globose or ellipsoid, and may be echinulate in some species. Both tramal hyphae and basidia in these fungi possess clamp connections (Corner, 1950, 1970; Petersen, 1978).

Species of *Clavulinopsis* are distributed worldwide and exhibit a range of growth forms including solitary, gregarious, or caespitose. These fungi are predominantly terrestrial, adapting to various ground substrates. However, some species also exhibit lignicolous habits, meaning they grow on or decompose wood, which showcases their ecological diversity and adaptability (Birkebak et al., 2016; He, 2019; Hyde et al., 2016).

C. aurantiaca Araujo-Neta, G.A. Silva & Gibertoni, found as solitary basidiomata on soil, is characterized by slender, flexible, orange basidiomata when fresh, becoming brittle when dry, and hyaline, mostly globose basidiospores. The specimens of Clavulinopsis aurantiaca form a distinct, well-supported clade closely related to Ramariopsis aurantio-olivacea, C. fusiformis, C. helvola, and C. laeticolor, though with low support. These related species share simple, orange basidiomata, but differ in spore morphology and geographic distribution. For instance, R. aurantio-olivacea has narrower basidiospores and is found only in New Zealand, while C. fusiformis, C. helvola, and C. laeticolor have been reported in the Neotropics. C. helvola differs by having angular basidiospores, C. fusiformis has larger, more globose spores, and C. laeticolor has broadly ellipsoid to subglobose spores. Other related species include C. aurantiocinnabarina, with pale yellow spores, C. calocera, with longer cylindrical spores, and C. amoena, with pale yellow basidiomata and subglobose spores (Hyde et al., 2016).

Specimens of *Clavulinopsis* collected in China were analyzed using morphological and molecular methods, leading to the identification of six new species, which includes *C. aspersa*, *C. bicolor*, *C. bispora*, *C. erubescens*, *C. incarnata*, and *C. tropicalis* as well as a new record of *C. trigonospora* in China. Phylogenetic analysis, based on internal transcribed spacer and nuclear ribosomal RNA large subunit sequences, confirmed that each new species formed an independent lineage, with Chinese *C. trigonospora* samples clustering with those from Italy. Detailed morphological descriptions, along with illustrations and photographs, are provided for these seven species, and a key to the known *Clavulinopsis* species in China is included, primarily through analysis of the internal transcribed spacer region (ITS, including the 5.8S gene) and nuclear large subunit ribosomal DNA (nuc-LSU-rDNA). Notably, these studies did not include protein-coding genes, which could provide additional insights into the phylogeny and taxonomy of the genus (Yan et al., 2023).

## 2.9 The Literature Review of Clavariadelphus

Clavariadelphus, established by Donk in 1933, is characterized by its non-gilled, club-shaped basidiomata. This genus is a member of the Clavariadelphaceae family within the Gomphales order. It is recognized for its unique macroscopic features, which include erect, simple, or branched fruit bodies. The genus is notable for its diverse species, displaying variations in color, morphology, and size, adapted to different environmental conditions ranging from temperate to alpine forests (Huang et al., 2020; Sher et al., 2018; Wen-Ying et al., 2020; Xia & Fan, 2020).

Recent studies have identified new species of *Clavariadelphus* in various regions, including China and Pakistan, enhancing the understanding of its distribution and morphological diversity. For instance, *Clavariadelphus elongatus* was described from Pakistan with distinctive large subcylindrical basidiomata and a unique color spectrum (Sher et al., 2018). Similarly, studies in China have expanded the known diversity within the region, describing species like *Clavariadelphus griseoclavus* based on both morphological and molecular data (Huang et al., 2020; Xia & Fan, 2020).

Molecular techniques have significantly contributed to refining the taxonomy and phylogeny of *Clavariadelphus*. DNA sequencing, particularly of the ITS region, has supported the classification and identification of several new and existing species. These studies have revealed complex phylogenetic relationships within the genus, underscoring the importance of integrating molecular data with traditional morphological approaches for species delimitation (Huang et al., 2020; Sher et al., 2018; Xia & Fan, 2020).

Clavariadelphus species are found predominantly in forest ecosystems, where they play crucial ecological roles. While some species are noted for their saprotrophic capabilities, contributing to wood decomposition and nutrient cycling, others are suspected to form symbiotic relationships with forest trees. The conservation of these fungi is important due to their ecological roles and the sensitivity of their habitats to environmental changes (Huang et al., 2020; Wen-Ying et al., 2020).

The genus *Clavariadelphus* exemplifies the dynamic interplay between morphological innovation and ecological adaptation in fungi. Ongoing research continues to uncover the rich diversity of this genus, highlighting its significance in mycological studies and forest ecology. Future research should focus on the ecological functions of these fungi, their conservation needs, and the potential impacts of environmental change on their populations.

#### 2.10 The Literature Review of *Lentaria*

Lentaria, a genus within the Gomphales order of Basidiomycota, comprises lignicolous fungi crucial for forest ecosystems due to their role as decomposers. Recent studies have expanded the known diversity of this genus in China, identifying several species through combined morphological and molecular approaches. This genus, initially described by Corner in 1950, has since been redefined to include species with characteristic branched basidiomata and elongate basidiospores, contributing significantly to its ecological niche as wood decomposers (Liu et al., 2017).

Research has identified five *Lentaria* species in China, with two newly described species, *Lentaria bambusina* and *Lentaria uncispora*, enriching the understanding of the genus's diversity. This work not only helps in recognizing the morphological variability among species but also in cataloguing species based on distinct habitats and geographic distribution. *Lentaria patouillardii* was also confirmed as a new record for China, adding to the known floristic diversity (Liu et al., 2017).

Molecular techniques, particularly the analysis of ITS sequences, have been instrumental in delineating the phylogenetic relationships within *Lentaria*. These studies have shown that *Lentaria* does not form a monophyletic group within the Gomphales but instead splits into distinct clades that suggest complex evolutionary histories. The inclusion of tropical and temperate species in these analyses highlights the adaptive diversification of *Lentaria* across different environmental gradients (Liu et al., 2017).

The ecological significance of *Lentaria* species, primarily as decomposers in forest ecosystems, underscores the importance of accurate taxonomic characterization for ecological studies and conservation efforts. These fungi contribute to nutrient cycling and biomass decomposition, processes vital for ecosystem health and resilience. Furthermore, the documentation of new species and their specific ecological roles can

aid in targeted conservation strategies, particularly in biodiverse but ecologically sensitive regions like China (Liu et al., 2017).

The genus *Lentaria* exemplifies the complex interplay between taxonomy, phylogeny, and ecology in fungi. The recent expansions in taxonomic knowledge, combined with molecular phylogenetic insights, provide a deeper understanding of its diversity and ecological roles. Continued research is crucial for unraveling the full ecological and evolutionary significance of *Lentaria* in global forest ecosystems, particularly in the face of changing climate and habitat loss.



### **CHAPTER 3**

### RESEARCH METHODOLOGY

## 3.1 Sample Collection

Samples were collected during the rainy season (June to October) from various locations in China (Beijing, Chongqing, Fujian, Gansu, Guangxi, Hebei, Heilongjiang, Hubei, Inner Mongolia, Jilin, Sichuan, Xizang, Yunnan, and Zhejiang) and Thailand (Bangkok, Chanthaburi, Chiang Mai, Chiang Rai, Kanchanaburi, Nakhon Si Thammarat, and Tak). Photographs of each specimen were taken immediately in situ. Basidiomes were either wrapped in foil or placed separately in plastic boxes. Each specimen was thoroughly dried in a dryer at 50°C before being stored in a plastic ziplock bag.

The collected samples from Thailand were deposited in the herbarium of Mae Fah Luang University (MFLU), while the Chinese samples were deposited in the herbarium of Mycology at the Institute of Microbiology, Chinese Academy of Sciences, Beijing, China (HMAS). Additional collections were loaned from other herbaria for study, including those from the herbarium of Cryptogams at the Kunming Institute of Botany, Chinese Academy of Sciences (HKAS); the herbarium of Mycology at the Institute of Microbiology, Chinese Academy of Sciences, Beijing, China (HMAS); and the herbarium of the Meise Botanic Garden, Belgium (BR).

# 3.2 Morphological Studies

Morphological characteristics such as odor, basidiome size, color, and chemical reactions were recorded from fresh basidiomes. Color codes follow the standards set by Kornerup and Wanscher (1978).

Microscopic features, including basidiospores, basidia, and cystidia, were observed on parts of the dried specimens that are carefully excised with a razor blade under a MOTIC SMZ-168 stereomicroscope. The specimens are sectioned and mounted in 5% KOH and 1% Congo red and examined using light microscopy with Olympus CX31 or BX53 compound microscope equipped with a Leica DFC450 camera.

Measurements are taken for at least 50 basidiospores, 20 basidia, and 20 cystidia. Basidiospore descriptions follow a specific notation: [x/y/z] indicates x spores measured from y basidiomata from z collections. The notation (a–) b–c (–d) describes basidiospore dimensions, where b–c represents the range for 95% of the measured values, with "a" and "d" as extreme values. The Q value refers to the length/width ratio of an individual basidiospore, and Q<sub>m</sub> denotes the average Q value of all measured basidiospores, plus or minus the standard deviation. All protocols for morphological study and chemical reactions adhere to the methodologies established by Largent (1986).

# 3.3 DNA Extraction, PCR Amplification and Sequencing

Genomic DNA of every specimen was extracted by an E.Z.N.A. Forensic DNA Extraction Kit (D3591-01, Omega Bio-Tek) following the manufacturer's protocol. Phylogenetic analyses were conducted for six loci: internal transcribed spacer region (ITS, including the 5.8S gene), nuclear large subunit ribosomal DNA (nrLSU), Mitochondrial small subunit ribosomal DNA (mtSSU), translation elongation factor 1α (EF-1α), DNA-directed RNA polymerase II subunit 2 (RPB2), mitochondrial ATPase subunit 6 (ATP6). PCR amplification was performed as follows. (1) The primers ITS1 or ITS1F or ITS5) and ITS4 were used for the ITS. The PCR cycling conditions for the ITS locus were: 5 min initial denaturation at 94°C, followed by 34 cycles of 40 s at 94 °C, 40 s at 53°C, and 60 s at 72°C, with a final extension step for 10 min at 72°C (Gardes & Bruns, 1993; White, 1990). (2) The primers LR0R and LR5 were used for nrLSU. The PCR conditions for the nrLSU locus were: 5 min initial denaturation at 94°C, followed by 34 cycles of 40 s at 94 °C, 40 s at 53°C, and 60 s at 72°C, with a final extension step for 10 min at 72°C (Vilgalys & Hester, 1990). (3) The primers MS1 and

MS2 were used for mrSSU. The PCR conditions for the mrSSU locus were: 5 min initial denaturation at 94°C, followed by 34 cycles of 40 s at 94 °C, 40 s at 53°C, and 60 s at 72°C, with a final extension step for 10 min at 72°C. (4) The primers 526F or 983F) and 1567R or 2218R were used for EF-1α. The PCR cycling conditions for the EF-1α locus were: 5 min initial denaturation at 94°C, followed by 34 cycles of 40 s at 94 °C, 40 s at 56°C, and 60 s at 72°C, with a final extension step for 10 min at 72°C (Rehner & Buckley, 2005). (5) The primers RPB2-6F or bRPB2-6F and RPB2-7R or fRPB2-7cR, bRPB2-7R) were used for the RPB2. The PCR cycling conditions for the RPB2 locus were: 1 min initial denaturation at 95°C, followed by 34 cycles of 1 min at 95 °C, 1 min at 55°C, and 1 min 72.0 C + 1 sec/cycle, with a final extension step for 10 min at 72°C (Matheny, 2006). (6) The ATP6 locus was amplified using two sets of primers. The first set was ATP6-1 or ATP6-3 and ATP6-2 or ATP6-4. Using this set of primers, the PCR cycling conditions were: 2 min initial denaturation at 96°C, followed by 35 cycles of 1 min at 94 °C, 1 min at 57 °C, and 1 min at 72 °C, with a final extension step for 5 min at 72°C (Kretzer & Bruns, 1999). The second set of ATP6 primers was ATP6-1M40F—ATP6-2M, which correspond to ATP6-1 and ATP6-2 primers to which a tail was added to improve sequencing results. ATP6-1 is tailed with the universal primer sequence M13F-pUC (-40), and ATP6-2 is tailed with the universal primer sequence M13F (-20). Using these primers, the PCR cycling conditions were: 2 min at 95°C; five cycles of 45 s at 95°C, 60 s at 42 °C, 30 s at 72°C; 35 cycles of 20 s at 95°C, 30 s at 55°C, 30 s+1 s/cycle at 72°C; 3 min at 72 °C (Raspé et al., 2016). All PCR products were detected by 2% agarose gel electrophoresis and then sent to various companies for sequencing. The newly generated sequences were assembled and edited using SeqMan or Geneious Prime version 2024.0.5 (Fehér et al., 2022) with generic-level identities for sequences confirmed via Blast queries of GenBank.

## 3.4 Sequence Alignment and Phylogenetic Analyses

Sequences of clavarioid fungi, both newly generated and retrieved from GenBank, were aligned using MAFFT version 7 (Katoh & Standley, 2013). The alignments were subsequently reviewed and manually adjusted using BioEdit version

7.0.5 (Hall, 2007), Geneious Prime version 2024.0.5 (Fehér et al., 2022), or AliView version 3.0 (Larsson, 2014).

Phylogenetic analyses were initially conducted on single-gene alignments using the Maximum Likelihood method with RAxML-HPC2 version 8.2.12 (Stamatakis, 2014), with 1,000 rapid bootstrap resampling on the CIPRES Science Gateway (Miller et al., 2010). Following confirmation that there were no significant conflicts (bootstrap support  $\geq 70\%$ ) among single-gene topologies, the sequences were concatenated using Sequence Matrix (Vaidya et al., 2011). A partitioned Maximum Likelihood analysis was then performed on the concatenated dataset.

Bayesian Inference was employed to further refine the phylogenetic assessment, with optimal substitution models for each character set determined using jModelTest 2.3 (Nylander et al., 2004). The Bayesian analysis was conducted on partitioned matrices in MrBayes version 3.2.7a (Ronquist et al., 2005), involving two runs of five chains each for 8,000,000 generations, sampling trees every 200 generations. The analysis was set to terminate when the standard deviation of split frequencies fell below 0.01. Clades were considered strongly supported if they showed bootstrap support values (BS)  $\geq$  70% and posterior probabilities (PP)  $\geq$  0.90. The resulting phylogenetic trees were visualized and refined in FigTree v. 1.4.0 (Rambaut, 2012).

## **CHAPTER 4**

### RESEARCH RESULTS

### 4.1 Phaeoclavulina

### 4.1.1 Phylogenetic Analyses

In this study, 461 sequences derived from five loci (nrITS, nrLSU, mtSSU, tef1 and ATP6) were used sequencing of *Phaeoclavulina*, including 196 for ITS, 142 for nrLSU, 32 for mtSSU, 44 for ATP6 and 47 for tef1 representing 54 species from *Phaeoclavulina* (Table 4.2). The dataset of nrITS comprised 826 characters including gaps and contains 181 specimens which represent 36 species of *Phaeoclavulina*, and 6 species of *Ramaria* were chosen as outgroup taxa. The dataset of combined ITS and nrLSU comprised 1776 characters including gaps (nrITS: 1–826, nrLSU: 827–1776) and contains 206 specimens which represent 54 species of *Phaeoclavulina*, and 6 species of *Ramaria* were chosen as outgroup taxa. The Maximum likelihood tree was showed in Figures 4.1 and 4.2.

Table 4.1 Summary of data sets of ITS, nrLSU, mtSSU, tefl and ATP6

Properties	ITS1+ITS2	nrLSU+5.8S	mtSSU	tef1	ATP6
Characters included	470	1028	353	952	700
(with gaps)					
Conserved positions	124	760	232	713	415
Parsimony informative	320	213	89	195	256
positions (%)					
Uninformative variable	346	268	121	239	285
position					
Nucleotide substitution	GTR+G	GTR+I+G	GTR+I+G	GTR+I+G	GTR+I+G
models					

The phylogeny topologies of *Phaeoclavulina* based on ITS, ITS + nrLSU, sequences respectively with ML bootstrap support values ≥ 70% are shown in Figures 4.1–4.2. There were 86 taxa included in the ITS dataset, 114 taxa included in the nrLSU dataset.

Table 4.2 GenBank accession number of specimen used in this study

Š •	Voucher	G		Gen	Bank accessio	ns				
Species	Voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1			
Phaeoclavulina abietina	STU:SMNS-STU-F-0901132	Germany	OM152331	N/A	N/A	N/A	N/A			
P. abietina	STU:SMNS-STU-F-0900006	Germany	OM152302	N/A	N/A	N/A	N/A			
P. abietina	AMB 18530	Italy	MT055914	MT053205	N/A	N/A	N/A			
P. abietina	OSC 112178	USA	KY510818	KY354707	N/A	N/A	N/A			
P. abietina	OSC 109282	USA	KP658149	N/A	N/A	N/A	N/A			
P. abietina	OSC 140661	N/A	JX310379	JX287479	N/A	N/A	N/A			
P. abietina	OSC 134649	N/A	JX310378	JX287478	N/A	N/A	N/A			
P. abietina	RLE2017_2894	BG	ITS	LSU	N/A	ATP6	N/A			
P. abietina	AF1521	BG	ITS	LSU	N/A	ATP6	N/A			
P. aeruginea	MHHNU6887*	China	ON262784	ON262781	N/A	N/A	N/A			
P. aeruginea	MHHNU8909*	China	ON262785	ON262782	N/A	N/A	N/A			
P. aeruginea	G1	N/A	OM469312	N/A	N/A	N/A	N/A			
P. africana	TENN39621	N/A	N/A	AY574653	AY574726	AY574796	N/A			
P. alboapiculata	AMB 18590*	Italy	MT055971	MT053248	N/A	N/A	N/A			
P. alboapiculata	AMB 18585*	Italy	MT055964	MT053242	N/A	N/A	N/A			
P. alboapiculata	AMB 18613	Italy	MT452509	N/A	N/A	N/A	N/A			
P. angustata	BPI2	N/A	N/A	AY577847	N/A	N/A	N/A			
P. apiahyna	LPS13259	N/A	N/A	AY577840	N/A	N/A	N/A			
P. arcosuensis	AMB 18532	Italy	MT055916	MT053207	N/A	N/A	N/A			
P. arcosuensis	MA-Fungi 48049	Spain	AJ408394	N/A	N/A	N/A	N/A			
P. argentea	TENN41370	N/A	N/A	AY577839	N/A	N/A	N/A			
P. bicolor	MHHNU10702	China	PP809798	PP800475	N/A	N/A	N/A			
P. bicolor	MHHNU10703	China	PP809799	PP800476	N/A	N/A	N/A			
P. campestris	TNS1502	N/A	N/A	AY577851	N/A	N/A	N/A			
P. campoi	LPS39622	N/A	N/A	AY577842	N/A	N/A	N/A			

Table 4.2 (continued)

G •	¥7 l	C: A:		Genl	Bank accession		
Species	Voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1
P. capucina	GH288	N/A	N/A	AY577845	N/A	N/A	N/A
P. carovinacea	AMB 18533*	Italy	MT055917	N/A	N/A	N/A	N/A
P. carovinacea	AMB 18534*	Italy	MT055918	N/A	N/A	N/A	N/A
P. carovinacea	AMB 18551	Italy	MT055933	N/A	N/A	N/A	N/A
P. carovinacea	AMB 18550	Italy	MT055932	N/A	N/A	N/A	N/A
P. caroviridula	AMB 18535*	Italy	MT055919	MT053208	N/A	N/A	N/A
P. caroviridula	AMB 18536*	Italy	MT055920	MT053209	N/A	N/A	N/A
P. cinnamomea	MHHNU10376*	China	ON262786	ON262783	N/A	N/A	N/A
P. clavarioides	ERD-9641	Portugal	OQ703628	N/A	N/A	N/A	N/A
P. clavarioides	PRM:945441	Czech Republic	LR723647	N/A	N/A	N/A	N/A
P. clavarioides	PRM:945440	Czech Republic	LR723646	LR723645	N/A	N/A	N/A
P. nigricans	AMB 18589*	Italy	MT055970	N/A	N/A	N/A	N/A
P. cokeri	MA:Fungi:79893	Spain	MH322666	N/A	N/A	N/A	N/A
P. coniferarum	AMB 18531*	Italy	MT055915	MT053206	N/A	N/A	N/A
P. coniferarum	AMB 18562*	Italy	MT055942	N/A	N/A	N/A	N/A
P. curta	STU:SMNS-STU-F-0900025	Germany	OM152312	N/A	N/A	N/A	N/A
P. curta	STU:SMNS-STU-F-0900023	Germany	OM152310	N/A	N/A	N/A	N/A
P. curta	AMB 18641	Italy	MW115423	MW092704	N/A	N/A	N/A
P. curta	AMB 18605	Italy	MT452501	N/A	N/A	N/A	N/A
P. curta	UBC F32034	Canada	KX236126	N/A	N/A	N/A	N/A
P. curta	MA-Fungi 48081	Spain	AJ408359	N/A	N/A	N/A	N/A
P. curta	MA-Fungi 48029	Spain	AJ408358	N/A	N/A	N/A	N/A
P. cyanocephala	TH9064	Guyana	KT339249	KT339290	N/A	N/A	N/A
P. echinoflava	HKAS 45984	China	PP809801	PP800478	N/A	N/A	N/A
P. echinoflava	HKAS 45992	China	PP809800	PP800477	N/A	N/A	N/A

Table 4.2 (continued)

G •	<b>Y</b> 7 <b>1</b>	<b>C</b>		Genl	Bank accession	ns				
Species	Voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1			
P. eumorpha	STU:SMNS-STU-F-0901134	Germany	OM152319	N/A	N/A	N/A	N/A			
P. eumorpha	STU:SMNS-STU-F-0901127	Germany	OM152327	N/A	N/A	N/A	N/A			
P. eumorpha	STU:SMNS-STU-F-0901129	Germany	OM152320	N/A	N/A	N/A	N/A			
P. eumorpha	STU:SMNS-STU-F-0900015	Germany	OM152305	N/A	N/A	N/A	N/A			
P. eumorpha	STU:SMNS-STU-F-0900014	Germany	OM152304	N/A	N/A	N/A	N/A			
P. eumorpha	GLM:GLM-F116666	Germany	OM152300	N/A	N/A	N/A	N/A			
P. eumorpha	MQ18R020-QFB30103	Canada	MN992241	N/A	N/A	N/A	N/A			
P. eumorpha	ANT057-QFB28646	Canada	MN992499	N/A	N/A	N/A	N/A			
P. eumorpha	MQ22-KEG037-HRL3458	Canada	OQ321907	N/A	N/A	N/A	N/A			
P. eumorpha	ANT290-QFB28813	Canada	MN992483	N/A	N/A	N/A	N/A			
P. flaccida	STU:SMNS-STU-F-0901133	Germany	OM152322	N/A	N/A	N/A	N/A			
P. flaccida	GLM:GLM-F116675	Germany	OM152299	N/A	N/A	N/A	N/A			
P. flaccida	STU:SMNS-STU-F-0900019	Germany	OM152309	N/A	N/A	N/A	N/A			
P. flaccida	STU:SMNS-STU-F-0900018	Germany	OM152308	N/A	N/A	N/A	N/A			
P. flaccida	STU:SMNS-STU-F-0900017	Germany	OM152307	N/A	N/A	N/A	N/A			
P. flaccida	STU:SMNS-STU-F-0900016	Germany	OM152306	N/A	N/A	N/A	N/A			
P. flaccida	AMB 18544	Italy	MT055926	MT053213	N/A	N/A	N/A			
P. flaccida	AMB n. 17686	Italy	MK806692	N/A	N/A	N/A	N/A			
P. flaccida	AMB n. 17671	Italy	MK796107	MK796156	N/A	N/A	N/A			
P. flaccida	AMB n. 18209	Italy	MF288928	MF288936	N/A	N/A	N/A			
P. flaccida	MA-Fungi 48020	Spain	AJ408390	N/A	N/A	N/A	N/A			
P. flaccida	MA-Fungi 48076	Spain	AJ408371	N/A	N/A	N/A	N/A			
P. flaccida	AMB 18643	Italy	MW115426	MW092707	N/A	N/A	N/A			
P. flaccida	AMB 18645	Italy	MW115424	MW092705	N/A	N/A	N/A			
P. flaccida	AMB 18540	Italy	MT055922	MT053210	N/A	N/A	N/A			

Table 4.2 (continued)

G •	Y l	<b>G</b>		Ger	Bank accessio	ns					
Species	Voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1				
P. flaccida	AMB 18537	Italy	MT055921	N/A	N/A	N/A	N/A				
P. flaccida var. fraceolens	AMB 18552*	Italy	MT055934	MT053219	N/A	N/A	N/A				
P. flaccida	AMB 18542	Italy	MT055924	N/A	N/A	N/A	N/A				
P. flaccida	EL61-03 (GB)	Sweden	JN649369	N/A	N/A	N/A	N/A				
P. flaccida	AF1529	BG	ITS	LSU	N/A	N/A	N/A				
P. gigantea	FH109	N/A	N/A	AY574703	AY574776	AY574845	N/A				
P. grandis	OSC122773	N/A	N/A	DQ218618	N/A	DQ218904	DQ219252				
P. guadelupensis	FH120	N/A	N/A	AY574682	AY574755	N/A	N/A				
P. guyanensis	FH84	N/A	N/A	AY574706	N/A	AY574848	N/A				
P. insignis	FH104	N/A	N/A	AY574704	AY574774	AY574846	N/A				
P. jilinensis	MHHNU9149	China	PP809802	PP800479	N/A	N/A	N/A				
P. jilinensis	MHHNU9164	China	PP809803	PP800480	N/A	N/A	N/A				
P. jilinensis	MHHNU10504	China	PP809804	PP800481	N/A	N/A	N/A				
P. liliputensis	209	N/A	N/A	MT214492	MT214626	N/A	N/A				
P. liliputensis	207	N/A	N/A	MT214491	MT214625	N/A	N/A				
P. liliputensis	206	N/A	N/A	MT214490	MT214624	N/A	N/A				
P. liliputensis	205	N/A	N/A	MT214489	MT214623	N/A	N/A				
P. liliputensis	204	N/A	N/A	MT214488	MT214622	N/A	N/A				
P. longicaulis	TENN33826	N/A	N/A	AY574700	AY574773	AY574842	N/A				
P. macrospora	AMB 18614	Italy	MT452510	N/A	N/A	N/A	N/A				
P. minutispora	STU:SMNS-STU-F-0900024	Germany	OM152311	N/A	N/A	N/A	N/A				
P. minutispora	AMB 18588*	Italy	MT055969	N/A	N/A	N/A	N/A				
P. minutispora	AMB 18586*	Italy	MT055965	N/A	N/A	N/A	N/A				
P. minutispora	AMB 18579*	Italy	MT055959	N/A	N/A	N/A	N/A				
P. minutispora	GT21030	Belgium	OQ749903	N/A	N/A	N/A	N/A				

Table 4.2 (continued)

G .		Voucher Country -	GenBank accessions				
Species	Voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1
P. minutispora	LD5028	Belgium	OQ729761	N/A	N/A	N/A	N/A
P. minutispora	ERD-9651	Spain	OQ702320	N/A	N/A	N/A	N/A
P. minutispora	TUR-A 209242	Italy	ON561381	N/A	N/A	N/A	N/A
P. minutispora	JM_SN_513755	BG	ITS	N/A	N/A	N/A	N/A
P. minutispora	AF3841	BG	ITS	LSU	N/A	ATP6	TEF1
P. ochracea	Christan1868	Spain	MH384905	N/A	N/A	N/A	N/A
P. ochracea	AH:48374	Spain	MH322686	N/A	N/A	N/A	N/A
P. coniferarum	GENARD_22	BG	ITS	LSU	N/A	ATP6	N/A
P. pancaribbea	TENN31836	N/A	N/A	AY574707	N/A	AY574849	N/A
P. pseudozippelii	BBH 43575*	Thailand	MG214661	MG214663	N/A	N/A	N/A
P. pseudozippelii	BBH 43576	Thailand	MG214660	MG214662	N/A	N/A	N/A
P. pseudozippelii	THAI-STO-2019-429	Thailand	ITS	LSU	N/A	N/A	TEF1
P. roellinii	PRM:945445	Czech Republic	LR723649	N/A	N/A	N/A	N/A
P. roellinii	PRM:945446	Czech Republic	LR723648	N/A	N/A	N/A	N/A
P. sp.	ARF-4974	USA	OP580189	N/A	N/A	N/A	N/A
P. sp.	ARF-4963	USA	OP580188	N/A	N/A	N/A	N/A
P. subabietina	HBAU15196	N/A	MZ157225	N/A	N/A	N/A	N/A
P. subabietina	HBAU15175	N/A	MZ157224	N/A	N/A	N/A	N/A
P. subabietina	HBAU15741	N/A	MZ157223	N/A	N/A	N/A	N/A
P. subabietina	HBAU15749	N/A	MZ157222	N/A	N/A	N/A	N/A
P. subabietina	HBAU15328	N/A	MW862330	N/A	N/A	N/A	N/A
P. subabietina	XH005	China	MW947479	N/A	N/A	N/A	N/A
P. subabietina	HBAU15760	China	MW855922	N/A	N/A	N/A	N/A
P. subabietina	ZRL20151834	China	ITS	LSU	N/A	ATP6	N/A
P. subabietina	ZRL20151868	China	ITS	LSU	N/A	N/A	N/A

Table 4.2 (continued)

Species	Variable	Commen		GenBank accessions				
Species	Voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1	
P. subabietina	ZRL20151909	China	ITS	LSU	N/A	N/A	TEF1	
P. subabietina	ZRL20151944	China	ITS	LSU	N/A	ATP6	N/A	
P. subabietina	ZRL20151969	China	ITS	LSU	N/A	ATP6	N/A	
P. subabietina	ZRL20160398	China	ITS	LSU	N/A	ATP6	N/A	
P. subabietina	ZRL20160473	China	ITS	LSU	N/A	ATP6	TEF1	
P. subabietina	ZRL20160525	China	ITS	LSU	N/A	ATP6	N/A	
P. subabietina	ZRL20160599	China	ITS	LSU	N/A	N/A	TEF1	
P. subabietina	ZRL20160613	China	ITS	LSU	N/A	N/A	TEF1	
P. subabietina	ZRL20160653	China	ITS	LSU	N/A	N/A	TEF1	
P. subabietina	ZRL20160655	China	ITS	LSU	N/A	N/A	TEF1	
P. subabietina	ZRL20161151	China	ITS	LSU	N/A	N/A	TEF1	
P. subabietina	ZRL20161175	China	ITS	LSU	N/A	N/A	TEF1	
P. subabietina	ZRL20161184	China	ITS	LSU	SSU	N/A	TEF1	
P. subabietina	ZRL20161263	China	ITS   S	LSU	N/A	ATP6	N/A	
P. subabietina	ZRL20170146	China	ITS	LSU	N/A	ATP6	N/A	
P. subabietina	ZRL20170242	China	ITS	LSU	N/A	N/A	N/A	
P. subminutispora	ZRL20181570	China	ITS	LSU	N/A	N/A	TEF1	
P. subminutispora	ZRL20181988	China	ITS	LSU	SSU	N/A	TEF1	
P. sp11	UBC F16560	Canada	FJ627035	N/A	N/A	N/A	N/A	
P. sp11	HC-PNNT-231	Mexico	KT307859	N/A	N/A	N/A	N/A	
P. sp11	HC-PNNT-076	Mexico	KT307858	N/A	N/A	N/A	N/A	
P. sp11	GO-2009-173	Mexico	KT307857	N/A	N/A	N/A	N/A	
P. sp11	ASIS23208	N/A	KP004921	N/A	N/A	N/A	N/A	
P. sp2	KG117	China	OQ450440	N/A	N/A	N/A	N/A	
P. sp2	HBAU15347	N/A	OL455055	N/A	N/A	N/A	N/A	

Table 4.2 (continued)

C	Wanaha :	Compte		Ger	nBank accession	ns	
Species	Voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1
P. sp2	HMAS 293470	China	OR237005	N/A	N/A	N/A	N/A
P. sp2	EF503	China	PP734675	N/A	N/A	N/A	N/A
P. sp2	AH:48373	Spain	MH322662	N/A	N/A	N/A	N/A
P. sp2	MA-Fungi 48119	Spain	AJ408383	N/A	N/A	N/A	N/A
P. sp2	MA-Fungi 48090	Spain	AJ408376	N/A	N/A	N/A	N/A
P. sp2	ZRL20161270	China	ITS	LSU	N/A	N/A	TEF1
P. sp2	ZRL20162107	China	ITS	LSU	N/A	N/A	TEF1
P. sp2	ZRL20180859	China	ITS	LSU	N/A	N/A	TEF1
P. sp2	ZRL20180915	China	ITS	LSU	N/A	N/A	TEF1
P. sp2	ZRL20180916	China	ITS	N/A	N/A	N/A	TEF1
P. sp2	ZRL20181116	China	ITS	LSU	N/A	N/A	TEF1
P. sp2	ZRL20200016	China	ITS	LSU	N/A	ATP6	TEF1
P. sp2	ZRL20221359	China	ITS	LSU	N/A	N/A	TEF1
P. sp2	MAs2010_11	BG	ITS 8	LSU	N/A	ATP6	N/A
P. sp2	JL_02111999	BG	ITS	LSU	N/A	ATP6	N/A
P. sp2	MAs_2015_03	BG	ITS	LSU	N/A	N/A	N/A
P. qilianensis	QL20170222	China	ITS	LSU	N/A	N/A	N/A
P. qilianensis	QL20170327	China	ITS	LSU	N/A	N/A	TEF1
P. qilianensis	ZRL20181076	China	ITS	LSU	N/A	N/A	TEF1
P. qilianensis	ZRL20181083	China	ITS	LSU	SSU	N/A	N/A
P. qilianensis	ZRL20181339	China	ITS	LSU	N/A	N/A	TEF1
P. qilianensis	ZRL20181406	China	ITS	LSU	SSU	N/A	TEF1
P. qilianensis	ZRL20181428	China	ITS	LSU	SSU	N/A	TEF1
P. qilianensis	ZRL20181555	China	ITS	LSU	N/A	N/A	TEF1
P. qilianensis	ZRL20181572	China	ITS	LSU	N/A	N/A	N/A

Table 4.2 (continued)

C	Vossakas.	Commenter		GenBank accessions				
Species	Voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1	
P. qilianensis	ZRL20181589	China	ITS	LSU	N/A	N/A	TEF1	
P. qilianensis	ZRL20181906	China	ITS	LSU	N/A	N/A	TEF1	
P. sterigmata	QL20170281	China	ITS	LSU	SSU	N/A	N/A	
P. sp5	ZRL20221337	China	ITS	LSU	N/A	N/A	TEF1	
P. sp6	LE-2016-004	Thailand	ITS	LSU	N/A	ATP6	TEF1	
P. jilongensis	ZRL20220525	China	ITS	LSU	N/A	N/A	N/A	
P. jilongensis	ZRL20220569	China	ITS	LSU	SSU	N/A	TEF1	
P. subcarovinacea	QL20170375	China	ITS	LSU	SSU	N/A	TEF1	
P. subcarovinacea	ZRL20181031	China	ITS	LSU	SSU	N/A	TEF1	
P. subcarovinacea	ZRL20181309	China	ITS	LSU	SSU	N/A	TEF1	
P. subcarovinacea	ZRL20181629	China	ITS	LSU	SSU	N/A	TEF1	
P. subcarovinacea	ZRL20181633	China	ITS	LSU	SSU	N/A	TEF1	
P. subcarovinacea	ZRL20181909	China	ITS	LSU	SSU	N/A	N/A	
P. subclaviformis	BR079159-07	N/A	N/A	AY574679	AY574752	N/A	N/A	
P. subdecurrens	iNat66937861	Canada	ON943314	N/A	N/A	N/A	N/A	
P. subdecurrens	QHU20063	N/A	OM986855	N/A	N/A	N/A	N/A	
P. subdecurrens	STU:SMNS-STU-F-0901139	Germany	OM152336	N/A	N/A	N/A	N/A	
P. subdecurrens	STU:SMNS-STU-F-0901125	Germany	OM152335	N/A	N/A	N/A	N/A	
P. subdecurrens	AH:48370	Spain	MH322691	N/A	N/A	N/A	N/A	
P. subdecurrens	AMB 18548	Italy	MT055930	N/A	N/A	N/A	N/A	
P. subdecurrens	ZRL20200931	China	ITS	LSU	N/A	ATP6	TEF1	
P. viridis	PERTH4302	N/A	N/A	AY574677	AY574750	AY574819	N/A	
P. viridis	FH1853	N/A	N/A	AY574676	AY574749	AY574818	N/A	
P. viridis	OSC97708	N/A	N/A	AY574675	AY574748	AY574817	N/A	
P. zealandica	PDD43383	N/A	N/A	AY577849	N/A	N/A	N/A	

Table 4.2 (continued)

Species	Voucher	Country		Gen	Bank accession	ns	
Species	voucher	Country	ITS	nLSU	mitSSU	ATP6	TEF1
P. zippelii	FH2	N/A	N/A	AY577844	N/A	N/A	N/A
Ramaria botrytis	JL_25082000	BG	ITS	LSU	N/A	N/A	N/A
R. flava	FD_SN_1132920	BG	ITS	LSU	N/A	ATP6	N/A
R. fumigata	Mas_2007_23	BG	ITS	LSU	N/A	ATP6	N/A
R. fumigata	MAs_2004_65	BG	ITS	LSU	N/A	ATP6	TEF1
R. stricta	AF3491	BG	ITS	LSU	N/A	ATP6	TEF1

**Note** "\*" following a species name indicates that the specimen is the holotype of that species; "N/A" indicates sequence miss. The newly generated sequences are shown in bold.

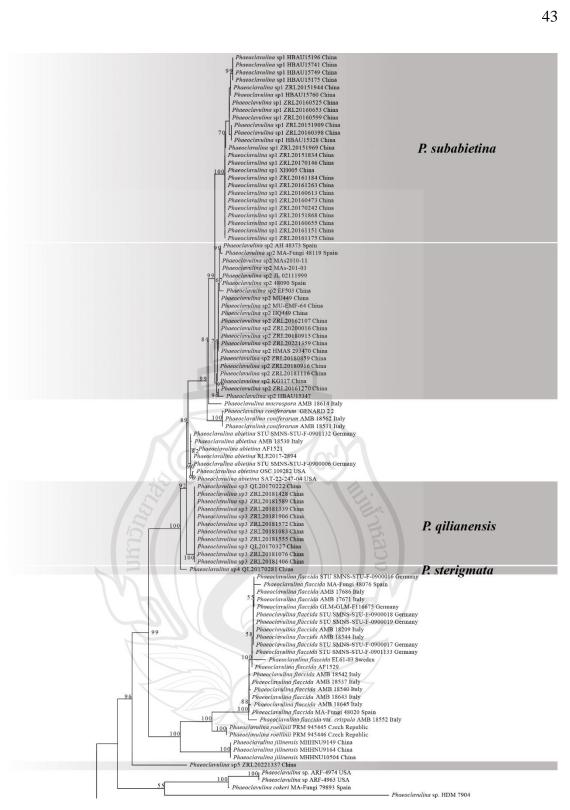


Figure 4.1 ITS phylogeny tree of Phaeoclavulina

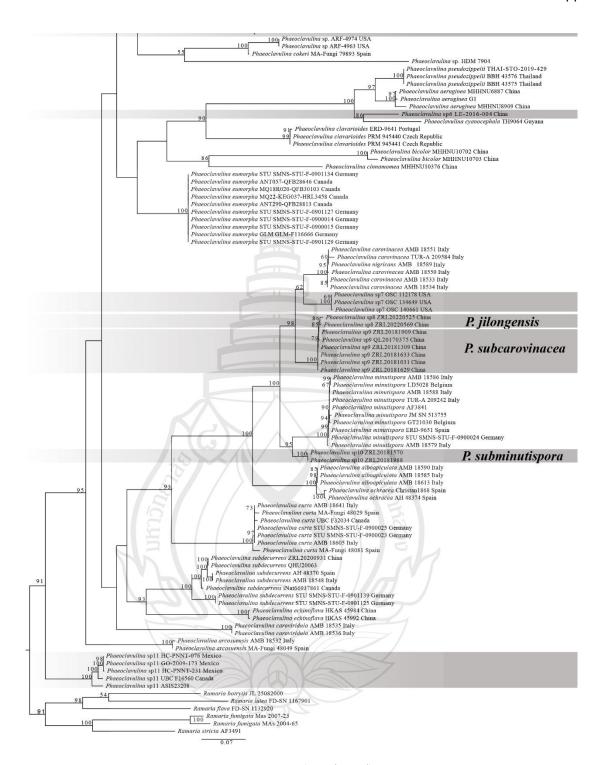


Figure 4.1 (continued)

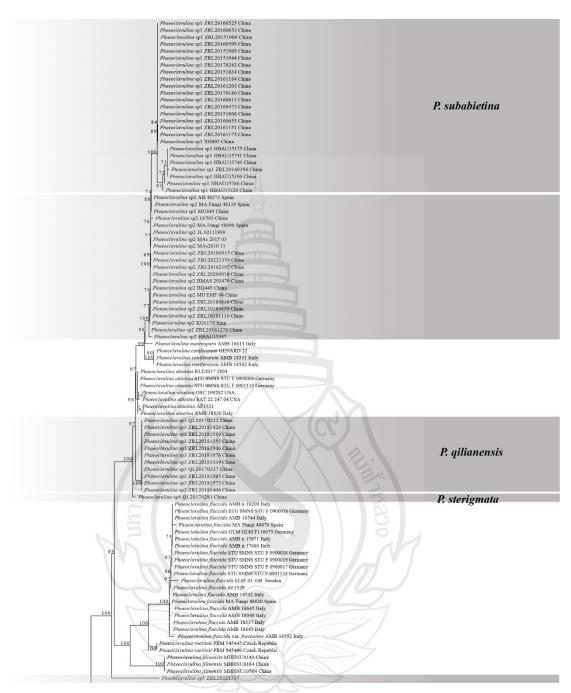


Figure 4.1 (continued)

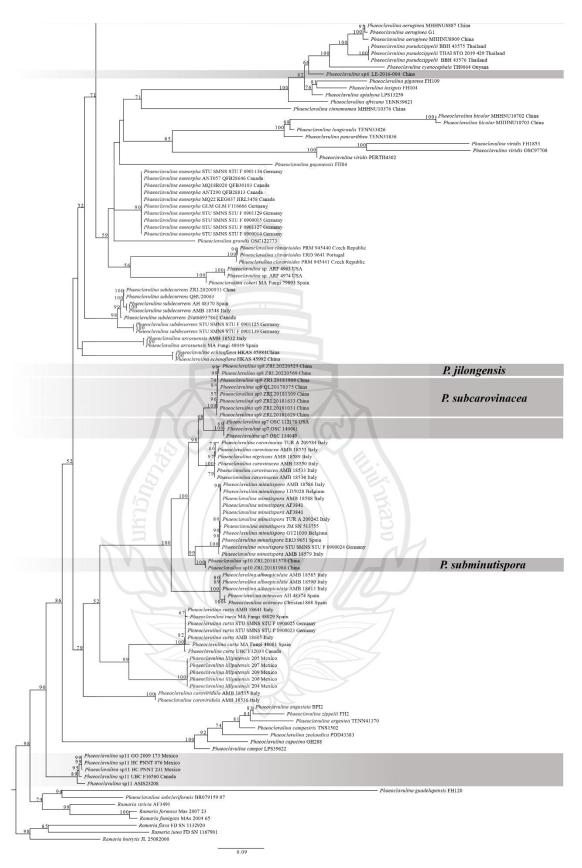


Figure 4.2 ITS + nrLSU phylogeny tree of *Phaeoclavulina* 

### 4.1.2 Taxonomy

Phaeoclavulina Brinkmann, Jahresbericht des Westfälischen Provinzialvereins für Wissenschaft und Kunst 25: 197, 1897

MycoBank MB 18213.

Type species: Phaeoclavulina macrospora Brinkmann.

Description: Phaeoclavulina is monophyletic and have diverse basidiome forms, which include ramarioid, unipileate, and merismatoid types. The basidiomes of Phaeoclavulina vary in color, ranging from white and brown green to pale or dark orange-yellow. These structures can adopt shapes such as infundibuliform or flabelliform and may be glabrous or subtomentose. The hymenium of these fungi varies in color from yellow to violet and can present as smooth or irregularly wrinkled, adding to their distinctive appearance. On a microscopic level, Phaeoclavulina is distinguished by its clamped hyphae and basidia, which can bear one to four sterigmata. The spores are notable for their golden yellow to ferruginous color and exhibit cyanophilic ornamentation when stained with cotton blue.

Phaeoclavulina subabietina X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.3

**Etymology.** The epithet "subabietina", from the Latin sub = near, referring to its similarity to P. abietina.

Holotype. China. Jilin Province: Chaoxianzu city, collected by R.L. Zhao (ZRL20160613).

**Diagnosis.** Differs from other *Phaeoclavulina* species in light yellow basidiome.

**Description.** Basidiome 35–60 × 20–30 mm, ramarioid (Figure 4.3), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and v-shape axils. Primary branches 20 × 2 mm, cylindrical to flattened, from light yellow [4A4] when young and orange yellow[4A7] in age; secondary branches 8 × 2 mm, cylindrical to flattened, mirror the morphology and coloration of the primary branches; terminal branches from cylindrical to flattened, concolorous with primary branches when young and light yellow [4A4] in age, with acute, dichotomous to polychotomous darker apices, from light yellow [4A4] to pale

yellow [4A3]. *Stipe* 8–10 × 4–5 mm, cylindrical, whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

*Basidia* 32.2–36.7 × 5.0–5.9 μm, subclavate, hyaline, multiguttulate, with four straight sterigmata. *Spores* 5.6–7.4 × 2.7–3.5 μm, [ $x = 6.2 \pm 0.4 \times 3.1 \pm 0.2$ , Q = 1.7–2.5,  $Q = 2.0 \pm 0.2$ ,  $Q = 2.0 \pm 0.2$ , Q = 2.0, Q

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. China. Jilin Province: Changchun city, collected by R.L. Zhao (ZRL20161184).

**Notes:** *Phaeoclavulina subabietina* is characterized by its variable basidiome colour. It is initially light yellow when young. When it matures, the primary and secondary branches darken gradually, while the terminal branches retain their light yellow. Additionally, the base of the basidiome features conspicuous white rhizomorphs. Microscopically, the basidiospores  $5.6-7.4 \times 2.7-3.5 \mu m$ , with prominent verrucose ornamentation rather than fine spines. The basidia are typically four-sterigmata.

In the phylogenetic tree, *Phaeoclavulina subabietina* forms a sister clade with *P. abietina*. However, the two species can be distinguished by their macroscopic features: *P. subabietina* has a light yellow basidiome, whereas *P. abietina* displays a yellow-brown coloration and undergoes color change upon bruising, a characteristic not observed in *P. subabietina*. Additionally, *P. subabietina* is closely related to *P. coniferarum*, but the latter species has a distinct ochraceous yellow basidiome, making them easily to be differentiated.

Morphologically, *P. liliputiana* also exhibits a light yellow, dichotomous to polychotomous structure that makes it challenging to distinguish from *P. subabietina*. However, they can be differentiated based on spore size, *P. liliputiana* has smaller spores (3.9-) 4.3–6.2 (-7) × (1.3-) 2.7–3.5 (-4) µm. Furthermore, the spore surface of *P. liliputiana* is finely spiny, while that of *P. subabietina* is verrucose. In terms of spore size, *P. nigricans*  $(5.5-8.3 \times 2.8-3.9 \, \mu m)$  is similar to *P. subabietina*, but *P. nigricans* has a darker basidiome color, described as buff.

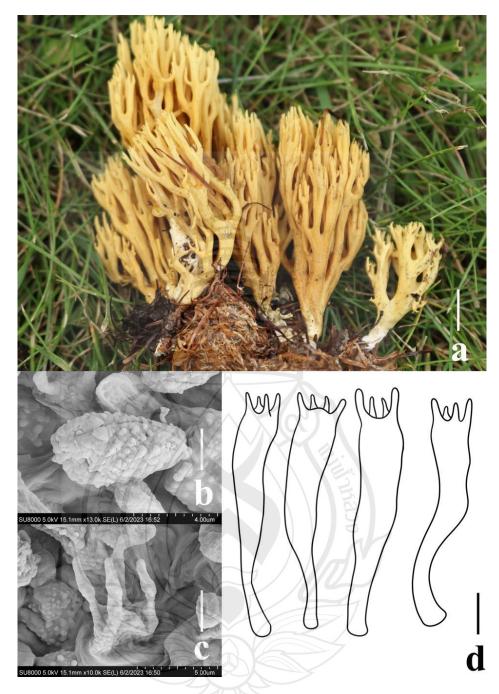


Figure 4.3 Phaeoclavulina subabietina. a Basidiome; b Basidiospores; c-d Basidia

Phaeoclavulina qilianensis X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.4

**Etymology.** The epithet "qilianensis" refers to Qilian Mountain where the type specimen is from.

**Holotype.** China. Gansu Province: Zhangye city, Sunan County, 25 August 2018, collectded by J.X. Li & B. Cao (**ZRL20181906**).

**Diagnosis.** Differs from other *Phaeoclavulina* species in cylindrical spores uniformly covered with fine spines.

**Description.** Basidiome 70–120  $\times$  35–60 mm, ramarioid (Figure 4.4), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and v-shape axils. *Primary branches* 15  $\times$  4 mm, cylindrical to flattened, from pale yellow [4A3] to yellowish write [4A2]; secondary branches 40  $\times$  3 mm, cylindrical to flattened, mirror the morphology and coloration of the primary branches; terminal branches from cylindrical to flattened, concolorous with primary branches, with acute, dichotomous to polychotomous apices, from pale yellow [4A3] to yellowish write [4A2]. Stipe 1–3  $\times$  1–2 mm, very short to almost absent, cylindrical, whitish, with a basal white tomentum and few white rhizomorphs. Context fleshy, whitish. Odour & taste not recorded. Macrochemical reactions not recorded.

*Basidia* 40.0–50.3 × 5.7–8.9 μm, subclavate, hyaline, multiguttulate, with two or four straight sterigmata. *Spores* 8.7–10.9 × 3.5–5.0 μm, [ $x = 9.7 \pm 0.7 \times 4.2 \pm 0.4$ , Q = 2.0–2.8, Q m = 2.3 ± 0.2, n =20], yellow-brown when seen in KOH, cylindric; when seen with SEM conical, with a sharply pointed tip ornamentation, evenly distributed on the spore surface. *Context* with generative hyphae in parallel arrangement, 2.0–4.3 μm broad, thinwalled, hyaline, with clamp connections.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

**Additional material examined.** China. Gansu Province: Zhangye city, Sunan County, 25 August 2017, collected by J.X. Li & B. Cao (**QL20170327**).

**Notes:** *Phaeoclavulina qilianensis* is characterized by cylindrical spores uniformly covered with fine spines, and its basidiome is light yellow with consistent coloration between the main branches and tips. Notably, the basidiome shows a distinct color change upon handling or bruising.

In the phylogenetic tree, *Phaeoclavulina qilianensis* is closely related to *P. abietina*. The two species are difficult to distinguish based on macromorphological features, including basidiome color and bruising response. The most notable difference lies in spore size—*P. qilianensis* has larger spores compared to *P. abietina*, whose spores  $(5.5)7.0-9.0(11) \times (3.3)3.7-4.5(4.8)$  µm. Additionally, *P. qilianensis* is similar to *P. subabietina*, but *P. qilianensis* has a paler basidiome and larger spores.

Morphologically, *Phaeoclavulina qilianensis* is most similar to *P. abietina*, as discussed above. Furthermore, it also shares a similar light yellow basidiome with *P. liliputiana*, and both exhibit a color change upon bruising. However, *P. liliputiana* has significantly smaller spores (3.9-) 4.3–6.2 (-7) × (1.3-) 2.7–3.5 (-4) µm, making it easy to differentiate between the two based on spore size.

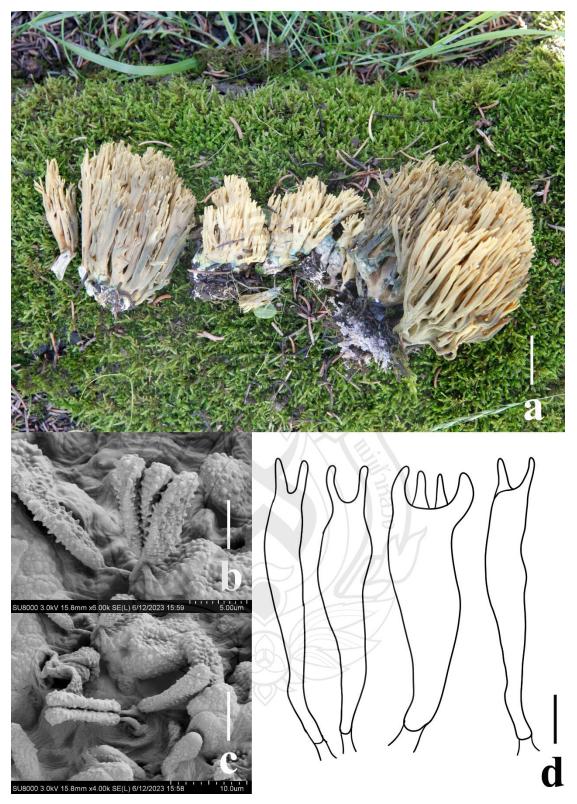


Figure 4.4 Phaeoclavulina qilianensis. a Basidiome; b Basidiospores; c–d Basidia

Phaeoclavulina sterigmata X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.5

Etymology. The epithet "sterigmata" refers to special five-sterigmata structure.

**Holotype.** China. Gansu Province: Zhangye city, Sunan County, 25 August 2017, collected by J.X. Li & B. Cao (QL20170281).

**Diagnosis.** Differs from other *Phaeoclavulina* species in the basidia commonly have five sterigmata.

**Description.** Basidiome 100–120 × 60–80 mm, ramarioid (Figure 4.5), repeatedly branched, with up to three levels of branching, polychotomous, with unparallel arrangement, and rounded axils. Primary branches 30 × 15 mm, cylindrical, from bronze [5E5] to yellowish brown [5E8]; secondary branches 30 × 10 mm, cylindrical, from reddish [5C4] to yellow ochre [5C7]; terminal branches from cylindrical, concolorous with secondary branches, with acute, polychotomous apices, from pale yellow [4A3] to yellowish write [4A2]. Stipe 1–3 × 1–2 mm, very short to almost absent, cylindrical, whitish, with a basal white tomentum and few white rhizomorphs. Context fleshy, whitish. Odour & taste not recorded. Macrochemical reactions not recorded.

*Basidia*  $40.6-56.3 \times 6.1-9.4$  μm, subclavate, hyaline, multiguttulate, with four or five straight sterigmata. *Spores*  $7.7-10.4 \times 3.2-4.3$  μm, [x =  $9.2 \pm 0.7 \times 3.9 \pm 0.3$ , Q = 2.0-2.7, Q m =  $2.4 \pm 0.2$ , n = 20], yellow-brown when seen in KOH, cylindric; when seen with SEM conical, with a sharply pointed tip ornamentation, evenly distributed on the spore surface. *Context* with generative hyphae in parallel arrangement, 2.2-3.6 μm broad, thin-walled, hyaline, with clamp connections.

Habitat and distribution. Scattered on the ground, known from China.

Additional material examined. N/A.

**Notes:** *Phaeoclavulina sterigmata* is characterized by its non-dichotomous, polychotomous basidiome, which ranges in color from brown to dark brown. The basidiome also changes color upon bruising. The branches are short and robust, and the spores exhibit evenly distributed verrucae. The basidia commonly have five sterigmata.

Only a single specimen of *Phaeoclavulina sterigmata* was collected, but due to its distinctive characteristics, it has been proposed as a new species. In the phylogenetic

Morphologically, *P. sterigmata* resembles *P. abietina*, as both species exhibit a color change upon bruising and have brown basidiomes. However, *P. sterigmata* has larger spores, and its basidia typically have five sterigmata, which is a distinguishing feature.



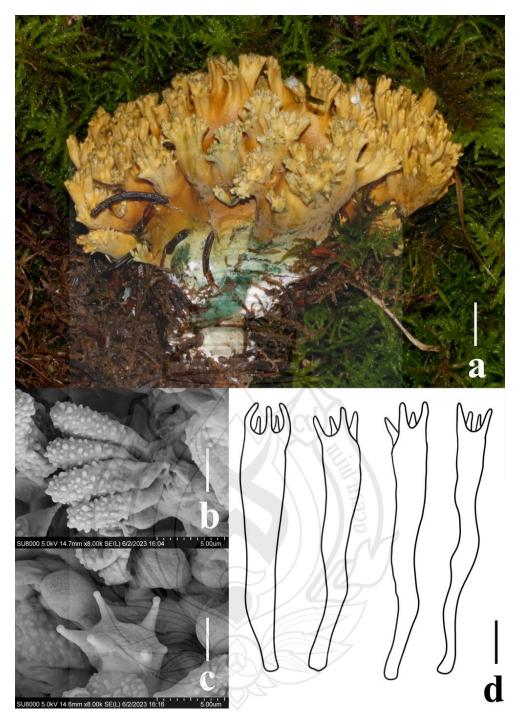


Figure 4.5 Phaeoclavulina sterigmata. a Basidiome; b Basidiospores; c–d Basidia

Phaeoclavulina jilongensis X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.6

**Etymology.** The epithet "*jilongensis*" refers to Jilong County where the type specimen is from.

**Holotype.** China. Xizang Province: Rikaze city, collected by X.Y. Zhu & R.L. Zhao (ZRL20220569).

**Diagnosis.** Differs from other *Phaeoclavulina* species in greenish yellow basidiome.

**Description.** Basidiome 45–50 × 25–30 mm, ramarioid (Figure 4.6), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and v-shape axils. Primary branches 10 × 4 mm, cylindrical to flattened, from greenish yellow [1A8] to greyish yellow [1B7] when young; secondary branches 15 × 4 mm, cylindrical to flattened, mirror the morphology and coloration of the primary branches; terminal branches from cylindrical to flattened, concolorous with primary branches when young, with acute, dichotomous to polychotomous apices, from greenish yellow [1A8] to greyish yellow [1B7]. Stipe 20–25 × 4–8 mm, cylindrical, whitish, with a basal white tomentum and few white rhizomorphs. Context fleshy, whitish. Odour & taste not recorded. Macrochemical reactions not recorded.

*Basidia* 40.5–43.6 × 5.8–6.8 μm, subclavate, hyaline, multiguttulate, with two or four straight sterigmata. *Spores* 5.8–7.5 × 2.–3.9 μm, [ $x = 6.4 \pm 0.5 \times 3.2 \pm 0.2$ , Q = 1.6–2.5,  $Q = 2.0 \pm 0.2$ ,  $Q = 2.0 \pm 0.2$ , Q = 2.0, Q = 2.0

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

**Additional material examined.** China. Xizang Province, Rikaze city, 1 August 2022, collected by X.Y. Zhu & R.L. Zhao (**ZRL20220525**).

**Notes:** *Phaeoclavulina jilongensis* is characterized by its greenish yellow basidiome, which has slender and sparse branches. The spore surface exhibits prominent verrucae, and the basidia are predominantly 2-4 sterigmate.

In the phylogenetic tree, *Phaeoclavulina jilongensis* forms a sister clade with *P. subcarovinacea*. However, these two species can be distinguished by basidiome color— *P. subcarovinacea* has a cream basidiome, while *P. jilongensis* is greenish yellow. Additionally, *P. jilongensis* is closely related to *P. carovinacea*, but

*P. carovinacea* is yellow brown or cinnamon in color, making the two species easily distinguishable.

Morphologically, *Phaeoclavulina jilongensis* resembles *P. abietina* in basidiome color; however, the spores of *P. abietina*  $(7.0-9.0 \times 3.7-4.5 \,\mu\text{m})$  are larger compared to those of *P. jilongensis*. *P. jilongensis* also has a similar basidiome morphology to *P. liliputiana*, but *P. liliputiana* is yellow to olive in color, which is darker, making them easy to differentiate.



Figure 4.6 Phaeoclavulina jilongensis. a Basidiome; b Basidiospores; c-d Basidia

Phaeoclavulina subcarovinacea X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.7

**Etymology.** The epithet "subcarovinacea" refers from the Latin sub = near, referring to its similarity to *P. carovinacea*.

**Holotype.** China. Gansu Province: Zhangye city, Sunan County, Z.L. Ling & Y.Y. Ling & R.L. Zhao (**ZRL20181909**).

**Diagnosis.** Differs from other *Phaeoclavulina* species in cream basidiome.

**Description.** *Basidiome* 65–78 × 44–51 mm, ramarioid (Figure 4.7), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 13.7 × 4.2 mm, cylindrical to flattened, from cream [4A3] to light yellow [4A4] when young; *secondary branches* 6.3 × 3.1 mm, cylindrical to flattened, concolorous with primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with primary branches when young, with acute, dichotomous to polychotomous darker apices, from butter yellow to light yellow [4A5] when young. *Stipe* 1–3 × 1–2 mm, very short to almost absent, cylindrical, whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

*Basidia* 38.8–43.4 × 5.4–6.4 μm, subclavate, hyaline, multiguttulate, with two or four straight sterigmata. *Spores* 5.8–7.8 × 2.8–4.1 μm, [ $x = 6.8 \pm 0.6 \times 3.6 \pm 0.4$ , Q = 1.6–2.2,  $Q = 1.9 \pm 0.2$ ,  $Q = 1.9 \pm 0.2$ , Q = 1

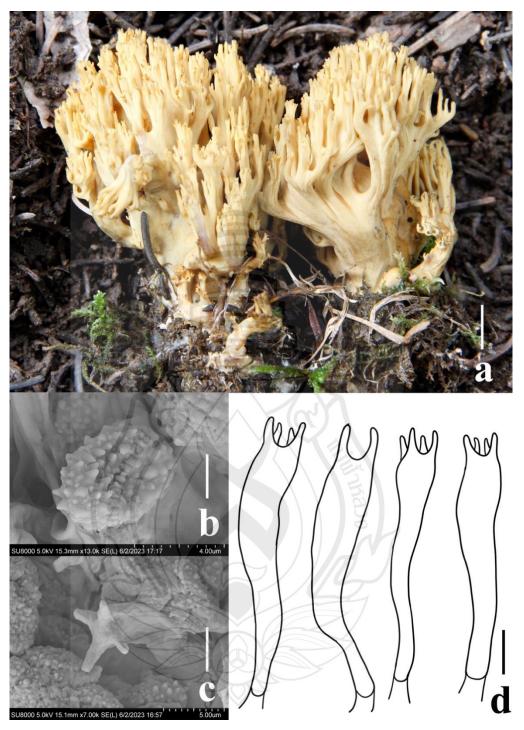
**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. China. Gansu Province: Zhangye city, Sunan County, 25 August 2018, collected by J.X. Li & B. Cao (ZRL20181629). (ZRL20181031). (ZRL20181633). (ZRL20181309).

**Notes:** *Phaeoclavulina subcarovinacea* is characterized by its cream basidiome with dense branching, with an indistinct or absent stipe. The basidiome does not change color upon bruising. The spore surface features prominent verrucae, and the basidia are two or four sterigmata.

In the phylogenetic tree, *Phaeoclavulina subcarovinacea* forms a sister clade with *P. jilongensis*. However, they can be distinguished by basidiome color. Additionally, *P. subcarovinacea* is closely related to *P. carovinacea*, and the two have similar spore sizes, but *P. carovinacea* has a darker basidiome, ranging from yellow brown to cinnamon, which makes them easy to differentiate by color. Morphologically, *P. subcarovinacea* resembles *P. liliputiana*, but the latter has smaller spores  $4.3-6.2 \times 2.7-3.5 \mu m$ . *Phaeoclavulina subcarovinacea* shares a similar spore size with *P. nigricans*, but the two can be easily differentiated by basidiome color.





**Figure 4.7** *Phaeoclavulina subcarovinacea.* a Basidiome; b Basidiospores; c–d Basidia. Scale bars

Phaeoclavulina subminutispora X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.8

**Etymology.** The epithet "subminutispora" refers from the Latin sub = near, referring to its similarity to *P. minutispora*.

**Holotype.** China. Gansu Province, Wuwei city, Xiama County, 21 August 2018, collected by Z.L. Ling, Y.Y. Ling & R.L. Zhao (**ZRL20181570**).

**Diagnosis.** Differs from other *Phaeoclavulina* species in pale orange to light orange basidiome.

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.8), repeatedly branched, with up to six levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from pale orange [5A3] to light orange [5A4] when young and brownish yellow in age [5C7]; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, from light orange [5A5] to orange [5A6] when young and brownish yellow in age [5C7]; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous darker apices, from greyish orange [5B5–6] when young and brown in age [5E7]. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, surface bruising dark brown [6F8], with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

*Basidia* 28–33 × 4.8–6.7 μm, subclavate, hyaline, multiguttulate, with two or four straight sterigmata. *Spores* 5.1–6.7 × 2.4–3.9 μm, [ $x = 5.7 \pm 0.5 \times 3.1 \pm 0.5$ , Q = 1.5–2.3,  $Q = 1.9 \pm 0.2$ ,  $Q = 1.9 \pm$ 

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

**Additional material examined.** China. Gansu Province, Zhangye city, Sunan County, 25 August 2018, collected by J.X. Li & B. Cao & R.L. Zhao (**ZRL20181988**).

**Notes.** *Phaeoclavulina subminutispora* is characterized by the pale orange to light orange basidiome, with a basal white tomentum and few white rhizomorphs, basidia mostly 4–spored, rarely 2–spored, subellipsoid basidiospores (5.1–6.7  $\times$  2.4–3.9  $\mu$ m) with a slightly blunt tip ornamentation.

In phylogenetic analysis, *Phaeoclavulina subminutispora* is a clade, distinguished from other *P.* species, it forms a sister clade with *P. minutispora*, but *P. subminutispora* has larger spores  $(5.1–6.7 \times 2.4–3.9 \, \mu m)$  than those of *P. minutispora*  $(3.7–5.0 \times 2.5–3.6 \, \mu m)$ . *Phaeoclavulina subminutispora* is similar to *P.* abietina in them medium-sized basidiome. However, *P. abietina* has lager spores  $(7–9 \times 3.7–4.5 \, \mu m)$ .



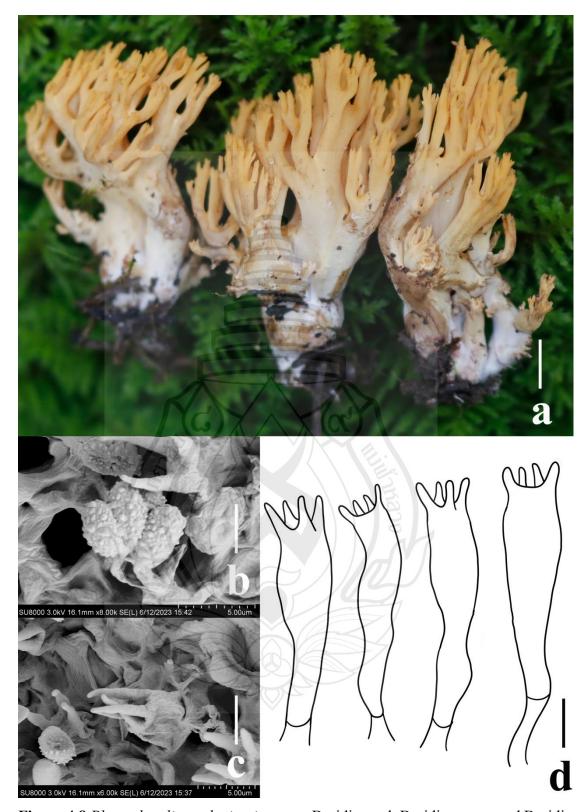


Figure 4.8 Phaeoclavulina subminutispora. a Basidiome; b Basidiospores; c–d Basidia

## 4.2 Gomphus, Turbinellus and Gloeocantharellus

### **4.2.1** Phylogenetic Analyses

In this study, 336 sequences derived from three loci (ITS, nrLSU, tef1) were used to reconstruct phylogenetic trees of *Gomphus*, *Turbinellus* and *Gloeocantharellus*, including 121 for ITS, 131 for nrLSU and 84 for tef1 representing 41 species from *Gomphus*, *Turbinellus* and *Gloeocantharellus*. Newly generated 94 sequences, including 31 for ITS, 36 for nrLSU and 27 for tef1 representing 5 species from *Gomphus*, *Turbinellus* and *Gloeocantharellus*. (Table 4.3). The combined three-gene dataset (ITS+nrLSU+ tef1) included sequences from 146 specimens representing 41 species from *Gomphus*, *Turbinellus* and *Gloeocantharellus*, and *Clavariadelphus ligula* (Schaeff.) Donk, *Lentaria dendroidea* (O.R. Fr.) J.H. Petersen, *Phaeoclavulina abietina* (Pers.) Giachini and *Phaeoclavulina flaccida* (Fr.) Giachini were chosen as outgroup based on previous phylogenetic studies. The best-fit evolutionary models selected for the three character sets were GTR+I+G (ITS1+ITS2), GTR+I+G (nrLSU+5.8S) and GTR+I+G (tef1). These models were applied in Bayesian analyses for the combined dataset.

The phylogeny topologies of *Gomphus*, *Turbinellus* and *Gloeocantharellus* based on ITS + nrLSU + tef1, sequences respectively with ML bootstrap support values  $\geq 70\%$  are shown in Figure 4.9, there were 146 taxa.

**Table 4.3** GenBank accession number of specimen used in this study for *Gomphus*, *Turbinellus* and *Gloeocantharellus* 

Taxon	Voughor	Voucher Location -	GenBank Accession Number			
Taxon	voucher	Location	ITS	nrLSU	tef1a	
Clavariadelphus ligula	AMB18570	Italy	MT055950	MT053231	DQ219239	
Gautieria monticola	OSC 65121;	USA: California	AF377105	AY574651	N/A	
	SNF 95CA					
Gloeocantharellus	FLOR 49692	Brazil	KU884896	N/A	N/A	
aculeatus						
Gloeocantharellus	FLOR 59113	Brazil	KU884897	N/A	N/A	
aculeatus						
Gloeocantharellus	FLOR 47977	Brazil	KU884895	N/A	N/A	
aculeatus						

 Table 4.3 (continued)

Taxon	Voucher	Location	GenBank Accession Number			
Taxon	voucher		ITS	nrLSU	tef1a	
Gloeocantharellus	FCME 14883	Mexico:	N/A	MT261809	N/A	
albidocarneus		Campeche				
Gloeocantharellus	K 255527	Madagascar:	MW506830	N/A	N/A	
andasibensis		Toamasina				
Gloeocantharellus	FCME 19868	Mexico:	N/A	MT261810	N/A	
calakmulensis		Campeche				
Gloeocantharellus	FLOR 47978	Brazil	KU884898	N/A	N/A	
corneri						
Gloeocantharellus	CGE 16041	Solomon Islands	KU884899	N/A	N/A	
echinosporus						
Gloeocantharellus	GDGM 70585	China	MK358821	MK358816	N/A	
neoechinosporus						
Gloeocantharellus	GDGM 75321	China	MK358820	MK358815	N/A	
neoechinosporus						
Gloeocantharellus	GDGM 75322	China	MK358819	MK358814	N/A	
neoechinosporus						
Gloeocantharellus	ZT 68-657	Switzerland	N/A	AF261548	N/A	
novae-zelandiae						
Gloeocantharellus	CGE 16046	Solomon Islands	KU884900	N/A	N/A	
okapaensis						
Gloeocantharellus	K 255526	Papua New	MW506831	AF261548	N/A	
okapaensis		Guinea				
Gloeocantharellus	TLXM 1924	N/A	N/A	MT261811	N/A	
pleurobrunnescens						
Gloeocantharellus	TENN 60053	USA	AY872281	AY574683	N/A	
purpurascens						
Gloeocantharellus	REH 6904	USA	KU884901	AY574684	N/A	
purpurascens						
Gloeocantharellus	TH 0817	Panama:	MW386076	N/A	N/A	
salmonicolor		Chiriqui				
Gloeocantharellus sp1	GX20170056	China	ITS	LSU	N/A	
Gomphus brunneus	BR 034190-46	s.n.	N/A	AY574680	N/A	
Gomphus clavatus	GB EL64/03	Sweden	EU118628	N/A	N/A	
Gomphus clavatus	HKAS 54852	China: Yunnan	OQ858438	OQ858505	OQ84760	
Gomphus clavatus	HKAS 6187	China: Tibet	N/A	N/A	N/A	
Gomphus clavatus	HKAS 76574	China: Gansu	OQ858440	N/A	N/A	
Gomphus clavatus	HKAS 80749	China: Tibet	OQ858436	N/A	N/A	
Gomphus clavatus	HKAS 82547	China: Sichuan	OQ858433	OQ858500	OQ84759	

 Table 4.3 (continued)

Town	Vouchon	Location	GenBank Accession Number			
Taxon	Voucher	Location	ITS	nrLSU	tef1a	
Gomphus clavatus	HKAS 90876	China: Sichuan	OQ858439	OQ858506	OQ847601	
Gomphus clavatus	HKAS 90958	China: Tibet	OQ858432	OQ858499	OQ847594	
Gomphus clavatus	HKAS 94030	China: Tibet	OQ858435	OQ858503	OQ847598	
Gomphus clavatus	HKAS 96161	Austria	OQ858441	OQ858507	N/A	
Gomphus clavatus	HKAS 106799	China: Tibet	OQ858437	OQ858504	OQ847599	
Gomphus clavatus	HKAS 116246	China: Tibet	N/A	OQ858502	OQ847597	
Gomphus clavatus	HKAS 122603	China: Yunnan	OQ858431	OQ858498	OQ847593	
Gomphus clavatus	HKAS 122961	China: Yunnan	OQ858434	OQ858501	OQ847596	
Gomphus clavatus	ZRL20191189	China	ITS	LSU	TEF1	
Gomphus clavatus	ZRL20200718	China	ITS	LSU	TEF1	
Gomphus clavatus	ZRL20200882	China	ITS	LSU	TEF1	
Gomphus clavatus	ZRL20200996	China	ITS	LSU	TEF1	
Gomphus clavatus	ZRL20211238	China	N/A	LSU	TEF1	
Gomphus crassipes	MA 79908	Spain	MH322660	N/A	N/A	
Gomphus ludovicianus	TENN 69175	USA: Texas	KJ655571	KJ655578	N/A	
Gomphus ludovicianus	TENN 69174	USA: Louisiana	KJ655572	KJ655579	N/A	
Gomphus ludovicianus	TENN 69161	USA: Louisiana	NR169658	NG059516	N/A	
Gomphus matijun	HKAS 122604	China: Guizhou	OL673002	OL672986	OQ847588	
Gomphus matijun	HKAS 122605	China: Guizhou	OL673001	OL672985	N/A	
Gomphus orientalis	HKAS 83567	China: Tibet	OQ858425	OQ858493	OQ847589	
Gomphus orientalis	HKAS 68646	China: Yunnan	OQ858426	OQ858494	OQ847590	
Gomphus orientalis	HKAS 18144	China: Yunnan	OQ858427	N/A	N/A	
Gomphus orientalis	ZRL20200623	China	ITS	LSU	TEF1	
Gomphus violaceus	HKAS 104313	China: Yunnan	OQ858428	OQ858495	OQ847591	
Gomphus violaceus	HKAS 122947	China: Yunnan	OQ858429	OQ858496	OQ847592	
Gomphus violaceus	HKAS 53267	China: Yunnan	OQ858430	OQ858497	N/A	
Lentaria dendroidea	SJ 98012	Sweden	EU118640	EU118641	N/A	
Phaeoclavulina abietina	AMB 18530	Italy: Cesuna	MT055914	MT053205	N/A	
Phaeoclavulina flaccida	AMB 18544	Italy: Cerbaie	MT055926	MT053213	N/A	
Ramaria botrytis	AMB 18204	Italy: La Secchia	KY626153	KY626154	N/A	
Ramaria botrytis	AMB 18201	Italy: Folgarida	KY626151	KY626152	N/A	
Turbinellus flavidus	HKAS 99946	China: Hunan	N/A	OQ858531	OQ847619	
Turbinellus floccosus	MICH 5588	USA: Oregon	N/A	AY574660	N/A	
Turbinellus floccosus	OSC 70579	USA	N/A	EU669263	N/A	
Turbinellus floccosus	OSC 97562	USA	N/A	AY577833	N/A	
Turbinellus fujisanensis	OSA MY-1842	Japan	N/A	AY574669	N/A	
Turbinellus fulvus	HKAS 57625	China: Yunnan	OQ858452	OQ858520	OQ847610	
Turbinellus imbricatus	HKAS 95099	China: Yunnan	OQ858442	OQ858508	OQ847602	

 Table 4.3 (continued)

Toron	Voucher Location	Laastian	GenBank Accession Number			
Taxon		Location	ITS	nrLSU	tef1a	
Turbinellus imbricatus	HKAS 85905	China: Yunnan	OQ858443	OQ858509	OQ847603	
Turbinellus kauffmanii	MICH 10069	USA	N/A	AY574671	N/A	
Turbinellus kauffmanii	OSC 97561	USA	N/A	AY577837	N/A	
Turbinellus longistipes	HKAS 82569	China: Yunnan	OQ858463	OQ858532	OQ847620	
Turbinellus longistipes	HKAS 87956	China: Yunnan	OQ858465	OQ858534	OQ847622	
Turbinellus longistipes	HKAS 113226	China: Yunnan	OQ858464	OQ858533	OQ847621	
Turbinellus longistipes	HKAS 122957	China: Yunnan	OQ858466	OQ858535	OQ847623	
Turbinellus parvisporus	HKAS 89475	China: Yunnan	OQ858450	OQ858516	OQ847607	
Turbinellus parvisporus	HKAS 122952	China: Yunnan	OQ858448	OQ858514	N/A	
Turbinellus parvisporus	HKAS 122954	China: Yunnan	OQ858449	OQ858515	OQ847606	
Turbinellus solidus	HKAS 86006	China: Yunnan	N/A	OQ858518	N/A	
Turbinellus solidus	HKAS 92450	China: Yunnan	N/A	OQ858517	OQ847608	
Turbinellus solidus	HKAS 140801	China: Yunnan	OQ858451	OQ858519	OQ847609	
Turbinellus sp1	ZRL20190385	China	ITS	LSU	N/A	
Turbinellus squamosus	HKAS 70249	China: Yunnan	OQ858444	OQ858510	OQ847604	
Turbinellus squamosus	HKAS 71334	China: Yunnan	OQ858446	OQ858512	N/A	
Turbinellus squamosus	HKAS 122950	China: Yunnan	OQ858445	OQ858511	N/A	
Turbinellus squamosus	HKAS 122955	China: Yunnan	OQ858447	OQ858513	OQ847605	
Turbinellus szechwanensis	ZRL20151545	China	N/A	LSU	TEF1	
Turbinellus szechwanensis	ZRL20231876	China	ITS	N/A	N/A	
Turbinellus szechwanensis	HKAS 51324	China: Tibet	OQ858472	OQ858544	OQ847630	
Turbinellus szechwanensis	HKAS 68200	China: Yunnan	OQ858481	OQ858553	N/A	
Turbinellus szechwanensis	HKAS 76579	China: Gansu	OQ858483	OQ858555	OQ847640	
Turbinellus szechwanensis	HKAS 77970	China: Hubei	OQ858485	OQ858557	OQ847642	
Turbinellus szechwanensis	HKAS 77988	China: Hubei	OQ858486	OQ858558	OQ847643	
Turbinellus szechwanensis	HKAS 82602	China: Yunnan	OQ858479	OQ858551	OQ847637	
Turbinellus szechwanensis	HKAS 82614	China: Yunnan	OQ858476	OQ858548	OQ847634	
Turbinellus szechwanensis	HKAS 93982	China: Sichuan	OQ858482	OQ858554	OQ847639	
Turbinellus szechwanensis	HKAS 94040	China: Tibet	OQ858473	OQ858545	OQ847631	
Turbinellus szechwanensis	HKAS 99484	China: Sichuan	OQ858484	OQ858556	OQ847641	
Turbinellus szechwanensis	HKAS 101035	China: Tibet	OQ858475	OQ858547	OQ847633	
Turbinellus szechwanensis	HKAS 116137	China: Tibet	OQ858478	OQ858550	OQ847636	
Turbinellus szechwanensis	HKAS 116225	China: Tibet	OQ858480	OQ858552	OQ847638	
Turbinellus szechwanensis	HKAS 122959	China: Yunnan	OQ858474	OQ858546	OQ847632	
Turbinellus szechwanensis	HKAS 122960	China: Yunnan	OQ858477	OQ858549	OQ847635	
Turbinellus szechwanensis	ZRL2015526	China	N/A	LSU	TEF1	
Turbinellus szechwanensis	ZRL20161519	China	ITS	LSU	N/A	
Turbinellus szechwanensis	ZRL20190389	China	ITS	LSU	TEF1	

 Table 4.3 (continued)

Tayon	Taxon Voucher Location		GenBank Accession Number			
Taxon	voucher	Location	ITS	nrLSU	tef1a	
Turbinellus szechwanensis	ZRL20190579	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20190616	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20190624	China	ITS	LSU	N/A	
Turbinellus szechwanensis	ZRL20190662	China	ITS	LSU	N/A	
Turbinellus szechwanensis	ZRL20190728	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20190729	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20191464	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20191601	China	ITS	LSU	N/A	
Turbinellus szechwanensis	ZRL20200481	China	N/A	LSU	TEF1	
Turbinellus szechwanensis	ZRL20200489	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20200492	China	N/A	LSU	TEF1	
Turbinellus szechwanensis	ZRL20200507	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20200574	China	ITS	LSU	N/A	
Turbinellus szechwanensis	ZRL20210734	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20210798	China	ITS	LSU	TEF1	
Furbinellus szechwanensis	ZRL20210808	China	ITS	LSU	TEF1	
Furbinellus szechwanensis	ZRL20211011	China	ITS	LSU	TEF1	
Furbinellus szechwanensis	ZRL20211040	China	N/A	LSU	TEF1	
Furbinellus szechwanensis	ZRL20211047	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20211102	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20220310	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20220444	China	ITS	LSU	TEF1	
Turbinellus szechwanensis	ZRL20221033	China	ITS	LSU	N/A	
Turbinellus szechwanensis	ZRL20221239	China	ITS	LSU	N/A	
Turbinellus tomentosipes	HKAS 70002	China: Yunnan	OQ858456	OQ858524	N/A	
Turbinellus tomentosipes	HKAS 71332	China: Yunnan	OQ858455	OQ858523	N/A	
Turbinellus tomentosipes	HKAS 87066	China: Yunnan	OQ858454	OQ858522	OQ8476	
Turbinellus tomentosipes	HKAS 95222	China: Yunnan	OQ858457	OQ858525	OQ8476	
Turbinellus tomentosipes	HKAS 113156	China: Yunnan	OQ858453	OQ858521	OQ8476	
Turbinellus verrucosus	HKAS 54742	China: Yunnan	OQ858467	OQ858539	OQ8476	
Turbinellus verrucosus	HKAS 55476	China: Yunnan	OQ858471	OQ858543	N/A	
Turbinellus verrucosus	HKAS 56888	China: Yunnan	OQ858468	OQ858540	OQ8476	
Turbinellus verrucosus	HKAS 74860	China: Yunnan	N/A	OQ858538	N/A	
Turbinellus verrucosus	HKAS 87257	China: Yunnan	OQ858470	OQ858542	OQ8476	
Turbinellus verrucosus	HKAS 97554	China: Yunnan	N/A	OQ858537	OQ8476	
Turbinellus verrucosus	HKAS 101185	China: Yunnan	N/A	OQ858536	OQ8476	
Turbinellus verrucosus	HKAS 122949	China: Yunnan	OQ858469	OQ858541	OQ8476	
Turbinellus yunnanensis	HKAS 18142	China: Yunnan	OQ858460	OQ858528	OQ8476	

Table 4.3 (continued)

Taxon	Voucher	Location	GenBank Accession Num		umber	
Taxon	voucher	Location	ITS	nrLSU	tef1a	
Turbinellus yunnanensis	HKAS 52916	China: Yunnan	OQ858462	OQ858530	OQ847618	
Turbinellus yunnanensis	HKAS 79785	China: Yunnan	OQ858461	OQ858529	OQ847617	
Turbinellus yunnanensis	HKAS 87913	China: Yunnan	OQ858459	OQ858527	OQ847615	
Turbinellus yunnanensis	HKAS 122962	China: Yunnan	OQ858458	OQ858526	OQ847614	

**Note** "\*" following a species name indicates that the specimen is the holotype of that species; "N/A" indicates sequence miss. The newly generated sequences are shown in bold.



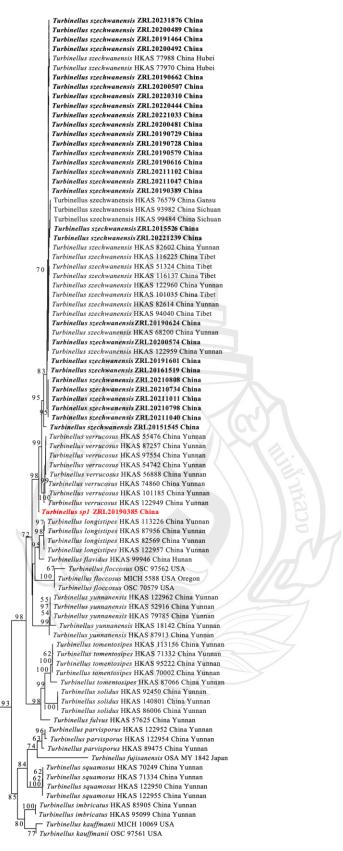


Figure 4.9 ITS + nrLSU + TEF1 phylogeny tree of Gomphus, Turbinellus and Gloeocantharellus

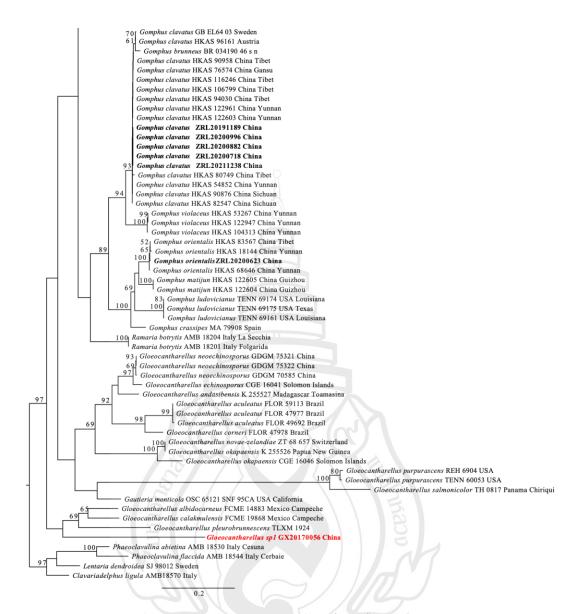


Figure 4.9 (continued)

## 4.2.2 Taxonomy

Turbinellus subflavidus X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.10

**Etymology.** The epithet "subflavidus" refers to the Latin adjective, subflavidus, referring to the yellowish basidioma.

**Holotype.** China. Sichuan Province, Liangshan city, 21 August 2019, collected by R.L. Zhao (**ZRL2010385**).

**Diagnosis.** Differs from other *Turbinellus* species in pale orange to light orange basidiome.

**Description.** Basidiome 3.5–4.5 cm in heigh. Tapering downward with a single pileus. Pileus diameter 1.5–2.5 cm, funnel-shaped with a central depression, light yellow (3A4) to orange-yellow (4A4–6), sparsely covered in small appressed scales arranged in a somewhat radial manner; margin uplifted and undulating. Hymenium creamy (3A2–3), wrinkled and irregularly reticulate, extending onto the upper stipe; sparse, reaching the upward margin. Stipe length 1.5–1.8 cm, width 0.4–0.6 cm, nearly cylindrical, solid, orange-yellow (4A4); smooth above the base; pliable context, thin, creamy (3A2), not changing when exposed; white basal mycelium (1A1).

*Basidiospores* 12–14 × 5.5–8 μm; Q = 1.9–2.0; Qm =  $1.9 \pm 0.2$ ; elliptic-fusiform, inequilateral side view with a distinct suprahilar depression; ellipsoid ventrally; non-amyloid; light yellowish in KOH; strongly verrucose, coarse warts. *Basidia* 60–80 × 12–18 μm; clavate, with 2–4 spores; sterigmata 5–10 μm long. *Hymenial cystidia* absent. *Pileipellis* comprises many inflated hyphae (7–30 μm in diameter) with ampulliform swellings, along with some uninflated hyphae (3–6 μm in diameter); simple branching; constricted at septa; repent; more or less arranged parallel to the pileal context; abundant gloeoplerous hyphae, yellowish in water.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

#### Additional material examined. N/A

**Notes.** *Turbinellus subflavidus* is distinguished by its basidiome color, from pale orange to orange-yellow, which clearly differentiates it from other species. Additionally, its relatively large spores make it easily identifiable.

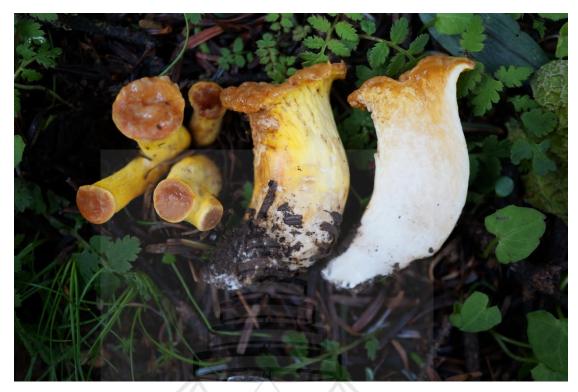


Figure 4.10 The Basidiome of Turbinellus subflavidus

Gloeocantharellus flavidus X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.11

Etymology. The epithet "flavidus" refers to the yellowish basidioma

**Holotype.** China. Guangxi Province, Shiwandashan, 21 August 2017, collected by R.L. Zhao (GX20170056).

**Diagnosis.** Differs from other *Gloeocantharellus* species in basidiome exhibits color change upon bruising.

**Description.** Basidiome 3–5.5 cm in height, showing color change upon bruising. Pileus single, tapering downward, 1.2–2.1 cm in diameter, funnel-shaped with a central depression, ranging from light yellow (3A4) to orange-yellow (4A4–6). Surface sparsely covered with small appressed scales, somewhat radially arranged; margin uplifted and undulate. Hymenium creamy (3A2–3), wrinkled, irregularly reticulate, extending onto the upper stipe; sparse and reaching the upward margin. Stipe 1.5–1.7 cm long, 0.5–0.8 cm wide, nearly cylindrical, solid, orange-yellow (4A4), smooth above the base; pliable context, thin (0.1–0.2 cm), creamy (3A2), unchanged

upon exposure; basal mycelium white (1A1).

Basidiospores 14–18 × 6–8  $\mu$ m; Q = 1.8–2.1; Qm = 1.9  $\pm$  0.1; elliptic-fusiform, inequilateral in side view with a distinct suprahilar depression; ellipsoid in ventral view; non-amyloid; light yellowish in KOH; strongly verrucose with coarse warts. Basidia 55–100 × 10–15  $\mu$ m, clavate, with 2–4 spores; sterigmata 5–10  $\mu$ m long. Hymenial cystidia absent.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

#### Additional material examined. N/A

Notes. Gloeocantharellus flavidus showing color change upon bruising



Figure 4.11 The Basidiome of Gloeocantharellus flavidus

## Gomphus orientalis R.H. Petersen & M. Zang 1996

Figure 4.12

#### Description.

Basidiome up to 17 cm in height, unipileate at the base and becoming merismatoid with 5–15 subpilei. *Pileus* irregularly fan-shaped, up to 15 cm wide; surface ranges from orangish brown to vinaceous brown to creamy violet; either

glabrous or covered in minute patches towards the crenate or undulate margin. *Hymenium* gray-violet to violet or vinaceous brown, wrinkled, irregularly reticulate to nearly poroid, extending onto the upper stipe. *Stipe* off-white to pale violet, glabrous at the apex but tomentose to hispid towards the white base; context off-white.

*Basidiospores* (9–) 10–15 (–17) × (4–) 5–7.5 μm, oblong in side view, ellipsoid in ventral view; non-amyloid with verrucose ornamentation. *Basidia* 60–95 × 8.5–12 μm, clavate, (2–) 4-spored. *Pileipellis* composed of uninflated hyphae, with pileocystidia 3–4.5 (–5.5) μm in diameter, protruding 50–120 μm from the surface.

Habitat and distribution. Scattered, gregarious or cespitose on the ground, known from China.

**Additional material examined.** China. Sichuan Province, Ganzi city, 25 August 2020, collected by R.L. Zhao (**ZRL20200623**).

**Notes.** G. orientalis has a grayish violet context, larger basidiospores (15–18  $\times$  7–9  $\mu$ m) and the rare presence of pileocystidia in pileipellis.



Figure 4.12 The Basidiome of Gomphus orientalis

#### Gomphus clavatus (Pers.) Gray 1821

Figure 4.13

**Description.** Basidiome up to 16 cm, initially presenting a single pileus at the base which subsequently develops into a merismatoid structure with 6–14 subpilei. Pileus spans up to 15 cm in width, demonstrating an irregularly fan-shaped morphology. Its surface exhibits a color gradient from orangish brown to vinaceous brown, progressing to creamy violet, and may be glabrous or display minute patches near the crenate or undulate margin. Hymenium, characterized by a gray-violet to violet or vinaceous brown hue, displays a wrinkled texture and an irregularly reticulate to almost poroid pattern that extends to the upper stipe region. Stipe itself varies from off-white to pale violet, with a glabrous apex transitioning to a tomentose or hispid texture towards the white base. The internal stipe context is off-white.

Basidiospores  $10-15 \times 5-7.5$  μm, appearing oblong in lateral view and ellipsoid in ventral perspective. These spores are non-amyloid and exhibit a verrucose surface ornamentation. Basidia, clavate, measuring  $60-95 \times 8.5-12$  μm, and predominantly 4-spored, although occasionally 2-spored forms are observed. Pileipellis consists of uninflated hyphae, with pileocystidia ranging from 3–4.5 (up to 5.5) μm in diameter, projecting 50-120 μm from the pileus surface. Clamp connections, up to 12 μm in width, are observed throughout the basidioma, facilitating inter-hyphal connectivity.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

**Additional material examined.** China. Sichuan Province, Ganzi city, 25 August 2020, collected by R.L. Zhao (**ZRL20200996**).

**Notes.** This species has been documented in southwestern China, historically identified as either *G. orientalis* or *G. clavatus*. A comprehensive study, incorporating both molecular and morphological analyses of 13 specimens from this group, substantiated the presence of *G. clavatus* in this region. Misidentification with *G. orientalis* was common due to overlapping features such as merismatoid basidiomata, an irregularly fan-shaped pileus, and a purplish hymenium. Nonetheless, distinctions exist: *G. clavatus* is characterized by an off-white context, smaller basidiospores measuring  $10-15 \times 5-7.5 \,\mu\text{m}$ , and the frequent occurrence of pileocystidia in the pileipellis. Conversely, *G. orientalis* exhibits a grayish violet context, larger basidiospores ( $15-18 \times 7-9 \,\mu\text{m}$ ), and infrequent

pileocystidia. Phylogenetic analysis clearly delineates *G. orientalis* as an independent lineage from *G. clavatus*.



Figure 4.13 The Basidiome of Gomphus clavatus

# Turbinellus szechwanensis (R.H. Petersen) Xue Ping Fan & Zhu L. Yang 2023

Figure 4.14

**Description.** Basidiome height of 14–25 cm, occasionally reaching up to 30 cm; structure is unipileate and tapers downwards. Pileus up to 17 cm in diameter, adopts a funnel shape. Its surface is colored orange-ochre to brownish orange and has a pellicle-like texture. Hymenium surface, clay-colored and densely configured, features strong wrinkles and an irregularly reticulate pattern that extends longitudinally to the upper stipe. Stipe is roughly cylindrical, hollow, and tapers to a rounded base. Coloration transitions from off-white in the upper part to reddish towards the base, with a glabrous surface above the base and a white internal context.

Basidiospores  $16-19.5 \times 7.5-11$  µm, oblong and inequilateral in side view, featuring a distinct suprahilar depression, and ellipsoid in ventral view. The spores are non-amyloid and turn a dull ochre when treated with KOH; their surface is distinctly

ornamented with very coarse ridges or warts. *Basidia*, clavate,  $85-110 \times 10-13$  µm, and typically bear 2–4 spores. No hymenial cystidia are present.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

**Additional material examined.** China. Sichuan Province, Ganzi city, 25 August 2020, collected by J.X. Li & B. Cao & R.L. Zhao (**ZRL20200489**).

**Notes.** Gomphus floccosus (Schwein.) Singer, previously referred to as Cantharellus floccosus Schwein., was first recorded in China by Patouillard in 1895 following a collection by M. Farges in Tchen-KéouTin (now Kangding) in 1894. This specimen was initially regarded as a distinct species, Gomphus szechwanensis, by Petersen and later by Zang et al. However, Giachini and subsequently Giachini and Castellano argued for synonymizing G. szechwanensis with T. floccosus, a species originally described in North America, based on morphological similarities. Despite these classifications, our research combining morphological and molecular data recognizes it as distinct from T. floccosus, prompting the proposal of a new combination and the designation of an epitype to clarify the species concept.

According to Petersen, *T. szechwanensis* is notable for its large basidioma, often exceeding 30 cm in height, with a pileus up to 17 cm in diameter, characterized by a pellicle-like surface and basidiospores that are larger and coarsely ornamented. In contrast, *T. floccosus* features significantly smaller basidiospores, as reported by Arora and Bessette et al., and differs substantially in morphological details from *T. szechwanensis*.

Phylogenetically, *T. szechwanensis* is closely related to *T. verrucosus*, yet distinguishable by the latter's smaller stature and narrower pileus with verrucous scales, along with smaller basidiospores. Ecologically, *T. szechwanensis* is predominantly found at higher altitudes of 3200–4000 meters in forests dominated by Abies, Picea, and Pinus densata, unlike its phylogenetic relatives that inhabit lower elevations.

As of the latest research, only *T. szechwanensis* and *T. flavidus* have been identified in the central regions of China, underscoring the unique ecological and geographic distribution within the genus.



Figure 4.14 The Basidiome of Turbinellus szechwanensis

#### 4.3 Ramaria

### 4.3.1 Phylogenetic Analyses

In this study, 376 sequences derived from three loci (ITS, nrLSU, mtSSU) were used to reconstruct phylogenetic trees of *Ramaria*, including 273 for ITS, 75 for nrLSU and 28 for mtSSU representing 134 species from *Ramaria*. Newly generated 177 sequences, including 75 for ITS, 75 for nrLSU and 28 for mtSSU representing 26 species from *Ramaria*. (Table 4.4). The ITS included sequences from 282 specimens representing 134 species from *Ramaria*, and *Mutinus elegans* (Mont.) E. Fisch. 1888, *Phallus dongsun* T.H. Li, T. Li, Chun Y. Deng, W.Q. Deng & Zhu L. Yang were chosen as outgroup based on previous phylogenetic studies. The best-fit evolutionary models selected were GTR+I+G (ITS1+ITS2). These models were applied in Bayesian analyses for the combined dataset.

The phylogeny topologies of *Ramaria* based on ITS sequences respectively with ML bootstrap support values  $\geq 70\%$  are shown in Figure 4.15.

Table 4.4 GenBank accession number of specimen used in this study for Ramaria

Taxon	Voucher	Country	ITS	LSU	SSU
Mutinus elegans	ME.BST	USA	OQ694424	N/A	N/A
Phallus dongsun	GDGM 75402	China	MN307397	N/A	N/A
Ramaria abetonensis	MCVE 28638	Italy	KT357472	N/A	N/A
Ramaria abetonensis	AH 48006	Spain	MH322661	N/A	N/A
Ramaria acris	strain UT-36052-T	USA	OM238175	N/A	N/A
Ramaria acrisiccescens	OSC 112057	USA	KY354738	N/A	N/A
Ramaria acrisiccescens	RLE2005-100	USA	KY986440	N/A	N/A
Ramaria acrisiccescens	OSC 87690	USA	AY102857	N/A	N/A
Ramaria acrisiccescens	OSC 87692	USA	AY102858	N/A	N/A
Ramaria admiratia	TFB14450	USA	KJ416133	N/A	N/A
Ramaria admiratia	TENN 69114	USA	KJ416133	N/A	N/A
Ramaria albidoflava	AMB 18606	France	MT452502	N/A	N/A
Ramaria albidoflava	ZT Myc 55621	Spain	MK493033	N/A	N/A
Ramaria amyloidea	OSC 96384	USA	EU697257	N/A	N/A
Ramaria amyloidea	OSC 66957	USA	EU697258	N/A	N/A
Ramaria anziana	TENN 43401	New Zealand	MF564295	N/A	N/A
Ramaria apiculata	MA-Fungi 48064	Spain	AJ408385	N/A	N/A
Ramaria apiculata	HC-PNNT-263	Mexico	KT307869	N/A	N/A
Ramaria araiospora	OSC 104945	USA	EU669243	N/A	N/A
Ramaria araiospora	OSC 134758	USA	KY354758	N/A	N/A
Ramaria atractospora	AMB 18598	Spain	MT055979	N/A	N/A
Ramaria aurantiisiccescens	CB 08113	Mexico	KT307875	N/A	N/A
Ramaria aurantiisiccescens	HC-PNNT-250	Mexico	KT307873	N/A	N/A
Ramaria aurantiisiccescens	OSC 97400	USA	KP658121	N/A	N/A
Ramaria aurantiisiccescens	OSC 112055	USA	KY354744	N/A	N/A
Ramaria aurea	MA-Fungi 48120	Germany	AJ408387	N/A	N/A
Ramaria barenthalensis	130822MFBPC356	China	MW554136	N/A	N/A
Ramaria barenthalensis	AMB 17386	Spain	MK493039	N/A	N/A
Ramaria bataillei	MA-Fungi 48075	Spain	AF441082	N/A	N/A
Ramaria boreimaxima	H, Kytovuori 96-525	Finland	KJ464996	N/A	N/A
Ramaria botrytis	SNF 213	USA	AF377055	N/A	N/A
Ramaria botrytis	DGUM 29001	South Korea	AY588247	N/A	N/A
Ramaria botrytis	DARD-112	India	KJ184344	N/A	N/A
Ramaria botrytis	MA-Fungi 47951	Spain	AJ292294	N/A	N/A
Ramaria botrytis	AMB 18201	Italy	KY626151	N/A	N/A
Ramaria botrytis	NIFoS1018	Korea	MF421105	N/A	N/A
Ramaria botrytis	JL 25082000	BG	ITS	LSU	N/A
Ramaria brunneolilacina	AMB 18584	Spain	MT055963	N/A	N/A
Ramaria brunneolilacina	AMB 18591	Spain	MT055903	N/A	N/A
Ramaria orunneoniacina Ramaria calvodistalis	TENN 69095	USA	KJ416132	N/A	N/A
Ramaria canobrunnea	ZT Myc 54981	Spain	MT055899	N/A	N/A
Ramaria cartilaginea	WTU 43208	USA	KY986436	N/A	N/A
Ramaria cartitaginea Ramaria caulifloriformis	BEP01 (TENN)	USA	MF755270	N/A	N/A
Ramaria cedretorum	MA-Fungi 48074	Spain	AJ408353	N/A	N/A

Table 4.4 (continued)

Taxon	Voucher	Country	ITS	LSU	SSU
Ramaria cedretorum	ZT Myc, Schild 1902	Italy	AJ408392	N/A	N/A
Ramaria celerivirescens	Isolate 137.5	USA	DQ365647	N/A	N/A
Ramaria celerivirescens	OSC 1064227	USA	EU525995	N/A	N/A
Ramaria cistophila	AH 47781	Spain	MF564292	N/A	N/A
Ramaria cistophila	AH 47765	Spain	MF564293	N/A	N/A
Ramaria claviramulata	WTU-F-043055	USA	KX574472	N/A	N/A
Ramaria claviramulata	OSC 1064080	USA	EU525991	N/A	N/A
Ramaria comitis	MA-Fungi 47970	Spain	AF442095	N/A	N/A
Ramaria comitis	AH 48341	Portugal	MH322667	N/A	N/A
Ramaria conjunctipes	OSC 96488	USA	EU846302	N/A	N/A
Ramaria conjunctipes	OSC 119381	USA	EU846304	N/A	N/A
Ramaria conjunctipes	OSC 105346	USA	EU846301	N/A	N/A
Ramaria conjunctipes	OSC 110613	USA	KC346861	N/A	N/A
Ramaria coulterae	TENN 45771	USA	KX574462	N/A	N/A
Ramaria coulterae	OSC 70059	USA	KY354736	N/A	N/A
Ramaria cyaneigranosa	OSC 140651	USA	JX310397	N/A	N/A
Ramaria cyaneigranosa	WTU-F-043056	USA	KX574465	N/A	N/A
Ramaria cystidiophora	UBC F15182	Canada	DQ384590	N/A	N/A
Ramaria cystidiophora	UBC OGTR0419s	Canada	EU597077	N/A	N/A
Ramaria dendrophora	GM19094	Patagonia	OP177715	N/A	N/A
Ramaria dendrophora	GM20020	Patagonia	OP177716	N/A	N/A
Ramaria edwinii	ZT Myc 54975	Spain	MK493034	N/A	N/A
Ramaria fagetorum	MA-Fungi 48117	Spain	AJ408362	N/A	N/A
Ramaria fagetorum	MA-Fungi 48118	Spain	AJ408363	N/A	N/A
Ramaria fennica	MA-Fungi 47996	Spain	AJ408352	N/A	N/A
Ramaria flava	MA-Fungi 48072	Spain	AJ408367	N/A	N/A
Ramaria flava	ZT Myc 55613	Germany	KY626146	N/A	N/A
Ramaria flavescens	TENN 36864	Germany	KY626140	N/A	N/A
Ramaria flavescens	ZT Myc, Schild 1517	Slovenia	MH322680	N/A	N/A
Ramaria flavescens	FD_SN_1132920	BG	ITS	LSU	N/A
Ramaria flavescentoides	MH-2013	Pakistan	MG760617	N/A	N/A
Ramaria flavicingula	AMB 18607	France	MT452503	N/A	N/A
Ramaria flavigelatinosa	MA-Fungi 48083	Spain	AJ408357	N/A	N/A
Ramaria flavinedulis	GM19056	Patagonia	OP177717	N/A	N/A
Ramaria flavinedulis	GM19117	Patagonia	OP177718	N/A	N/A
Ramaria flavissima	ZT Myc 57157	Spain	MT055966	N/A	N/A
Ramaria flavobrunnescens	iNat63604655	USA	ON479744	N/A	N/A
Ramaria flavoides	MA-Fungi 47972	Spain	AJ408380	N/A	N/A
Ramaria flavoides	MA-Fungi 47971	Spain	AJ408381	N/A	N/A
Ramaria flavosalmonicolor	ZT Myc 54973	Switzerland	KY626135	N/A	N/A
Ramaria flavosalmonicolor	AH 47740	Spain	MH322681	N/A	N/A
Ramaria flavosaponaria	AHB3	USA	MT196969	N/A	N/A
Ramaria formosa	OSC 1064203	USA	EU525994	N/A	N/A
Ramaria formosa	MA-Fungi 48087	Spain	AJ408393	N/A	N/A

Table 4.4 (continued)

Taxon	Voucher	Country	ITS	LSU	SSU
Ramaria formosa	AMB 18199	Italy	KY626155	N/A	N/A
Ramaria fumigata	AH:47767	Spain	MH322669	N/A	N/A
Ramaria fumigata	NIFoS2370	Korea	KX814451	N/A	N/A
Ramaria fumigata	MAs_2004_65	BG	ITS	LSU	N/A
Ramaria fumosiavellanea	WTU-F-063048	USA	MK169345	N/A	N/A
Ramaria gelatiniaurantia	OSC 65737	USA	KP658144	N/A	N/A
Ramaria gelatiniaurantia	WTU-F-063049	USA	KX574474	N/A	N/A
Ramaria gracilioides	AMB 18543	Italy	MT055925	N/A	N/A
Ramaria gracilis	-	Mexico	EU258553	N/A	N/A
Ramaria gracilis	OSC 134659	USA	JX310399	N/A	N/A
Ramaria gracilis	ZRL20151444	China	ITS	LSU	N/A
Ramaria gracilis	ZRL20160164	China	ITS	LSU	SSU
Ramaria gracilis	ZRL20160174	China	ITS	LSU	SSU
Ramaria gracilis	ZRL20160271	China	ITS	LSU	SSU
Ramaria gracilis	ZRL20160323	China	ITS	LSU	SSU
Ramaria gracilis	ZRL20220939	China	ITS	LSU	SSU
Ramaria gracilis	ZRL20220940	China	ITS	LSU	SSU
Ramaria ichnusensis	AMB 18582	Italy	MT055961	N/A	N/A
Ramaria ignicolor	MA-Fungi 47978	Spain	AJ408386	N/A	N/A
Ramaria inedulis	isolate 12648	Chile	OP177723	N/A	N/A
Ramaria inedulis	GM19047	Argentina	OP177722	N/A	N/A
Ramaria inquinata	ZT Myc 55614	Slovenia	KY626147	N/A	N/A
Ramaria intimorosea	ZT Myc 57155	Slovenia	KY626148	N/A	N/A
Ramaria kafaensis	FR-0246021	Äthiopien	MT542981	N/A	N/A
Ramaria lacteobrunnescens	MA-Fungi 48470	Spain	MH322682	N/A	N/A
Ramaria largentii	OSC 109294	USA	KP658126	N/A	N/A
Ramaria largentii	OSC 67012	USA	KP658130	N/A	N/A
Ramaria largentii	ZRL20231337	China	ITS	N/A	N/A
Ramaria leptoformosa	SAT-21-290-06	USA	OP205430	N/A	N/A
Ramaria leptoformosa	WTU-F-063036	USA	MN809535	N/A	N/A
Ramaria longispora	iNat63913396	USA	ON479741	N/A	N/A
Ramaria longispora	iNAT:17234752	USA	OM522294	N/A	N/A
Ramaria lorithamnus	PDD 95771	New Zealand	HQ533039	N/A	N/A
Ramaria lorithamnus	ZRL20150133	China	ITS	LSU	SSU
Ramaria lutea	FD SN 1167901	BG	ITS	LSU	N/A
Ramaria luteoaurantiaca	AMB 18525	Italy	MT055906	N/A	N/A
Ramaria luteovernalis	MCVE 28637	Italy	KT357471	N/A	N/A
Ramaria maculatipes	OSC 69937	USA	KP658151	N/A	N/A
Ramaria maculatipes	WTU-F-063042	USA	KX574476	N/A	N/A
Ramaria magnifica	MA-Fungi 26386	Spain	AJ408354	N/A	N/A
Ramaria magnipes	WTU 063057	Spain	MK493040	N/A	N/A
Ramaria magnipes	WTU-F-063057	USA	MK169351	N/A	N/A
Ramaria magnipes Ramaria mediterranea	MA-Fungi 39877	Spain	AJ408370	N/A	N/A
Ramaria obtusissima	TENN 69158	USA	KJ655554	N/A	N/A

Table 4.4 (continued)

Taxon	Voucher	Country	ITS	LSU	SSU
Ramaria ossolana	AMB 1852	Italy	MT055908	N/A	N/A
Ramaria pallida	IZS19097028/8-94	Italy	MZ005501	N/A	N/A
Ramaria pallida	AMB n. 18211	Italy	MF288931	N/A	N/A
Ramaria pallida	ZRL20200675	China	ITS	LSU	N/A
Ramaria pallida	ZRL20200740	China	ITS	LSU	N/A
Ramaria pallida	ZRL20211294	China	ITS	LSU	SSU
Ramaria pallidissima	ZT Myc 55616	Italy	MT055967	N/A	N/A
Ramaria pallidosaponaria	TENN 36849	Italy	KY626142	N/A	N/A
Ramaria parabotrytis	ZT Myc 58930	Spain	MH216040	N/A	N/A
Ramaria parabotrytis	AMB n. 18281	Spain	MH216039	N/A	N/A
Ramaria paraconcolor	AMB 18546	Italy	MT055928	N/A	N/A
Ramaria patagonica	GM19095	Argentina	OP177714	N/A	N/A
Ramaria patagonica	GM19106	Argentina	OP177713	N/A	N/A
Ramaria pinicola	isolate 139.1	USA	DQ365649	N/A	N/A
Ramaria polonica	L 0053314	Spain	MT055947	N/A	N/A
Ramaria praecox	AH 47804	Spain	MF564298	N/A	N/A
Ramaria primulina	AMB 17480	Spain	MK493043	N/A	N/A
Ramaria primulina	TENN 038182	Spain	MK493042	N/A	N/A
Ramaria pseudoflava	AMB 17392	Spain	MK493046	N/A	N/A
Ramaria pseudoflava	AMB 17390	Spain	MK493045	N/A	N/A
Ramaria pseudogracilis	MA-Fungi 48067	Spain	AJ408384	N/A	N/A
Ramaria pumila	MA-Fungi 47983	Spain	AJ408388	N/A	N/A
Ramaria rainierensis	KA12-1702	South Korea	KR673634	N/A	N/A
Ramaria rainierensis	WTU-F-063041	USA	KX574466	N/A	N/A
Ramaria rasilispora	S12B1602	USA	KU574735	N/A	N/A
Ramaria rasilispora	S12B1601	USA	KU574736	N/A	N/A
Ramaria rasilisporoides	iNat62919302	USA	ON479762	N/A	N/A
Ramaria rasilisporoides	WTU-F-043029	USA	MK169346	N/A	N/A
Ramaria rielii	AMB n. 17268	Italy	MK100905	N/A	N/A
Ramaria rielii	AMB n. 17163	Italy	MK046801	N/A	N/A
Ramaria rubella	OSC 140659	USA	JX310405	N/A	N/A
Ramaria rubella	OSC 110600	USA	KC346860	N/A	N/A
Ramaria rubiginosa	Isolate 170.3	USA	DQ365650	N/A	N/A
Ramaria rubribrunnescens	CB 08258	Mexico	KT307881	N/A	N/A
Ramaria rubribrunnescens	CB 08392	Mexico	KT307882	N/A	N/A
Ramaria rubribrunnescens	OSC 119676	USA	EU652352	N/A	N/A
Ramaria rubribrunnescens	OSC 140575	USA	JX310406	N/A	N/A
Ramaria rubribrunnescens	OSC 66051	USA	KY354750	N/A	N/A
Ramaria rubribrunnescens	OSC 131274	USA	EU837231	N/A	N/A
Ramaria rubribrunnescens	OSC 105345	USA	KP658107	N/A	N/A
Ramaria rubricarnata	iNat82256995	USA	ON975053	N/A	N/A
Ramaria rubricarnata	WTU F 043061	Spain	MT055913	N/A	N/A
Ramaria rubrievanescens	AH 47481	Spain	MH322689	N/A	N/A
Ramaria rubrievanescens	OSC 134654	USA	JX310408	N/A	N/A

Table 4.4 (continued)

Taxon	Voucher	Country	ITS	LSU	SSU
Ramaria rubrievanescens	OSC 140637	USA	JX310409	N/A	N/A
Ramaria rubripermanens	OSC 130793	USA	JX310412	N/A	N/A
Ramaria rubripermanens	OSC 134755	USA	KY510828	N/A	N/A
Ramaria rufescens	AMB 18554	Spain	MT055936	N/A	N/A
Ramaria rufescens	AMB 18608	France	MT452504	N/A	N/A
Ramaria sandaracina	OSC 1064136	USA	EU525992	N/A	N/A
Ramaria sandaracina	WTU-F-063058	USA	KX574484	N/A	N/A
Ramaria sanguinea	MA-Fungi 48080	Spain	AJ408373	N/A	N/A
Ramaria sanguinea	AMB 18200	Italy	KY626159	N/A	N/A
Ramaria sardiniensis	ZT Myc 57149	Italy	KY626138	N/A	N/A
Ramaria sp.	ZRL20160741	China	N/A	LSU	SSU
Ramaria sp.	ZRL20161511	China	ITS	LSU	SSU
Ramaria sp.	ZRL20200443	China	N/A	LSU	N/A
Ramaria sp.	ZRL20200473	China	N/A	LSU	N/A
Ramaria sp.	ZRL20200948	China	N/A	LSU	SSU
Ramaria sp.	ZRL20200990	China	N/A	LSU	N/A
Ramaria sp.	ZRL20201005	China	N/A	LSU	N/A
Ramaria sp.	ZRL20201156	China	N/A	LSU	N/A
Ramaria sp.	ZRL20201229	China	N/A	LSU	N/A
Ramaria sp.	ZRL20210958	China	ITS	LSU	N/A
Ramaria sp.	ZRL20211292	China	ITS	LSU	N/A
Ramaria sp.	ZRL20221278	China	N/A	LSU	N/A
Ramaria sp.	ZRL20231531	China	ITS	N/A	N/A
Ramaria sp1	ZRL20161335	China	ITS	LSU	N/A
Ramaria sp1	ZRL20161415	China	ITS	LSU	N/A
Ramaria sp10	ZRL20211306	China	ITS	LSU	SSU
Ramaria sp10	ZRL20211328	China	ITS	LSU	N/A
Ramaria sp10	ZRL20211330	China	ITS	LSU	N/A
Ramaria sp11	ZRL20211304	China	ITS	LSU	N/A
Ramaria sp12	ZRL20152266	China	ITS	LSU	N/A
Ramaria sp12	ZRL20201350	China	ITS	LSU	N/A
Ramaria sp12	ZRL20201440	China	ITS	LSU	N/A
Ramaria sp12	ZRL20211327	China	ITS	LSU	SSU
Ramaria sp13	ZRL20201140	China	ITS	LSU	N/A
Ramaria sp13	ZRL20201142	China	ITS	LSU	N/A
Ramaria sp13	ZRL20201196	China	ITS	LSU	N/A
Ramaria sp13	ZRL20201407	China	ITS	LSU	N/A
Ramaria sp13	ZRL20201425	China	ITS	LSU	N/A
Ramaria sp13	ZRL20201425	China	ITS	LSU	N/A
Ramaria sp13	ZRL20211243 ZRL20211251	China	ITS	LSU	N/A
Ramaria sp14	ZRL20211231 ZRL20200747	China	ITS	LSU	N/A
Ramaria sp15	ZRL20200747 ZRL20200110	China	ITS	LSU	N/A
Kamaria sp15 Ramaria sp16	ZRL20200110 ZRL20201128	China	ITS	LSU	SSU
Kamaria sp10 Ramaria sp17	ZRL20201128 ZRL20211333	China	113	LSU	330

Table 4.4 (continued)

Taxon	Voucher	Country	ITS	LSU	SSU
Ramaria sp18	2021073008	Thailand	ITS	LSU	N/A
Ramaria sp18	ZRL20211310	China	ITS	LSU	N/A
Ramaria sp18	ZRL20211311	China	ITS	LSU	N/A
Ramaria sp18	ZRL20211332	China	ITS	LSU	N/A
Ramaria sp18	ZRL20221358	China	ITS	LSU	N/A
Ramaria sp19	ZRL20200548	China	ITS	LSU	N/A
Ramaria sp19	ZRL20200710	China	ITS	LSU	N/A
Ramaria sp19	ZRL20200801	China	ITS	LSU	N/A
Ramaria sp19	ZRL20200872	China	ITS	LSU	N/A
Ramaria sp2	ZRL20161627	China	ITS	LSU	N/A
Ramaria sp3	GX20170642	China	ITS	LSU	SSU
Ramaria sp3	ZRL20120667	China	ITS	LSU	SSU
Ramaria sp3	ZRL20120693	China	ITS	LSU	SSU
Ramaria sp4	ZRL20160212	China	ITS	LSU	SSU
Ramaria sp4	ZRL20180942	China	ITS	LSU	SSU
Ramaria sp4	ZRL20181612	China	ITS	LSU	N/A
Ramaria sp5	ZRL20160984	China	ITS	LSU	SSU
Ramaria sp6	ZRL20160169	China	ITS	N/A	SSU
Ramaria sp7	ZRL20201808	China	ITS	LSU	N/A
Ramaria sp7	ZRL20211319	China	ITS	N/A	N/A
Ramaria sp7	ZRL20211321	China	ITS	LSU	SSU
Ramaria sp7	ZRL20211331	China	ITS	LSU	N/A
Ramaria sp8	ZRL20200278	China	ITS	LSU	N/A
Ramaria sp8	ZRL20231064	China	ITS	N/A	N/A
Ramaria sp9	ZRL20200739	China	ITS	LSU	SSU
Ramaria sp9	ZRL20200954	China	ITS	LSU	SSU
Ramaria spinulosa	MA-Fungi 47990	Spain	AJ292293	N/A	N/A
Ramaria stricta	MA-Fungi 33215	Spain	AF442097	N/A	N/A
Ramaria stricta	MA-Fungi 48068	Spain	AJ408372	N/A	N/A
Ramaria stricta	AF3491	BG	ITS	LSU	N/A
Ramaria stuntzii	OSC 73315	USA	KP658122	N/A	N/A
Ramaria stuntzii	WTU-F-063050	USA	KX574478	N/A	N/A
Ramaria subalpina	KD-14-006	India	KT824242	N/A	N/A
Ramaria subalpina	STO2019428	China	ITS	N/A	SSI
Ramaria subaurantiaca	FLAS:F-70702-MES-4176	USA	OP339697	N/A	N/A
Ramaria subbotrytis	OSC 1064182	USA	EU525993	N/A	N/A
Ramaria subtilis	AH 48020	Spain	MF564300	N/A	N/A
Ramaria subtilis	MA-Fungi 48010	Spain	MF564301	N/A	N/A
Ramaria suecica	MA-Fungi 48078	Spain	AJ408360	N/A	N/A
Ramaria suecica	DG 1218	USA	KU574731	N/A	N/A
Ramaria suecica	ZRL20160362	China	ITS	LSU	SSI
Ramaria suecica	ZRL20202006	China	ITS	LSU	SSU
Ramaria synaptopoda	WTU-F-063037	USA	KX574485	N/A	N/A
Ramaria testaceoflava	4441 SL	USA	KU574732	N/A	N/A

Table 4.4 (continued)

Taxon	Voucher	Country	ITS	LSU	SSU
Ramaria thalliovirescens	AMB 18523	Spain	MT055904	N/A	N/A
Ramaria thalliovirescens	AMB 18519	Spain	MT055898	N/A	N/A
Ramaria thiersii	OSC 47006	USA	KP658143	N/A	N/A
Ramaria thiersii	OSC 112045	USA	KY354761	N/A	N/A
Ramaria thindii	CAL 1786	India	MN046114	N/A	N/A
Ramaria thindii	ZRL20231967	China	ITS	N/A	N/A
Ramaria thindii	ZRL20231982	China	ITS	N/A	N/A
Ramaria tsugina	iNat63859415	USA	ON479753	N/A	N/A
Ramaria tsugina	WTU-F-043052	USA	KX574467	N/A	N/A
Ramaria velocimutans	WTU-F-063045	USA	KX574487	N/A	N/A
Ramaria verlotensis	WTU-F-063047	USA	KX574480	N/A	N/A
Ramaria vinosimaculans	OSC 73528	USA	KP658155	N/A	N/A
Ramaria vinosimaculans	WTU-F-063043	USA	KX574488	N/A	N/A
Ramaria violacea	AMB 18564	Spain	MT055944	N/A	N/A
Ramaria violacea	AMB 18563	Spain	MT055943	N/A	N/A
Ramaria xanthosperma	IMG5012-18	USA	MW680289	N/A	N/A
Ramaria xanthosperma	ALV16744	Spain	MK408625	N/A	N/A
Ramaria_formosa	Mas_2007_23	BG	ITS	LSU	N/A

**Note** "\*" following a species name indicates that the specimen is the holotype of that species; "N/A" indicates sequence miss. The newly generated sequences are shown in bold.

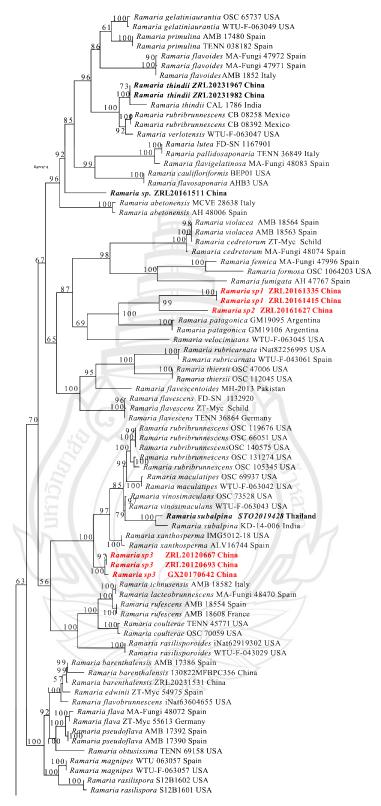


Figure 4.15 ITS phylogeny tree of Ramaria

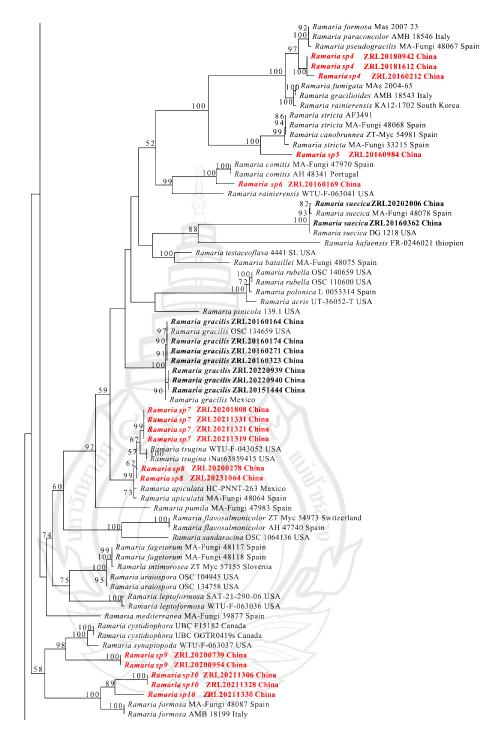


Figure 4.15 (continued)

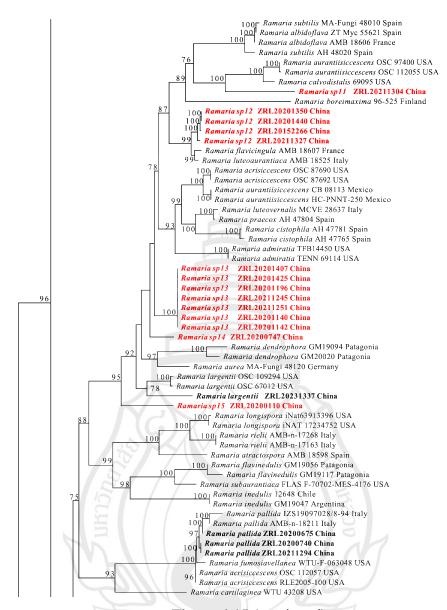


Figure 4.15 (continued)

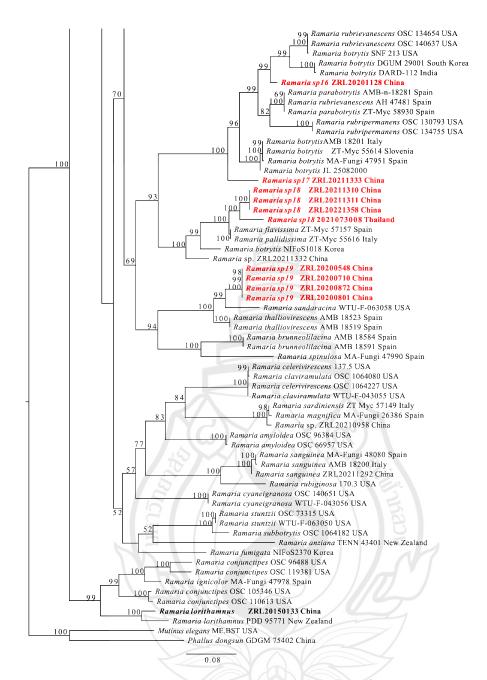


Figure 4.15 (continued)

## 4.3.2 Taxonomy

Ramaria sp1 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.16

**Holotype.** China. Zhejiang Province, Lishui city, 21 August 2016, collected by R.L. Zhao (**ZRL20161335**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.16), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from pale pink when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

Habitat and distribution. Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. China. Zhejiang Province, Lishui city, 21 August 2016, collected by R.L. Zhao (ZRL20161475)

**Notes.** *Ramaria sp1* is characterised by light pink basidiome.



Figure 4.16 The Basidiome of Ramaria sp1

Ramaria sp2 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.17

**Holotype.** China. Zhejiang Province, Lishui city, 21 August 2016, collected by R.L. Zhao (**ZRL20161627**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.17), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from pale pink when young; secondary branches 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; terminal branches from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. Stipe 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. Context fleshy, whitish to slightly brown. Odour & taste not recorded. Macrochemical reactions not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

#### Additional material examined. N/A

**Notes.** *Ramaria sp2* is characterised by light pink basidiome.



Figure 4.17 The Basidiome of Ramaria sp2

Ramaria sp3 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.18

**Holotype.** China. Guangxi Province, 21 August 2017, collected by R.L. Zhao (**GX20170642**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.18), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from pale white when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal

white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. (ZRL20120667). (ZRL20120693).

**Notes.** *Ramaria sp3* is characterised by light white basidiome.



Figure 4.18 The Basidiome of Ramaria sp3

Ramaria sp4 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.19

**Holotype.** China. Gansu Province, Sunan city, 21 August 2018, collected by R.L. Zhao (**ZRL20180942**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.19), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from pale white when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches,

with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe*  $7.8–9.9 \times 4.3–7.3$  mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. (ZRL20181612). (ZRL20160212).

**Notes.** *Ramaria sp4* is characterised by light white basidiome.



Figure 4.19 The Basidiome of Ramaria sp4

Ramaria sp5 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.20

**Holotype.** China. Jilin Province, Yedian city, 21 August 2016, collected by R.L. Zhao (**ZRL20160984**).

**Description.** basidiome 44–57  $\times$  18–32 mm, ramarioid (Figure 4.20), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8  $\times$  7.5 mm, cylindrical to flattened, from pale white when young; *secondary branches* 6.2

× 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

## Additional material examined. N/A

**Notes.** *Ramaria sp5* is characterised by light white basidiome.

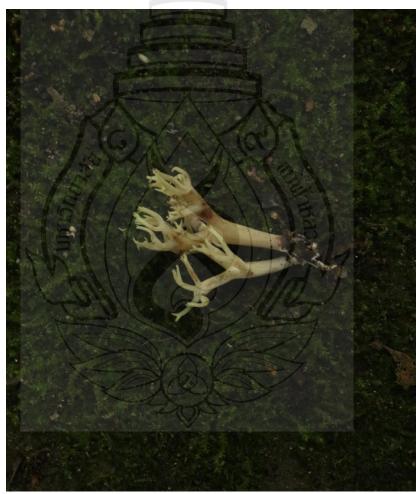


Figure 4.20 The Basidiome of Ramaria sp5

Ramaria sp6 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.21

**Holotype.** China. Heilongjiang Province, Yichun city, 21 August 2016, collected by R.L. Zhao (**ZRL20160169**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.21), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from pale white when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

# Additional material examined. N/A

**Notes.** Ramaria sp6 is characterised by light white basidiome.



Figure 4.21 The Basidiome of Ramaria sp6

Ramaria sp7 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.22

**Holotype.** China. Yunnan Province, Dali city, 21 August 2021, collected by R.L. Zhao (**ZRL20211331**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.22), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from pale white when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

# Additional material examined. (ZRL20211329) (ZRL20211319)

**Notes.** Ramaria sp7 is characterised by light white basidiome.



Figure 4.22 The Basidiome of Ramaria sp7

Ramaria sp8 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.23

**Holotype.** China. Yunnan Province, Dali city, 21 August 2023, collected by R.L. Zhao (**ZRL20231064**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.23), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from light yellow when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. (ZRL20200278)

**Notes.** Ramaria sp8 is characterised by light yellow basidiome.



Figure 4.23 The Basidiome of Ramaria sp8

Ramaria sp9 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.24

**Holotype.** China. Sichuan Province, Ganzi city, 21 August 2020, collected by R.L. Zhao (**ZRL20200739**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.24), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from light yellow when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

## Additional material examined. (ZRL20200954)

**Notes.** Ramaria sp9 is characterised by light yellow basidiome.



Figure 4.24 The Basidiome of *Ramaria sp9* 

Ramaria sp10 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.25

**Holotype.** China. Yunnan Province, Dali city, 21 August 2021, collected by R.L. Zhao (**ZRL20211306**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.25), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from light yellow when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal

white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

## Additional material examined. (ZRL20211328) (ZRL20211330)

**Notes.** *Ramaria sp10* is characterised by light yellow basidiome.



Figure 4.25 The Basidiome of Ramaria sp10

Ramaria sp11 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.26

**Holotype.** China. Yunnan Province, Dali city, 21 August 2021, collected by R.L. Zhao (**ZRL20211304**).

**Description.** basidiome 44–57  $\times$  18–32 mm, ramarioid (Figure 4.26), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8  $\times$  7.5 mm, cylindrical to flattened, from light yellow when young; *secondary branches* 6.2  $\times$  2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches,

with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

## Additional material examined. N/A

**Notes.** Ramaria spl1 is characterised by light yellow basidiome.



Figure 4.26 The Basidiome of Ramaria sp11

Ramaria sp12 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.27

**Holotype.** China. Sichuan Province, Ganzi city, 21 August 2020, collected by R.L. Zhao (**ZRL20201350**).

**Description.** basidiome 44–57  $\times$  18–32 mm, ramarioid (Figure 4.27), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8  $\times$  7.5 mm, cylindrical to flattened, from light yellow when young; *secondary branches* 

6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. (ZRL20201440) (ZRL20152266) (ZRL20211327)

Notes. Ramaria sp12 is characterised by light yellow basidiome.



Figure 4.27 The Basidiome of Ramaria sp12

Ramaria sp13 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.28

**Holotype.** China. Sichuan Province, Ganzi city, 21 August 2020, collected by R.L. Zhao (**ZRL20201407**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.28), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from light yellow when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. (ZRL20201425) (ZRL20201196) (ZRL20211245)

Notes. Ramaria sp13 is characterised by light yellow basidiome.



Figure 4.28 The Basidiome of Ramaria sp13

Ramaria sp14 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.29

**Holotype.** China. Sichuan Province, Yanjiang city, 21 August 2020, collected by R.L. Zhao (**ZRL20200707**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.29), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from orange yellow when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

#### Additional material examined. N/A

**Notes.** *Ramaria sp14* is characterised by orange yellow basidiome.



Figure 4.29 The Basidiome of Ramaria sp14

Ramaria sp15 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.30

**Holotype.** China. Sichuan Province, Yanjiang city, 21 August 2020, collected by R.L. Zhao (**ZRL20200110**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.30), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from orange yellow when young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

#### Additional material examined. N/A

**Notes.** *Ramaria sp15* is characterised by orange yellow basidiome.



Figure 4.30 The Basidiome of Ramaria sp15

Ramaria sp16 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.31

**Holotype.** China. Sichuan Province, Yanjiang city, 21 August 2020, collected by R.L. Zhao (**ZRL20201128**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.31), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from light brown young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal

white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

## Additional material examined. N/A

**Notes.** Ramaria sp16 is characterised by orange light brown basidiome.



Figure 4.31 The Basidiome of Ramaria sp16

Ramaria sp17 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.32

**Holotype.** China. Sichuan Province, Yanjiang city, 21 August 2020, collected by R.L. Zhao (**ZRL20211333**).

**Description.** basidiome 44–57 × 18–32 mm, ramarioid (Figure 4.32), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from light yellow young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches,

with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

## Additional material examined. N/A

**Notes.** Ramaria sp17 is characterised by orange light yellow basidiome.



Figure 4.32 The Basidiome of Ramaria sp17

Ramaria sp18 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.33

**Holotype.** China. Beijing Province, 21 August 2020, collected by R.L. Zhao (**ZRL20211310**).

**Description.** basidiome 44–57  $\times$  18–32 mm, ramarioid (Figure 4.33), repeatedly branched, with up to five levels of branching, from dichotomous to polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8  $\times$  7.5 mm, cylindrical to flattened, from light yellow young; *secondary branches* 6.2  $\times$ 

2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

# Additional material examined. (ZRL20211311) (ZRL20221358)

**Notes.** *Ramaria sp18* is characterised by orange light yellow basidiome.



Figure 4.33 The Basidiome of Ramaria sp18

## Ramaria sp19 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

Figure 4.34

**Holotype.** China. Sichuan Province, Ganzi City, 21 August 2020, collected by R.L. Zhao (**ZRL20200548**).

**Description.** basidiome  $44-57 \times 18-32$  mm, ramarioid (Figure 4.34), repeatedly branched, with up to five levels of branching, from dichotomous to

polychotomous, with parallel arrangement, and rounded axils. *Primary branches* 8.8 × 7.5 mm, cylindrical to flattened, from light yellow young; *secondary branches* 6.2 × 2.3 mm, cylindrical to flattened, concolorous with Primary branches when young; *terminal branches* from cylindrical to flattened, concolorous with secondary branches, with acute, dichotomous to polychotomous, concolorous with Primary branches when young. *Stipe* 7.8–9.9 × 4.3–7.3 mm, cylindrical, white [6A1] to whitish, with a basal white tomentum and few white rhizomorphs. *Context* fleshy, whitish to slightly brown. *Odour & taste* not recorded. *Macrochemical reactions* not recorded.

Habitat and distribution. Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. (ZRL20200710) (ZRL20200872) (ZRL20200801)

**Notes.** Ramaria sp19 is characterised by orange light yellow basidiome.





Figure 4.34 The Basidiome of Ramaria sp19

# 4.4 Clavulinopsis

## 4.4.1 Phylogenetic Analyses

For this study, forty-three new sequences covering ITS, LSU, and ATP6 markers were generated from *Clavulinopsis* species and submitted to GenBank, as detailed in Table 4.5. The ITS dataset comprised 243 specimens across 50 species, while the combined ITS-LSU-ATP6 dataset included 46 specimens from 31 species. We conducted two phylogenetic analyses: one utilizing the 5.8S, ITS1+ITS2 dataset and another employing the 5.8S+LSU, ITS1+ITS2, and ATP6 datasets. The complete ITS alignment spanned 687 positions, with 170 positions dedicated to 5.8S and 517 to ITS1+ITS2. *Mucronella flava* Corner was selected as the outgroup based on previous phylogenies. Model selection for the 5.8S-ITS1-ITS2 dataset by mrModelTest recommended SYM for 5.8S and GTR+I+G for ITS1+ITS2. The Maximum likelihood tree was showed in Figures 4.35 and 4.36.

**Table 4.5** GenBank accession number of specimen used in this study for *CLavulinopsis* 

Species	Voucher/isolate	ITS	LSU	ATP6
Clavulinopsis. umbrinella	DJH23-19	PP379250	-	-
C. sp.	HAY-F-000883	PP318586	-	-
C. sp.	HAY-F-002187	PP294801	-	-
C. fusiformis	OMDL K. Canan iNaturalist # 184217542	PP156206	-	-
C. sp.	OMDL K. Canan iNaturalist # 179616249	OR987436	-	-
C. sp.	OMDL K. Canan iNaturalist # 179616324	OR987435	-	-
C. sp.	OMDL K. Canan iNaturalist # 183113638	OR987428	-	-
C. sp.	OMDL K. Canan iNaturalist # 186222778	OR987427	-	-
C. sp.	OMDL K. Canan iNaturalist # 184334398	OR987426	-	-
C. sp.	OMDL K. Canan iNaturalist # 183269112	OR987424	-	-
C. appalachiensis	OMDL K. Canan iNaturalist # 181609493	OR987423	-	-
C. sp.	OMDL K. Canan iNaturalist # 174375821	OR987404	-	-
C. sp.	OMDL K. Canan iNaturalist # 179176209	OR987388	-	-
C. sp.	OMDL K. Canan iNaturalist # 177411637	OR945112	-	-
C. sp.	HAY-F-001858	OR882703	-	-
C. sp.	HAY-F-001914	OR859442	-	-
C. sp.	HAY-F-000254	OR853534	-	-

Table 4.5 (continued)

Species	Voucher/isolate	ITS	LSU	ATP
C. fusiformis	JBRI-M23-159	OR852545	-	-
C. sp.	OMDL K. Canan Mushroom Observer # 520977	OR825682	-	-
C. helvola	iNat176186010	OR800134	-	-
C. sp.	HAY-F-000744	OR778455	-	-
C. tropicalis	MHHNU:10722	OQ703793	OQ703810	-
C. incarnata	MHHNU:11330	OQ703787	OQ703804	-
C. bispora	MHHNU:11188	OQ703782	OQ703799	-
C. bicolor	MHHNU:10381	OQ703780	OQ703797	-
C. aspersa	MHHNU:10342	OQ703778	OQ703795	-
C. sp.	HAY-F-003728	OR750608	-	-
C. sp.	HAY-F-003726	OR750595	-	-
C. sp.	MCCNNU00955	OP681086	OP677993	-
C. sp.	MES-1703	KY462526	-	-
C. sp.	MES-1672	KY462518	-	-
C. sp.	MES-1617	KY462502	-	-
C. antillarum	PDD:112016	OR567709	OR567798	-
C. novozealandica	PDD:112004	OR567708	OR567797	-
C. simplex	PDD:111999	OR567707	OR567796	-
C. sp.	PDD:111981	OR567705	OR567795	-
C. sulcata	PDD:111978	OR567703	OR567793	-
C. sulcata	PDD:111965	OR567702	OR567792	-
C. sulcata	PDD:111950	OR567701	OR567791	-
C. novozealandica	PDD:111932	OR567700	OR567790	-
C. amoena	PDD:108445	OR567698	OR567788	-
C. sp.	PDD:107630	OR567697	OR567787	-
C. sp.	PDD:113964	OR567656	OR567783	-
C. persicina	PDD:113957	OR567655	OR567782	-
C. persicina	PDD:113916	OR567654	OR567781	-
C. simplex	PDD:113718	OR567651	OR567779	-
C. persicina	PDD:113340	OR567643	OR567773	-
C. sp.	PDD:113060	OR567640	OR567771	-
C. depokensis	PDD:113053	OR567638	OR567769	-
C. simplex	PDD:112953	OR567633	OR567765	-
C. persicina	PDD:107130	OR567615	OR567753	-
C. sp.	PDD:107103	OR567606	OR567749	-
C. sp.	PDD:107079	OR567597	OR567746	-
C. persicina	PDD:107077	OR567595	OR567745	-
C. sp.	PDD:107073	OR567591	OR567744	-
C. depokensis	PDD:107070	OR567588	OR567743	-
C. sp.	PDD:106531	OR567583	OR567740	-
C. archeri	PDD:106510	OR567580	OR567737	_

Table 4.5 (continued)

Species	Voucher/isolate	ITS	LSU	ATP6
C. sp.	PDD:106506	OR567577	OR567736	-
C. sp.	PDD:106958	OR567576	OR567735	-
C. sulcata	PDD:106852	OR567575	OR567734	-
C. depokensis	PDD:106922	OR567574	OR567733	-
C. sulcata	PDD:107023	OR567572	OR567732	-
C. sulcata	PDD:107022	OR567571	OR567731	-
C. novozealandica	PDD:107021	OR567570	OR567730	-
C. archeri	PDD:106252	OR567565	OR567725	-
C. simplex	PDD:106044	OR567563	OR567722	-
C. sp.	PDD:106040	OR567560	OR567720	-
C. sp.	PDD:105661	OR567558	OR567719	-
C. sp.	PDD:105592	OR567557	OR567718	-
C. sp.	PDD:121240	OR567711	-	-
C. persicina	PDD:111985	OR567706	-	-
C. sp.	PDD:83118	OR567693	-	-
C. persicina	PDD:81499	OR567689	-	-
C. sp.	PDD:81207	OR567687	-	-
C. depokensis	PDD:80484	OR567685	-	-
C. sp.	PDD:115068	OR567683	-	-
C. sp.	PDD:115064	OR567681	-	-
C. sp.	PDD:114996	OR567679	-	-
C. sulcata	PDD:114975	OR567678	-	-
C. archeri	PDD:114972	OR567676	-	-
C. persicina	PDD:114966	OR567675	1 -	-
C. persicina	PDD:114964	OR567674	-	-
C. sp.	PDD:114939	OR567673	_	-
C. antillarum	PDD:114901	OR567671	-	-
C. simplex	PDD:114878	OR567669	-	-
C. depokensis	PDD:114826	OR567663	-	-
C. sp.	PDD:114362	OR567659	-	-
C. persicina	PDD:114050	OR567657	-	-
C. depokensis	PDD:113829	OR567653	-	-
C. sp.	PDD:113497	OR567645	-	-
C. sp.	PDD:113062	OR567641	-	-
C. sp.	PDD:112920	OR567631	-	-
C. depokensis	PDD:107106	OR567608	-	-
C. archeri	PDD:107104	OR567607	-	-
C. sulcata	PDD:107085	OR567602	-	-
C. depokensis	PDD:107084	OR567601	-	-
C. sp.	PDD:107082	OR567600	-	-
C. simplex	PDD:107080	OR567598	_	_

Table 4.5 (continued)

Species	Voucher/isolate	ITS	LSU	ATP6
C. sp.	PDD:107078	OR567596	-	-
C. persicina	PDD:107074	OR567592	-	-
C. simplex	PDD:107072	OR567590	-	-
C. persicina	PDD:107071	OR567589	-	-
C. antillarum	PDD:106508	OR567578	-	-
C. sulcata	PDD:107024	OR567573	-	-
C. sulcata	PDD:106041	OR567561	-	-
C. depokensis	PDD:105693	OR567559	-	-
C. depokensis	PDD:96712	OR567557	-	-
C. persicina	PDD:96251	OR567554	-	-
C. sp.	PDD:87597	OR567550	-	-
C. sp.	PDD:83770	OR567547	-	-
C. fusiformis	TENN:071596	MF992158	-	-
C. corallinorosacea	PBM3380 (TENN)	KP257144	-	-
C. tropicalis	MHHNU10721	OQ703792	OQ703809	-
C. trigonospora	MHHNU10198	OQ703791	OQ703808	-
C. trigonospora	MHHNU9200	OQ703790	OQ703807	_
C. trigonospora	MHHNU9186	OQ703789	OQ703806	_
C. incarnata	MHHNU11331	OQ703788	OQ703805	-
C. incarnata	MHHNU9813	OQ703786	OQ703803	-
C. incarnata	MHHNU9314	OQ703785	OQ703802	-
C. erubescens	MHHNU10290	OQ703784	OQ703801	-
C. erubescens	MHHNU8040	OQ703783	OQ703800	_
C. bispora	MHHNU11181	OQ703781	OQ703798	_
C. aspersa	MHHNU11103	OQ703779	OQ703796	_
C. aspersa	MHHNU10153	OQ703777	OQ703794	_
C. sp.	KFRI MH1519	OR224623	-	_
C. sp.	S.D. Russell ONT WCMB23 iNaturalist # 147370979	OR168885	-	-
C. sp.	S.D. Russell ONT WCMB23	OR168813	-	-
C. sp.	iNaturalist # 147647505 S.D. Russell ONT WCMB23 iNaturalist # 147689103	OR162455	-	-
C. miyabeana	BMS12BM	OR099734	-	-
C. fusiformis	BMS13AM	OR099733	-	-
C. fusiformis	BMS13F	OR099728	-	-
C. miyabeana	BMS12F	OR099726	-	-
C. umbrinella	DJH22-100	OQ875816	-	-
C. sp.	FLAS-F-69299-C.	OQ725183	-	-
C. umbrinella	HFRG_EJ191214_3_FRDBI 17588114	OQ133539	OQ133591	-
C. sp.	iNat66898216	ON943319	-	-
C. sp.	S.D. Russell ONT iNaturalist 136438210	OP749759	-	-

Table 4.5 (continued)

Species	Voucher/isolate	ITS	LSU	ATP6
C. sp.	S.D. Russell ONT iNaturalist	OP749635	-	-
C. appalachiensis	136439713 S.D. Russell ONT iNaturalist 136703747	OP749256	-	-
C. sp.	S.D. Russell ONT iNaturalist 136438756	OP749034	-	-
C. aurantiocinnabarina	NEMF 2018 iNaturalist # 14815641	ON416905	-	-
C. fusiformis	1.5.176-1	OP538830	-	-
C. fusiformis	1.2.122-2	OP538806	-	-
C. sp.	2.1.38	OP538789	-	-
C. fusiformis	1.1.26	OP538780	-	-
C. fusiformis	2.1.17	OP538776	-	-
C. cf. subtilis	2.1.161	OP538774	-	-
C. fusiformis	KN_310	OP538733	-	-
C. cf. subtilis	KN_250	OP538726	-	-
C. luteoalba	BSI13_147a	OP538704	-	-
C. helvola	2.0.24	OP538699	-	-
C. fusiformis	HKAS122736	ON794462	-	-
C. fusiformis	HKAS122627	ON794403	-	-
C. sp.	LD2021-6-9	OK643821	OK643695	-
C. helvola	KA12-1320	KR673550	-	-
C. sp.	39	ON650114	-	-
C. aurantiocinnabarina	38	ON650113	-	_
C. sp.	PUL:PUL00036002	ON650111	-	-
C. sp.	37	ON650110	-	_
C. sp.	36	ON650109	1 -	_
C. gracillima	20	ON650091	_	_
C. trigonospora	AMB 18587	MT055968	_	_
C. trigonospora	AMB 18557	MT055939	MT053223	_
C. sp.	MES-3040	ON383352	-	_
C. sp.	iNAT:100085413	ON206855	-	-
C. sp.	S.D. Russell iNaturalist 56326333	ON059217	-	-
C. sp.	S.D. Russell iNaturalist 56636002	ON059182	-	-
C. helvola	S.D. Russell iNaturalist 99178003	OM987379	-	_
C. helvola	MICH340330	OM985825	-	-
C. sp.	279	OM972550	-	_
C. sp.	86	OM972357	-	_
C. appalachiensis	151	OM809324	-	-
C. sp.	TENN:075845	OM677709	-	-
C. sp.	S.D. Russell iNaturalist # 57068093	OM473893	-	-
C. sp.	S.D. Russell iNaturalist # 56684784	OM473813	-	-
C. sp.	WML2021-8-25-2	OL998888	-	-
C. amoena	KN23	OL638253	-	_

Table 4.5 (continued)

Species	Voucher/isolate	ITS	LSU	ATPO
C. sulcata	26	OL616149	-	-
C. sulcata	MG10	OK446763	-	-
C. helvola	BRA:CR-12763	-	GU299510	-
C. appalachiensis	iNAT:31157503	MZ318380	-	-
C. appalachiensis	iNAT:15755704	MZ171335	-	-
C. sp.	MCCNNU 00952	MT587809	MT587811	-
C. sp.	MCCNNU 00948	MT587808	MT587810	-
C. fusiformis	Taxon 35	MW899401	-	-
C. umbrinella	DJH20-20	MW685504	-	-
C. gracillima	UWO:HA5 (MO 215748)	KY706170	-	-
C. umbrinella	BRACR-17991	-	MK277709	-
C. sp.	NL-5157	-	MK277708	-
C. sp.	CNV55	MT345232	-	-
C. sp.	CNV46	MT345223	-	-
C. appalachiensis	TENN:074980	MT196965	-	-
C. fusiformis	ANT002-QFB28551	MN992315	-	-
C. sulcata	HFJAU-TD330	MN622711	-	-
C. sp.	FLAS-F-61269	MH399871	-	-
C. amoena	ZP-2400	MK427063	-	-
C. fusiformis	ZP-1145	MK427062	-	-
C. helvola	ZP-2101	MK427061	-	-
C. sulcata	ZP-2119	MK427060	-	-
C. miyabeana	ZP-2118	MK427059	-	-
C. sp.	inaturalist.org/observations/19901249	MK640605	1 -	-
C. sp.	Mushroom Observer # 235637	MK607506	-	-
C. fusiformis	SDR NAMA 2017-125	MK575451	-	-
C. helvola	420526MF0990		MG712389	-
C. helvola	420526MF0997		MH141387	-
C. helvola	420526MF0737	</td <td>MH141369</td> <td>-</td>	MH141369	-
C. helvola	420526MF0618	>7	MH141352	-
C. helvola	420526MF0469	<del>-</del>	MH141331	-
C. sp.	MES-2825	MH930297	-	-
C. sp.	MES-2986	MH930283	-	-
C. cf. amoena	MES-2695	MH930255	-	-
C. sp.	MES-2900	MH930223	-	-
C. aurantiaca	URM <bra>:84216</bra>	-	KX227750	-
C. sp.	610723MF0060	KY950493	-	-
C. helvola	h12	-	-	-
C. fusiformis	PBM 2804 (CUW)	-	EF535273	-
C. aurantiaca	URM <bra>:84212</bra>	-	KX227749	-
C. helvola	Lueck6	KP965770	KP965788	_

Table 4.5 (continued)

Species	Voucher/isolate	ITS	LSU	ATP6
C. fusiformis	2718	KM248914	-	-
C. sp.	MEL:2382732	KP012914	-	-
C. fusiformis	TUB 019060	-	-	KF147767
C. flavella	URM 84216	KC348464	-	-
C. luteoalba	BRACR16669	-	JQ415959	-
C. sp.	L-Lob-H10	JN569120	-	-
C. sp.	L-Lob-G3	JN569119	-	-
C. helvola	TRTC157008	JN020997	-	-
C. fusiformis	MGW672; TENN064110	-	HQ877717	-
C. antillarum	PBM3446	-	HQ877710	-
C. sulcata	PBM3379	-	HQ877709	-
C. gracillima	JMB10071002; TENN065662	-	HQ877708	-
C. corallinorosacea	PBM3380	-	HQ877707	-
C. aff.	PBM3010		HQ877706	-
Aurantiocinnabarina C. aff. Aurantiocinnabarina	JMB08171006		HQ877705	-
C. aff. Aurantiocinnabarina	JMB08171004		HQ877704	-
C. aff. Aurantiocinnabarina	JMB08240901	(CC-) \	HQ877703	-
C. amoena	PBM3381	<del>-</del>	HQ877702	-
C. novozealandica	TENN043575	1 - 1	HQ877693	-
C. helvola	RD990908	AY463397	AY586647	-
C. miyabeana	198-506	AB509804	-	-
C. miyabeana	197-490	AB509796	-	-
C. miyabeana	198-280	AB509666	7 -	-
C. helvola	EL 111/04 (GB)	EU118617	_	-
C. fusiformis	Farlow EP96-004	11/10	-	-
C. sulcata	PDD78241		DQ284904	-
C. fusiformis	TENN62211	FJ596792	-	_
Mucronella flava	IO.16.84	MT232354	MT232307	_

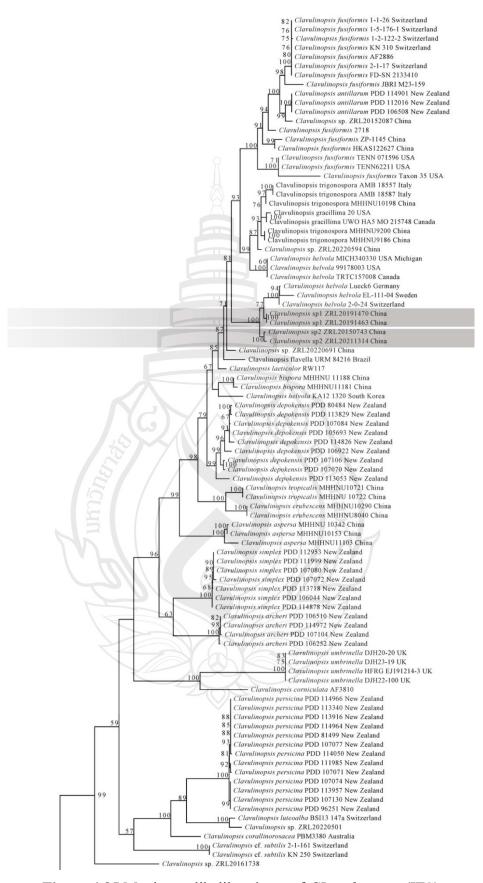


Figure 4.35 Maximum likelihood tree of *CLavulinopsis* (ITS)

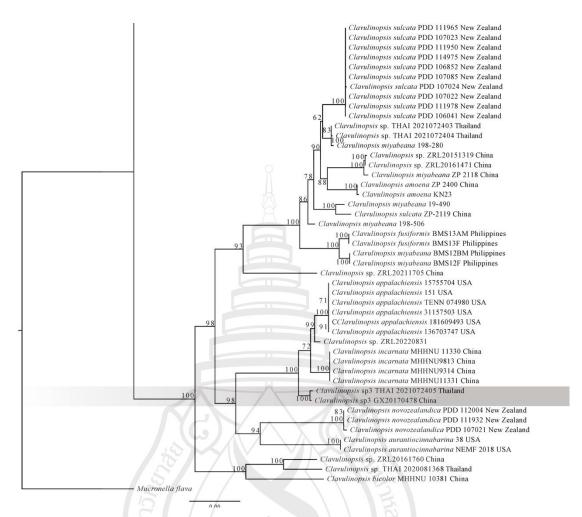


Figure 4.35 (continued)

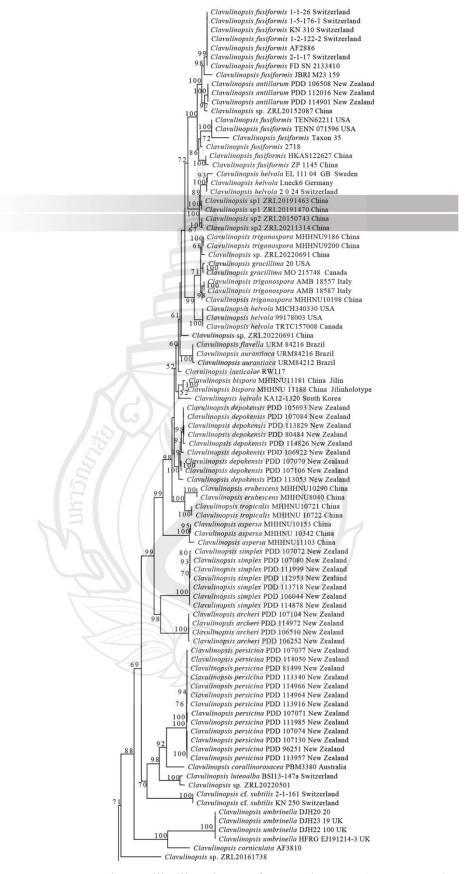


Figure 4.36 Maximum likelihood tree of *CLavulinopsis* (ITS, nrLSU)

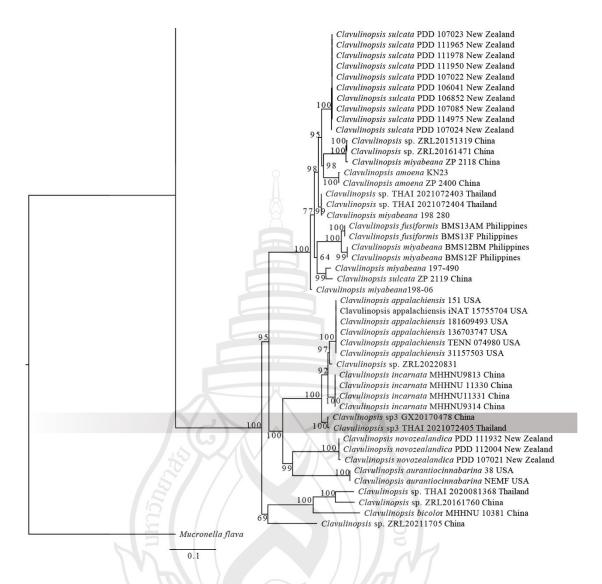


Figure 4.36 (continued)

#### 4.4.2 Taxonomy

CLavulinopsis sp1 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.37

Etymology. The epithet "sp1" refers to.

Holotype. China. Sichuan Province: Ganzi city, Z.L. Ling & Y.Y. Ling (ZRL20191470).

**Diagnosis.** Differs from other *Clavulinopsis* species in.

**Description.** The structures range in size from 50.5 to 60.6 mm in height and 3.8 to 5.5 mm in diameter, presenting a simple configuration as shown in Figure 4.37.

The fertile section transitions from subcylindrical to fusiform, often displaying a mild curvature or slight flexure accompanied by a pronounced longitudinal depression, colored from yellowish to a more distinct yellow. The apex, either rounded or ranging from obtuse to acute upon maturity, aligns in color or is slightly lighter, darkening as it ages. The sterile section appears narrow and less defined, often curved, matching or lighter than the fertile part, and lacks both tomentum and mycelial patches at the base. The overall context is fragile, with the hymenium maintaining consistent coloration. Neither odors nor tastes have been documented, nor have macrochemical reactions been noted.

*Basidia* 54.2–62.4 × 5.6–9.3 μm, subclavate, hyaline, multiguttulate, with four straight sterigmata. *Spores* 4.5–7.4 × 3.2–6.6 μm, [ $x = 6.0 \pm 0.8 \times 4.9 \pm 0.9$ , Q = 0.9–1.5,  $Q = 1.2 \pm 0.2$ , Q = 0.9–1.5, Q =

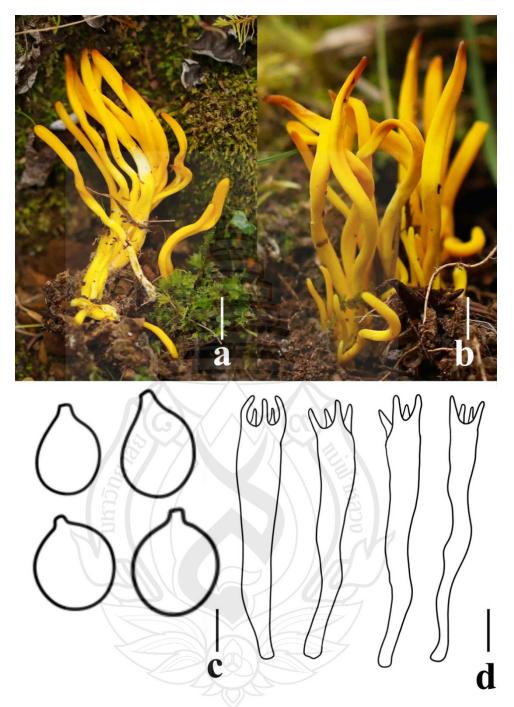
**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. China. Sichuan Province: Ganzi city, Z.L. Ling & Y.Y. Ling (ZRL20191463).

**Notes.** Clavulinopisi sp1 is distinguished by its light yellow basidiome, particularly noticeable at the tips. Sterile part concolorous or paler than the upper part. The basidia four sterigmata, with spores  $4.5-7.4 \times 3.2-6.6 \mu m$ .

In our phylogenetic tree, *Clavulinopisi sp1* and *Clavulinopisi helvola* form a sister clade. These two species can be distinctly differentiated by spore, with *Clavulinopisi helvola* has a spiny spore.

Clavulinopisi sp1 is similar to C. erubescens in them same spore size. However, C. erubescens has red basidiome.



Note a,b Basidiome; c Basidiospores; d Basidia.

Figure 4.37 Clavulinopisi sp1 sp. nov. macroscopic and microscopic features

CLavulinopsis sp2 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.38

Etymology. The epithet "sp2" refers to.

Holotype. China. Yunnan Province: Diqing city, H. Zhao (ZRL20211314).

**Diagnosis.** Differs from other *Clavulinopsis* species in.

**Description.** Measuring between 50.5 and 60.6 mm in height and 3.8 to 5.5 mm across, these structures exhibit a simple form as illustrated in Figure 4.38. The fertile area transitions from subcylindrical to fusiform, with occasional mild bends or flexes, marked by a clear longitudinal depression, and colored from yellow to dark yellow. The apex, which matures from rounded to either obtuse or acute, typically matches or is slightly lighter than the rest, and tends to darken over time. The sterile zone is slender, subtle, typically lighter than or similar to the fertile section, and may curve slightly, lacking any tomentum or mycelial base patches. The internal context is delicate, with the hymenial layer uniformly colored. No odor or taste characteristics have been noted, and macrochemical tests have not been conducted.

*Basidia* 54.7–61.0 × 5.6–8.3 μm, subclavate, hyaline, multiguttulate, with four straight sterigmata. *Spores* 5.1–7.2 × 4.6–7.0 μm, [ $x = 6.2 \pm 0.5 \times 5.9 \pm 0.6$ , Q = 0.9–1.2,  $Q = 1.1 \pm 0.2$ , Q = 0.9–1.2, Q = 0.9–1.2, Q = 0.9–1.2, Q = 0.9–1.3 μm broad, thin-walled, hyaline, with clamp connections.

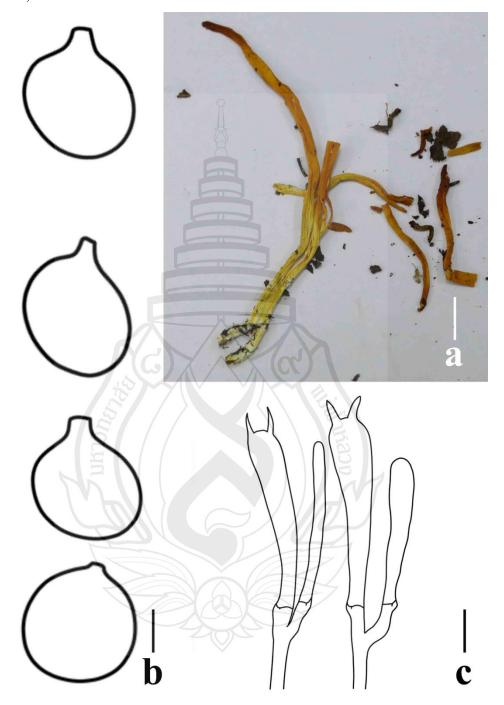
Habitat and distribution. Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. China. Sichuan Province: Luding city, Z.L. Ling & Y.Y. Ling (ZRL20150743).

**Notes.** Clavulinopisi sp2 is distinguished by its light yellow basidiome, particularly noticeable at the tips. Sterile part concolorous or paler than the upper part. The basidia four sterigmata, with spores  $5.1-7.2 \times 4.6-7.0 \mu m$ .

In our phylogenetic tree, *Clavulinopisi sp2* and *Clavulinopisi helvola* form a sister clade. These two species can be distinctly differentiated by spore, with *Clavulinopisi helvola* has a spiny spore.

Clavulinopisi sp2 is similar to C. erubescens in them same spore size. However, C. erubescens has red basidiome.



Note a Basidiome; b Basidiospores; c,d Basidia.

Figure 4.38 Clavulinopisi sp2 sp. nov. macroscopic and microscopic features

CLavulinopsis sp3 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.39

Etymology. The epithet "sp3" refers to.

Holotype. China. Guangxi Province: Cenwang city, R.L. Zhao (GX20170478).

**Diagnosis.** Differs from other *Clavulinopsis* species in.

**Description.** Dimensions range from 50.5 to 60.6 mm in height and 3.8 to 5.5 mm in diameter, described simply in Figure 4.13. The fertile segment is shaped from subcylindrical to fusiform, often exhibiting a slight bend or flexibility and characterized by a prominent longitudinal depression, with hues ranging from light pink to pink. The apex, rounded or shifting from obtuse to acute upon maturation, remains consistent in color or may appear slightly lighter, gradually darkening as it ages. The sterile portion is slim and subtle, matching or lighter than the fertile area, occasionally bent, and lacks both tomentum and mycelial patches at the base. The context is noted for its delicacy, with the hymenium maintaining a uniform color. No sensory details such as odor or taste have been documented, and macrochemical tests were not performed.

*Basidia* 28.1–39.5 × 7.1–10.1 μm, subclavate, hyaline, multiguttulate, with four straight sterigmata. *Spores* 6.9–8.4 × 5.8–7.7 μm, [x = 7.6 ± 0.4 × 6.8 ± 0.5, Q = 1.0–1.3, Q m =  $1.1 \pm 0.1$ , n =20], hyaline in KOH, subellipsoid and usually more or less lacrymoid in shape. *Context* with generative hyphae in parallel arrangement, 2.6–4.3 μm broad, thinwalled, hyaline, with clamp connections.

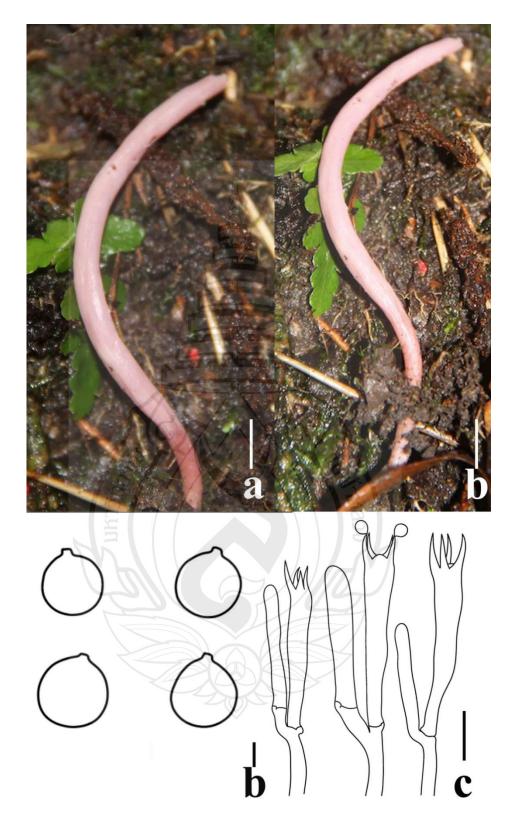
**Habitat and distribution.** Scattered or cespitose on the ground, known from China and Thailand.

Additional material examined. Thailand. S.M. Tang (THAI2017072405).

**Notes.** Clavulinopisi sp3 is distinguished by its pink basidiome, particularly noticeable at the tips. Sterile part concolorous or paler than the upper part. The basidia four sterigmata, with spores  $6.9-8.4 \times 5.8-7.7 \, \mu m$ .

In our phylogenetic tree, *Clavulinopisi sp3* and *Clavulinopisi incarnata* form a sister clade. These two species can be distinctly differentiated basidiome color, *Clavulinopisi incarnata* has light pink basidiome.

Clavulinopisi sp3 is similar to C. lignicola in them same basidiome color. However, C. lignicola generally has a bifurcate basidioma and smaller spores  $(2.8-3.2 \times 2.1-2.3 \mu m)$ 



Note a Basidiome; b Basidiospores; c,d Basidia.

Figure 4.39 Phaeoclavulina sp3 sp. nov. macroscopic and microscopic features

# 4.5 Clavariadelphus

# 4.5.1 Phylogenetic Analyses

In this study, 100 sequences derived from two loci (ITS, nrLSU) were used to reconstruct phylogenetic trees of *Clavariadelphus*, including 73 for ITS and 27 for nrLSU representing 26 species from *Clavariadelphus*. Newly generated 54 sequences, including 27 for ITS and 27 for nrLSU representing 7 species from *Clavariadelphus*. (Table 4.6). The ITS dataset included sequences from 73 specimens representing 26 species from *Clavariadelphus*, and *Ramaria luteovernalis* Franchi, M. Marchetti & Bottoni were chosen as outgroup based on previous phylogenetic studies. The best-fit evolutionary models selected for the character sets were GTR+I+G (ITS1+ITS2. These models were applied in Bayesian analyses for the dataset.

The phylogeny topologies of based on ITS, sequences respectively with ML bootstrap support values  $\geq 70\%$  are shown in Figure 4.40.

**Table 4.6** GenBank accession number of specimen used in this study for *Clavariadelphus* 

Taxon	Voucher	Location	ITS
Clavariadelphus alpinus	HKAS 57396	China, Yunnan	MK705888
Clavariadelphus americanus	TENN NCD02	USA	MF755266
Clavariadelphus americanus	SD Russell MycoMap # 1288	USA	MK575228
Clavariadelphus amplus	HKAS 54876	China, Yunnan	MK705857
Clavariadelphus amplus	HKAS 46120	China, Tibet	MK705862
Clavariadelphus amplus	ZRL20191029	China	ITS
Clavariadelphus amplus	ZRL20201256	China	ITS
Clavariadelphus amplus	ZRL20201286	China	ITS
Clavariadelphus amplus	ZRL20201349	China	ITS
Clavariadelphus amplus	ZRL20201521	China	ITS
Clavariadelphus amplus	ZRL20201546	China	ITS
Clavariadelphus amplus	ZRL20201595	China	ITS
Clavariadelphus amplus	ZRL20201617	China	ITS
Clavariadelphus amplus	ZRL20220860	China	ITS
Clavariadelphus amplus	ZRL20221551	China	ITS
Clavariadelphus aurantiacus	MHHNU 9256 (holotypus)	China	MT580787
Clavariadelphus aurantiacus	OHU20137	China	OM974114
Clavariadelphus aurantiacus	ZRL20191474	China	ITS
Clavariadelphus elongatus	LAH 31397	Pakistan	MG768847
Clavariadelphus elongatus	SWAT 000559 (holotypus)	Pakistan	MG768846
Clavariadelphus elongatus	HMAS 260746	China, Yunnan	MK705845
Clavariadelphus elongatus	ZRL20201168	China	ITS
Clavariadelphus elongatus	ZRL20211065	China	ITS

Table 4.6 (continued)

Taxon	Voucher	Location	ITS
Clavariadelphus	AMB 18559	Italy	MT434359
flavoimmaturus Clavariadelphus flavoimmaturus	AMB 18560	Italy	MT434360
Clavariadelphus gansuensis	HKAS 76487	China, Gansu	MK705847
gunsuensis Clavariadelphus griseoclavus	BJTC FM965	China	MT302371
griseociavas Clavariadelphus griseoclavus	BJTC FM964 (holotypus)	China	MT302370
griseociavas Clavariadelphus griseoglaucus	AMB 19280 (holotypus)	Italy	ON693224
griseogiaucus Clavariadelphus griseoglaucus	AMB 19282	Italy	ON693225
griseoguucus Clavariadelphus himalayensis	HKAS 50684	China, Yunnan	MK705863
nimatayensis Clavariadelphus himalayensis	HKAS 58811	China, Yunnan	MK705864
nimaiayensis Clavariadelphus khinganensis	MHHNU 7789	China, Inner Mongolia	MK705865
kninganensis Clavariadelphus khinganensis	MHKMU H.Y. Huang 368	China, Jilin	MT447468
kninganensis Clavariadelphus khinganensis	ZRL20200073	China	ITS
Clavariadelphus ligula	KHL 8560	Sweden	AF347099
Clavariadelphus ligula	AMB 18570	Italy	MT055950
Clavariadelphus mucronatus	OSC 1064138	USA	EU526000
mucronatus Clavariadelphus occidentalis	OSC 104664	USA, the Pacific Northwest	EU669308
Clavariadelphus occidentalis	OSC 114281	USA, the Pacific Northwest	EU846242
Clavariadelphus pakistanicus	MH 129901 (holotypus)	Pakistan	HQ379937
Clavariadelphus pistillaris	AMB 18609	Italy	MT452505
Clavariadelphus pistillaris	AMB 18610	Italy	MT452506
pistitiaris Clavariadelphus pistillaris	AMB 18611	Italy	MT452507
pistituris Clavariadelphus pistillaris	FLAS F 60521	USA	MH281842
pistitiaris Clavariadelphus pistillaris	NAMA 2017 123	USA	MH979250
olsuuaris Clavariadelphus sachalinensis	p058i	USA	EU624411
sacnatinensis Clavariadelphus sachalinensis	p061i	USA	EU624408
Clavariadelphus sachalinensis	MHHNU 7816	China, Inner Mongolia	MK705866
Clavariadelphus sp1	ZRL20200074	China	ITS
Clavariadelphus sp2	ZRL20211329	China	ITS
Clavariadelphus subfastigiatus	MICH 73554	USA	JX275756
suojastigiatus Clavariadelphus subfastigiatus	OSC 119587	USA	EU669207
Clavariadelphus tenuis	MHHNU 9900	China	MT580793
Clavariadelphus tenuis	MHHNU 9934	China	MT580790

Table 4.6 (continued)

Taxon	Voucher	Location	ITS
Clavariadelphus	CB 08379	Mexico	KT874983
truncatus			
Clavariadelphus	AMB 18612	Italy	MT452508
truncatus			
Clavariadelphus unicolor	Mushroom Observer #112193	USA, Indiana	MN906166
Clavariadelphus	ZT Myc 54987	Switzerland	MT055901
xanthocephalus	(holotypus)		
Clavariadelphus	HKAS 57731	China, Yunnan	MK705871
yunnanensis			
Clavariadelphus	HKAS 77288	China, Yunnan	MK705887
yunnanensis			
Clavariadelphus	ZRL20200147	China	ITS
yunnanensis			
Clavariadelphus	ZRL20200202	China	ITS
yunnanensis			
Clavariadelphus	ZRL20200203	China	ITS
yunnanensis			
Clavariadelphus	ZRL20200311	China	ITS
yunnanensis	TTT	CI.	TTT-0
Clavariadelphus	ZRL20200332	China	ITS
yunnanensis	7DI 20200226	CI.	ITC
Clavariadelphus	ZRL20200336	China	ITS
yunnanensis Claumi alalahan	7DI 20200476	Cl.:	ITS
Clavariadelphus	ZRL20200476	China	115
yunnanensis Clavariadelphus	ZRL20200734	China	ITS
yunnanensis	ZKL20200734	Cilila	113
Clavariadelphus	ZRL20201683	China	ITS
yunnanensis	ZKL20201083	Cilita	113
Clavariadelphus	ZRL20201685	China	ITS
yunnanensis	212220201003		110
Clavariadelphus	ZRL20201894	China	ITS
yunnanensis			
Ramaria luteovernalis	MCVE 28637	Italy	NR_155720

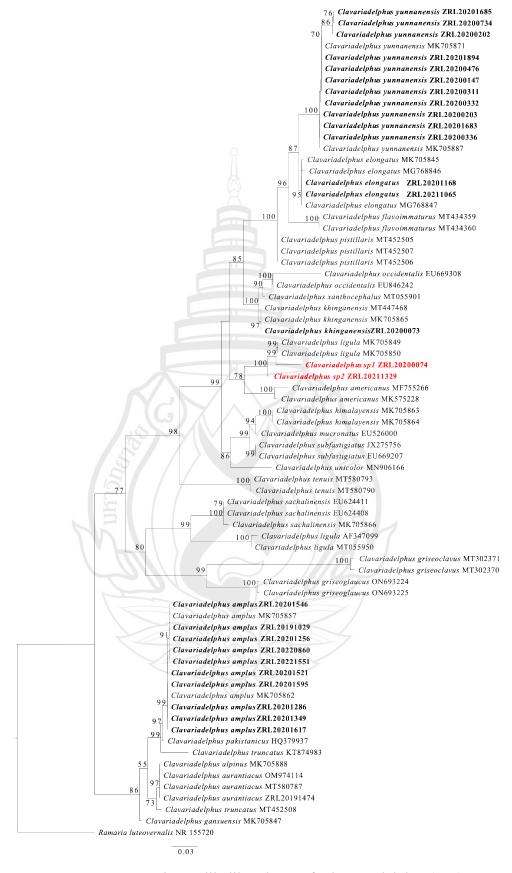


Figure 4.40 Maximum likelihood tree of Clavariadelphus (ITS)

# 4.5.2 Taxonomy

Clavariadelphus sp1 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.41

**Etymology.** The epithet "sp1", from.

Holotype. China. Sichuan Province: Ganzi city, collected by R.L. Zhao (ZRL20200074).

**Diagnosis.** Differs from other *Clavariadelphus* species in light yellow basidiome.

**Description.** Basidiome 40–10 mm, 8–12 mm in diameter, exhibit a subcylindrical shape that tapers upward to a subobtuse to obtuse apex. The base is terete, particularly noticeable in younger specimens, and can be either tapering or non-tapering. Some specimens may appear somewhat flattened in the middle. The surface of the basidiome is smooth in young specimens but becomes rugose to rugulose upon maturation. Initially straight, the basidiome tend to become more flexuous with age, often bending downward at the tip. The color transitions from light yellowish-pink in young specimens to moderate reddish-orange or grayish-reddish orange in mature ones.

*Basidiospores*,  $8.5-10 \times 6.5-7.5$  μm, (Q) 1.22-1.4, are ovoid in face view and ellipsoid in side view, featuring a prominent apiculus. The spores contain granular contents and are hyaline in KOH, lightly staining in Congo Red, inamyloid, and smooth. *Basidia* are narrowly clavate, ranging from  $55-85 \times 7-10$  μm, tetrasterigmate, and hyaline in KOH, displaying light golden brown guttules. *Sterigmata* are  $\leq 10$  μm long, with basal clamp connections present. *Leptocystidia* are frequent, mostly cylindrical to somewhat flexuous, rarely narrowly clavate, measuring  $45-75 \times 5-10$  μm.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

### Additional material examined. N/A

**Notes:** Clavariadelphus sp1 is characterized by its variable basidiome colour.

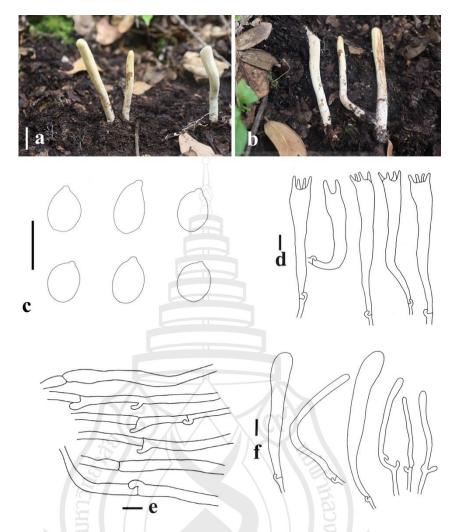


Figure 4.41 Clavariadelphus spl. a, b Basidiome; c Basidiospores; d Basidia

Clavariadelphus sp2 X.Y. Zhu, Raspé & R.L. Zhao, sp. nov.

MycoBank No:

Figure 4.42

**Etymology.** The epithet "sp2", from.

**Holotype.** China. Yunnan Province: Diqing city, collected by R.L. Zhao (ZRL20211329).

**Diagnosis.** Differs from other *Clavariadelphus* species in light yellow basidiome.

**Description.** Basidiome 40–10 mm, 8–12 mm in diameter, exhibit a subcylindrical shape that tapers upward to a subobtuse to obtuse apex. The base is terete, particularly noticeable in younger specimens, and can be either tapering or non-tapering.

Some specimens may appear somewhat flattened in the middle. The surface of the basidiome is smooth in young specimens but becomes rugose to rugulose upon maturation. Initially straight, the basidiome tend to become more flexuous with age, often bending downward at the tip. The color transitions from light yellowish-pink in young specimens to moderate reddish-orange or grayish-reddish orange in mature ones.

*Basidiospores*,  $8.5-10 \times 6.5-7.5$  μm, (Q) 1.22-1.4, are ovoid in face view and ellipsoid in side view, featuring a prominent apiculus. The spores contain granular contents and are hyaline in KOH, lightly staining in Congo Red, inamyloid, and smooth. *Basidia* are narrowly clavate, ranging from  $55-85 \times 7-10$  μm, tetrasterigmate, and hyaline in KOH, displaying light golden brown guttules. *Sterigmata* are  $\leq 10$  μm long, with basal clamp connections present. *Leptocystidia* are frequent, mostly cylindrical to somewhat flexuous, rarely narrowly clavate, measuring  $45-75 \times 5-10$  μm.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

Additional material examined. N/A

Notes: Clavariadelphus sp2 is characterized by its variable basidiome colour.



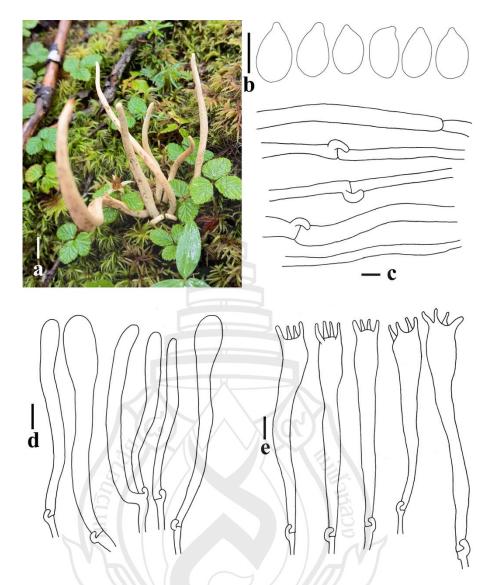


Figure 4.42 Clavariadelphus sp2. a, b Basidiome; c Basidiospores; d Basidia

## 4.6 Lentaria

# **4.6.1** Phylogenetic Analyses

In this study, 64 sequences derived from ITS were used to reconstruct phylogenetic trees of *Lentaria*, including 64 for ITS representing 21 species from *Lentaria*. Newly generated 5 sequences, including 5 for ITS representing 3 species from *Lentaria*. (Table 4.7). The ITS dataset included sequences from 64 specimens representing 21 species from *Lentaria*, and *Dictyophora rubrovolvata* M. Zang, D.G. Ji & X.X. Liu were chosen as outgroup based on previous phylogenetic studies. The best-fit evolutionary models were GTR+I+G (ITS1+ITS2). These models were applied in Bayesian analyses for the combined dataset.

The phylogeny topologies of *Lentaria* based on ITS, sequences respectively with ML bootstrap support values  $\geq 70\%$  are shown in Figure 4.43.

**Table 4.7** GenBank accession number of specimen used in this study for *Gomphus*, *Turbinellus* and *Gloeocantharellus* 

Taxon	Voucher	Location	ITS
Dictyophora rubrovolvata	YZS043	Guizhou, China	KF939504
Lentaria afflata	TUF114597	Estonia	UDB034986
Lentaria afflata	TUF114596	Estonia	UDB035003
Lentaria albovinacea	TUF109615	Estonia	UDB031119
Lentaria bambusina	MHHNU 6794	Sangzhi, Hunan, China	KU870448
Lentaria bambusina	MHHNU 7302	Liuyang, Hunan, China	KU324496
Lentaria byssiseda	TENN61159-C2	Tennessee, USA	FJ596785
Lentaria byssiseda	TENN61159-C3	Tennessee, USA	FJ596786
Lentaria byssiseda	TENN:075057	USA: Tennessee, Rock Islnd State Park, Bluff Trail	MT196983
Lentaria byssiseda	Mushroom Observer 487464	USA: Arizona, Cochise Co.	OP297818
Lentaria byssiseda	(51)	USA: Indiana, Morgan County, Martinsville	ON650132
Lentaria byssiseda	PUL:PUL00033973	USA: Indiana, Morgan County, Martinsville, Morgan-Monroe State Forest	ON209231
Lentaria byssiseda	TUF118502	Estonia	UDB018199
Lentaria byssiseda	ZRL20200504	China	ITS
Lentaria byssiseda	ZRL20221444	China	ITS
Lentaria dendroidea	SJ 98012 (GB)	Sweden	EU118640
Lentaria gossypina	FCME27625	Mexico: Veracruz, Los Tuxtlas	MK253199
Lentaria gossypina	FCME27623	Mexico: Campeche, Calakmul	MK253203
Lentaria gossypina	FCME27627	Mexico: Veracruz, Los Tuxtlas	MK253202
Lentaria gossypina	FCME27621	Mexico: Chiapas	MK253201

Table 4.7 (continued)

Taxon	Voucher	Location	ITS
Lentaria gossypina	FCME27626	Mexico: Veracruz, Los Tuxtlas	MK253200
Lentaria gossypina	FCME27624	Mexico: Veracruz, Los Tuxtlas	MK253198
Lentaria gossypina	FCME27628	Mexico: Veracruz, Los Tuxtlas	MK253197
Lentaria gossypina	FCME27622	Mexico: Veracruz, Los Tuxtlas	MK253196
Lentaria gossypina	FCME27620	Mexico: Tabasco, Parque Estatal Agua Blanca	MK253195
Lentaria micheneri	S.D. Russell ONT NAMA2022 iNaturalist # 137768095	USA: Missouri, Ste. Genevieve County, Sainte Genevieve	OP743566
Lentaria micheneri	RRD6 (TENN)	USA: Tennessee, Big Ridge State Park	MF773634
Lentaria patouillardii	MHHNU 7829	Baihaba, Xinjiang, China	KU324498
Lentaria patouillardii	HMJAU 26892	Hexigten, Inner Mongolia, China	KU870449
Lentaria patouillardii	MA-Fungi 48032	Spain	AJ292290
Lentaria patouillardii	HMAS 290111	N/A	MK966659
Lentaria pinicola	MushroomObserver.org/355909	USA: California, Sonoma Co., Occidental, CYO McGucken Camp	MW871706
Lentaria pinicola	MushroomObserver.org/193851	USA: California, Nevada Co., Grizzly Creek	MG979400
Lentaria soluta	TUF118501	Estonia	UDB017940
Lentaria sp.	(77)	USA: Indiana, Marshall County, Plymouth	OM972348
Lentaria sp.	RA708-21	USA: Arkansas	MK217455
Lentaria sp.	PDD 95856	Mid Canterbury, New Zealand	HQ533048
Lentaria sp.	MA-Fungi 48116	Equatorial Guinea	AJ292289
Lentaria sp.	TUF103919	Cameroon	UDB014007
Lentaria sp.	ARF-4975	USA: Florida	OP580239
Lentaria sp.	ARF-4968	USA: Florida	OP580231
Lentaria surculus	MHHNU 8721	Xishuangbanna, Yunnan, China	KU870450
Lentaria surculus	FHMU 880	Dinghushan, Guangdong, China	KU870451
Lentaria surculus	PDD 95856	Mid Canterbury, New Zealand	HQ533048
Lentaria surculus	THAI20190042	Thailand	ITS
Lentaria uncispora	MHHNU 7707	Kangding, Sichuan, China	KU324497
Lentaria uncispora	ZRL20220129	China	ITS
Lentaria uncispora	ZRL20220293	China	ITS
Lentaria variabilis	FCME21524	Mexico: Campeche, Calakmul	MK253189
Lentaria variabilis	FCME21526	Mexico: Campeche, Calakmul	MK253194
Lentaria variabilis	FCME21522	Mexico: Campeche, Calakmul	MK253193
Lentaria variabilis	FCME21525	Mexico: Campeche, Calakmul	MK253188
Lentaria variabilis	FCME21518	Mexico: Campeche, Xpuhil	MK253192
Lentaria variabilis	FCME19861	Mexico: Campeche, Calakmul	MK253191
Lentaria variabilis	FCME27619	Mexico: Campeche, Calakmul	MK253190
Lentaria variabilis	FCME21520	Mexico: Campeche, Calakmul	MK253186
Lentaria variabilis	FCME21516	Mexico: Campeche, Calakmul	MK253187
Lentaria variabilis	FCME19864	Mexico: Campeche, Calakmul	MK253185
Lentaria variabilis	FCME19862	Mexico: Campeche, Calakmul	MK253184

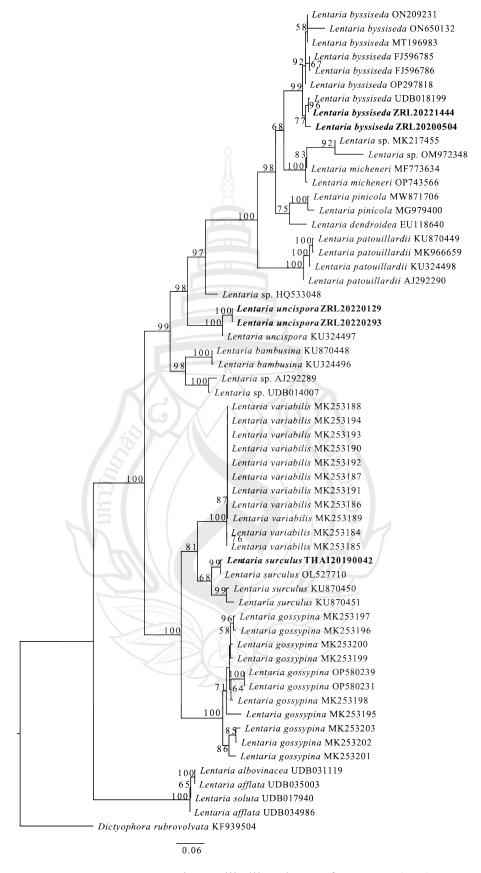


Figure 4.43 Maximum likelihood tree of *Lentaria* (ITS)

# 4.6.2 Taxonomy

# Lentaria byssiseda Corner 1950

Figure 4.44

**Description.** Basdidiome 2–4 cm, length from 1.5–3 cm, singly, cespitosely, or in groups. Felty white mycelial layer within the substrate, displaying a cinnamon buff coloration. Stipe is off-white, appearing either solitary or conjunct, with dimensions up to  $1.0 \times 0.3$  cm. Occasionally, the stipe may be very short or absent, maintaining a terete shape, and exhibiting a puberulous surface originating from the mycelium. The flesh of the stipe is white, soft yet tough, and dries to a lighter shade. The branching structure of the basidiome is dichotomous, arranged in 2–4 ranks, with branches erect and internodes that diminish gradually upwards. The branches are rounded in cross-section and fleshy tan in color, turning brown upon bruising. The apices of these branches are awl-shaped, dichotomous, and vary in color from pallid ochraceous to yellowish cream. The taste of the mushroom is bitter, while the odor is negligible.

Basidiospores cylindrical,  $12-15.5 \times 3.5-4.5$  μm, slightly sway-backed, rounded and blunt at the apex, subacute at the base, smooth, colorless, hyaline, thin-walled, and non-amyloid, with a gradual, inconspicuous hilar appendix. Basidia 50–60  $\times$  9–11 μm, clavate in shape, clamped, and thin-walled, each terminating in four sterigmata. The rhizomorph hyphae are 2–4 μm in diameter, occasionally swelling up to 8 μm, hyaline, and thick-walled, with the walls measuring up to 1 μm thick and featuring conspicuous clamped connections. The subhymenium consists of clamped hyphae, 2–3 μm in diameter.

Habitat and distribution. Scattered, gregarious or cespitose on the ground.

Additional material examined. China. Sichuan Province, Ganzi city, 25 August 2020, collected by R.L. Zhao (ZRL20200504).

**Notes.** Lentaria byssiseda is widely distributed in the northern regions of Eurasia and North America. It is a commonly observed clavarioid fungus in coniferous forests of northern China. This species has spore dimensions similar to those of *L. surculus*. However, the latter species has slenderer and more relaxed fruitbodies. More importantly, they are distributed in different regions. Lentaria byssiseda is also easily confused with several Ramaria taxa of subgenus Lentoramaria; however, Ramaria taxa differ because they have ornamental and thick-walled spores.



Figure 4.44 The Basidiome of Lentaria byssiseda

# Lentaria uncispora P. Zhang & Zuo H. Chen 2017

Figure 4.45

**Description.** Basidiome, 5–10 cm height and 3–5 cm in width, exhibit branching in 3–4 ranks and are either cespitose or densely gregarious. Initially fleshy tan, they mature to a cinnamon buff color, emerging from extensive white resupinate patches with rhizomorphs on the substrate. Stipe is usually conjunct, up to  $1.0 \times 0.5$  cm, irregularly rounded, and covered by a felty mycelial layer, with off-white flesh. Major branches, numbering 3–6, are erect and irregularly rounded, somewhat paler than the stipe, and colored flesh pink to pale ochraceous. The branches' surface is rugose and diminishes gradually upward, ending in awl-shaped or dichotomous apices colored blue-green. The taste is faintly bitter, and the odor is negligible.

Basidiospores,  $24-27 \times 3.5-4$  µm, sigmoid with a strongly bent upper part and a curved lower part, smooth, colorless, hyaline, thin-walled, and non-amyloid. Rhizomorph hyphae are 2-5 µm in diameter, with walls up to 0.5 µm thick, conspicuously clamped, and tightly packed. Branch tramal hyphae, also 2-5 µm in diameter and occasionally swelling up to 10 µm, are hyaline, thin- to thick-walled (up

to 0.4  $\mu$ m thick), with common ampulliform clamp connections swelling up to 12  $\mu$ m, arranged parallel. *Subhymenium* consists of clamped hyphae 2–3  $\mu$ m in diameter. *Basidia* measuring 56–76  $\times$  10–12  $\mu$ m, thin-walled, and four sterigmata 7–10  $\mu$ m long. There are no cystidia.

**Habitat and distribution.** Scattered, gregarious or cespitose on the ground, known from China.

**Additional material examined.** China. Sichuan Province, Ganzi city, 25 August 2020, collected by R.L. Zhao (**ZRL20220129**).

**Notes.** This species is characterized by its stout fruitbodies, blue-green branch apices and large and strongly bent basidiospores. Only *L. macrospora* Corner from Lipore approaches this taxon in basidiospore size. *Lentaria macrospora* spores were  $20-30 \times 3.7-5.5 \, \mu m$ . However, its spores are not strongly bent, and its branch apices are not green.



Figure 4.45 The Basidiome of Lentaria uncispora

# Lentaria surculus (Berk.) Corner 1950

Figure 4.46

**Description.** *Basidiome* 3–12 cm high, 2–8 cm broad, found singly or in clusters, initially pinkish flesh-colored, becoming pale ochraceous with maturity, arising from a felty white mycelial layer. *Stipe* distinct, solitary or connected, cylindrical, up to  $3.0 \times 0.4$  cm, off-white to cinnamon buff, with a villous base. *Branches* erect, rounded in cross-section, gray-drab to pinkish tan, sometimes with a purplish ochraceous tinge, becoming paler upward; flesh off-white, tough, pliable, and elastic. *Apices* elongated, flagelliform to awl-shaped, off-white to pale pinkish cinnamon. Taste is bitter; odor is negligible.

*Basidiospores* are  $12-16 \times 3-4.5$  μm, cylindrical, slightly curved, rounded at the apex, subacute at the base, smooth, colorless, hyaline, thin-walled, non-amyloid, with an inconspicuous hilar appendix. *Hymenium* is thickening; basidia are  $50-60 \times 9-11$  μm, clavate, clamped, and thin-walled, with four sterigmata. *Rhizomorph* hyphae are 2-5 μm in diameter, occasionally swollen to 8 μm, thin- to thick-walled, clamped, straight, tightly packed, with crystalline deposits. *Branch* tramal hyphae are 3-10 μm in diameter, hyaline, thick-walled with ampulliform clamp connections swollen up to 14 μm, parallel. Subhymenium consists of clamped hyphae 2-3 μm in diameter.

Habitat and distribution. Scattered, gregarious or cespitose on the ground.

**Additional material examined.** Thailand. ChiangMai Province, 25 August 2019, collected by X.Y. Zhu (**THAI20190042**).

**Notes.** Lentaria surculus was first described from the Philippines by Berkeley in 1842. It is a typical tropical species, widely reported in tropical regions of Asia, America, and Africa (Petersen, 2000). This species is characterized by its slender fruiting bodies and spore dimensions. Petersen (2000) also reported two variants of Lentaria surculus, both from tropical America.

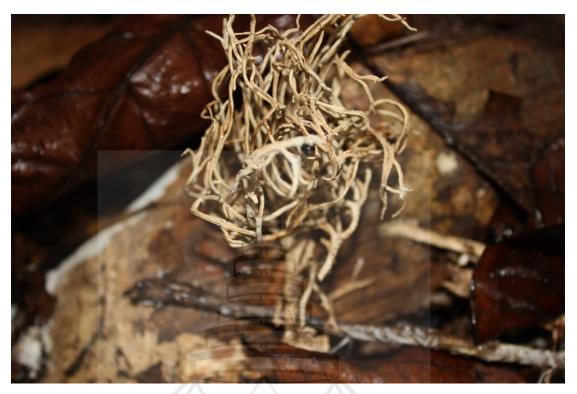


Figure 4.46 The Basidiome of Lentaria surculus



### **CHAPTER 5**

## **CONCLUSION AND DISCUSSION**

# 5.1 Conclusion

- 5.1.1 In this study, we introduce six new *Phaeoclavulina* species (*Phaeoclavulina* subabietina, *P. qilianensis*, *P. sterigmata*, *P. jilongensis*, *P. subcarovinacea and P. subminutispora*) based on morphology and phylogenetic analysis. *Phaeoclavulina* phylogenetic framework has been established.
- 5.1.2 In this study, we introduce two new Gomphoid fungi species (*Turbinellus sp1* and *Gloeocantharellus sp1*) and three known species (*Gomphus orientalis*, *Gomphus clavatus* and *Turbinellus szechwanensis*) based on morphology and phylogenetic analysis. The difference in characters of these two new species and closely related species are discussed herein. Gomphoid fungi phylogenetic framework has been established.
- 5.1.3 In this study, we introduce nineteen new *Ramaria* species and seven known species based on morphology and phylogenetic analysis. *Ramaria* phylogenetic framework has been established.
- 5.1.4 In this study, we introduce three new *Clavulinopsis* species (*C. sp1*, *C. sp2* and *C. sp3*) based on morphology and phylogenetic analysis. The difference in characters of these three new species and closely related species are discussed herein. *Clavulinopsis* phylogenetic framework has been established.
- 5.1.5 In this study, we introduce two new *Clavariadelphus* species and five known species based on morphology and phylogenetic analysis. The difference in characters of these two new species and closely related species are discussed herein. *Clavariadelphus* phylogenetic framework has been established.
- 5.1.6 In this study, we introduce three known *Lentaria* species based on morphology and phylogenetic analysis. *Lentaria* phylogenetic framework has been established.

## 5.2 Discussion

### 5.2.1 Phaeoclavulina

With the advancement of molecular biology, the description of new *Phaeoclavulina* species has significantly accelerated, as demonstrated by recent studies (Deng et al., 2024; Franchi & Marchetti, 2019; A. González-Ávila et al., 2020; P. González-Ávila et al., 2013; Liu et al., 2022; Maneevun et al., 2012; Wannathes et al., 2018). Due to the limited number of morphologically distinctive and taxonomically informative features in *Phaeoclavulina*, molecular analyses have become essential tools for species classification and identification within this genus. In this study, we employed both single-gene (ITS1+ITS2 and 5.8S) and multi-locus (ITS, nrLSU) phylogenetic analyses to evaluate the taxonomy of *Phaeoclavulina* species found in China and Thailand. This comprehensive molecular approach resulted in discovering six new species, *Phaeoclavulina subabietina*, *P. qilianensis*, *P. sterigmata*, *P. jilongensis*, *P. subcarovinacea*, and *P. subminutispora*.

In addition to the discovery of these six new species, we conducted detailed analyses of several unique species, including *Phaeoclavulina abietina*. This is a species originally described in Europe and has been reported in Americas and Asia. In the past, a lot of specimens collected in China were initially identified as *Phaeoclavulina abietina*. In this study, we thoroughly examined the European samples (AF1521 et al.) and employed multigene sequencing, incorporating data from the ATP6 gene. Concurrently, numerous specimens identified as *Phaeoclavulina abietina* were collected in China. Using these specimens for comparative purposes, we were able to precisely determine the phylogenetic placement of *Phaeoclavulina abietina* and update its related molecular data and findings.

This revised approach, utilizing both traditional morphological examination and modern molecular techniques, has not only enhanced our understanding of the species diversity within *Phaeoclavulina* but also clarified the relationships among these newly discovered and previously known species. Our findings highlight the importance of integrating molecular data to address taxonomic ambiguities and ensure accurate species identification in fungi with limited morphological variability. Our study may be significant in terms of stimulating further research of *Phaeoclavulina* and macrofungi in China and Thailand.

### **5.2.1** Gomphoid Fungi

In this research, we identified two new species within the Gomphoid group, designated as *Turbinellus sp1* and *Gloeocantharellus sp1*, along with reevaluating three established species—*Gomphus orientalis*, *Gomphus clavatus*, and *Turbinellus szechwanensis*—utilizing both morphological features and phylogenetic data. Traditionally, species within the *Gomphus* genus are significant yet frequently misidentified members of the Gomphaceae family.

Recent phylogenetic research suggests that the broader classification of *Gomphus* results in a paraphyletic assembly in relation to *Ramaria* sensu lato. To preserve the monophyletic nature of *Gomphus*, several species have been reassigned to *Gloeocantharellus*, and the *Turbinellus* genus has been reinstated. This study confirms the monophyletic status of both *Gomphus* and *Turbinellus*, in alignment with

earlier findings. Our phylogenetic evaluations reveal a sister group relationship between *Gomphus* and *Turbinellus*, diverging from earlier studies that grouped *Turbinellus* with other Gomphaceae genera as sisters to *Gomphus* or with multiple *Ramaria* species. The earlier expansive classification of gomphoid fungi, which included *Gloeocantharellus*, is now considered inaccurate.

The analysis conducted in this study upholds the monophyly of gomphoid fungi under a more restricted definition, solely encompassing *Gomphus* and *Turbinellus*. Predominantly found in the northern hemisphere, notably North America, which Corner and Petersen have identified as this group's diversity hotspot, recent research acknowledges only four North American species from this group. Our study incorporates an extensive array of Asian specimens, shedding light on the phylogenetic ties among the majority of known gomphoid species. As per the findings of this and previous studies, there are now 23 recognized gomphoid species across Africa, Asia, Europe, and North America.

### 5.2.2 Ramaria

In this research, we expand the phylogenetic landscape of the *Ramaria* genus by introducing nineteen new species and revisiting the classification of seven known species based on both morphological characteristics and phylogenetic analysis. The *Ramaria* genus, traditionally known for its colorful and extensively branched basidiocarps, exhibits a wide phenotypic diversity and ecological significance, which our study further elucidates.

Our findings parallel those of Humpert et al. (2001), who explored the paraphyletic nature of *Ramaria* in relation to other genera such as *Clathrus* and *Gomphus*, highlighting the evolutionary complexity within the Gomphales. In line with their research, our phylogenetic framework also shows that *Ramaria*, with its newly identified species, continues to be a paraphyletic group, emphasizing a dynamic and complex taxonomic structure that challenges conventional classification paradigms. The addition of new species in our study emphasizes the diversity and morphological variations within *Ramaria*, showcasing a range from gelatinous to fibrous textures among the basidiocarps, as previously described by Marr and Stuntz (1973). Furthermore, the spore characteristics, such as color and ornamentation, align with the broader phylogenetic traits identified in the family, reaffirming the evolutionary trajectories proposed by Petersen (1971) and subsequent studies.

Moreover, this study findings challenge and extend the morphological classifications by revealing cryptic diversity within known species, suggesting that morphological traits alone may not adequately reflect the phylogenetic and ecological complexities of the *Ramaria* species. This underlines the necessity for integrating robust phylogenetic methods to capture the full spectrum of diversity within this group, echoing the sentiments from earlier foundational works on fungal phylogenetics.

In conclusion, the expanded phylogenetic analysis presented here not only contributes to a deeper understanding of the *Ramaria* genus but also sets a framework for future taxonomic revisions and ecological studies. It underscores the importance of continuous revision and exploration within fungal taxonomy, especially for genera as complex and ecologically significant as *Ramaria*.

## 5.2.3 Clavulinopsis

In this research, we utilized detailed molecular phylogenetic analyses, employing both single-gene markers (ITS1+ITS2 and 5.8 S ribosomal RNA) and multi-locus genetic sequences (including ITS, nrLSU, and ATP6), to thoroughly explore the taxonomy of the genus *Clavulinopsis* across regions in China and Thailand. This rigorous approach led to the discovery and identification of three previously unknown species within the genus, specifically identified as *P. sp1*, *P. sp2*, *P. sp3*. Due to the limited number of morphological traits that are taxonomically informative in *Clavulinopsis*, these molecular techniques are

essential for the accurate classification and identification of species within this genus. The expansion in the description of new species within the genus *Clavulinopsis* has been significantly accelerated by advancements in molecular analysis methods, as highlighted by several recent publications (Hyde et al., 2016; Kautmanová et al., 2012; Yan et al., 2023).

In our comprehensive research on the genus *Clavulinopsis*, we have not only identified three new species within this genus but have also focused extensively on certain species that present taxonomic uncertainties, such as *Clavulinopsis fusiformis* (Sowerby) Corner. Initially discovered in Europe, this species has been subsequently reported across a global range. Furthermore, a significant number of sequences from this species are currently available in the GenBank database. However, a major challenge has been that most specimens are either accompanied only by sequences without detailed morphological descriptions or are morphological documented but lack accompanying molecular data. This lack of detailed and integrative data substantially impedes in-depth research on this species.

To address these issues, our study involved the construction of a comprehensive multi-gene phylogenetic tree for European specimens of *Clavulinopsis fusiformis*, coupled with detailed observations of their microscopic morphologies. We precisely determined their phylogenetic positioning and conducted comparative analyses with other species within the genus to delineate both morphological distinctions and similarities.

The species *Clavulinopsis helvola* (Pers.) Corner 1950 encountered similar challenges. Our approach involved an exhaustive examination of all sequences associated with this species, an analysis of the geographic locations of discovery, and a thorough review of existing literature. These efforts culminated in a definitive placement of this species on the phylogenetic tree.

Concerns regarding the taxonomic placement of *Clavulinopsis miyabeana* (S. Ito) S. Ito 1955 also emerged during our study. Originally discovered in Japan, we found a notable absence of relevant molecular data from Japan itself. Despite this, the species has been identified in other regions, including China and the Philippines. Our research efforts focused on elucidating the relationships of this species with other members of the genus, enhancing our understanding of its taxonomic and phylogenetic context.

### 5.2.4 Clavariadelphus

In this investigation, we present the characterization of two newly identified *Clavariadelphus* species, which have been distinguished from five known species through comprehensive morphological descriptions and phylogenetic analyses. The phylogenetic framework developed in this study follows recent methodological advancements, like the approaches utilized by Xia and Fan (2020), Sher et al. (2018), and Huang et al. (2020), which underscore the integration of molecular data to resolve species relationships within *Clavariadelphus*.

Morphologically, the new species exhibit distinct characteristics that set them apart from closely related species within the genus. This differentiation is akin to the observations made by Xia and Fan (2020) where *Clavariadelphus griseoclavus* was delineated based on unique coloration and spore measurements. Similarly, our findings highlight unique morphological traits such as basidiome structure and spore geometry that are critical for species identification.

Phylogenetically, the use of ITS sequences has allowed for a more refined understanding of the genus's structure. This approach follows the methodology described by Sher et al. (2018), who also utilized ITS regions to establish the phylogenetic placement of *Clavariadelphus* elongatus. Our analyses support the monophyly of the newly introduced species within the *Clavariadelphus* genus, reinforcing the phylogenetic framework established by Huang et al. (2020), which expanded the known diversity of the genus in China and provided a key for species identification based on molecular and morphological data.

The taxonomic clarity provided by this study is crucial for the accurate classification of *Clavariadelphus*, facilitating further ecological and biogeographical research. Understanding the specific attributes and distribution of each species aids in conservation efforts and in understanding their ecological roles within their respective environments.

### 5.2.5 Lentaria

In this study, we revisit the classification and phylogenetic positioning of three known *Lentaria* species, expanding on the phylogenetic framework previously established for this genus. Our research integrates detailed morphological examinations and molecular phylogenetic analyses to refine the understanding of these species within the *Lentaria* genus.

In line with Liu et al. (2017), our analyses have established robust phylogenetic relationships among the studied *Lentaria* species. By using ITS region sequences, we were able to confirm the monophyletic nature of the species within this genus and their evolutionary relationships with other members of the Gomphales order. This molecular evidence is crucial as *Lentaria* species often exhibit subtle morphological differences that can complicate classification based solely on physical characteristics. Moreover, the detailed morphological descriptions and comparison with closely related species enable a deeper understanding of *Lentaria* diversity. As Liu et al. (2017) highlighted, the majority of *Lentaria* species are lignicolous and play significant roles as decomposers in forest ecosystems, which underpins the ecological importance of accurate species identification.

To conclude, the integration of detailed morphological characterizations with phylogenetic analyses provides a clearer picture of *Lentaria* taxonomy and its ecological roles. This approach not only aligns with the methodologies, but also enhances our capacity to monitor and study biodiversity within fungal communities, ensuring that ecological assessments and conservation efforts are based on precise taxonomic knowledge.

# 5.3 Suggestions

## 5.3.1 Potential benefits or application of the study's outcomes.

In numerous areas across China, some species of the genus *Phaeoclavulina* are recognized as edible, owing to their palatable taste, rich protein content, and the ease with which they can be harvested. These attributes have established them as superior edible mushroom resources in the marketplace, where they are greatly appreciated by a wide array of consumers.

*Phaeoclavulina* species produce various enzymes, including cellulases, amylases, and proteases, which have potential applications in biotechnology and industrial processes. These enzymes can be used in biofuel production, bioremediation, food processing, and other biotechnological applications.

Phaeoclavulina species are widely recognized as ectomycorrhizal fungi, forming mutualistic associations with tree roots. They play a vital role in forest ecosystems by enhancing nutrient uptake, improving tree growth, and facilitating nutrient cycling. Phaeoclavulina species are often considered indicators of healthy and diverse forest ecosystems.

Clavulinopsis species have demonstrated the ability to accumulate and degrade various contaminants, including heavy metals and organic pollutants. This suggests their potential application in bioremediation efforts to clean up polluted soils and sites.

Further research on *Phaeoclavulina* and *Clavulinopsis* species diversity and their potential benefits may uncover additional applications and insights. It is important to note that the practical utilization of these fungi requires thorough investigation, including safety and efficacy evaluations, before their implementation in various applications.

5.3.2 Recommendations for further research to more comprehensively address other aspects of the problem. The holotype of some *Phaeoclavulina* species were lost. New collections are needed for epitypification and fixing the species concept for these species. Previous studies on *Phaeoclavulina* species mainly focused on taxonomy. Further studies on the relationships between *Phaeoclavulina* and termites are needed. Ongoing research on *Clavulinopsis* species diversity, still have many *Clavulinopsis* species need description based on our collection.

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# **APPENDIX A**

# CHEMICAL REAGENTS AND MEDIA

# 1. Malt Extract Agar (MEA) used for fungal cultivation

Agar 15 g

Peptone 0.78 g

Glycerol 2.35 g

Dextrin 2.75 g

Maltose, Technical 12.75 g

Suspend 33.6 g of malt extract agar in distilled water and mix thoroughly. Heat with frequent agitation and boil for 1 minute to completely dissolve the power and bring volume to 1000 ml. Autoclave at 121°C for 15 minutes

# 2. Potato dextrose agar (PDA) used for fungal cultivation

Potato starch (from the infusion) 4 g

Dextrose 20 g

Agar 15 g

Suspend 39 g of Potato dextrose agar in distilled water and mix thoroughly. Heat with frequent agitation and boil for 1 minute to completely dissolve the powder and bring volume to 1000 ml. Autoclave at 121°C for 15 minutes.

### APPENDIX B

## ABSTRACT OF PUBLICATIONS







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### Two new species of Cyclocybe (Agaricales, Tubariaceae) from China

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### Abstract

Cyclocybe encompasses 12 species which are distributed worldwide. In this study, two new species named C. suberebia and C. dinggvensis are introduced from China. Phylogenetic analyses based on nrITS, nrLSU, tef1-α, and rpb2 data show their placement within Cyclocybe in two distinct lineages. Cyclocybe suberebia is characterized by its dark brown to light brown pileus, smaller spore size, clampless hyphae. Cyclocybe dinggyensis is characterized by a slender basidioma, tetrasporic basidia and clampless hyphae. Descriptions, colour photographs and line drawings of both new species are presented.

Key words: China, new taxon, phylogeny, taxonomy

### Introduction

Cyclocybe Velen, (Velenovský 1939) part of the Tubariaceae family within the Agaricales order and typified by C. erebia (Fr.) Vizzini & Matheny-currently comprises 12 species (He et al. 2019, Niveiro et al. 2020, Liu et al. 2021). Compared with the other genera of Tubariaceae, species of Cyclocybe differ by a membranous ring and smooth basidiospores with a rudimentary or absent germ-pore (Pegler 1983, Singer 1986, Largent & Baroni 1988, Nauta 2005, Ryman 2008, Vizzini et al. 2014).

Before the advent of molecular phylogenetic studies, Cyclocybe was considered as a subgenus in Agrocybe of the family Strophariaceae, genus which is characterized by collybioid to tricholomatoid basidiomes usually with yellowbrown or brown tinges, regular hygrophanous pileus, dull brown spore print, basidiospores often with a broad germ pore (sometimes quite reduced), distinct hymenial cystidia and a hymenidermal pileipellis (Singer 1986, Nauta 2005, Ryman 2008, Kiyashko 2022). However, several molecular phylogenetic studies indicated that the genus Agrocybe is polyphyletic (Moncalvo et al. 2002, Walther et al. 2005, Matheny et al. 2006, Tóth et al. 2013, Vizzini et al. 2014). Vizzini et al. (2014) carried out a phylogenetic study (nrITS- and nrLSU based) on Agrocybe subg. Aporos, resurrected the genus Cyclocybe for accommodating A. erebia, A. cylindracea (DC.) Maire, A. aegerita (V. Brig.) Singer A. parasitica G. Stev., and A. salicaceicola Zhu L. Yang, M. Zang & X.X. Liu, and described the new species Cyclocybe erebioides Angelini & Vizzini. All these species are distinguished by a membranous ring and basidiospores with a reduced or absent germ-pore. In a subsequent phylogenetic study, Frings et al. (2020) added the protein-coding genes rpb2 and tef1-α for the first time to distinguish species in the Cyclocybe aegerita complex.





# New Insights into Lichenization in Agaricomycetes Based on an Unusual New Basidiolichen Species of Omphalina s. str.

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Abstract: The genus Omphalina is an ideal genus for studying the evolutionary mechanism of lichenization. Based on molecular phylogeny using ITS and nuLSU sequences by means of Bayesian and maximum likelihood analyses and morphological examination, combining the existence of green algae in basidiomata stipe and a Botrydina-type vegetative thallus, we described a bryophilous new basidiolichen species, Omphalina licheniformis, from a residential area of Jiangxi Province, China. This finding of unusual new basidiolichen species updated our understanding of the delimitation of Omphalina, indicating that both non-lichen-forming and lichen-forming fungal species are included simultaneously. The presence of algal cells in the basidiomata should receive more attention, as this would be helpful to distinguish more potential basidiolichens and explore the cryptic species diversity. This work provides new insights and evidence for understanding the significance of lichenization during the evolution of Agaricomycetes.

Keywords: agaricales; basidiolichen; basidiomycota; fruiting body; green algae; phenotype; systematics; new taxon



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### 1. Introduction

Lichens are symbionts of fungi (mycobionts) and algae and/or cyanobacteria (photobionts), among which only 0.9% species belong to the Basidiomycota [1]. Omphalina Quél. is an undisputedly important genus when talking about basidiolichen species, because it included both non-lichenized and lichenized species originally, and was subsequently separated into non-lichenized Omphalina s. str. and lichenized genera such as Lichenomphalia Redhead, Lutzoni, Moncalvo & Vilgalys [2] and Agonimia Zahlbr. (syn. Marchandiomphalina Diederich, Manfr. Binder & Lawrey [3]). In addition, Omphalina also includes saprophytic, parasitic, and bryophilous species [4]. Therefore, Omphalina has been regarded as an ideal genus for studying the evolutionary mechanisms associated with lichenization [4,5].

Recently, molecular phylogenetic analyses pointed out that the classical concept of Omphalina, mainly based on morphological features [6-9], includes several omphalinoid genera nested inside the order Agaricales [2,10-14], as well as Hymenochaetales Oberw. [15-18]. Inside the Agaricales there are omphalinoid taxa in the suborders Hygrophorineae (family Hygrophoraceae, subfamily Lichenomphaloideae [13]), Marasmiineae (family Porotheleaceae [19,20]) and Tricholomatineae (family Omphalinaceae [21]). Rickenellaceae is the family encompassing omphalinoid taxa in the Hymenochaetales [17,18,22]. Omphalina was

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