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Morphological and Molecular Systematics of Resupinatus (Basidiomycota)

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Morphological and Molecular Systematics of *Resupinatus* (*Basidiomycota*)

(Thesis format: Integrated Article)

by

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Graduate Program in Biology

A thesis submitted in partial fulfillment
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The School of Graduate and Postdoctoral Studies
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Abstract

Cyphelloid fungi (small, cup-shaped *Agaricomycetes* with a smooth spore-bearing surface) are, compared to their gilled relatives, poorly studied and understood. Within the tribe *Resupinateae* (which has included the genera *Resupinatus*, *Stigmatolemma*, *Aphyllotus* and *Stromatocyphella*), little is known about the evolution of the cyphelloid fruit body form. How many times has this reduced morphology evolved within the group? Do all cyphelloid members that are currently treated in this group belong there? Are there other described species of cyphelloid fungi currently treated in other genera that belong within the *Resupinateae*? This study presents phylogenies of the cyphelloid and small lamellate members of the *Resupinateae* based on rDNA sequences (ITS1, 5.8S, ITS2 and the D1/D2 region of the nuclear large subunit rRNA gene) to illustrate the evolution of reduced basidiomata in the *Resupinateae*. This study also provides an analysis of traditional morphological characters used to distinguish species (fruit body colour and size, and spore size, shape, ornamentation and colour) and compares morphological and DNA-based classifications. A total of 10 species new to science (representing approximately 20% of herbarium specimens examined) were discovered as a result of this study, and 24 species belonging in the *Resupinateae* were "rediscovered" (species previously described but forgotten since their initial description) amongst herbarium collections and in the literature. Based on the phylogenetic analysis of the group, all members of the *Resupinateae* fall into a single genus, *Resupinatus*, including *Stigmatolemma* and *Stromatocyphella* as synonyms, whereas the genus *Aphyllotus* is excluded from the group based on morphology. The cyphelloid fruit body morphology has evolved at least four separate times within the group. This study highlights the significance of herbaria as repositories of unknown and undocumented biodiversity, and shows that the evolution of different fruit body morphologies in the *Fungi* is not a linear pattern of simple to complex.

Keywords

Systematics, Molecular Systematics, Taxonomy, Fungi, *Basidiomycota*, *Resupinatus*, *Agaricales*, Fruit Body Morphology, Herbarium Specimens, Natural History

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When The Beatles sang the songs "With a Little Help from My Friends" and "All You Need Is Love" they were obviously thinking about the graduate students I share an office with (Sarah Allan, Sara Asmail, Asma Asemaninejad, Michael Del Vasto, Chris Hay, Jason Lehrer, and Nimalka Weerasuriya), as well as all of the current and past graduate students with whom I have shared a lab. You have all helped keep me sane over my time here, and for that I thank you very much. I have also shared a lab with work-study and volunteer students too numerous to name, but I would like to officially acknowledge one: Terry Dongkeun Kim. You got me excited to do lab work again. Thank you.

Last but certainly not least, I would like to thank my family for supporting me during my time in graduate school: my parents, grandparents, aunts, uncles, cousins, and those that I lost along the way.

To Dorothy Saunders: I wish you were still here to share in the joy of my accomplishments. I know you would have been so proud. I dedicate this thesis to you.

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Statement of Co-Authorship

All of the labwork and writing in this thesis is the work of the primary author (JVM) with the following exceptions:

I had assistance with sequence concatenation by three undergraduate students (R. Beretta, A. Chatterjee, and D. Sinov), and assistance by five students in generating sequences used throughout this study (M. Anderson, R. Beretta, A. Gorth, T. Dongkeun Kim, and D. Sinov). The table caption for Table 2.1 indicates which sequences were generated by the author (JVM, in regular font), which sequences were generated by the most productive work-study student (TDK, in bold font), and which sequences were generated by the rest of the undergraduate students in the lab as a group (in italics). Cultures of fungi obtained through culture collections, as well as those generated as a result of this study, were maintained by lab volunteers and work-study students.

In Chapter 6, herbarium collections received on loan not belonging in the *Resupinateae* were originally identified and annotated by RGT. In the "Taxonomy" section of that chapter, all observations of species or collections were made by the author except where clearly noted (for example, the observations for *Hydnopolyporus palmatus*).

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List of Abbreviations

(!): Denotes a type specimen was seen in this study

AD: State Herbarium of South Australia (Adelaide, Australia)

Ant-PDA: Antibiotic Potato Dextrose Agar

ARIZ: Herbarium, School of Plant Sciences, University of Arizona (Tucson, Arizona, USA)

B: Botanical Garden and Botanical Museum in Berlin-Dahlem, Zentraleinrichtung der Freien Universität Berlin (Berlin, Germany)

BPI: U.S. National Fungus Collections (Beltsville, Maryland, USA)

BSC: Biological Species Concept

C: Natural History Museum of Denmark (Copenhagen, Denmark)

CANB: Australian National Herbarium (Canberra, Australia)

CFMR: U.S. Forest Service, Northern Research Station (Madison, Wisconsin, USA)

DNA: Deoxyribonucleic Acid

EDTA: Ethylenediaminetetraacetic Acid

EF1-α: Elongation Factor 1-α

ESC: Evolutionary Species Concept (in the context of this study; may also be used to refer to the Ecological Species Concept)

EtBr: ethidium bromide

FH: Harvard University Herbarium (Cambridge, Massachusetts, USA)

GBIF: Global Biodiversity Information Facility (Copenhagen, Denmark)

GJO: Universalmuseum Joanneum (Graz, Austria)

HO: Tasmanian Museum and Art Gallery (Hobart, Australia)

ICMP: International Collection of Microorganisms from Plants (Auckland, New Zealand)

INPA: Instituto Nacional de Pesquisas da Amazônia (Manaus, Brazil)

ITS: Internal Transcribed Spacer (of ribosomal DNA)

ITS1: Internal Transcribed Spacer region 1, or a forward primer targeting the ITS region of ribosomal DNA

ITS1-F: a forward primer targeting the ITS region of ribosomal DNA, specifically designed for fungi

ITS6F: a forward primer targeting the ITS region of ribosomal DNA

ITS8R: a reverse primer targeting the ITS region of ribosomal DNA

K: Royal Botanic Gardens (Kew, England)

KOH: potassium hydroxide

L: Nationaal Herbarium Nederland, Leiden University branch (Leiden, Netherlands)

LR3: a reverse primer targeting the large subunit of ribosomal DNA

LR3R: a forward primer targeting the large subunit of ribosomal DNA

LR5: a reverse primer targeting the large subunit of ribosomal DNA

LS1: a forward primer targeting the large subunit of ribosomal DNA

LS1R: a reverse primer targeting the large subunit of ribosomal DNA

LSU: Large Subunit of the ribosomal DNA

MCMC: Markov chain Monte Carlo simulation

MEA: Malt Extract Agar

MEB: Malt Extract Agar with Benomyl

MEGA6.0: Molecular Evolutionary Genetics Analysis version 6.0

MEL: Royal Botanic Gardens (Melbourne, Australia)

μm: micrometer (or micron)

MSC: Morphological Species Concept

NCU: University of North Carolina Herbarium (Chapel Hill, North Carolina, USA)

NL4: a reverse primer targeting the large subunit of ribosomal DNA

NYBG: New York Botanical Garden (Bronx, New York, USA)

O: Botanical Museum (Oslo, Norway)

PC: Muséum National d'Histoire Naturelle (Paris, France)

PDA: Potato Dextrose Agar

PDD: Landcare Research (Auckland, New Zealand)

rDNA: Ribosomal DNA

PCR: Polymerase Chain Reaction

PH: Academy of Natural Sciences (Philadelphia, Pennsylvania, USA)

PRC: Charles University in Prague (Praha, Czech Republic)

PRM: National Museum (Praha, Czech Republic)

PSC: Phylogenetic Species Concept

Q: the ratio of spore length to width

S: Swedish Museum of Natural History (Stockholm, Sweden)

SSU: Small Subunit of the ribosomal DNA

STR: Institut de Botanique (Strasbourg, France)

TAE: Tris base, acetic acid and EDTA buffer

TE: Tris base and EDTA buffer

TENN: University of Tennessee Herbarium (Knoxville, Tennessee, USA)

UPS: Uppsala University Herbarium (Uppsala, Sweden)

UWO: University of Western Ontario Herbarium (London, Ontario, Canada)

Preface

The purpose of taxonomy and systematics is obvious: to correctly name, describe, and classify species. This is not a new effort, as biologists since the beginning of Biology as we know it have been naming, describing, drawing, and classifying species. The importance of this effort today takes on a new meaning: we are in the middle of a mass extinction, and many of the species we are losing we don't even know exist. Botanists and zoologists name and describe new species on a regular basis, but they are far more focused on conservation as they already know about much of the hypothesized diversity that exists on the planet. Mycologists, on the other hand, are in a league of their own. There are an estimated 1.5 million species of fungi on the planet, yet we only know of approximately 97,000 species. Unfortunately, fungal taxonomy, fungal systematics, and fungal classification have all been made more difficult by the naming practices of the past. Mycologists would do "smash and grabs" on expeditions, attempting to collect and name everything they came across. This led to the species being named more than once, worthless species descriptions (sometimes as few as three words), and species being lost in the literature of the 1700s and 1800s.

Erwin F. Smith, a mycologist in the 1890s, said it best:

"The labors of the 'all naming' mycologists of the past have filled this part of systematic botany with a mass of rubbish mountain high, and still the brave work goes on, exactly as if it were not known that fungi are exceedingly variable organisms, or that it is possible by holding on to the old notion of fixity of species to make half a dozen new ones out of the product of a single spore by a little variation of the substratum, or even without the latter divide by drawing up separate descriptions of old and young and large, small and medium sized spores. Is it not indeed time we should have a reform and begin to *reduce* the number of species by carefully studying those with which have been badly described (by far the large number), learning their life history and the extent of their variability under ordinary conditions, and throwing out the synonyms? This method carefully applied would unquestionably reduce the number of so-called species of fungi and bacteria nearly or quite one-half. This must necessarily form a large part of the work of the next generation of mycologists, and no one familiar with the ground can doubt that the task of properly classifying these plants would be immensely easier if half the descriptions had never been written."

(The American Society of Naturalists, volume 30, p. 225)

(March 1896)

Chapter 1

1   General Introduction and Literature Review

1.1   Overview and Broad Classification of Macrofungi

Biological organisms can be divided into three main groups called domains, as demonstrated by molecular evidence (Woese, 1990): the Archaea (a group of prokaryotic, unicellular organisms with no nucleus or other cell-bound organelles, formerly thought to live in extreme environments but now associated with a broad range of hosts and environments; Bang & Schmitz, 2015), the Eubacteria (a group of prokaryotic, unicellular organisms with no nucleus or other cell-bound organelles, and like the Archea they can be found in a wide variety of environments; Rappé & Giovannoni, 2003; Sears, 2005; Glud et al., 2013), and the Eukarya (a group of unicellular or multicellular organisms with many membrane-bound organelles; Nelson & Cox, 2005). The Eukarya are divided into supergroups (Burki et al., 2007; Burki et al., 2008), and the Fungi fall into the Opisthokont supergroup with the Animals (Steenkamp et al., 2006).

The Kingdom Fungi is a group of eukaryotic organisms that occupy a wide variety of habitat types. Some fungi cause devastating diseases in crops, which can have an enormous indirect impact on human health by decreasing the amount of food available worldwide, whereas others play an integral role in plant survival and growth. Some species of fungi form symbiotic associations with plant roots, called mycorrhizae. This mutualism is hypothesized to have been the major contributing factor for plants being able to colonize the land from water, approximately 400 million years ago (Malloch et al., 1980; Pirozynski & Malloch, 1975; Read et al., 2000; Remy et al., 1994; Simon et al.; 1993). Fungi are also the single most important group of organisms in the world for decomposition of dead plant matter due to their enzymatic ability to digest cellulose and lignin, and their physical ability to penetrate solids through their filamentous growth form ((Floudas et al., 2012). Without the decomposition of plant wastes by fungi, humans and other life would be buried under millions of tons of dead plant material (Schwarze et al., 2000).

The classification of the fungi was historically based on the morphology - both macroscopic and microscopic - of their spores and spore-bearing structures. Fungi with macroscopic fruit bodies - i.e., at least 1 mm in some dimension - were classified on the basis of the shape of these fruit bodies and the arrangement of their spore-bearing tissues. Many form spores in a distinct surface layer called a hymenium (the "Hymenomycetes"), whereas the puffballs and their relatives (the "Gasteromycetes") form their spores internally in an amorphous mass called a gleba (Kirk et al., 2008). With the advent of DNA-based phylogenetic studies, it was confirmed that "Gasteromycetes" were derived multiple times from within the "Hymenomycetes" (Hibbett et al., 1997).

Within the "Hymenomycetes", fungi with fruit bodies shaped like an umbrella, with the hymenium covering blades or ridges (called gills, or lamellae) that radiate beneath the cap (or pileus), were classified as "agarics", the gilled mushrooms. Other fruit body forms and the broad categories based on them include: cup-shaped, with the hymenium lining the interior of the cup/apothecium ("cup fungi"); stalked or sessile, with the hymenium lining downward-facing pores ("polypores" if tough, and "boletes" if fleshy and centrally stipitate); club- or coral-shaped (the "coral fungi"); and crustlike, with a smooth or wrinkled hymenium (the "crust fungi"). In very early classifications, one genus or a very few genera would contain all of the species of each of these broad groups of macrofungi, e.g., *Peziza*[1] for most of the cup-fungi, and *Agaricus* for most of the gilled mushrooms (Persoon 1801; Fries, 1821-1832). With the added information of molecular phylogenetics, each of the broad groups listed above is recognized to be highly diverse and polyphyletic (Schoch et al., 2009; Hibbett et al., 2014).

Microscopy revealed how and where the spores of macrofungi were produced: inside a tubular or swollen sac called an ascus (plural asci), or on prongs (sterigmata) external to a typically club-shaped cell called a basidium (pl. basidia). Micheli (1729) was the first to illustrate the ascus, and Hedwig (1789) illustrated ascospores within asci (which he

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[1] Authorities (the authors of taxon names) are provided for taxa that are central to this thesis in Tables 1.1 and 1.2, and in lists of synonymy in Chapters 2-6. For all others, see Kirk et al. (2008) or indexfungorum.org

termed 'thecae'). Around the same time, the pegs or sterigmata (singular sterigma) on which basidiospores are formed were described by Schaeffer (1759), and the arrangement of spores in fours on the sterigmata of the basidium were illustrated by Müller (1780). Persoon (1794) introduced the idea that there was a specific location within the fruit body that all spores are produced; he termed this area the hymenium. Unfortunately, he forced a step backwards in fungal classification by saying that all spores must be borne in the 'thecae', and this was only corrected by Léveillé (1837) when he interpreted the difference between asci (in which spores are produced internally) and basidia (on which spores are produced externally). These are now recognized as the fundamental characters of the phyla *Ascomycota* (meiospores borne inside asci) and *Basidiomycota* (meiospores borne on basidia) (Kirk et al., 2008). Some focal taxa of this thesis produce small, cup-shaped fruit bodies and were originally classified in *Peziza* or some of its segregates, but produce their spores on basidia, not in asci Léveille (1837; see Table 1.2). So, instead of being members of the *Ascomycota*, they belong in the *Basidiomycota*.

1.2   Historical Classification of the *Agaricales*

The gilled mushrooms, all producing basidia and basidiospores, gradually became known as the order *Agaricales* of the class *Basidiomycetes*, and later the phylum *Basidiomycota* (Kirk et al., 2008). Fries (1821-1832) often used genera in a broad way, for example, placing all gilled mushrooms in the genus *Agaricus*, and then divided these genera into tribes or series based on other macroscopic characters (such as the colour of the spores when shed onto a piece of white or black paper). There was little attention paid to microscopic characters.

Lucien Quélet (1832-1899) and Victor Fayod (1860-1900) both used microscopic characters to divide the genus *Agaricus* into 108 genera. The characters included spore size, shape, colour and ornamentation, and unusual hyphal characteristics, all characters that we still use today to describe and delimit species (Quélet, 1888; Fayod, 1889). Fayod especially placed great emphasis on the outer layers of the fruit body cap (pileus) and stem (stipe), and the structure of the gill trama (the ground tissue of the gills, supporting the subhymenium and hymenium); he believed that these characters together placed great doubt of the membership of Fries' genera (Fayod, 1889; Lamoure & Miller, 1999). This

allowed for species with dramatically different macromorphology to be linked by common micromorphological characters.

The concept of micromorphological characters being a better predictor of phylogeny than macromorphological characters was maintained in the literature with the further division of the *Agaricales* by Rolf Singer (1906-1994) and Robert Kühner (1903-1996). Kühner used cytological studies of both cultures and fresh fruit bodies to determine affinities of genera to families. The characters used revolved mostly around characters relating to spores: spore wall features such as the layers and ornamentation of the spore wall(s), nuclear content and behavior in basidia and basidiospores, chemical reactions of the spores or other cells or tissues, and ontogenic characters such as the development of the fruit body and hymenium (Kühner, 1984). Singer (e.g., 1936; 1951; 1975; 1986) used these characters as well as information from the arrangement of cells in the hymenial layer, trama (flesh) of gills and cap, and surface of the cap (pileipellis) and stipe (stipitopellis), and the use of stains to determine chemical makeup of the cell walls. Using these characters, Singer (1948: p. 30) first named the tribe *Resupinateae* to include the genera *Resupinatus* and *Hohenbuehelia,* both of which have a gelatinous layer in the flesh of their caps, and colourless spores (white in print) that do not react with iodine (are inamlyoid). Later, Singer (1975; 1986) included cyphelloid genera (basidiomycetes with cup-shaped fruit bodies so small that they have no room for gills) together with the gilled genera that he thought were their natural relatives based on micromorphological and biochemical characters. This was a radical departure from earlier classifications, in which the cyphelloid fungi were assigned to the families *Thelephoraceae* or *Cyphellaceae* of the order *Aphyllophorales* (literally, the non-gilled mushroom fungi) (Burt, 1914; Pilát, 1924; Cunningham, 1953; Talbot, 1956; Donk, 1959; Cooke, 1961; Donk, 1962; Reid, 1964; Donk, 1966), quite separate from the gilled mushrooms in the *Agaricales*. In the case of the *Resupinateae*, this included the cyphelloid genera *Aphyllotus, Stigmatolemma,* and *Stromatocyphella*, treated together with the lamellate *Hohenbuehelia*, *Resupinatus,* and *Asterotus* (which he later treated as a synonym of *Resupinatus*; Singer 1975; 1986). Singer's classification was visionary, but in many cases he and others created artificial groups due to the misinterpretation of convergent characters (homoplasies) or ancestral

characters (symplesiomorphies) as shared, derived character states (synapomorphies; Matheny et al., 2007).

1.2.1   Defining the *Agaricales* using molecular techniques

Classifications of the *Agaricales* that were based primarily on morphological characters differed widely in their recognition of genera and families (Kühner, 1980; Jülich, 1981; Singer, 1986; or Bas, 1998). Since the 1990s, DNA sequence data have been used to estimate the evolutionary relations of the gilled fungi and to determine how close or disparate these estimates are from established classifications. Hibbett et al. (1993) studied the phylogeny of various species of gilled fungi that had been classified in the genus *Lentinus* based on partial sequences of the nuclear gene for the large ribosomal subunit (LSU rDNA), and showed that these were polyphyletic, with some species being related to polypores (now *Polyporales*) and others scattered in different groups of *Agaricales*. Later, Hibbett et al. (1997) demonstrated that different fruit body morphologies have evolved multiple times within the *Basidiomycota* as predicted by Kühner (1980), Singer (1986) and others. This was accomplished with sequences from nuclear small subunit rDNA and mitochondrial small subunit rDNA of different genera of fungi within the *Basidiomycota*, and comparing the phylogenetic relationships of these sequences to patterns suggested by their fruit body morphology (Hibbett et al., 1997). It was found that the gilled hymenium, believed by Fries to represent the genus *Agaricus* in the strict sense and later by most other mycologists to represent the *Agaricales*, has evolved at least six separate times over the evolutionary history of the *Basidiomycota* (Hibbett et al., 1997). It was also found that the hymenium of the *Basidiomycota* has changed morphologies, switching back and forth from a gilled or pored hymenium to a smooth one multiple times. The only constraint seems to be with the gasteromycetes (or the "puffballs") that lost the ability to discharge spores forcibly from the basidia; once this ability has been lost it cannot be regained (Hibbett et al., 1997).

Moncalvo et al. (2000) focused on using nlrDNA sequences to determine the relationships among families within the *Agaricales*. The monophyly of the major families of *Agaricales* was tested by constructing phylogenetic trees according to various tree construction algorithms, and all determined that the main families of *Agaricales*, ones we

still use today (*Tricholomataceae, Cortinariaceae,* and *Hygrophoraceae*), were not monophyletic (Moncalvo et al., 2000). It also demonstrated that major genera in use since the time of Fayod (*Clitocybe, Omphalina*, and *Marasmius*) were also not monophyletic (Moncalvo et al., 2000). Further study was required, and in 2002 another analysis using more taxa was performed to determine the major clades (which could represent families, tribes and/or genera) of *Agaricales* (Moncalvo et al., 2002). They determined that at least one hundred and seventeen distinct clades were present in the *Agaricales*, and that the largest of the families, the *Tricholomataceae*, represented at least ten distinct clades (Moncalvo et al., 2002). The idea that the *Tricholomataceae* was not a natural group is not new; since the 1970s it had been referred to as a group of mushrooms that were brought together on the basis of negative characters (characters that are not present and which preclude membership of the species in other groups) as opposed to any one positive character (a character that would include a species in a group; Marr & Stuntz, 1973). Using data from six gene regions, Matheny et al. (2007), proposed six major clades and thirty families within the *Agaricales*. These families have been adopted in the literature and will be used herein except when more recent molecular analyses show conflicting results.

1.2.2   Species concepts in *Agaricales* and other Fungi

The morphological species concept (MSC) was historically used in the identification, delineation, and circumscription of fungal species. When two collections shared many morphological characters, they were deemed to be the same species (Cronquist, 1978). This species concept was once favoured in the biological community due to ease of use; it has since been replaced by other species concepts due to large numbers of cases of convergent evolution. Despite this fact, the MSC is still heavily relied upon when describing and delimiting fungal species; of the 97,000 species currently described, upwards of 70,000 rely on morphological characters alone (Pitt, 1979; Hawksworth et al., 1996). Because the MSC can only circumscribe species based on divergent morphological characters (which may or may not be reflective of common ancestry), other species concepts have been examined as they relate to the fungi. That being said,

the MSC is still relied on heavily for the identification of fungal species, and is used extensively in this study.

The standard species concept used to define species in metazoan animals and many plants is the biological species concept (BSC) developed by Mayer (1942), which states that two organisms are members of the same species if they can interbreed and produce fertile offspring. Unfortunately, although this species concept - at least, the preliminary test of mating compatibility, rather than production of fertile offspring - has been very useful in some groups of *Basidiomycota* (e.g. Petersen & Hughes, 1997; Petersen et al., 1999; Petersen, 2000; Mata et al., 2004; and Kruger et al., 2006), it is difficult to test in some others. During the majority of their life cycle, each cell within the hyphal network is dikaryotic (two genetically distinct nuclei in each cell). Monokaryons derived from single haploid basidiospores often do not grow well in culture, and so testing spore compatibility for many species is difficult (Choi et al., 1999). This has been done for only one species of *Resupinatus* (Thorn & Barron, 1986).

The development of DNA sequencing technologies has allowed mycologists to define species based on two additional species concepts: the evolutionary species concept (ESC; a lineage evolving separately from other lineages and with its own evolutionary role and tendencies, Simpson, 1961) and the phylogenetic species concept (PSC; the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent, Cracraft, 1983; Taylor et al., 2000). Another approach is to use sequence data as multiple characters by which to recognize clusters of individuals that represent species, between which are gaps that aid in recognition of the species clusters. This approach has come to be called "barcoding" (Hebert et al., 2003), but was in fact commonplace among fungal systematists long before the term was coined (e.g. Vilgalys et al., 1990; Gardes & Bruns, 1993; Haynes et al., 1995). Unfortunately, the limit of a species is still arbitrary. What has been colloquially termed "Kurtzman's Rule" states that a variation of three or fewer substitutions in the sequence of the D1/D2 variable domains of the 5' end of the nuclear large ribosomal subunit DNA indicates that individuals are of the same species. A 1% or greater difference in this same region indicates individuals are of a different species (Kurtzman & Robnett, 1998). It has been found that this is an

appropriate operational rule for many species of fungi. In some cases, the large subunit rDNA region often does not have enough variation to distinguish species, although it allows separation of genera or families (Haynes et al., 1995; Kurtzman & Robnett, 1998; Moncalvo et al., 2000). The ITS region was recently selected as the universal fungal barcode at the Barcode of Life meeting in Amsterdam (Schoch et al., 2012). DNA sequencing performed in this study targeted the ITS and D1/D2 regions, but because it was not possible to obtain DNA sequences from all specimens or taxa, both the MSC and the PSC are used herein.

1.3   A Synopsis of the *Resupinateae*

The *Resupinateae* are a tribe (a group between family and genus) of *Agaricales* occurring in all continents around the world, excluding Antarctica (Cooke, 1961; Singer, 1986). The tribe was first designated by Rolf Singer in *Diagnoses fungorum novorum Agaricalium* (1948), and included two genera: *Resupinatus* and *Hohenbuehelia*. By the time of Singer's last major publication, the fourth edition of his Agaricales in Modern Taxonomy (Singer, 1986), four additional genera had been added to the group: *Aphyllotus*, *Asterotus*, *Stigmatolemma*, and *Stromatocyphella*. The group has been largely ignored since then, with only a very recent effort made to clarify phylogenetic relationships amongst members of the group (Thorn et al., 2000; Thorn et al., 2005). *Hohenbuehelia* was shown to be a sister genus to *Pleurotus* (*Pleurotaceae*) (Thorn et al., 2000), and *Asterotus* and *Stigmatolemma* were shown to be synonyms of *Resupinatus* (Thorn et al., 2000; 2005).

1.3.1   *Resupinatus* (including *Asterotus*)

Until recently, the name *Resupinatus* was used for a genus of fungi with 33 species names that are not considered synonyms of each other or placed in alternate genera, in which the hymenium (the spore-bearing surface) is folded into gills (lamellae) or pores (indexfungorum.org/Names/Names.asp). This differs from the development of most other species within the *Agaricales* in which gill production is usually completed within the mushroom primordium, and gills only become larger (either wider, longer, or both) during development and not more numerous (e.g. Moore 1987; Reijnders, 1948, 1963).

The fruit bodies (commonly called "mushrooms") are small; the smallest species, *Resupinatus kavinii*, forms gregarious cups 1-2 mm in diameter while the largest species examined in this study, *Resupinatus violaceogriseus*, forms groups of much larger fruit bodies up to 3 cm across (Pilàt, 1931; Thorn & Barron, 1986; Grgurinovic, 1997). The number of lamellae can differ dramatically between species, with some fully-developed fruit bodies having as few as three lamellae and some as many as 75 lamellae (Pilàt, 1931; Grgurinovic, 1997). This number can also vary based on stage of fruit body development, such that gill number is not a good taxonomic character to use to distinguish species in agarics (Largent, 1986). Along the edge of the gills are cells called cheilocystidia, which are sterile cells believed to play a role in antimycophagy (Nakamori & Suzuki, 2007). The cheilocystidia in *Resupinatus* are clavate-shaped single cells with finger-like projections (that may or may not be branched (Thorn et al., 2005). The spores are hyaline (clear), inamyloid (do not react with a colour change when stained with Melzer's solution), and range from being globose or subglobose in some species to elliptical or cylindrical in others (Thorn et al., 2005). Spore shape and size vary only slightly within species and greatly between species, and consequently can be used as a taxonomic character to distinguish species when used in combination with other characters (Largent et al., 1977). The colour of the fruit body also varies between species, with some species, such as *Resupinatus applicatus*, being a light tan-brown and other species, such as *Resupinatus alboniger*, being nearly black (Thorn & Barron, 1986). The trama of the gills and cap is gelatinized (has cell walls that are glutinous and expand with moisture) (Thorn et al., 2005). The substrate on which the fruit bodies develop is most often well rotted wood of gymnosperms or dicotyledonous trees (in the form of logs on the forest floor of old-growth forests), but can rarely be on cones of gymnosperms, standing dead trees, the wood of live trees, and the surface of dead heavily lignified tissues of bamboo (Singer, 1962; Singer, 1975; Singer, 1986; Thorn & Barron, 1986; Thorn et al., 2005). Historically, species that are now placed in *Resupinatus* have been classified in 18 genera that are now placed in at least 7 families of 3 orders of the phylum *Basidiomycota* (see Table 1.1).

The genus *Asterotus* was described by Singer (1943) and distinguished from *Resupinatus* by possession of a pseudostipe (a stem-like extension of the pileus) and by the form of

the hyphae in the pileipellis: in *Asterotus* there are asterostromelloid hyphae with cylindric protrusions branching at right angles and resembling an asterisk, whereas in *Resupinatus* the pileipellis hyphae are knobby or have a few irregularly tapering branches but not in the pattern of an asterisk. By 1969, five species had been described or transferred into the genus (indexfungorum.org/Names/Names.asp). Later, Singer (1973; 1975; 1986) treated *Asterotus* as a subgenus of *Resupinatus*. Thorn and Barron (1986) treated *Asterotus* as a separate, monotypic genus including only the type species *A. dealbatus*, and listed three of the other species as members of *Resupinatus* (*A. chilensis* and *A. graminis* as close to *Resupinatus striatulus, A. argentinus* as a synonym of *R. alboniger*), and the fourth (*A. bicolor*) as a synonym of *A. dealbatus*. Sequence data of *Asterotus dealbatus* placed it within *Resupinatus* (Thorn et al., 2000), so this study follows these authors and Singer (1973) in treating *Asterotus* as a synonym of *Resupinatus*.

Table 1.1 Genera historically containing members of the genus *Resupinatus* (in its current sense) and their current classification (Singer, 1986; Kirk et al., 2008).

Genus	Family	Order	Class	Phylum	Current name
Acanthocystis (Fayod) Kühner	*Pleurotaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Hohenbuehelia*
Agaricus L.	*Agaricaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Asterotus Singer	*Tricholomataceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Resupinatus*
Calathinus Quél.	*Tricholomataceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Resupinatus*
Calyptella Quél.	*Marasmiaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Campanella Henn.	*Marasmiaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Dendrosarcus Paulet	*Pleurotaceae (or Omphalotaceae)*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Pleurotus* (or *Omphalotus*)[2]
Geopetalum Pat.	*Pleurotaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Hohenbuehelia*
Hohenbuehelia Schulzer	*Pleurotaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Lentinellus P. Karst.	*Auriscalpiaceae*	*Russulales*	*Agaricomycetes*	*Basidiomycota*	
Marasmiellus Murrill	*Marasmiaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Panellus P. Karst.	*Mycenaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Phyllotus P. Karst.	*Tricholomataceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Resupinatus*
Pleurotopsis (Henn.) Earle	*Tricholomataceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Resupinatus*
Pleurotus (Fr.) P. Kumm.	*Pleurotaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Scytinotopsis Singer	*Tricholomataceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Resupinatus*
Urceolus Velen.	*Tricholomataceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Resupinatus*
Urospora Fayod	*Mycenaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Panellus*

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[2] The type species of *Dendrosarcus* (itself a nomen nudum) has been contested, as *D. carpini* (a synonym of *Omphalotus olearius*; Earle, 1909) or *D. nigrescens* (a synonym of *Pleurotus ostreatus*; Singer & Smith, 1946). According to Donk (1962), Paulet applied his genus *Dendrosarcus* in the same sense as a broadly defined *Pleurotus*.

The lamellate members of *Resupinatus* have been shown to be paraphyletic in the few molecular studies that have been done (Thorn et al., 2000; 2005) as *Asterotus* and several members of the cyphelloid genus *Stigmatolemma* were nested within *Resupinatus*.

1.3.2   *Stigmatolemma*

The name *Stigmatolemma* (now a synonym of *Resupinatus*; Thorn et al., 2005) was used until recently for a genus of 11 species with cyphelloid (cup-shaped) fruit bodies and a smooth hymenium. It is hypothesized based on the development of *Resupinatus* that the hymenium remains smooth because it does not have enough space within the fruit body to fold into lamellae (Donk, 1962). The fruit bodies are much smaller than those of the lamellate *Resupinatus*, rarely growing larger than 250 μm in diameter, 100-150 μm tall and occur in groups of 50 to more than 1,000 fruit bodies (Thorn et al., 2005). These fruit bodies are embedded in or seated on a white or cream mat of hyphae called a subiculum that can be thin, with the substrate visible through the subiculum, to very thick and almost as deep as the cups are high (Cunningham, 1953). As the fruit bodies of *Stigmatolemma* have no gills, they cannot have cheilocystidia. They do, however, have cystidia along the top edge of the cup (a homologous structure to a gill edge) that are identical in morphology to those in *Resupinatus* (Redhead, 1973). The colour of the cups ranges from a tan-brown in *Stigmatolemma poriaeforme* to almost black in *Stigmatolemma incanum*, the type species (Donk, 1962). The trama, as in *Resupinatus*, is gelatinized and hyaline in section in all species (Thorn et al., 2005). The substrate on which it develops, as in *Resupinatus*, is very well rotted wood of gymnosperms or dicotyledonous trees, and one species is known to grow on the bark of old grape vines (Cooke, 1957; Singer, 1986; Schweinitz, 1822). Historically, species of *Stigmatolemma* have been identified as belonging to 15 genera that are now placed in 11 families of 6 orders of the phyla *Ascomycota* and *Basidiomycota* (see Table 1.2).

The first (and only) molecular study involving more than one species of *Stigmatolemma* was performed by Thorn et al. (2005) and showed that the few species of *Stigmatolemma* treated were paraphyletic (possibly polyphyletic), nested within *Resupinatus*. Only three species previously classified in *Stigmatolemma* were included (*S. poriaeforme*, *S.*

Table 1.2: Genera historically containing members of the genus *Stigmatolemma* and their current classification (Cooke, 1957; Singer, 1986; Kirk et al., 2008)

Genus	Family	Order	Class	Phylum	Current name
Boletus L.	*Boletaceae*	*Boletales*	*Agaricomycetes*	*Basidiomycota*	
Chaetocypha Corda	*Tricholomataceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Cellypha*[3]
Cyphella Fr.	*Cyphellaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Henningsomyces Kuntze	*Marasmiaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Lachnella Fr.	*Niaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Maireina W.B. Cooke	*Niaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	
Peziza Dill. ex Fr.	*Pezizaceae*	*Pezizales*	*Pezizomycetes*	*Ascomycota*	
Phaeoglabrotricha W.B. Cooke	*Inocybaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Pellidiscus*
Poria Pers.	*Polyporaceae*	*Polyporales*	*Agaricomycetes*	*Basidiomycota*	
Porotheleum Fr.	*Meripilaceae*	*Polyporales*	*Agaricomycetes*	*Basidiomycota*	
Rhodocyphella W.B. Cooke	*Tricholomataceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Resupinatus*
Solenia Pers.	*Marasmiaceae*	*Agaricales*	*Agaricomycetes*	*Basidiomycota*	*Henningsomyces*
Stromatoscypha Donk	*Meripilaceae*	*Polyporales*	*Agaricomycetes*	*Basidiomycota*	*Porotheleum*
Tapesia (Pers.) Fuckel	*Dermateaceae*	*Helotiales*	*Leotiomycetes*	*Ascomycota*	*Mollisia* (or *Tapesia*)[4]
Theleporus Fr.	*Grammotheleaceae*	*Polyporales*	*Agaricomycetes*	*Basidiomycota*	

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[3] Saccardo (1888) treated the type species of *Chaetocypha*, *C. variabilis* Corda, as a synonym of *Cellypha* (*Cyphella*) *goldbachii*

[4] The type species of *Tapesia* is *Peziza fusca* Pers., which is sometimes treated as *Mollisia*, but sometimes left in *Tapesia*; the two genera differ primarily in the presence (in *Tapesia*) or absence (in *Mollisia*) of a subiculum (Breitenbach and Kränzlin, 1981; indexfungorum.org).

urceolatum, and a sequence of a collection identified as *S. conspersum*), and so it cannot be considered a comprehensive analysis of the group. This study aims to determine if the cyphelloid habit – representing *Stigmatolemma* – is multiply derived within *Resupinatus*, or whether *Stigmatolemma* could be recognized as a monophyletic group within *Resupinatus* once more molecular information is added to the phylogenetic tree.

1.3.3   *Stromatocyphella*

Stromatocyphella conglobata is the only species in a monotypic genus (a genus that contains only one species; Kirk et al., 2008). The fruit bodies of the species are small and cyphelloid, 300-500 µm in diameter and 250-400 µm high, and are found in groups of 3-30 on a common stroma that is raised off the substrate (Reid, 1964). The fruit bodies are a very dark brown (almost black), and the raised stroma-like subiculum is a dusty grey (Burt, 1914). The trama are gelatinized and hyaline as in *Resupinatus* and *Stigmatolemma* (Burt, 1914). Clavate-diverticulate cystidia are located along the edge of each of the cups (Reid, 1964). Previous to this study, *S. conglobata* was only known from North America, primarily on dead *Alnus* spp. (where it erupts out of the lenticels in the bark; Burt, 1914), although Cooke (1961) reported it on multiple woody angiosperm hosts.

Due to the unique morphology of this species, it has been classified in only one other genus (*Cyphella* Fr., *Basidiomycota*, *Agaricomycetes*, *Agaricales*, *Cyphellaceae*; Burt, 1914), and this was at the time of its original description. When Cooke (1961) described the genus *Stromatocyphella*, he included two other species, but Reid (1964) transferred them out of the genus: *Stromatocyphella lataensis* as a synonym of *Calathella eruciformis* (*Marasmiaceae*) and *Stromatocyphella aceris* as a member of *Cyphellopsis* (now a synonym of *Merismodes, Niaceae*).

A goal of this study is first to place *Stromatocyphella conglobata* in the correct location in the fungal tree of life based on morphological and molecular analyses. It has been hypothesized to belong in the *Resupinateae* due to morphological similarities (i.e., Singer, 1973; Thorn & Barron, 1986; Singer, 1986). Singer (1945) suggested that there be a delay in the creation of a new generic name for *Cyphella conglobata* Burt until the *Cyphellaceae* were reorganized, but agreed with Burt (as stated in his original species

description) that this species likely belonged in a separate genus. Singer (1945) commented that this species shared many morphological similarities with the genera *Campanella* and *Favolaschia*, and his comment may be the reason that the genus is classified in the *Marasmiaceae* by Kirk et al. (2008).

1.3.4   *Aphyllotus*

Aphyllotus campanelliformis is also the only species in a monotypic genus (Singer, 1973). The fruit bodies are cup-shaped and singular or in small groups of two or three fruit bodies, with no basal subiculum (Singer, 1986). The pseudostipe (the fruit body narrows as it nears the substrate but does not have the morphology of a true stipe) is eccentric (off-centre) or absent in some fruit bodies (Singer, 1986). The hymenium is smooth, occasionally wrinkled with age (but not folded into gills) (Singer, 1986). The trama is gelatinized, but not all hyphae in the trama have this gelatinization (Singer, 1973). The surface hairs are a Rameales-structure, occasionally asterostromelloid, and there are no cystidia along the edge of the fruit bodies (Singer, 1973).

The classification of *Aphyllotus* has alternated between the *Resupinateae* (Singer, 1975; 1986) and the *Marasmiaceae* (Kirk et al., 2008). The latter is likely correct; there is nothing to suggest that *Aphyllotus* belongs in the *Resupinateae* other than a convergent morphology. The spores of this species also show affinities with the genus *Campanella* (*Marasmiaceae*); they have an eccentric bulge, which is typical of this genus (Singer, 1986). This study will determine if *Aphyllotus* belongs with the *Resupinateae*, and if not suggest where the genus belongs.

1.4   Goals of this work

One of the central questions in the evolution of the fungi is the direction of change between complex and simple forms: in agarics, did taxa with complex fruit body forms develop from ancestors with simpler ones, or was there a simplification of fruit body forms from complex ancestors? Singer (1975; 1986) believed that simpler, cyphelloid forms arose from complex ancestors, and did so multiple times, such that he recognized "reduced series" within multiple families and tribes of the *Agaricales*, including the *Resupinateae*. This hypothesis has been supported by limited molecular studies in

cyphelloid fungi such as that by Bodensteiner et al. (2004), who found that cyphelloid agarics were found in 11 different clades, and within the very small sample of sequences generated from species in the *Resupinateae*, the cyphelloid fruit body form had evolved twice (Bodensteiner et al., 2004). Within the *Resupinateae*, preliminary analyses suggested that at least some species of *Stigmatolemma* (not including the type species, for which no sequences were available) were nested within the genus *Resupinatus* (Moncalvo et al., 2002; Bodensteiner et al., 2004; Thorn et al., 2005). On this basis, Thorn et al. (2005) chose to treat *Stigmatolemma* as a synonym of *Resupinatus*, but their study left a number of questions unanswered: first, did the cyphelloid habit arise just once or multiple times within *Resupinatus*? Second, what is the phylogenetic placement of the type species of *Stigmatolemma* (i.e., is *Stigmatolemma* truly a synonym of *Resupinatus*)? Third, with better taxon sampling could a monophyletic *Stigmatolemma* and *Resupinatus* be recognized? And fourth, what is the phylogenetic relationship of the other cyphelloid members of Singer's (1986) *Resupinateae*?

The main goals of this study are three-fold: first, to determine the number of times the cyphelloid fruit body morphology has evolved in the *Resupinateae*; second, to determine if there are other fruit body morphologies (aside from one poroid species, *Resupinatus porosus*, and the cyphelloid species formerly belonging to *Stigmatolemma*) present in the group; and third, to determine how the taxa belonging to the *Resupinateae* should be classified and if any morphological characters are valuable in defining or recognizing taxonomic groups. These main goals will answer the questions arising from the work of Thorn et al. (2005) in that if the species with cyphelloid fruit bodies are derived multiple times within the *Resupinateae*, the species formerly classified in *Stigmatolemma* would not form a monophyletic group and would validate the synonymizing of *Stigmatolemma* and *Resupinatus,* and a better taxon sampling would determine if Singer's *Resupinateae* was also monophyletic. Better resolution of the phylogenetic relationships of the *Resupinateae* would also suggest if the ancestor of the group was more likely to be a species with lamellate fruit bodies (and thus the cyphelloid fruit body form was either multiply or singly derived) or a species with cyphelloid fruit bodies (and the lamellate form was either multiply or singly derived).

The issue of "orphaned" species in the literature has also been raised recently with the renewed push to discover the missing diversity of the fungi (Hawksworth, 2001). Saccardo (1882-1931) published an encyclopedia of all known names of fungal species at the time, and recorded as many as 117,000 species: 52,157 species as of 1901 (Arthur, 1902), 100,000 species as of 1995 (Rossman, 1995), and 117,000 species as of 2006 (Farr & Rossman, 2014). Not all of these have been analyzed to determine synonymy with the accepted 97,000 species in Dictionary of the Fungi (Kirk et al., 2008), so a significant number of these species may have been "orphaned" (described once briefly, often only with a few words or merely a mention of the substrate, then forgotten) in the literature. This study attempts to rediscover some of this orphaned diversity and determine their correct classification according to modern taxonomy (using molecular analyses when possible).

This study comprises five main parts to answer the above questions. First, an analysis of the group as a whole using molecular and morphological characters will be performed, and the status of each genus in Singer's *Resupinateae* will be addressed as to whether or not it is a synonym of *Resupinatus* (Chapter 2). Second, an analysis of host specificity and geographic location of different species in the *Resupinateae* will be used as indicators of species limits, for the purpose of species range limits and species delineation in identification (Chapter 3). Third, a thorough analysis of the small lamellate and all species with cyphelloid fruit bodies in the *Resupinateae* in Australia and New Zealand will be performed, describing new species as necessary (Chapter 4). Fourth, a discussion of all other species in the *Resupinateae* with small fruit bodies will be performed using molecular methods (when possible) and/or morphological methods (Chapter 5). Lastly, species excluded via molecular and/or morphological analyses will be discussed, as will species that could not be studied (Chapter 6). These studies will contribute to our knowledge of the evolution of different fruit body morphologies: the reversibility of the development of different fruit body morphologies (from lamellate to cyphelloid and back again, or the reverse), the diversity of different fruit body morphologies in a single genus of fungi, and the diversity within a group that can be discovered by examining natural history collections preserved in herbaria.

1.5   References

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Chapter 2

2   The *Resupinateae* Singer: *Resupinatus* Gray

The *Resupinateae* are a group of fungi believed to be monophyletic within the *Agaricales*. While there have been broad studies examining the phylogeny and classification of the *Agaricales* (Hibbett et al., 1997; Moncalvo et al., 2000; Moncalvo et al., 2002; Matheny et al., 2007) and many in depth studies on particular groups of *Agaricales*, none have looked in depth at the *Resupinateae*. This chapter will examine the membership of the *Resupinateae* and of each genus that has been included in the *Resupinateae*.

2.1   Introduction

Since Singer's last *Agaricales in Modern Taxonomy* was published (1986), the *Agaricales* (the mushroom-forming fungi) have been examined in detail, separating the order into at least one hundred and seventeen clades (Moncalvo et al., 2002). The most comprehensive analysis of the phylogeny of the *Agaricales* included five taxa from the *Resupinateae*, and these five taxa emerged as their own clade, /resupinatus, within the *Agaricales* (Moncalvo et al., 2002). Unfortunately, the area of the tree where /resupinatus fell was poorly resolved and resulted in a polytomy (an internal node of a phylogenetic tree which has more than two immediate descending branches), making it impossible to say with any level of certainty what fungi are the closest relatives of the *Resupinateae* (Moncalvo et al., 2002). Polytomies can result when too little phylogenetic information is used to construct the tree (too short a sequence, a radiation event from a single ancestral taxon, or a sequence that doesn't show enough variation). However, this was the first study to demonstrate the molecular evolutionary relationship between *Stigmatolemma* and *Resupinatus*, supporting the morphological analysis performed by Singer in his works (Moncalvo et al., 2002). Since then, a single representative of the *Resupinateae* was used in a multi-locus DNA analysis of the *Agaricales* and it was placed in the *Pleurotaceae* with a high Bayesian posterior probability (1.0) but low maximum parsimony bootstrap support (Matheny et al., 2007).

Over the years, cyphelloid members of the *Resupinateae* have been classified in a wide variety of genera and families. The first of these families was the *Thelephoraceae*, which at one point was the family used to group all fungi with smooth, exposed spore-bearing surface and regular (aseptate) basidia (Burt, 1914). Coker (1921), Talbot (1956), and Cunningham (1963) also placed the cyphelloid members of the *Resupinateae* in the family *Thelephoraceae*. Currently this family contains only a few genera closely related to *Thelephora* Ehrh. ex Wild., with warty and usually brown basidiospores, all species obligately ectomycorrhizal, not saprotrophic (Kirk et al., 2008).

The systematic analysis performed by Burt of the *Thelephoraceae*, published in 15 volumes between 1914 and 1926, is one of the most comprehensive morphological analyses ever performed of a group of fungi. He provided many suggestions relating to taxonomy in general in his introduction to the *Thelephoraceae*, not the least of which being that more detailed species descriptions must be made (as opposed to the two- or three-line descriptions produced by the likes of Berkeley, 1873, and Saccardo, 1889) and that species do not simply belong to a group because of a lack of care taken on the part of taxonomists before applying a name to a collection (Burt, 1914). He also mentioned the problem of bound exsiccati, sets of collections of dried fungal specimens made by botanists who would then send them out to herbaria around the world. These exsiccati could also be requested from the author, or sold (and were an important source of income for many prominent mycologists of the time). Often, exsiccati were assembled and sent without great care being paid to ensuring that multiple collections with a given species name, distributed among the various sets, were actually the same species! This problem noted by Burt is still a problem today; far too many herbarium collections are specimens that were identified macroscopically (often without even the use of a dissecting microscope) and bear an incorrect name.

Once some mycologists recognized that the *Thelephoraceae* was no longer an appropriate location for cyphelloid fungi, these fungi were all transferred to the families *Cyphellaceae* Lotsy or *Porotheleaceae* Murrill (e.g., Pilát, 1925; Bourdot & Galzin, 1927; Cunningham, 1953; Cooke, 1957 & 1961; Donk, 1962). Many species were treated in the genera *Cyphella, Solenia,* or *Porotheleum*. *Cyphella* is still a genus of fungi

in the *Cyphellaceae* (a family in the *Agaricales*), but *Solenia* Pers. (a later homonym of *Solena* Lour.) is a synonym of *Henningsomyces* Kuntze (Kirk et al., 2008). Phylogenetic analyses of DNA sequences place *Cyphella* in the /Cyphellaceae clade, *Henningsomyces*, and *Porotheleum* in the hydropoid clade, both of which are nested within the larger /marasmioid clade (IV) (Moncalvo et al., 2002; Matheny et al., 2007).

Cooke (1957) emphasized the taxonomic importance of the subiculum over all other microscopic characters and transferred all of the cyphelloid fungi with a prominent subiculum to the genus *Porotheleum*, in the *Porotheleaceae*. Donk (1962) noted that there was no morphological evidence other than similar fruit body morphology to suggest that *Porotheleum* and any other fungus producing cyphelloid fruit bodies with a subiculum were closely related, but he continued to use the family *Cyphellaceae* as a convenience for those that could not readily be connected elsewhere. Donk (1962) resurrected the genus *Stigmatolemma* (after a proper description of the type species, *Stigmatolemma incanum* Kalchbr., by Talbot, 1956), transferred the known members of the genus into it, and placed it in the *Cyphellaceae*.

At the same time, Singer was reorganizing the *Agaricales* into groups that better reflected shared morphological characters. He created the tribe *Resupinateae* within the *Pleurotaceae* (Singer, 1948) for the genera *Resupinatus* and *Hohenbuehelia*, which both had a gelatinous zone in the flesh of the cap. Singer (1962) then added *Asterotus* to the *Resupinateae*, but later synonymized this genus with *Resupinatus* (Singer, 1973). Based on the the similarities in micromorphology between *Resupinatus kavinii* (then classified in *Geopetalum*) and *Stigmatolemma poriaeforme* (then classified in *Solenia*), noted by Pilát (1935, p. 66), Singer (1975a) transferred *Stigmatolemma* to the *Resupinateae* in the 3rd edition of his *Agaricales in Modern Taxonomy* as a "reduced series" derived from the gilled genus *Resupinatus*. Molecular evidence has since supported the relationship of *Stigmatolemma* within the *Resupinateae* (Thorn et al., 2005), but also shown that fungi with cyphelloid fruit bodies have evolved multiple times within the *Agaricales* (Hibbett & Binder, 2002; Moncalvo et al., 2002; Bodensteiner et al. 2004). *Hohenbuehelia* was transferred to the *Pleurotaceae* (and thus out of the *Resupinateae*) as the sister genus to *Pleurotus* by Thorn et al. (2000) but Matheny et al. (2007) have since argued that

Resupinatus belongs within an expanded *Pleurotaceae*. This argument is not addressed in this thesis.

The goal of this study is to determine the membership of the *Resupinateae*. Singer (1975a, 1986) placed *Aphyllotus* and *Stromatocyphella* in the *Resupinateae*, and this hypothesis (made based on morphology alone) has never been tested using molecular data. This study will also test the monophyly of species classified as *Stigmatolemma* within *Resupinatus* and determine if the cyphelloid habit evolved once or multiple times within the *Resupinateae*.

2.2 Materials and Methods

2.2.1 Herbarium samples

Letters requesting dried specimens of *Resupinateae* for microscopic study were sent by the late Dr. Jane Bowles (UWO Herbarium) to herbaria around the world (AD, ARIZ, B, BPI, C, CANB, FH, GBIF, GJO, HO, INPA, K, L, MEL, NCU, NYBG, O, PC, PDD, PH, PRC, PRM, S, STR, TENN, UPS; herbarium acronyms following Holmgren et al., 1990; updated at http://sciweb.nybg.org/science2/IndexHerbariorum.asp). When there was sufficient material of collections made within the past 40 years, a request was also sent for DNA analysis. Herbarium collections were then analyzed for taxonomic characters (see section 2.2.2 Analysis of herbarium samples) and, when possible, DNA was extracted and amplified for sequencing (see section 2.2.5 DNA extraction and amplification). The species of fungi targeted for this study were the smaller members of *Resupinatus*, all species of *Stigmatolemma*, *Stromatocyphella conglobata*, *Aphyllotus campanelliformis*, and any other species believed to belong to the *Resupinateae*.

2.2.2 Analysis of herbarium samples

Among the most important characters for use in identification of the *Resupinateae* are the colour, size and shape of the fruit body; the colour, shape (including ornamentation) and size of surface hairs; the presence, colour and thickness of a gelatinous layer in a vertical section of the fruit body tissues; basidiospore shape, size and ornamentation; the size and

shape of basidia and the presence, shape and size of any other characteristic cells in the hymenium such as cheilocystidia, pleurocystidia, or metuloids.

Notes and measurements were taken of dried collections for fruit body size (in mm; a range from smallest mature fruit bodies to largest mature fruit bodies that show no signs of decomposition), colour and shape; location of attachment to the substrate; presence and characteristics of surface hairs; average number of gills (if present); presence of cheilocystidia visible through the dissecting microscope at 10x magnification (noted by the appearance of the gills being "frosted" along the top edges); and presence or absence of a subiculum or subiculum-like structure. Small portions of dried fruit bodies were rehydrated, and changes in colour of the fruit body and surface hairs were noted (often, fruit bodies are much darker in colour with surface hairs more visible when dry than when fresh). Photographs of the dried collections and rehydrated portions were taken using a Canon Rebel XS 10.0 MP camera and either an EF 50 mm 1:1.8 lens (photographs of the entire dried collection) or an EF 100mm 1:2.8 macro lens (macro photographs of fruit bodies). The rehydrated portions of the fruit body were sectioned by hand using a razor blade and squash-mounted on a microscope slide.

Two mounts were made on each microscope slide, each one being stained differently to emphasize different microscopic characters. The first group of sections were stained using Melzer's reagent (containing potassium iodide and iodine to stain starch and dextrin, chloral hydrate as a clearing agent to better visualize darkly pigmented fungal structures, and sterile distilled water; Largent, 1977), and the second group with a 2% potassium hydroxide solution (Largent, 1977). Melzer's reagent is used to visualize spore characteristics (shape, size, colour changes and spore ornamentation), hyphal characteristics (size, shape, colour, presence or absence of clamps, presence or absence of septa), and surface hair characteristics (size, shape, colour). Due to the difficulty separating cells in Melzer's even with light pressure, basidia and cheilocystidia were observed and measured in 2% (w/v) potassium hydroxide (KOH). Spore colour is also sometimes difficult to discern in Melzer's so basidiospore colour is confirmed in KOH. Due to the tendency of KOH to over-inflate cells, spore measurements were not taken as

this would change the average spore size range, potentially quite dramatically for some species.

All microscopic measurements are represented in micrometers (µm). Basidiospore (at least 30 measured per sample), basidium (all observed mature basidia were measured), cystidia (at least 10 per sample) and surface hair measurements (all intact surface hairs observed were measured) are represented as a range, with values in parentheses representing the smallest and largest values, and the size range representing values between the tenth and ninetieth percentiles (as per Thorn & Barron, 1986). The range of ratios of spore length to width is reported as Q. Other measurements (for example the diameter of hyphae, or the sterigma length and width) are represented as a range of values (smallest and largest measurements) based on observed collections. Microscopic characters were photographed using a Nikon Coolpix camera.

2.2.3　Fresh collections

During my studies I took trips with my supervisor, Dr. R.G. Thorn, to local forests (Meadowlily Woods, Medway Valley, Sifton Bog and Westminster Ponds in London, Ontario, Komoka Provincial Park, Pinery Provincial Park, Algonquin Provincial Park, Clearwater Conservation Area, Skunk's Misery Natural Area) to search for fresh specimens. When specimens were found, substrate, GPS location, and the surrounding plant community were noted. Fresh collections of *Stromatocyphella* were made in Newfoundland by R.G. Thorn and by A. Voitk (Corner Brook, Newfoundland) and brought or mailed to me in London. Collections were photographed using a Canon Rebel XS 10.0 MP camera with an EF-S 18-55mm 1:3.5-5.6 IS lens. Once back in the lab, portions of fresh fruit body were removed and placed in 2X CTAB DNA extraction buffer for later use (Allen et al., 2006). A spore-drop culture was also made on MEB agar (see section 2.2.4 Media and cultures).

2.2.4　Media and cultures

Malt extract agar (MEA; Nobles, 1948; Difco malt extract 12.5 g, agar 15 g, deionized water 1.0 L) and potato dextrose agar (PDA; Difco) were made and poured in 60 mm petri dishes for routine culturing. For spore-drop cultures, both MEB (malt extract agar

with 50 µg per mL chloramphenicol and 5 µg per mL benomyl added prior to pouring) and Ant-PDA (antibiotic PDA; 50 µg per mL chloramphenicol, 30 µg per mL streptomycin and 60 µg per mL chlortetracycline were added to potato dextrose agar before pouring) were made and poured in 35 mm plates. Spore-drop cultures were made by using a small amount of Vaseline to attach a small portion of fruit body to the lid of a Petri dish containing MEB agar, with the hymenium facing the agar. The fruit body was allowed to drop spores onto the agar overnight, and removed the next morning. Spores were allowed to germinate, then small portions of growth were transferred to new plates of either PDA or MEA or both. For DNA extraction, still cultures were grown in 25 mL malt extract broth (ME broth, 5 g malt extract, deionized water 1.0 L) in 100 mL glass jars (see section 2.2.5 DNA extraction and amplification).

2.2.5   DNA extraction and amplification

DNA was extracted from dried herbarium collections and fresh collections in the same way. Portions of the fruit body were placed on a microscope slide and rehydrated in sterile distilled water. Once the small portions were rehydrated, they were finely chopped using a sterilized razor blade. Fifty milligrams of fresh or rehydrated tissue was put into a micro-bead tube from the MoBio Bacterial DNA Isolation Kit (MO BIO Laboratories, Carlsbad, California) or Thermo Scientific GeneJET Plant Genomic DNA Purification Mini Kit (Thermo Fisher Scientific Inc., Waltham, Massachusetts) with added garnet beads in bead-tubes as an additional mechanical lysis step, and the rest of the steps from the respective kits were followed according to the published protocols (a combination of chemical lysis of cells using a solution of SDS and mechanical cell lysis using 0.25 mm diameter glass, ceramic or garnet beads).

DNA was extracted from liquid cultures using the same procedure and isolation kit with the following modifications. Mycelial mats were removed from liquid media and placed into a sterilized 1.5 mL microfuge tube. Liquid media was pipetted out of the tube, then the tube was centrifuged at 10,000 rpm for 1 minute to remove additional liquid medium. The resulting mycelial mat was weighed, and 50 mg of material was transferred into the micro-bead tube. The extraction kit protocol was then followed as published. Once DNA was isolated, the resultant extract was quantified using a Nanodrop 2000

spectrophotometer (Thermo Scientific, Wilmington, Delaware) and the extract was kept at 4 °C (overnight) or at -20 °C (for extended periods).

The DNA extract was amplified using a PCR protocol in a Biometra T1 Thermocycler (Montreal Biotech) according to Koziak et al. (2007) and the fungal primers ITS1 (5'—TCCGTAGGTGAACCTGCGG—3'; White et al., 1990) and LR5 (5'—ATCCTGAGGGAAACTTC—3'; Vilgalys & Hester, 1990). This primer pair amplifies ribosomal DNA from the 3' end of the small ribosomal subunit (SSU) through the ITS1, 5.8S, ITS2, and the 5' end of the large ribosomal subunit (LSU; including the D1/D2 variable domains). Presence or absence of a PCR product was determined using gel electrophoresis in a 1.5% agar gel made in TAE electrophoresis buffer containing 0.5 µg/mL ethidium bromide.

Once the presence of the desired size of PCR product was confirmed, the PCR products were cleaned using the QIAquick PCR purification kit (Qiagen, Mississauga, Ontario) or the BioBasic PCR purification kit (Bio Basic Canada Inc, Markham, Ontario). Each DNA extract was amplified in four PCR reactions of 30 µL to ensure a large amount of PCR product was obtained, and these four PCR tubes were pooled into one cleaned PCR product and quantified on the Nanodrop 2000.

2.2.6   Sequencing of PCR products

Cleaned PCR products were sent for sequencing at the Robarts Research Institute at Western University on an ABI Illumina sequencing platform (Applied Biosystems). Sample tubes were prepared according to the Sequencing Facility's instructions, and the resulting electropherograms were e-mailed.

Samples were prepared using an optimized amount of cleaned PCR product (approximately 200 ng of PCR product per 10 µL of sample, or a concentration of 20 ng/µL), and one sequencing primer at 2.0 mM. The target PCR product is 1800 bases and sequencing reactions on the ABI machine are only reliable for 600-800 bases and consequently each sample was sequenced using six different primers, to get three overlapping sequences on each strand (for proof-reading purposes during sequence

compilation). The primers used were ITS1 or ITS1-F (5'—
CTTGGTCATTTAGAGGAAGTAA—3'; Gardes & Bruns, 1993, LS1 (5'—
ACTACCCGCTGAACTTAAG—3'; Hausner et al., 1993) and LR3R (5'—
GTCTTGAAACACGGACC—3'; Vilgalys lab, Duke University) on the coding strand
and LR5, LR3 (5'—GGTCCGTGTTTCAAGAC—3'; Vilgalys & Hester, 1990) or NL4
(5'—GGTCCGTGTTTCAAGACGG—3'; Kurtzman & Robnett, 1997) and LS1R (5'—
CTTAAGTTCAGCGGGTA—3'; Hausner et al., 1993) on the complementary strand.
Once all six regions were sequenced, the sequences were cleaned and assembled in
SeqEd v1.03 (Applied Biosystems Software, Foster City, California).

2.2.7   Phylogenetic analysis

The sequences generated in this study (see Table 2.1) were aligned with those already
available in GenBank (see Table 2.2) using MEGA5 v5.05 for Mac (Tamura et al., 2011)
or MEGA6 v6.06 for Mac (Tamura et al., 2013). When applicable, alignments were
edited to improve the alignment. Species of *Bovista*, *Calvatia*, *Langermannia*, and
Lycoperdon were chosen to root the large LSU tree (including all sequences generated
from collections that turned out to excluded from the *Resupinateae*) based on GenBank
and BLAST search results. The ingroup used to construct the LSU tree consisted of 46
sequences of 24 different taxa, resulting in an alignment of 1763 characters. The dataset
was trimmed to 918 positions in order to ensure that all sequences were of the same
length in the alignment. Some sequences were combined ITS and LSU sequences (so the
ITS sequences were trimmed from the alignment), while others were elongated LSU
sequences (so those portions of the sequence that were not D1/D2 and the upstream
highly conserved sequence up to the LR5 primer site were trimmed off). The resulting
alignment file was exported for further analysis.

Phylogenetic analyses according to neighbour-joining, maximum likelihood and
maximum parsimony methods were performed in MEGA5/6. Node support in the
likelihood and parsimony analyses was assessed using bootstrapping, with 1000
replicates. Only bootstrap values of 70% or higher are shown. Trees were generated using
separated datasets (ITS and LSU data separate) and then using the combined dataset.
Separate trees are shown for the LSU region (ingroup and all associated outgroup taxa;

see Figure 2.1) and the ITS regions (presented in Chapter 4, see Figure 4.3). The primary goal of the construction of the large ingroup and outgroup tree was to correctly identify, using phylogenetic methods, the identity of unknown taxa, plus the placement of the *Resupinateae* in a subset of sequences in the *Agaricales*, so neighbour-joining was chosen as the best tree construction method for the LSU tree. The maximum composite likelihood model of nucleotide substitution was used, which included transitions and transversions in the analysis. It was assumed that rates of substitution were homogeneous between sites, and that the pattern of substitution among lineages was also homogeneous. Gaps were treated as complete deletions in the data, not as missing data.

2.3   Results and Discussion

In all tree-building algorithms used (maximum likelihood, maximum parsimony, and neighbour-joining), the *Resupinateae* emerged as a monophyletic group with strong bootstrap support within the *Agaricales*, but placed without bootstrap support close to the *Pleurotaceae, Entolomataceae,* and *Tricholomataceae* (see Figure 2.1). Forty-seven new sequences of *Resupinateae,* representing 24 species, were obtained in this part of the study (Table 2.1). Misidentification or "underidentification" (identification of sequences to the family level, an incorrect family at that, based on superficial morphological analysis) of sequences in GenBank is a problem for this group. The 24 available sequences of *Resupinateae* are misidentified to the species level more often than they are properly identified and only ten species out of the approximately fifty species hypothesized to be in the group were represented (Table 2.2).

Table 2.1 Sequences generated for this study. Sequence accession refers to the collection number (herbarium accession number or culture number) of the associated collection, not GenBank accession numbers. Under "sequence accession," it is specified whether the sequences were generated from fresh collections (F), dried herbarium specimens (H), or cultures (C). Identifications were made first based on morphological analysis (when the sequence was generated from a fresh or dried collection), then by sequence analysis. Species with numbers after the scientific name indicate species part of a species complex; when more than one morphospecies falls in numerous places in the tree (i.e. *Resupinatus applicatus*), the first number is associated with the sequence generated from a collection that is best representative of the type (either collection location, collection substrate, or both) and the rest are numbered in the order they appear on the tree, from top to bottom. Within the "Sequence Accession" column, sequences generated by the primary author of this study (JVM) are indicated in regular font. Sequences generated by a work-study student are indicated in bold font (TDK). Sequences generated by other lab members are indicated in italic font (see statement of co-authorship). T-919 remains as an "Unknown taxon" as no GenBank reference sequences more than 87% identical could be found, and the sequence never clustered with other sequences in any tree generated.

Sequence Accession	Primers used	Collection Information	Species ID	ID based on this study
007 (H: in UWO and SGO)	ITS1, B001	On *Nothofagus*, Aug. 3 2011; Patagonia, Chile	*Resupinatus* sp.	Patagonian campanelloid
100426 av01 (F: in UWO)	ITS1, LR3	On *Alnus*, Apr. 26 2010; Newfoundland, Canada	*Stromatocyphella conglobata*	*Stromatocyphella conglobata*
101129 av02 (F: in UWO)	ITS1, B001	On *Alnus*, Nov. 29 2010; Newfoundland, Canada	*Stromatocyphella conglobata*	*Stromatocyphella conglobata*
ADC55348 (H)	ITS1, LR5	On well-decayed wood, Jun. 28 2008; Kelly Hill Caves Conservation Park, Kangaroo Island, Australia	*Resupinatus* sp.	Australian lamellate *Resupinatus* 1
ADC56856 (H)	ITS1, LR5	On *Eucalyptus cladocalyx*, Jun. 25 2011; Kelly Hill Caves Conservation Park, Kangaroo Island, Australia	*Resupinatus* sp.	Australian lamellate *Resupinatus* 1
ADC57180 (H)	ITS1, LR5	On *Eucalyptus cladocalyx*, Jun. 23 2009; Kelly Hill Caves Conservation Park, Kangaroo Island, Australia	*Resupinatus* sp.	Australian lamellate *Resupinatus* 1
AN 012974 (H: in ARIZ)	ITS8-F, ITS6-R LS1, LR5	On *Juniperus virginiana*, Apr. 17 1986; East Baton Rouge Parish, Louisiana, USA	*Stigmatolemma taxi*	*Rhodocyphella cupuliformis*
FP102486 (C)	ITS1, B001	On hardwood, 1990; unknown location in Illinois, USA	*Resupinatus applicatus*	*Resupinatus applicatus* 3
ICMP 16593 (C)	ITS1, B001	On *Dacrycarpus*, May 29 2006; Waikato, New Zealand	*Rhodocyphella cupulaeformis*	Australian cyphelloid *Resupinatus* 1
J19 (H: in UWO and	ITS1, B001	On *Nothofagus*, Aug. 8 2010; Patagonia, Chile	*Resupinatus* sp.	Patagonian campanelloid

SGO)				
NZ9 (E8202; N. Bougher) (H)	ITS1, LR3	Jun. 12 2005; Paganoni Swamp, Karnup, Australia	*Resupinatus cinerascens*	*Resupinatus cinerascens*
NZ14 (E8427; N. Bougher) (H)	ITS1-F, LR3	Jun. 17 2007; West Bay Bushland, Leeuwin-Naturaliste National Park, Augusta, Australia	*Resupinatus* sp.	*Resupinatus subapplicatus*
O 65603 (H)	ITS1, B001	On aspen, Apr. 13 2002; Arendal, Norway	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*
O 65625 (H)	ITS1, LR3	On *Tilia*, Apr. 21 2002; Arendal, Norway	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*
P79 (H: in UWO and SGO)	ITS1, B001	On *Nothofagus* Jul. 24 2011; Patagonia, Chile	*Resupinatus* sp.	Patagonian campanelloid
P80 (H: in UWO and SGO)	ITS1, B001	On *Nothofagus*, Jul. 29 2011; Patagonia, Chile	*Resupinatus* sp.	Chilean *Hohenbuehelia* sp.
PDD 87046 (H)	ITS1, LR5	On dead wood, Apr. 30 2006; Banks Peninsula, New Zealand	*Resupinatus applicatus*	*Resupinatus* sp.
PDD 87197 (H)	ITS1, LR5	On *Kunzea ericoides*, Jun. 3 2006; Hinewai Reserve, Akaroa, New Zealand	*Marasmiellus violaceogriseus*	*Resupinatus violaceogriseus* 1
PDD 87379 (H)	ITS1, LR5	On *Ripogonum scandens*, May 10 2007; Waiohine Gorge, Wairarapa, New Zealand	*Marasmiellus violaceogriseus*	*Resupinatus violaceogriseus* 2
PDD 87473 (H)	ITS1, LR5	On *Pseudopanax crassifolius*, May 7 2007; Mt. Bruce, Wairarapa, New Zealand	*Resupinatus applicatus*	*Resupinatus subapplicatus*
RGT010805/01 (F: in UWO)	ITS1, B001	Aug. 5 2001;	Black *Hohenbuehelia*	Excluded
RGT010806/01 (F: in UWO)	ITS1, B001	Aug. 6 2001; collection information unknown	Cyphelloid	*Cyphellopsis/ Merismodes* sp.
RGT080820/01 (F: in UWO)	ITS1, LR3	Aug. 20 2008; London, Ontario, Canada	*Resupinatus urceolatus*	North American cyphelloid *Resupinatus*
RGT100622/01 (F: in UWO)	ITS1, B001	Jun. 22 2010; London, Ontario, Canada	*Resupinatus urceolatus*	North American cyphelloid *Resupinatus*
RGT100622/02 (F: in UWO)	ITS1, LR3	Jun. 22 2010; London, Ontario, Canada	*Resupinatus* sp.	*Resupinatus applicatus* 3
Silver Box (H: in UWO)	ITS8-F, ITS6-R LS1, LR5	On dead hardwood, Aug. 18 2010; Woodson County, Kansas, USA	*Resupinatus* sp.	*Resupinatus applicatus* 3
T-001 (RLG10761sp: in CFMR) (C)	ITS1, B001	On *Quercus hypoleucoides*, Sep. 7 1972; Turkey Creek, Chiracahua Mountains, Colorado National Forest, Arizona, USA	*Resupinatus* sp.	*Resupinatus* sp.
T-099 (DAOM	ITS1-F,	Oct. 17 1956; Ridge Road,	*Resupinatus*	*Resupinatus*

54231) (C)	B001	Gatineau, Quebec, Canada	*applicatus*	*applicatus* 1
T-129.7 (VT1364) (C)	ITS1, B001	Unknown location in USA	*Resupinatus alboniger*	*Resupinatus alboniger*
T-236 (RGT850901/08 in TRTC) (C)	ITS1, B001	Fallen beech branches, May 30 1989; Chanterelle hill, Blomidon Provincial Park, Nova Scotia, Canada	*Resupinatus striatulus*	*Resupinatus striatulus*
T-244 (RGT850908/01 in TRTC) (C)	ITS1, B001	On *Acer saccharum,* Sep. 8 1985; Eramosa Township, Ontario, Canada	*Stigmatolemma poriaeforme*	North American cyphelloid *Resupinatus*
T-919 (C)	ITS1, B001	On *Juniperus virginiana*, May 22 1997; Oakley House, near Baton Rouge, Louisiana, USA	*Stigmatolemma taxi*	Unknown taxon**
T-921.12 (C)	ITS1, B001	May 24 1997; New Brunswick, Canada	*Hohenbuehelia ?elegans*	*Hohenbuehelia elegans*
TENN2417 (C)	ITS1-F, B001	Oct. 20 1989; Jackson County, Illinois, USA	*Resupinatus applicatus*	*Resupinatus applicatus* 1
TENN2674 (C)	ITS1, B001	May 1990; New Zealand	*Resupinatus violaceogriseus*	*Resupinatus violaceogriseus* 1
TENN3003 (C)	ITS1, B001	July 10 1990; Macon County, North Carolina, USA	*Resupinatus* sp.	*Hohenbuehelia grisea*
TENN3547 (C)	ITS1-F, B001	May 16 1991; New South Wales, Australia	*Resupinatus* cf. *striatulus*	*Resupinatus subapplicatus*
TENN4102 (C)	ITS1, B001	July 18 1991; Macon County, North Carolina, USA	*Resupinatus alboniger*	*Resupinatus applicatus* 1
TENN4403 (C)	ITS1, B001	Mar. 1 1992; Anderson County, Tennessee, USA	*Resupinatus striatulus*	*Resupinatus applicatus* 2
TENN8870 (C)	ITS1, B001	Caucasia, Russia	*Resupinatus* sp.	*Resupinatus* sp. 2
TENN9124 (C)	ITS1, B001	May 25 1997; East Baton Rouge Parish, Louisiana, USA	*Cyphella* sp.	"*Cyphella*" sp.
TENN10127 (C)	ITS1-F, B001	Nov. 27 1998; Blount County, Tennessee, USA	*Resupinatus* sp.	*Resupinatus alboniger*
TENN12070 (C)	ITS1, B001	Aug. 8 2004; University of Tennessee Campus, USA	*Resupinatus alboniger*	*Resupinatus alboniger*
TENN12406 (C)	ITS1, B001	Jan. 14 2005; Great Smokey Mountains National Park, North Carolina, USA	*Resupinatus alboniger*	*Resupinatus* sp. 3
TENN12417 (C)	ITS1, B001	Feb. 23 2005; Great Smokey Mountains National Park, Tennessee, USA	*Resupinatus alboniger*	*Resupinatus alboniger*
TENN12972 (C)	ITS1, B001	Dec. 20 2005; Great Smokey Mountains National Park, Tennessee, USA	*Resupinatus alboniger*	*Resupinatus alboniger*
TENN12990 (C)	ITS1, B001	May 8 2006; Great Smokey Mountains National Park, Tennessee, USA	*Resupinatus alboniger*	*Resupinatus alboniger*

Table 2.2 Sequences obtained from GenBank of species in the *Resupinateae*.
Collection information includes the strain from which the sequence was obtained, and collection information, if known. Correct identification is based on phylogenetic analyses presented in this study (or, in some cases where a morphological analysis could be performed, identification was based on a combination of morphological characters and phylogenetic placement; these taxa are indicated with an asterisk in the "ID based on this study" column). Species with numbers after the scientific name indicate species part of a species complex; when more than one morphospecies falls in numerous places in the tree (i.e. *Resupinatus applicatus*), the first number is associated with the sequence generated from a collection that is best representative of the type (either collection location, collection substrate, or both) and the rest are numbered in the order they appear on the tree, from top to bottom. When possible, separate regions from the same species and strain were merged for a complete dataset. For a full list of sequences used see Appendix B.

GenBank Accession	Gene Region	Collection Information	GenBank ID	ID based on this study
AF042600	LSU	RV/JM s.n.; on *Liquidambar*, Durham, NC	*Resupinatus alboniger*	*Resupinatus alboniger*
FJ596893	ITS	TENN62044; Tennessee, USA	*Resupinatus alboniger*	*Resupinatus alboniger*
AY571059	ITS	PB335; France	*Resupinatus applicatus*	*Resupinatus applicatus* 2
AY571022	LSU	PB335; France	*Resupinatus applicatus*	*Resupinatus applicatus* 2
AM946461	LSU	TAA171569; Estonia	*Resupinatus applicatus*	*Resupinatus applicatus* 2
HQ533025	ITS	PDD95777; New Zealand	*Resupinatus applicatus*	*Resupinatus applicatus* 4
AF139944	LSU	RM930924/01; Aldo Leopold Preserve, Wisconsin, USA	*Resupinatus dealbatus*	*Resupinatus dealbatus*
DQ017064	LSU	PR6198; Puerto Rico, USA	*Resupinatus porosus*	*Resupinatus porosus**
DQ017063	ITS	PR5832; Puerto Rico, USA	*Resupinatus porosus*	*Resupinatus porosus**
AJ406557	LSU	GEL4221; collection info unknown	*Resupinatus trichotis*	*Resupinatus trichotis**
GQ142022	ITS	HMJAU2150; China	*Resupinatus trichotis*	*Resupinatus trichotis*
HQ533014	ITS	PDD95788; New Zealand	*Marasmiellus violaceogriseus*	*Resupinatus violaceogriseus* 1
AF042599	LSU	T-001, VT1520, RLG10761sp; on *Quercus*, Arizona	*Resupinatus* sp.	*Resupinatus* sp.
GQ142045	LSU	HMJAU7036; China	*Resupinatus* sp.	*Resupinatus* sp. 1
GQ142021	ITS	HMJAU7036; China	*Resupinatus* sp.	*Resupinatus* sp. 1
AY571024	LSU	C61852; Ecuador	*Resupinatus conspersus*	*Porotheleum cinereum*

AY571061	ITS	C61852; Ecuador	*Resupinatus conspersus*	*Porotheleum cinereum*
AY571025	LSU	T-244, CBS327.91; on *Acer*, Ontario	*Resupinatus poriiformis*	North American cyphelloid *Resupinatus**
AY571062	ITS	T-244, CBS327.91; on *Acer*, Ontario	*Resupinatus poriiformis*	North American cyphelloid *Resupinatus**
AF261372	LSU	RLG11556sp; on *Populus tremuloides*, Arizona	*Resupinatus poriiformis*	North American cyphelloid *Resupinatus*
AF261373	LSU	HHB3534sp, on *Quercus*, Michigan	Cyphellaceae sp.	North American cyphelloid *Resupinatus**

Figure 2.1 rDNA LSU Neighbor-Joining tree showing the relationship of the *Resupinateae* to selected other members of the *Agaricales*. Bootstrap values (1000 replicates) are only shown if above 70%. Identifications in bold font represent sequences obtained from GenBank (represented by their accession number, species name, and strain information if known). Identifications in regular font represent sequences generated in this study (represented by their strain number and species name as identified by me). Red lines in the ingroup designate taxa with cyphelloid fruit bodies (showing that the cyphelloid habit is multiply derived), and the light blue line in the ingroup designates the taxon with poroid fruit bodies. Coloured arrows are for reference only between pages; arrows of the same colour join two lines together across pages (e.g. the red arrow down in panel A connects the line with the red arrow up in panel B). Identifications of all species in regular font based on morphological identifications, and where the same morphospecies occurs in multiple places in the phylogenetic tree (i.e. *Resupinatus applicatus* and *Resupinatus violaceogriseus*), the morphospecies identical in location of collection and substrate (when known) is designated "1" and all others numbered sequentially as they appear in the tree. When applicable, sequences generated in this study are named based on GenBank sequences of teleomorphs (i.e. in the case of *Hohenbuehelia*), not anamorphs (*Nematoctonus*) to which they are most similar as per the One Taxon, One Name rules (Schoch et al., 2012).

TENN 8870 *Resupinatus* sp.

TENN 12406 *Resupinatus* sp.

99 — 100426 av01 *Stromatocyphella conglobata*

101129 av02 *Stromatocyphella conglobata*

AY571024 **Porotheleum cinereum** (C61852)

ADC55348 Australian *Resupinatus* 1

99 — ADC56856 Australian *Resupinatus* 1

ADC57180 Australian *Resupinatus* 1

AF139944 **Resupinatus dealbatus** (RM930924/01)

TENN 12972 *Resupinatus alboniger*

TENN 12990 *Resupinatus alboniger*

TENN 12070 *Resupinatus alboniger*

99 — TENN 10127 *Resupinatus alboniger*

TENN 12417 *Resupinatus alboniger*

AF042600 **Resupinatus alboniger** (RV/JM s.n.)

T-129 *Resupinatus alboniger*

TENN 2674 *Resupinatus violaceogriseus* 1

95 — Silver Box *Resupinatus* sp.

NZ9 *Resupinatus cinerascens*

88 — PDD87197 *Resupinatus violaceogriseus* 2

PDD87379 *Resupinatus violaceogriseus* 2

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GQ289189 *Entoloma sericatum* (isolate 28)

GQ289204 *Entoloma vezzenaense* (isolate 241)

AF042620 *Entoloma strictus* (M96/10)

GQ289186 *Entoloma readiae* (isolate 102)

KC176290 *Clitopilus scyphoides* (T-782b)

KC176282 *Clitopilus scyphoides* (T-777)

DQ389734 *Tricholoma orirubens* (RGC04-053)

FJ755224 *Clitocybe subtitopoda* (CZ482)

JN649350 *Lepista sordida* (EL4-03(GB))

HM035073 *Psilocybe coprophila* (CBS 417.82)

AB158636 *Psilocybe merdaria*

HM035078 *Psilocybe montana* (CBS 101791)

FJ904179 *Naucoria bohemica* (EL716-03)

KC176278 *Hypholoma capnoides* (T-773)

HM035080 *Psilocybe semilanceata* (CBS 101868)

HM035075 *Psilocybe cubensis* (CBS 590.79)

HM035076 *Psilocybe cyanescens* (CBS 295.94)

HM035072 *Psilocybe caerulescens* (CBS 837.87)

HM035077 *Psilocybe mexicana* (CBS 831.87)

AB158635 *Psilocybe fasciata*

74

81

97

85

79

73

45

AY213568 *Armillaria gallica* (M70)

99 — AY213583 *Armillaria cepistipes* (W113)

AY213567 *Armillaria sinapina* (ST13-B)

T-919 *"Noleana"* sp. [as *Stigmatolemma taxi*]

83 — AF042621 *Omphalotus nidiformis* (T1946.8)

89 — DQ470816 *Omphalotus olearius* (AFTOL-ID #1718)

AY745709 *Anthracophyllum archeri* (AFTOL-ID #973)

AY639426 *Gymnopus nonnullis* var. *attenuatus* (AWW05)

AY639435 *Marasmiellus synodicus* (DED5258)

AF261336 *Gymnopus biformis* (RV98/32)

FJ750252 *Rhodocollybia butyracea* (TENN 60927)

86 — AF042597 *Rhodocollybia maculata* (RV94/175)

AY639880 *Rhodocollybia maculata* (AFTOL-ID #540)

AY639413 *Gymnopus diminutus* var. *attenuatus* (AR099_SFSU)

AY256708 *Marasmiellus juniperinus*

P79 Patagonian campanelloid

99 — 007 Patagonian campanelloid

J19 Patagonian campanelloid

AY639422 *Gymnopus melanopus* (AWW54_SFSU)

89

AY256709 *Gymnopus luxurians*

AY639436 *Marasmius alliaceus* (BRNM568)

AY639437 *Marasmius applanatipes* (DED6628_SFSU)

AY635776 *Marasmius alliaceus* (AFTOL-ID #556)

AF261331 *Marasmius scorodonius* (JEJ.586)

AF261329 *Marasmiellus opacus* (JEJ.574)

AY639438 *Marasmius copelandii* (DED5607_SFSU)

AF042628 *Micromphale performans* (RV83/67)

AY256711 *Gymnopus fusipes*

AF261327 *Caripia montagnei* (JMCR.143)

AF042596 *Collybia polyphylla* (RV182.01)

AF261585 *Marasmius andosaceus* (HN4730)

AY639432 *Gymnopus vitellinipes* (AWW127)

AY207240 *Micromphale foetidum*

AF261328 *Micromphale foetidum* (JEJ.VA.567)

AF042595 *Collybia dryophila* (RV83/180)

AY639411 *Gymnopus bicolor* (AWW146)

AJ406581 *Dendrothele acerina* (GEL5350)

AY572005 *Calathella gayana* (ZT8836)

AY571014 *Lachnella villosa* (PB332)

AF261475 *Lachnella alboviolascens* (DAOM 223321)

AY571006 *Flagelloscypha minutissima* (CBS 823.88)

AY571000 *Cyphellopsis anomala* (PB318)

AY571015 *Merismodes fasciculata* (HHB11894)

RGT010806/01 *Merismodes* sp.

AY571016 *Merismodes fasciculata* (PB342)

AY570998 *Cyphellopsis anomala* (PB318)

47

DQ112621 *Bovista promontorii* (MJ7070)

74

DQ112620 *Bovista aestivalis* (MJ1122)

99

94

DQ112611 *Bovista cretacea* (ANMH 11622)

DQ112617 *Bovista minor* (Steike 951015)

DQ112624 *Calvatia candida* (MJ3514)

DQ112625 *Calvatia craniiformis* (Steike 001017)

DQ112623 *Langermannia gigantea* (MJ3566)

DQ112583 *Lycoperdon decipiens* (MJ850902)

0.01 changes

2.3.1 *Stigmatolemma* is polyphyletic and a synonym of *Resupinatus*

Within the *Resupinateae*, the cyphelloid fruit body morphology has evolved on at least three separate occasions, making the former *Stigmatolemma* polyphyletic within *Resupinatus*. Unfortunately, there are no available sequences or collections recent enough to amplify and sequence of the type species of *Stigmatolemma*, *S. incanum*, and so it is not possible to determine to which of these three cyphelloid lineages of *Resupinatus* the name *Stigmatolemma* applies. *Rhodocyphella cupuliformis* is often synonymized with *Resupinatus taxi* (Donk, 1962; Gilbertson & Blackwell, 1984; Ginns & Lefebvre, 1993; Lassoe, 2006) but my data show that these two species are not conspecific (see Figure 4.3 for a placement of *Resupinatus griseopallidus*, the correct name for *Resupinatus taxi*) and that there is in this complex a third species from New Zealand that requires a new name (Figure 2.1). All three species are members of the *Resupinateae*. The North American *Rhodocyphella cupuliformis* and its New Zealand counterpart (Australian cyphelloid *Resupinatus* 1; see Chapter 4) are sister species, and the European *Resupinatus griseopallida* (see Chapter 5) is unrelated to the previous two species (see Figure 2.1, Figure 4.3). Based on two sequences generated in this study, *Stromatocyphella conglobata* also belongs in the genus *Resupinatus* (see Figure 2.1).

2.3.2 The lamellate *Resupinatus* species

All lamellate species classified in *Resupinatus* examined in this study belong in the *Resupinateae* based on the phylogenetic analysis performed of the group. This includes *Resupinatus violaceogriseus*, which is usually treated as a species of *Marasmiellus* (/marasmioid clade, Moncalvo et al. 2002) following Horak (1971). Placement of the type species, *Resupinatus applicatus*, in the phylogenetic analyses is uncertain because there is no type specimen for that species, nor sequences of recent collections that can be unequivocally identified as conspecific with the material that Batsch (1786) described and illustrated. For further discussion of this species, see section 2.4 "Taxonomy" below.

Based on the trees generated here and using the LSU and ITS combined dataset in Chapter 4, there is no broad pattern of geographic distribution within the group (i.e.,

tropical species are interspersed with temperate species in the tree; see Chapter 4, Figure 4.3), nor is there a pattern of the evolution of fruit body size within the group (see Figure 2.1 and Figure 4.3).

2.3.3   Excluded species

Aphyllotus campanelliformis Singer is the only species in the monotypic genus *Aphyllotus*. Unfortunately, it has been collected very few times since its original description in 1973 (Singer, 1973) and no DNA sequences of it exist. The type material, while not too old to be considered suitable for molecular analysis (collected in 1968), is not a candidate for destructive sampling because there is little material left and because of the Field Museum's policy on destructive sampling from type material. Singer (1973) originally suggested that this species was likely closely related to *Campanella*, a member of the *Marasmiaceae*, which is how *Aphyllotus* is classified according to the leading taxonomic authority (Kirk et al., 2008). However, Singer later (1986) transferred *Aphyllotus* to the *Resupinateae*. Based on morphological data, my study confirms that this taxon belongs in the *Marasmiaceae*, not the *Resupinateae*. For a more thorough description and discussion of *Aphyllotus,* refer to Chapter 6: "Excluded species".

2.3.4   *Stromatocyphella conglobata*

There is not much known about the development of the fruit bodies of this species, as until recently this species had only been observed a handful of times (see Appendix A for a list of herbarium specimens that carry this name). Determining the process of carpophore development of this species was not a primary goal of this project, but was the result of culturing a fresh collection of this species from Newfoundland, Canada. The spore-drop culture was initially made of the specimen in October 2010, transferred to a new plate in December 2010, then sub-cultured twice more before being neglected in January 2013 (five cultures total were created from the initial spore-drop). When the plates were examined in June 2014, there were fruit bodies forming on the culture medium (MEA) in various stages of development (plates closer to the bottom of the stack, where it was more temperature stable and had higher humidity levels were more

advanced in development of the fruit bodies, while plates higher in the stack were less fully developed).

The process of fruit body development appears to be as follows: first, a droplet of liquid extracted by the fungus from the medium is formed on the surface of the vegetative hyphae (see Figure 2.2A). The vegetative hyphae begin to show "puffier" growth directly around this liquid droplet (resembling a fluffy subiculum that would normally be present if growing on a wood substrate), as opposed to the matted, very dense growth of the vegetative hyphae that are not in the presence of these liquid droplets. The cyphelloid fruit body begins to form around the liquid droplet, beginning as a white mass of hyphae and gradually gaining pigmentation to become dark brown, nearly black (see Figure 2.2b, 2.2c and 2.2d). As the fruit bodies mature and increase in diameter, the pileal surfaces start to fuse together. Once fruit body development is complete, herbarium specimens of this species appear to have a fruit body with a poroid hymenial surface. This is not the case, as each one of the "pores" developed individually. At the same time as pigmentation is occurring during the fruit body development, the liquid droplet either evaporates or is reabsorbed into the hyphal network (impossible to determine, as these are based on observations and not a controlled experimental design; see Figure 2.2e and 2.2f). Thus, the placement of *Stromatocyphella conglobata* is not only confirmed to be within *Resupinatus* based on the molecular analyses discussed above, but also due to the common developmental sequence of the fruit bodies.
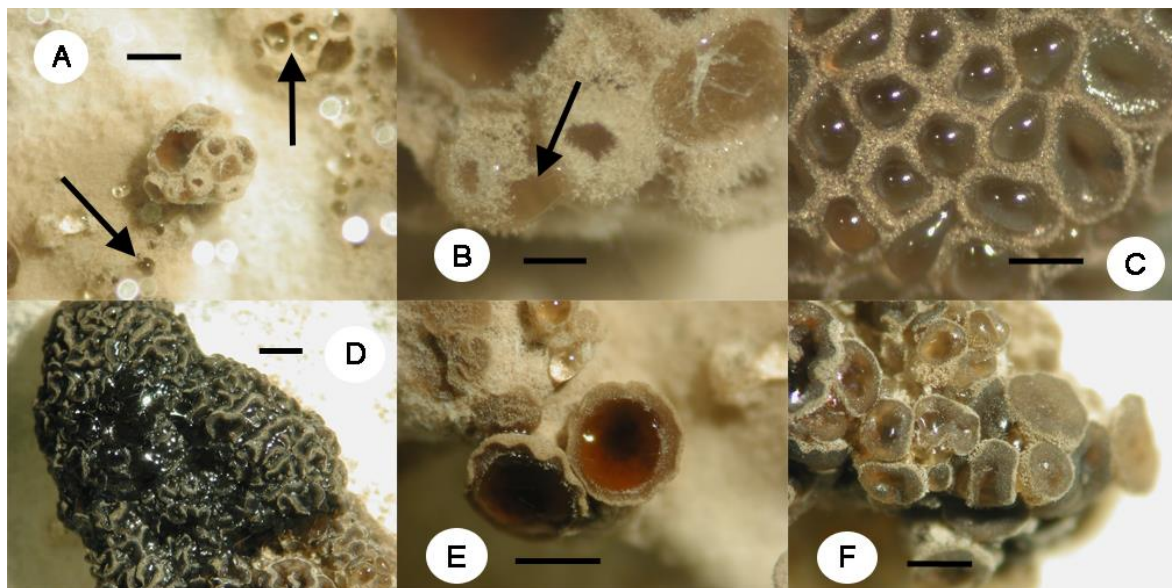
Figure 2.2 Growth and development of *Stromatocyphella conglobata* fruit bodies in culture. A. Dense mat of hyphae, forming a subiculum-like structure, forming liquid droplets on the surface of the vegetative hyphae (arrows); B. The individual fruit bodies forming via hyphal growth around each liquid droplet (arrow); C. Increase in pigmentation from cream to light tan, liquid droplets still visible inside each individual cyphelloid fruit body; D. Fully mature fruit bodies with full dark brown to black pigmentation, and the liquid droplets starting to disappear; E. Two individual fruit bodies with their inner liquid droplets starting to fuse together on the pileal surface; F. Fruit bodies with mature fruit bodies with and without their inner liquid droplets. All scale bars represent 1.5 mm.

2.4   Taxonomy

2.4.1   The tribe *Resupinateae* Singer

Tribus **Resupinateae** Singer, Sydowia 2: 30. 1948, emended herein

Characters: hymenophore lamellate, poroid or cyphelloid; with clavate or subclavate, 2- or 4-spored holobasidia. Spores hyaline, inamyloid, smooth-walled, ranging in shape from globose or subglobose to oblong or cylindric. Hyaline, diverticulate cheilocystidia present in all species with lamellate and poroid fruit bodies along gill or pore edges; equivalent structures present in most species with cyphelloid fruit bodies around the margin of the cups (Redhead, 1973); metuloids absent (with the exception of one taxon that has yet to be named, represented by a single sequence in GenBank, accession

AF042599). Stipe absent and fruit bodies directly attached by pileus to the substrate, or if present not fully developed and so termed a pseudostipe (eccentric to lateral) with decurrent gills. Pileal trama (flesh or context) soft, flexible and gelatinous when fresh. Surface hairs diverticulate, hyaline, inamyloid, of the same general shape as cheilocystidia but longer; in some species repeatedly dichotomously branched (asterostromelloid). Hyphae monomitic; thin-walled, with clamps, always branching from clamps.

Ecology: fruit bodies occurring most commonly on decaying wood of coniferous or dicotyledonous species, but rarely on other types of plant matter in the process of decomposition (reported from rotting bamboo stems and reproductive cones of *Banksia* in Australia; see Chapter 4, section 4.4 "Taxonomy").

Distribution: cosmopolitan, but some species showing geographic range restriction (some species only found in Australia and New Zealand, others restricted to tropical, temperate or boreal climates, etc.).

Classification: *Basidiomycota, Agaricomycotina, Agaricomycetes, Agaricales, Tricholomataceae* (based on the classification in Kirk et al., 2008; in the *Pleurotaceae* according to Matheny et al., 2007).

Membership: *Resupinatus* (40-50 species; now comprising species formerly classified in *Stigmatolemma*, a genus of species with cyphelloid fruit bodies; see Table 2.3), and *Stromatocyphella* (1 species) and *Rhodocyphella* (2 species) which should both be transferred to *Resupinatus*.

Members formerly included but now excluded: *Hohenbuehelia* (now classified in the *Pleurotaceae*; Thorn et al., 2000), *Nematoctonus* (the anamorphic genus of *Hohenbuehelia*, now an obligate synonym of *Hohenbuehelia* based on the "One Fungus = One Name" rule and the rule of priority; Hawksworth et al., 2011; Thorn, 2013), and *Aphyllotus* (placed in the *Marasmiaceae* based on morphology, see Table 2.3; Singer, 1973; Singer, 1975a and 1975b; Singer, 1986; Kirk et al., 2008).

Table 2.3 A list of selected species classified in the *Resupinateae*, with current Latin name, type of fruit body, and the chapter in which the species is discussed. Species now excluded are indicated in square brackets. For a full nomenclator, see Appendix A.

Latin name & Author	Type of fruit body	Chapter discussed
[*Aphyllotus campanelliformis* Singer]	Cyphelloid	Chapter 6
Cyphella tela (Berk. & Curtis) Massee	Cyphelloid	Chapter 5
Peziza pruinata Schwein.	Cyphelloid	Chapter 3
Porotheleum cinereum Pat.	Cyphelloid	Chapter 3
Resupinatus alboniger (Pat.) Singer	Lamellate	Chapter 5
Resupinatus applicatus (Batsch) Gray	Lamellate	Chapter 2
Resupinatus cinerascens (Clel.) Grgur.	Lamellate	Chapter 4
Resupinatus conspersus (Pers.) Thorn, Moncalvo & Redhead	Cyphelloid	Chapter 3
Resupinatus dealbatus (Berk.) Singer	Lamellate	Chapter 5
Resupinatus huia (G. Cunn.) Thorn, Moncalvo & Redhead	Cyphelloid	Chapter 4
Resupinatus hyalinus (Singer) Thorn, Moncalvo & Redhead	Cyphelloid	Chapter 5
Resupinatus incanus (Kalchbr.) Thorn, Moncalvo & Redhead	Cyphelloid	Chapter 2
Resupinatus kavinii (Pilát) M.M. Moser	Lamellate	Chapter 5
Resupinatus merulioides Redhead & Nagas.	Lamellate-merulioid	Chapter 4
Resupinatus poriaeformis (Pers.) Thorn, Moncalvo & Redhead	Cyphelloid	Chapter 3
Resupinatus porosus M.P. Martin, Lodge & Thorn	Poroid	Chapter 5
Resupinatus striatulus (Pers.) Murill	Lamellate	Chapter 5
Resupinatus subapplicatus (Cleland) Grgur.	Lamellate	Chapter 4
Resupinatus taxi (Lév.) Thorn, Moncalvo & Redhead (= *R. griseopallidus*)	Cyphelloid	Chapter 5
Resupinatus trichotis (Pers.) Singer	Lamellate	Chapter 5
Resupinatus urceolatus (Wallr. ex Fr.) Thorn, Moncalvo & Redhead	Cyphelloid	Chapter 3
Resupinatus vinosolividus (Segedin) J.A.	Lamellate	Chapter 4

Cooper		
Resupinatus violaceogriseus G. Stev.	Lamellate	Chapter 4
Rhodocyphella cupuliformis (Berk. & Ravenel) W.B. Cooke	Cyphelloid	Chapter 2
Rhodocyphella grisea (Petch) W.B. Cooke	Cyphelloid	Chapter 5
Solenia subporiaeformis Burt	Cyphelloid	Chapter 5
Stigmatolemma farinaceum (Kalchbr. & Cooke) D.A. Reid	Cyphelloid	Chapter 5
Stromatocyphella conglobata (Burt) W.B. Cooke	Cyphelloid	Chapter 2
Tapesia daedalea (Schwein.) Sacc.	Cyphelloid	Chapter 3

2.4.2   Genera in the *Resupinateae*

Resupinatus Gray, Nat. Arr. Brit. Pl. (London) 1: 617. 1821
= *Asterotus* Singer, Mycologia 35: 161. 1943 (according to Singer, 1975)
= *Calathinus* Quél., Enchir. fung. (Paris): 46. 1886 (according to Thorn and Barron, 1986)
= *Phyllotus* Karst., Bidr. Finl. Nat. Folk 32: 14. 1879 (according to Singer, 1951)
= *Rhodocyphella* W.B. Cooke, Beih. Sydowia 4: 105. 1961 (according to Donk, 1962)
= *Scytinotopsis* Singer *nom. nud.*, Ann. Mycol. 34: 335. 1936 (according to Singer, 1951)
= *Stigmatolemma* Kalchbr., Grevillea 10: 104. 1882 (according to Thorn et al., 2005)
= *Stromatocyphella* W.B. Cooke, Beih. Sydowia 4: 104. 1961 (this study)

Type species: *Resupinatus applicatus* (Batsch: Fr.) Gray, Nat. Arr. Brit. Pl. (London) 1: 617. 1821.

Characters: those of the tribus; hymenophore lamellate, poroid or cyphelloid, carpophores attached to the substrate directly via the pileus or by a lateral or eccentric pseudostipe; surface hairs repeatedly dichotomously branched or diverticulate; cheilocystidia diverticulate.

Distribution: cosmopolitan; some species show geographic patterns of distribution.

Observations: Historically, *Resupinatus* was restricted to species with lamellate or poroid fruit bodies, and those that were cyphelloid were placed in the genus

Stigmatolemma. The only molecular phylogenetic analysis to date prior to this study showed that *Stigmatolemma* was paraphyletic within *Resupinatus*, and so all members of the former genus were transferred into the latter (Thorn et al., 2005). Data from this study support this synonymy, and add the cyphelloid *Stromatocyphella* as another synonym of *Resupinatus*. The history of these cyphelloid genera is discussed below.

Species in *Hohenbuehelia* were initially separated from *Resupinatus* on the basis of morphological characters: the presence of metuloid cystidia (thick-walled, lanceolate, and often crystal-incrusted sterile cells in the hymenium) indicates a species belongs in *Hohenbuehelia* where an absence indicates the species belongs in *Resupinatus* (Singer, 1951; 1975a). Possession of a nematophagous anamorph (previously referred to as *Nematoctonus*) was added as a defining character of *Hohenbuehelia* by Thorn and Barron (1986), who treated in *Hohenbuehlia* some species that were previously thought to belong in *Resupinatus* due to their lack of conspicuous metuloids, such as *H. unguicularis*. Separation of *Hohenbuehelia* and *Resupinatus* has been supported by molecular phylogenetic analyses (e.g., Koziak et al. 2007). There is, however, at least one species of *Resupinatus* with metuloids (because of which the specimen was originally identified as *Hohenbuehelia nigra*), but no nematophagous anamorph. The sequence from this culture grouped with the *Resupinateae* and not in *Hohenbuehelia* (*Pleurotaceae*) so was deposited in GenBank as "*Resupinatus* sp." (Alberto et al., 1998; Thorn et al., 2000). *Asterotus* was once considered a separate genus from *Resupinatus* due to the unusual morphological characters: fruit bodies are stipitate and spoon-shaped, rather than astipitate, orbicular, and dorsally or laterally attached, and surface hairs are digitate to dichotomously branched rather than diverticulate (Singer, 1943). Singer (1975) later changed his mind and included *Asterotus* within *Resupinatus*, and this synonymy is supported by the placement of a sequence of the type species, *Asterotus dealbatus*, within *Resupinatus* (Moncalvo et al., 2002; Thorn et al., 2005; this study).

Stigmatolemma Kalchbr., Grevillea 10: 104. 1882
= *Resupinatus* Gray, Nat. Arr. Brit. Pl. (London) 1: 617. 1821. (Thorn et al., 2005; this
   study)

Type species: *Stigmatolemma incanum* Kalchbr., Grevillea 10: 104. 1882
≡ *Resupinatus incanus* (Kalchbr.) Thorn, Moncalvo & Redhead, in Thorn et al.,
   Mycologia 97(5): 1148. 2006

Observations: until Talbot's re-description of the type species (Talbot, 1956) the status
of the genus was considered doubtful (Donk, 1962). The original description by
Kalchbrenner was very brief (12 words), but did designate a type species (Kalchbrenner,
1882). Both Singer (1962) and Donk (1959) were satisfied with Talbot's re-description
after having also seen the small fragment of the holotype of *Stigmatolemma incanum* in
BPI.

Donk (1959) also remarked that the type species of this genus was likely to be closely
related to *Peziza conspersa* (now *Resupinatus conspersus*) and that this new cyphelloid
genus showed remarkable micromorphological similarity to the agaric genus
Resupinatus, a suggestion that was also made by Pilát (1935), Romagnesi (1950), Kühner
and Romagnesi (1953), and supported by Singer (1962). This suggestion that species with
a reduced morphology were closely related to species with what was regarded to be a
more "advanced" fruit body morphology (such as having gills, teeth, or pores) was not
widely adopted in fungal classifications until the first molecular studies demonstrated this
to be true (e.g., Hibbett and Binder, 2002; Bodensteiner et al., 2004). This study further
demonstrates that species with cyphelloid fruit body morphologies are multiply derived
within groups of species with lamellate or poroid fruit bodies (see Figure 2.1). This study
therefore supports that *Stigmatolemma* is a synonym of *Resupinatus*.

Stromatocyphella W.B. Cooke, Beih. Sydowia 4: 104. 1961.
= *Resupinatus* Gray, Nat. Arr. Brit. Pl. (London) 1: 617. 1821.

Type species: *Stromatocyphella conglobata* (Burt) W.B. Cooke, Beih. Sydowia 4: 104.
   1961
≡ *Cyphella conglobata* Burt, Ann. Mo. bot. Gdn 1: 375. 1915.

 Observations: at the time of its description, this genus originally contained three species. Reid (1964) reported that two of these (*Stromatocyphella lataensis* and *Stromatocyphella aceris*) do not belong in the genus, and are synonyms of *Calythella erucaeformis* and *Cyphellopsis anomala*, respectively. One other species, *Cyphella subgelatinosa,* may be a close relative. This species shares the common stroma-like hyphal mass, but has cups in smaller groups. A full discussion of *Cyphella subgelatinosa* can be found in Chapter 5.

There has also been disagreement in the literature about the correct classification of *Stromatocyphella conglobata*. In the type description, Burt (1914) commented that this species superficially resembles *Cyphella fasciculata* (now *Merismodes fasciculatus*, a member of the *Cyphellaceae*), but suggested that it might deserve a new genus. Singer (1945) supported this idea, and Cooke (1961) created the genus *Stromatocyphella*, which was supported by Donk (Donk, 1964). Unfortunately, Singer (1973) also stated that this species displayed strong affinities to *Campanella* and *Flavolaschia*, and so *Stromatocypella* has been classified with these genera in the *Marasmiaceae* ever since (as per Kirk et al., 2008), despite its morphology which places it as a close relative of *Resupinatus* (Singer, 1945, 1986). Molecular data (see Figure 2.1) now support its inclusion within *Resupinatus*.

Rhodocyphella W.B. Cooke, Beih. Sydowia 4: 105. 1961.
= *Resupinatus* Gray, Nat. Arr. Brit. Pl. (London) 1: 617. 1821.

Type species: *Rhodocyphella cupuliformis* (Berk. & Ravenel) W.B. Cooke, Beih.
    Sydowia 4: 105. 1961.
≡ *Cyphella cupuliformis* Berk. & Ravenel, Grevillea 2: 5. 1873 (as "*cupulaeformis*").
≡ *Chaetocypha cupuliformis* (Berk. & Ravenel) Kuntze, Rev. Gen. pl. (Leipzig) 2: 847.
    1891.

Observations: this genus is a synonym of *Resupinatus.* The name *Rhodocyphella cupuliformis* was originally used for all collections of cyphelloid fruit bodies lacking a subiculum found on *Juniperus*, regardless of geographic origin (Cooke, 1961), and was then treated as a synonym of *Resupinatus taxi* (Gilbertson & Blackwell, 1984), which is a later name for *Resupinatus griseopallidus* (Elborne, 2008). This is incorrect, as North American collections on *Juniperus* are *Rhodocyphella cupuliformis*, while European collections on a variety of substrates are *Resupinatus griseopallidus* (an unrelated species). *Rhodocyphella cupuliformis* has an identical sister species (Australian cyphelloid *Resupinatus* 1) found only in New Zealand on *Dacrycarpus* which requires a new name. The type species of this genus is discussed in further detail in section 2.4 "Taxonomy" (below), the Australian taxon (Australian cyphelloid *Resupinatus* 1) in Chapter 4, and *Resupinatus griseopallidus* in Chapter 5.

One other species, *Rhodocyphella grisea*, may be a close relative or even a synonym of *Resupinatus griseopallidus* as it is morphologically nearly identical, but was found in Sri Lanka. Unfortunately, it is only known from the type collection, precluding a molecular analysis. A more thorough description of this species may be found in Chapter 5.

Rhodocyphella cupuliformis is an example of what would have traditionally been considered an "intermediate" form between the lamellate species of *Resupinatus* and the cyphelloid gregarious species of *Stigmatolemma*: fruit bodies resemble *Resupinatus* in occuring singly or in small groups and lacking a subiculum, but are cyphelloid as in *Stigmatolemma*. The molecular data show that this species falls within *Resupinatus* (see Figure 2.1), making *Rhodocyphella* a synonym of *Resupinatus* and a member of the *Resupinateae*.

2.4.3　Type species of genera in the *Resupinateae*

All of the genera referred to below are now regarded to be synonyms of the genus
Resupinatus (see Figure 2.1) but the new combinations in *Resupinatus* are not made here
to avoid creating invalid names. Thus, currently accepted names according to Index
Fungorum (www.indexfungorum.org/Names/Names.asp) are used in this section.

Resupinatus applicatus (Batsch: Fr.) Gray, Nat. Arr. Brit. Pl. (London) 1: 617. 1821.
 ≡ *Agaricus applicatus* Batsch, Elench. fung., cont. prim. (Halle): 171. 1786.
 ≡ *Agaricus applicatus* Batsch: Fr., Syst. mycol. 1: 192. 1821.
 ≡ *Pleurotus applicatus* (Batsch: Fr.) P. Kumm., Fuhr. Pilzk. (Zerbst): 105. 1871.
 ≡ *Pleurotus applicatus* (Batsch: Fr.) P. Karst., Bidr. Kann. Finl. Nat. Folk 32: 94.
　　　1879.
 ≡ *Dendrosarcus applicatus* (Batsch: Fr.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 463.
　　　1898.
 ≡ *Calathinus applicatus* (Batsch: Fr.) Pat., in Duss, Enum. Champ. Guadeloupe
　　　(Lons-le-Saunier): 51. 1903.
 ≡ *Acanthocystis applicatus* (Batsch: Fr.) Kühner, Botaniste 17: 111. 1926.
 ≡ *Urospora applicata* (Batsch: Fr.) Singer, Beih. bot. Cbl., Abt. B 56: 145. 1936.
 ≡ *Geopetalum striatulum* var. *applicatum* (Batsch) Kühner & Romagn., Fl. Analyt.
　　　Champ. Supér. (Paris): 68. 1953.

Fruit Bodies: cupulate, 2-8 mm in diameter, with a lateral pseudostipe. Grey when dry
and non-striate, brown to black and non-striate when fresh. Hymenium folded into gills
that radiate from location of pseudostipe, macroscopically brown to dark brown when
fresh with white gill margins, composed of hyaline to pale brown basidia and basidioles
with hyaline cheilocystidia. Cuticle nonstriate when dry or fresh, with a grey coarse
tomentum at the point of attachment, glabrous at the margin. Flesh gelatinous between
epicutis and gill trama, hyphae in gelatinous zone a light brown and 2-4.5 μm in
diameter. Subhymenium dark brown, composed of gelatinized tightly packed hyphae 2.5-
4.5 μm in diameter. All hyphae with clamps, and branching from clamps. Cuticle covered
in hyaline, inamyloid, diverticulate hairs up to 80 μm long, 3-5 μm wide, with irregular
finger-like projections up to 4 μm long. Droplets on cheilocystidia and cuticular hyphae
have been reported from fruiting bodies (Thorn & Barron, 1986) but not observed in this
study

Basidia: with a basal clamp, 4-spored, hyaline to slightly pale brown in KOH, clavate, (18-)20-22(-29) x 4.5-5.5(-6) μm

Cystidia: numerous along gill edges, hyaline, cylindrical to clavate, diverticulate with fingerlike projections, 18-25 x 3.5-5 μm.

Spores: hyaline, inamyloid, smooth-walled, globose to subglobose, with central to slightly eccentric apiculus, (4.0-)4.4-5.2 x (4.0-)4.2-4.8 μm.

Substrate ecology: on living and dead dicotyledonous wood, specimens examined on *Acer*, *Carya, Eucalyptus, Fagus, Kunzea*, *Nothofagus*, *Pseudopanax*, *Pseudowintera*, *Quercus*, *Ripogonum, Salix*, and unidentified rotting wood.

Distribution of specimens examined: Australia, Canada (NS, ON, PQ), Germany, New Zealand, Tasmania, United States (IN, ME, NJ, NY, TN).

Specimens Examined: AD-C (10961, 10965, 55542, 55544, 55546, 55846), B (70 0000333), CANB (574876, 574880, 574881, 742140, 742279), DAR (14206), MEL (261051, 269113, 1052588, 2090235, 2300677, 2305275), PDD (70479, 79793, 86842, 86862, 87046, 87121, 87196, 87307, 87325, 87473). Collections found during this study: JVM062708/01, JVM061209/01, JVM072409/02, RGT060626/01, RGT080709/04, RGT100622/02

Observations: *Resupinatus applicatus* has been widely reported but the application of the name is uncertain. No holotype collection exists of this species, so a new type collection of the species sensu Batsch needs to be designated to cement the concept of the species. Batsch (1786, pl 123) published a watercolour painting done presumably of the type collection that can be used in the meantime as an iconotype (a photograph, painting or drawing of a type collection that was not deposited in a herbarium). If so designated, this iconotype could be compared to European specimens to determine a new type, which would be designated as an epitype. Based on molecular analysis of collections morphologically identified in this study as *Resupinatus applicatus*, there are five distinct, non-sister species that are part of this species complex, all found on hardwoods.

Sequences of *R. applicatus* 1 are known only from North America, *R. applicatus* 2 from Europe, *R. applicatus* 3 from North America and Europe, and *R. applicatus* 4 and 5 from Australia and New Zealand, which are both genetically distinct from *Resupinatus subapplicatus* (originally thought to be a synonym of this species; see Chapter 4 for more detail). Other than their geographic distribution, they are morphologically identical. Because of this, historic or recent collections lacking sequence data cannot be placed with certainty in any of the molecular species. Additional molecular sampling may extend the known ranges of the molecular species, particularly *R. applicatus* 1 and 2. Sequence data from a neotype for *R. applicatus* will be required to fix that name to one of these molecular species, so that the others may then be named.

The *Resupinatus applicatus* complex can be distinguished from *R. striatulus* morphologically in most circumstances, with *R. applicatus* having a felty grey tomentum over the back of the cap whereas *R. striatulus* has a pruinose white cap surface with many white hairs at the point of attachment. When fresh or rehydrated, collections of *R. applicatus* are not transparent or translucent whereas collections of *R. striatulus* are often translucent to transparent with strong striations along the back of the cup surface where the gills are located on the opposite side in the hymenium. The molecular data gathered in this study further supports the division between *Resupinatus striatulus* and *Resupinatus applicatus* in that the former is exclusively found on conifers and the latter exclusively on hardwoods. A GenBank sequence derived from a collection of *R. striatulus* on rotting coniferous wood is genetically distinct from all four *R. applicatus* species (see Figure 2.1 and Figure 4.3).

A culture of *Resupinatus applicatus* 1 produced jack-like cells on aerial hyphae (Thorn & Barron, 1986). This was not observed in this study, but similar spores were observed in *Resupinatus griseopallidus* and *Rhodocyphella grisea* in fruit bodies in herbarium collections. These spores (at least in *Resupinatus applicatus*) appear to be produced from dikaryotic hyphae and the spores are often empty so they presumably do not play a role in dormancy (Thorn & Barron, 1986).
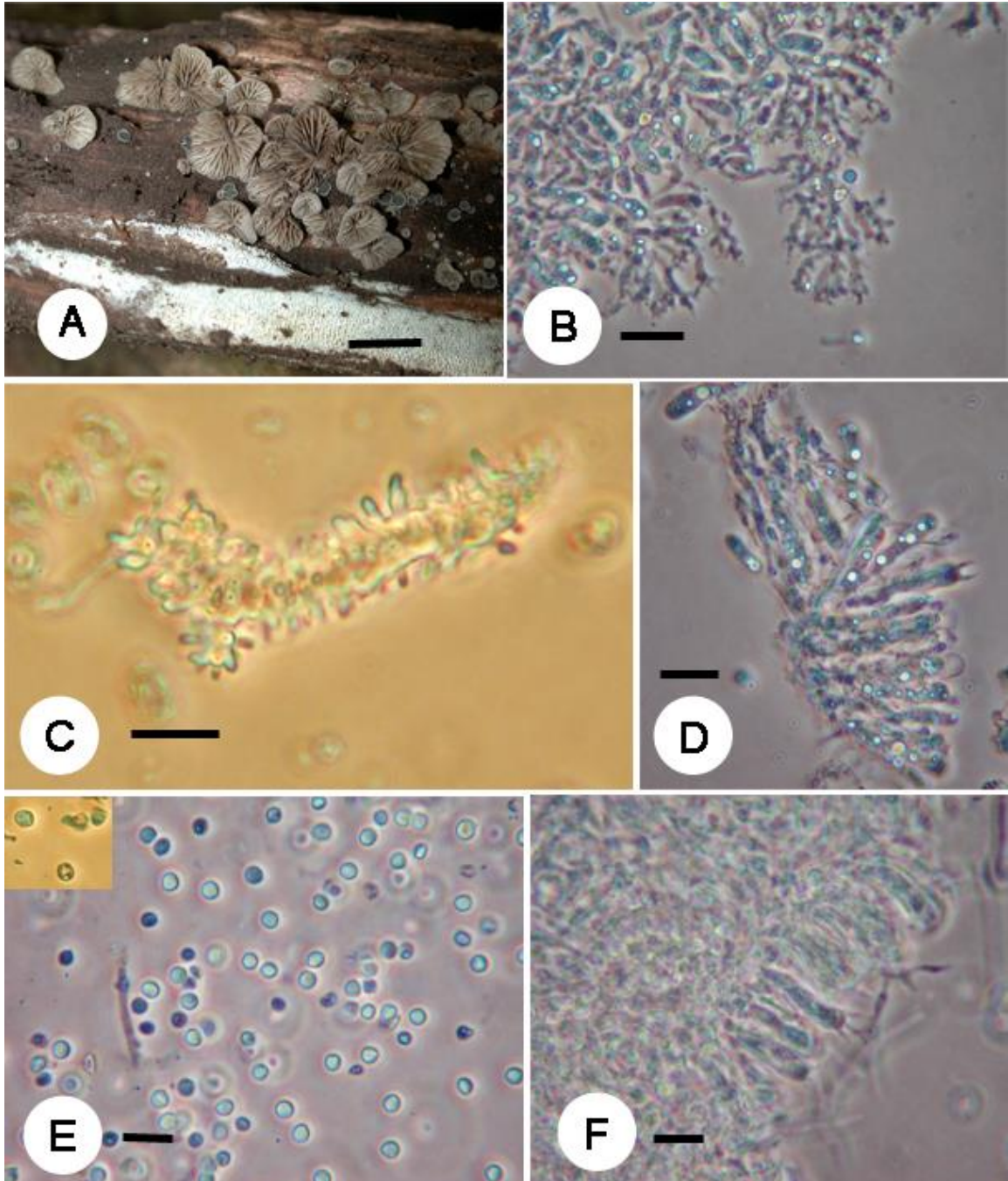
Figure 2.3 *Resupinatus applicatus* complex A. Fruit bodies (Bar = 1.5 cm, RGT060626/01). B. Rameales-like cheilocystidia present along gill edges (Bar = 10 μm, CANB 574880). C. Rameales-like surface hairs on the pileal surface (Bar = 15 μm, MEL 2059634). D. Mature basidium with two sterigma visible (Bar = 10 μm, MEL 2300677). E. Spores of two different collections, showing globose (main image) and subglobose (inset) spores (Bar = 10 μm, AD 10962 and MEL 1052588). F. Mature basidium with three of four sterigma visible (Bar = 10 μm, AD 10963).

Resupinatus incanus (Kalchbr.) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo, Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006.
≡ *Stigmatolemma incanum* Kalchbr., Grevillea 10(no. 55): 104. 1882.
≡ *Porotheleum incanum* (Kalchbr.) Sacc., Syll. fung. (Abellini) 6: 423. 1888.

Fruit Bodies: cupulate, sessile, grey to nearly black (or dark brown), 175-350 μm in diameter; cups seated on a common thick and dense white subiculum, margin of subiculum slightly filamentous, rolling slightly upwards; hyphae composing the subiculum are hyaline, 2-3 μm in diameter and coated in a fine encrustation made up of small cuboid crystals which appear to give the subiculum a "shiny" appearance when dry. Cups covered in hyaline diverticulate surface hairs up to 70 μm long, 2.5-3.5 μm in diameter, with finger-like projections up to 4 μm long. Trama gelatinized, composed of loosely-woven hyphae, hyaline, 2.5-4 μm in diameter. Subhymenium composed of slightly gelatinized hyphae, nearly black (dark brown in Melzer's), more tightly packed than in the trama, running parallel to the hymenium, hyphae 3-4.5 μm in diameter. Hymenium composed of tightly packed basidia and basidioles, with some basidioles showing elongated projections from the apex of the basidiole up to 25 μm long, 2-4 μm wide. All hyphae with clamps, and branching from clamps. When cut from the substrate, the fungus can be seen making fruit bodies on the interior of the substrates in pockets of air where all of the woody substrate has been rotted away; these cups lack a true subiculum but have a dense mat of white hairs at the base of the cup. The openings of these cups is scarcely larger than the diameter of a pin, and the cups themselves are much smaller than the fruit bodies on the exterior of the substrate (only 80-120 μm across). There were no mature basidia observed in these cups, and the basidioles were much smaller than basidioles measured on the reverse side of the collection (only up to 12 μm long, as opposed to up to 25 μm long); all other micromorphological characters identical to cups on the reverse side. This phenomenon is not observed in any other species in the *Resupinateae*.

Basidia: with clamps 4-spored, clavate, hyaline in KOH, (19-)20-24(-25) x (6.0-)6.5-7.5(-8) μm

Cystidia: none observed; surface hairs become shorter near the cup margins, more like cystidia but still in the epicutis, cylindrical, diverticulate, 12-24 x 3.5-5 μm.

Spores: hyaline, inamyloid, smooth-walled, oblong, (6.0-)6.5-8.0(-8.8) x (3.5-)4.4-5.2 μm

Substrate ecology: on rotting wood of unidentified dicot.

Distribution: South Africa

Holotype: BPI 323656 (!); collected on rotting wood in Somerset East, South Africa by MacOwan on an unknown date (prior to 1882).

Specimens Examined: the type is the only collection seen; other collections with this name were either misidentified or could not be examined (as in the case of *Porotheleum incanum* deposited in the PACA herbarium by Rick). The specimen used by Talbot to provide a more detailed description of the species (Talbot 1956) was collected in Knysna, South Africa, by A.M. Bottomley in 1939. Unfortunately, this collection could not be located for examination in this study but seems likely to belong to the same species. Another collection reported in the literature is by Rick from Brazil (Rick, 1960), but this likely represents a different species, *Porotheleum cinereum* Pat. (for a full description and discussion of that species, refer to Chapter 5).

Observations: This species is unique in the *Resupinateae*. The cupules erupting through the substrate into small air pockets in the wood are not observed in any other species in the group, lamellate or cyphelloid. Cooke (1957) synonymized this species with *Resupinatus poriaeformis*, which is erroneous in my opinion. This is a good species, and, despite the lack of molecular data due to the absence of recent collections, belongs in the *Resupinateae*. It is difficult to estimate its phylogenetic placement due to the number of times members of the *Resupinateae* have converged on the cyphelloid growth form, but *R. incanus* would probably group most closely to lamellate species with a very dense covering of white hairs when young, such as *Resupinatus violaceogriseus*.
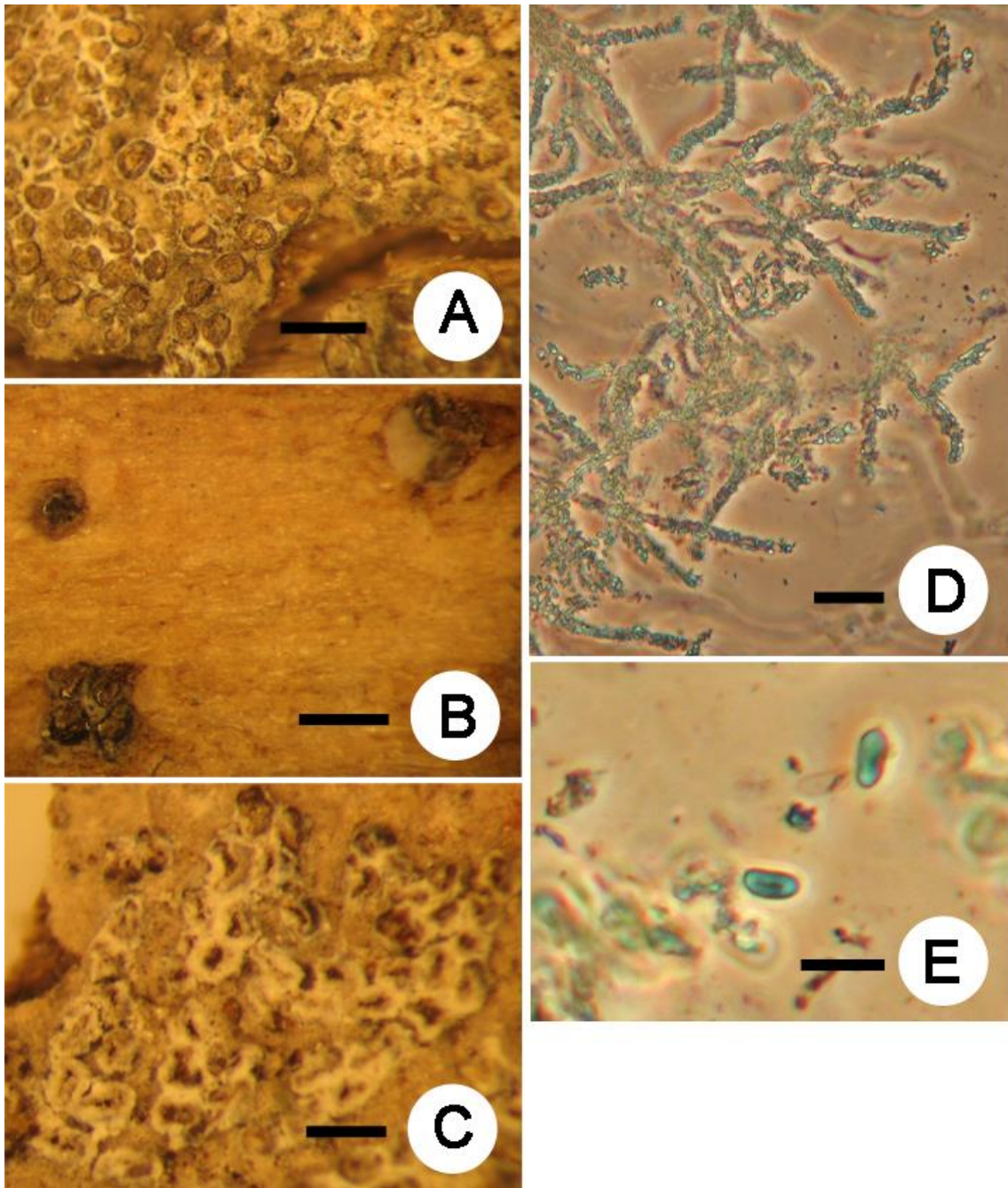
Figure 2.4 *Resupinatus incanus* A. Mature fruit bodies, showing the dense white subiculum that thins with age (Bar = 1 mm; BPI 323656). B. The underside of the substrate, showing the collection fruiting through the substrate and into open air spaces in the wood itself (Bar = 1 mm; BPI 323656). C. Younger fruit bodies than in A, showing the dense white hairs that cover young cups (Bar = 1 mm; BPI 323656). D. Densely encrusted surface hairs (Bar = 20 μm; BPI 323656). E. Basidiospores (Bar = 10 μm; BPI 323656).

Stromatocyphella conglobata (Burt) W.B. Cooke, Beih. Sydowia (ser II) 4: 104. 1961.
≡ *Cyphella conglobata* Burt, Ann. Mo.Bot. Gdn. 1: 375. 1914.

Fruit Bodies: hemispherical cups 0.3-1.0 mm in diameter, densely packed with a common stalk, erupting from lenticels of bark in groups of 3 to 25 cups. When dry, fruit bodies are grey and tomentose on exterior, hymenium becoming darker (almost black). Upon rehydrating, fruit bodies a dark caramel brown with hymenium a similar brown colour. Exterior covered in a dense covering of surface hairs, diverticulate (but less-so than other species in the group), hyaline, up to 40 μm long, 2.5-4 μm wide, with finger-like projections appearing more like warts on elongated hyphal tips 1.5-2.5 μm long. Hairs heavily encrusted with small cuboid crystals that dissolve almost immediately in KOH, less quickly in Melzer's. Subiculum very dense, appearing grey in mass but composed of hyaline or slightly brownish encrusted hyphae, 2.5-4.5 μm in diameter, raised off the substrate. Subhymenium a dark brown in KOH, hymenium hyaline. Hyphae strongly gelatinized in outer trama, hyaline, 1.5-4.0 μm in diameter, more or less perpendicular to hymenium, loosely woven. Inner trama has hyphae running parallel to hymenium, hyaline or slightly brownish, only slightly gelatinized, 1.5-3.5 μm in diameter, much more tightly packed than in the previous layer. All hyphae in trama have smooth walls, are thin-walled, with clamps and branching from clamps.

Basidia: 4-spored, hyaline in KOH, clavate, (19.0-)19.5-25(27) x (5.0-)5.5-7 μm

Cystidia: none seen

Spores: hyaline, inamyloid, smooth-walled, cylindrical, some slightly dented on one side while others have straight walls, rarely with an apiculus, (7.4-)8.0-9.2(-9.8) x 2.4-3.2-(3.6) μm

Substrate ecology: on dead hardwoods, observed from *Alnus* sp. and *A. incana*; also reported from *Betula* sp. and *Juglans cinerea* (Cooke, 1961)

Reported and observed distribution: Canada (BC, NB, NF, ON, PQ), United States (AK, MI, NC, NH, NY, PA).

Holotype: BPI 292800 (!); collected in Lower Bartlett, New Hampshire, USA in July 1907 by R. Thaxter

Specimens examined: BPI (292797, 292799, 292800, 292803, 332265), FH (258763, 258769). Collections found during this study: 10.04.26av01, 10.11.29av02, 11.11.04av01.

Observations: since Reid (1964), *Stromatocyphella* has been a monotypic genus that was easily identifiable by collectors. Historically, Reid (1964) remarked that the genus seems to be closely related to *Resupinatus*, and Singer (1975a) transferred it into the *Resupinateae* as a "reduced series". Phylogenetic analyses of ITS and LSU rDNA sequences place this species within *Resupinatus* (see Figure 2.1), and so it should be transferred to this genus.

Stromatocyphella conglobata was once considered rare, but we now know it is a common species. Habitat and time of fruiting were often disregarded when attempting to search for this fungus, but we now know that it fruits in the late fall or early winter in North America (depending on latitude, from early September to late November) and can be found in nearly every thicket of *Alnus* that contains rotting wood from older individuals. Throughout this study it was never found on a different substrate, although it was only found in Newfoundland, Canada. It is possible that searching further south would have yielded this species on different substrates, as evidenced by herbarium collections of this species on both *Betula* and *Juglans*. This species has also erroneously been recorded from Brazil by Rick in herbarium voucher collections (in BPI), but these collections do not represent the same species, nor are they members of the *Resupinateae* (see Chapter 6).
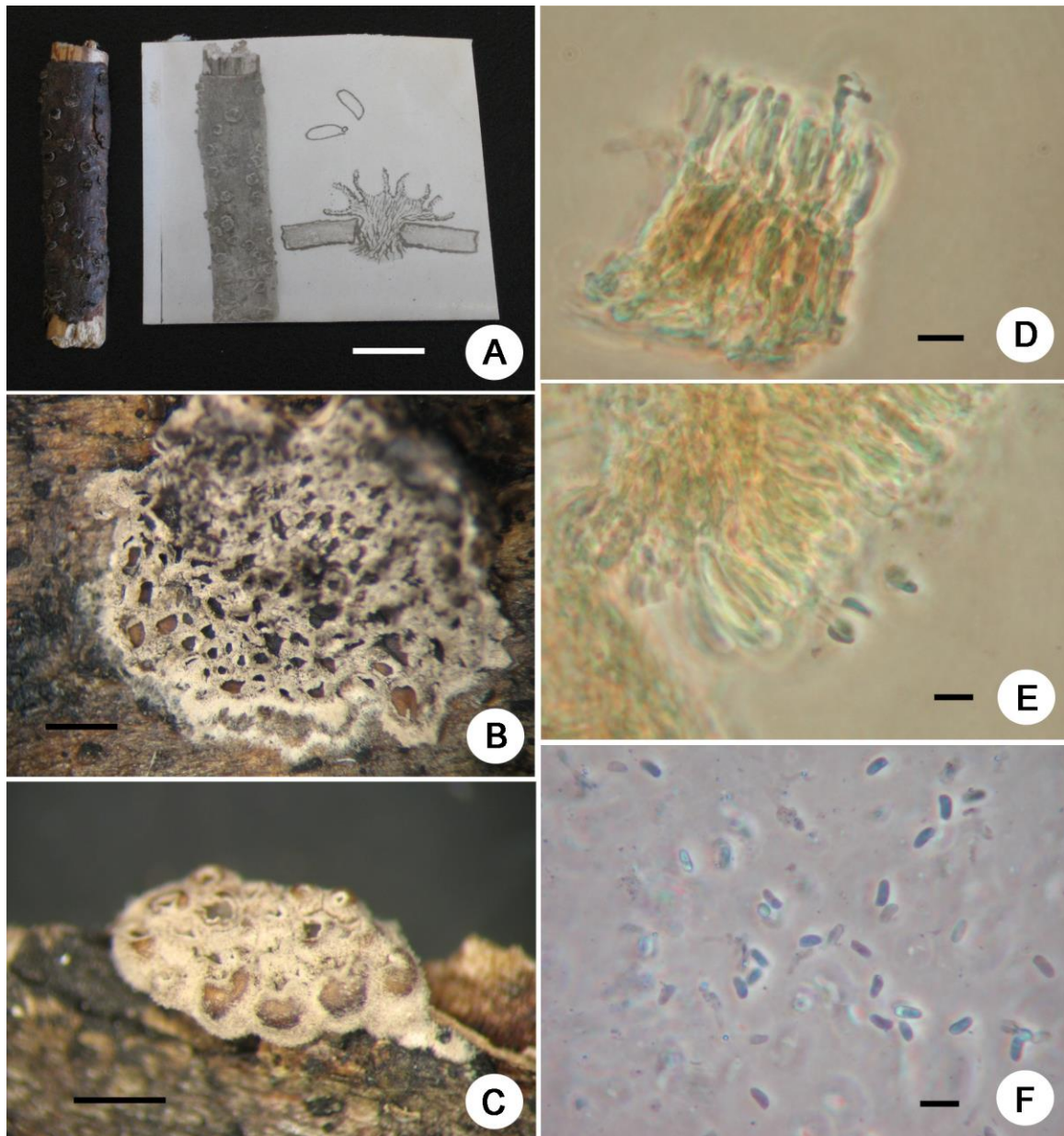
Figure 2.5 *Stromatocyphella conglobata*. A. Contents of the herbarium packet of the type collection, showing Burt's drawing of the development of the fruit bodies, the shape of the spores, and his original photograph of the type collection (Bar = 3 cm; BPI 292800). B. Mature fruit bodies erupting from a lenticel of *Alnus incana* (Bar = 1 mm; BPI 292800). C. Mature fruit bodies, side view, showing the raised subiculum off the substrate (Bar = 1 mm; BPI 292800). D. Diverticulate "cheilocystidia" around the edge of the fruit body with immature basidia (Bar = 10 μm; 11.11.04av01). E. Basidium with spores attached to sterigma (Bar = 10 μm; 11.11.04av01). F. Basidiospores in phase-contrast (Bar = 10 μm; 11.11.04av01).

Rhodocyphella cupuliformis (Berk. & Ravenel) W.B. Cooke, Beih. Sydowia 4: 105.
1961. (as *Rhodocyphella cupulaeformis*)

≡ *Cyphella cupuliformis* Berk. & Ravenel, Grevillea 2(no. 13): 5. 1873. (as *Cyphella
cupulaeformis*, an orthographical error to be corrected, Article 60.8, Rec.
60G.1, McNeil et al., 2012)

≡ *Chaetocypha cupuliformis* (Berk. & Ravenel) Kuntze, Revis. gen. pl. (Leipzig) 2:
847. 1891.

= *Resupinatus taxi*, *sensu* Burt (1914), Donk (1962), and Gilbertson & Blackwell
(1984).

≠ *Cyphella taxi* Lév., Annls. Sci. Nat., Bot., ser 3 8: 336. 1847. (this study)

Fruit Bodies: cups scattered, rarely in groups of three to seven cups, heavily crystal
encrusted, no subiculum. Cups 0.5-1.0 mm (rarely to 1.5 mm) across, approximately 0.5
mm high. Margin inrolling when dry. Exterior grey-brown, slightly greenish when visibly
high numbers of algae are present on the substrate (as evidenced by the substrate taking
on a greenish tint), with heavily encrusted diverticulate surface hairs up to 50 μm long, 2-
3.5 μm in diameter. Pileal trama slightly gelatinized, composed of loosely-woven hyaline
hyphae 2-3.5 μm in diameter. Hymenial trama brown, also slightly gelatinized but much
more densely packed than the previous layer, running parallel to the hymenium, 2-4 μm
in diameter. Hymenium appearing slightly darker than the exterior of the cup when dry
(dark brown to dark grey-brown), but microscopically composed of tightly packed
hyaline basidia and basidioles. All hyphae with clamps, and branching from clamps.

Basidia: clavate to subclavate, hyaline in KOH, 4-spored, 20-25 x 4-6 μm.

Cystidia: none seen.

Spores: hyaline, inamyloid, jack-shaped with six large spines 1.5-2(-3) μm long, 3.8-4.0
x 3.8-4.0 μm.

Substrate ecology: on bark of coniferous trees (Cupressaceae) in southeastern North
America, observed from *Juniperus* and *Thuja*

Distribution: Bermuda and the southeastern United States (FL, LA, OH, SC)

Isotype: FH 258736 (!); on dead bark, collected in Aiken, South Carolina in January
1873 by H.W. Ravenel

Specimens Examined: ARIZ (012974, 012975, 012976, 012977, 012978, 012979), BPI
(292807 [a portion of the type material]), FH (258736, 258738), K (166162 [co-
type of *R. cupuliformis*]), NYBG (152, 224, 300, 497, 511(1), 511(2), 1709),
PRM (560725)

Observations: This species has often been synonymized with *Resupinatus taxi* (Donk, 1962; Gilbertson & Blackwell, 1984; Ginns & Lefebvre, 1993; Thorn et al., 2005; Lassoe, 2006) but this study determines that *Rhodocyphella cupuliformis* is complex comprised of three different species: the first being all of the collections on *Cupressaceae* from southestern North America (this species, *Rhodocyphella cupuliformis*, Figure 2.6 A, B, and C for type material and J, K, and L for new material from which a sequence was derived), the second comprises collections on eutrophic angiosperms and some gymnosperms (one collection is reported on *Taxus*) in Europe (*Resupinatus griseopallidus*, formerly known as *Resupinatus taxi*; see Chapter 5, Figure 2.6 G, H, and I), and the third comprises collections on *Podocarpaceae* native to Australia and New Zealand (known as "Australian cyphelloid *Resupinatus* 1"; see Chapter 4, Figure 2.6 D, E, and F). This distinction is supported with molecular evidence, seen in Figure 2.1 and Chapter 4, Figure 4.3. The North American *Rhodocyphella cupuliformis* (AN 012974, as "*Resupinatus taxi*" in Figure 2.1) and "Australian cyphelloid *Resupinatus* 1" (ICMP 16593; as "*Rhodocyphella cupulaeformis*" in Figure 2.1) are sister species, while *Resupinatus griseopallidus* (R 12489; in Figure 4.3) is basal in *Resupinatus* and unrelated to the previous two species. An important morphological difference to note between *Resupinatus griseopallidus* and the other two species part of this complex are the spores: ovate spores (as reported by Léveillé, 1847) are borne on basidia instead of the jack-shaped spores of *Rhodocyphella cupuliformis* and "Australian cyphelloid *Resupinatus* 1" (as seen in Figure 2.6 I).

A full discussion of *Resupinatus griseopallidus* and its synonym *R. taxi*, can be found in Chapter 5. A full discussion of the New Zealand *Rhodocyphella cupuliformis* can be found in Chapter 4. *Rhodocyphella grisea* (from Sri Lanka) is also a possible synonym of *Resupinatus griseopallidus*, but only the type collection is known. A more thorough discussion of *Rhodocyphella grisea* can be found in Chapter 5.

As seen in Figure 2.6, there is a suggestion that these species are algal associates. Whether the host is *Juniperus* (Figure 2.6 A-C and J-L), *Dacrycarpus* (Figure 2.6 D-F), or *Syringa* (Figure 2.6 G-I), where there are fruit bodies formed there is also a dense layer of algal cells covering the surface of the substrate. Basidiomycete associations with algal cells have been documented previously (for example, Roskin, 1970; Hibbett & Thorn, 2001; Oberwinkler, 2001; Limpens et al., 2003; Ertz et al., 2008), but are rarer than their ascomycete counterparts (for example, of the approximately 14,000 species of lichen, nearly 95% of these species have an ascomycete mycobiont; Kirk et al., 2008). There needs to be more work done to examine if these species are algal associates - whether basidiolichens or algal parasites, or if this apparent association is mere coincidence.
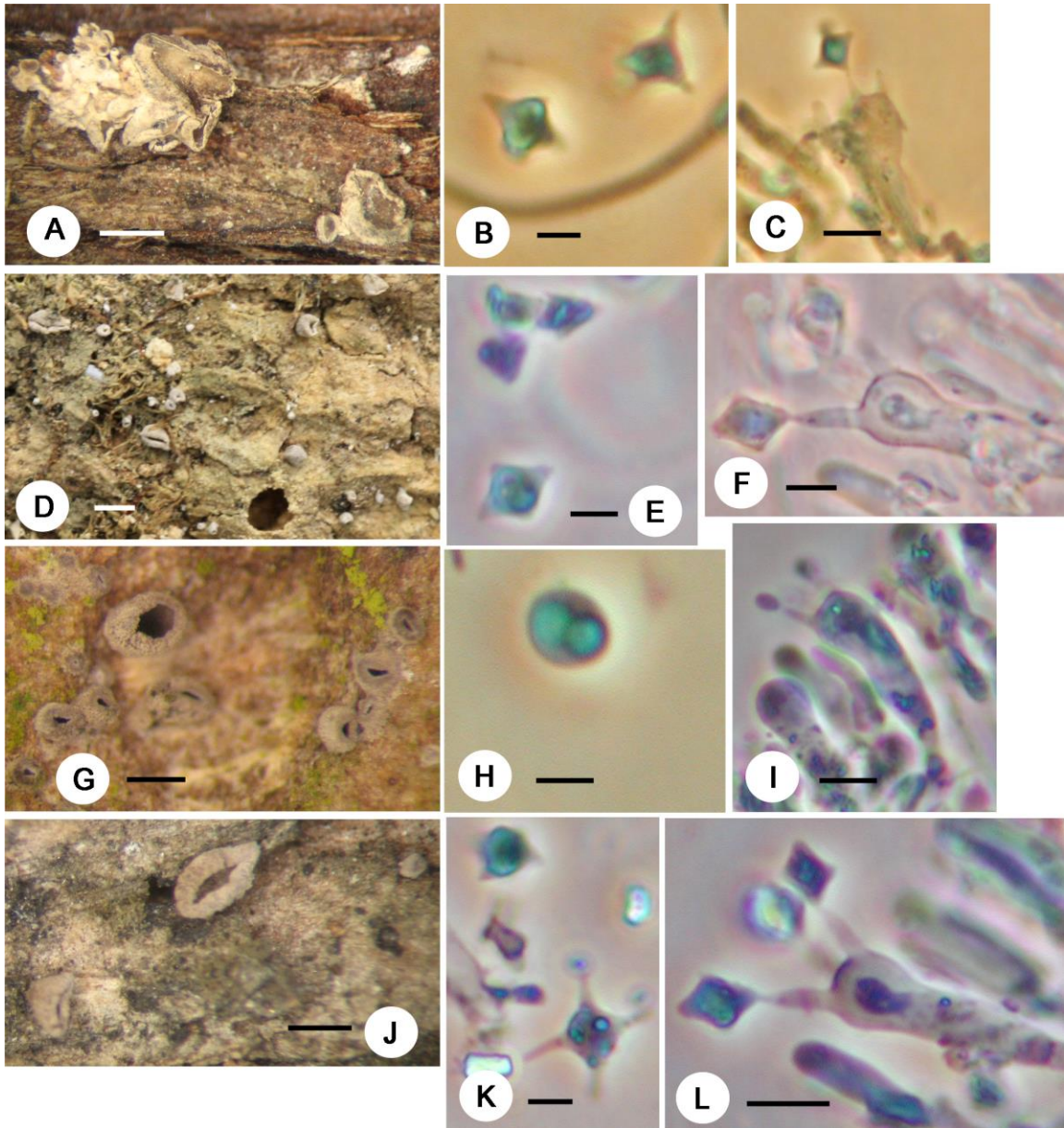
Figure 2.6 The *Rhodocyphella cupuliformis* species complex. A. Fruit body of a portion of the type material on *Juniperus* from SC, USA (Bar = 1.0 mm; BPI 292807). B. Basidiospores of the type material (Bar = 5 μm; BPI 292807). C. Basidium with attached basidiospores of the type material (Bar = 10 μm; BPI 292807). D. Fruit body of "Australian cyphelloid *Resupinatus* 1", on *Dacrycarpus* from New Zealand (Bar = 1.0 mm; PDD 88932). E. Basidiospores of the NZ species (Bar = 5 μm; PDD 88932). F. Basidium with attached basidiospores of the NZ material (Bar = 5 μm; PDD 88932). G. Fruit body of *Resupinatus griseopallida* from Denmark on *Syringa* (Bar = 1.0 mm; T. Lassoe). H. Basidiospore (Bar = 5 μm; T. Lassoe). I. Basidium with basidiospores attached (Bar = 10 μm; T. Lassoe). J. Fruit body of *Rhodocyphella cupuliformis* on *Juniperus* from FL, USA (Bar = 1.0 mm; ARIZ 012974). K. Basidiospores (Bar = 5 μm; ARIZ 012974). L. Basidium with basidiospores attached (Bar = 10 μm; ARIZ 012974).

2.5   Conclusions

It is now clear that the tribe *Resupinateae* consists of a single genus, *Resupinatus*, with approximately 40-50 species whose fruit bodies may be lamellate, poroid, merulioid, or cyphelloid. The cyphelloid habit in the *Resupinateae* is an example of a trait that has been multiply derived within a monophyletic group. This character was derived at least three separate times; once in the clade with *Resupinatus urceolatus* and *Resupinatus poriaeformis*, once in the clade with *Rhodocyphella cupuliformis* from North America and New Zealand, and once in the clade with *Stromatocyphella conglobata* and *Porotheleum cinereum*. Of the genera previously accepted in the *Resupinateae*, *Stromatocyphella* joins *Stigmatolemma* as a synonym of *Resupinatus,* whereas *Aphyllotus* and *Hohenbuehelia* should be excluded from the *Resupinateae* and transferred to the *Marasmiaceae* and *Pleurotaceae*, respectively. However, no sequences are as yet available of the type species of *Stigmatolemma* (*S. incanum*) nor of at least three other cyphelloid species (*S. farinaceum, S. huia,* and *S. hyalinum*), nor of the sole species of *Aphyllotus*, *A. campanelliformis*. A concerted effort should be made to obtain fresh collections and cultures of these species in order to obtain DNA sequences that could support or refute the taxonomic suggestions made here.

Many species thought to belong in the *Resupinateae* are still without sequences of voucher collections, as the herbarium collections available of these species are either only type collections or the collections are old enough that DNA extraction and amplification would be impossible. These species are covered in more detail in Chapter 5, but effort needs to be made to make recent collections of these species for DNA sequencing to demonstrate their membership in the group.

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Chapter 3

3 Host specificity and ecological distribution in the *Resupinateae*

With many species and groups of fungi, the distribution of taxa can be explained by interactions with other organisms: fungi will have the same or very similar distributions as their plant or insect host, or the same species range as the global distribution of the forest type in which they live (Bisby, 1943; Bissett & Parkinson, 1979; Amano, 1986; Koske, 1987). This distribution pattern does not seem to hold universally within the *Resupinateae*. This chapter will examine the patterns of geographic distribution and plant substrate relations in selected members of the group.

3.1 Introduction

The distribution of species of fungi around the world historically has been speculated to be similar to distributions of plants and animals: the highest diversity of fungi is expected to be in the tropics, where plant and insect diversity, as well as turnover of organic material in forest ecosystems, is the highest (Hawksworth, 1990; Hawksworth & Rossman, 1997; Frohlich & Hyde, 1999; Arnold et al., 2000; Hawksworth, 2001; Hyde, 2001; Parungao et al., 2002). It is also suggested that species that are often or easily overlooked (microfungi like molds, fungi with very small fruit bodies like in the *Resupinateae*, and fungi with very short-lived fruit bodies) could be much higher in diversity than currently known (Korf, 1997).

Host specificity is believed to be a strong factor in global diversity estimates, meaning that fungi specific to certain hosts (plant or animal) are greatly underrepresented in the literature with few exceptions. In Great Britain, one of the most highly studied areas in the world with respect to fungal diversity, for every one plant species there are approximately six fungal species known to exist (Hawksworth, 1990, based on data from Clapham et al., 1987; Sims et al., 1988). This ratio seems relevant to fungi growing on living substrates; whether or not this is the case for fungi found on decaying substrates is unknown.

Some species in the *Resupinateae* show ecological and host specificity (for example, *Resupinatus conspersus* is only known from the Alps and grows exclusively on *Abies*; Donk, 1962), while others are cosmopolitan and grow on many substrates (for example, *Resupinatus poriaeformis* is known from over 15 different host plants and has been collected on at least three continents; Burt, 1924; Bourdot & Galzin, 1927; Cooke, 1957; Cunningham, 1963; Agerer, 1978; Thorn & Barron, 1986; Ginns & Lefebvre, 1993). Traditional definitions of species limits in terms of taxonomic delineation have been challenged in the literature, first by the suggestion that *Resupinatus poriaeformis* differs from *Resupinatus urceolatus* in continental distribution (Donk, 1962), and second by the report that *Resupinatus conspersus* was collected in tropical South America (Bodensteiner et al., 2004).

What generalizations can we make, if any, about the patterns of species distribution in the *Resupinateae*? Are they a group of fungi that are underrepresented due to their small fruit bodies? Do they display host specificity, do they occur on a mixture of hosts, or do different species display a range of affinities to a host from host-specificity to host generalists? Can other morphological characters such as the subiculum or spore size and shape be consistently used for taxonomic delineation of species? This chapter will examine species in the *Resupinateae* whose distributions are thought to be based on host, ecological, or geographical specificity.

3.2   Materials and Methods

3.2.1   Herbarium samples

Dried specimens of the *Resupinateae* and candidates that might belong to that group, were requested for microscopic study through letters sent by the late Dr. Jane Bowles (UWO Herbarium) to herbaria around the world (AD, B, BPI, CANB, C, FH, GBIF, GJO, HO, INPA, K, L, MEL, NCU, NYBG, O, PC, PDD, PH, PRC, PRM, S, STR, TENN, UPS; herbarium acronyms following Holmgren et al., 1990, updated at http://sciweb.nybg.org/science2/IndexHerbariorum.asp). Species targeted for this study were *Resupinatus conspersus, Resupinatus urceolatus, Resupinatus poriaeformis,*

Porotheleum cinereum, and their synonyms. Herbarium collections were then analyzed for taxonomic characters.

3.2.2 Herbarium collection analysis

The most important characters for use in identification of species in *Resupinatus* are the colour, size and shape of the fruit body, the colour, shape (including ornamentation) and size of surface hairs, the presence, colour and thickness of a gelatinous layer in a vertical section of the fruit body tissues, basidiospore shape, size and ornamentation, and the size and shape of basidia.

Notes and measurements were taken of dried collections for fruit body size (in µm; a range from smallest mature fruit bodies to largest mature fruit bodies that show no signs of decomposition), colour and shape; presence and distribution of surface hairs; and presence or absence of a subiculum or subiculum-like structure (a mat of hyphae on the surface of the substrate at the base of the fruit bodies). Small portions of fruit bodies of dried collections were rehydrated, and changes in colour of the fruit body and surface hairs were noted (often, fruit bodies are much darker in colour with surface hairs more visible when dry than when fresh). Photographs of the dried collections were taken. Rehydrated portions of the fruit body were sectioned by hand using a razor blade and squash-mounted on a microscope slide.

Two sections were made on each microscope slide, in different mountants: one in Melzer's reagent (containing potassium iodide and iodine to stain starch, cellulose and dextrose, chloral hydrate as a clearing agent to better visualize darkly pigmented fungal structures, and sterile distilled water; Largent, 1977), and the other in 2% potassium hydroxide solution (KOH; Largent, 1977). Melzer's reagent was used to visualize spore characteristics (shape, size, colour changes and spore ornamentation), hyphal characteristics (size, shape, colour, presence or absence of clamps, presence or absence of septa), and surface hair characteristics (size, shape, colour). Due to the difficulty of spreading cells in Melzer's even with application of light pressure to the coverslip, basidia and cystidia are difficult to observe and measure in this mountant. Separation of cells in these tissues is much more effective in potassium hydroxide, so the latter was

used to visualize characteristics of basidia (size, shape, and colour) and cheilocystidia (size, shape, colour, ornamentation).

All microscopic measurements are represented in micrometers (µm). Basidiospore, basidium, cystidia and surface hair measurements are represented as a range, with values in parentheses representing the smallest and largest values, and the size range representing values between the tenth and ninetieth percentiles (as per Thorn and Barron, 1986). Other measurements (for example the diameter of hyphae, or the length and width of sterigmata) are represented as a range of values, the smallest and largest observed.

3.3   Results

3.3.1   *Resupinatus conspersus* and *Porotheleum cinereum*

Collections of each of these species can be separated based on geographic origin of the collections as well as substrate. Tropical collections represent *Porotheleum cinereum*, a member of the *Resupinateae* (demonstrated through phylogenetic analysis in Chapter 2, Figure 2.1), and temperate collections from the Alps on *Abies* represent *Resupinatus conspersus*. The morphological analysis in this study has resulted in the discovery of a third species of this complex, *Tapesia daedalea*. While morphologically identical to *R. conspersus* and *P. cinereum*, the difference is seen in substrate and geographic distribution as it is present in temperate to sub-tropical climates in North America on hardwoods. Unfortunately, none of the collections of *Tapesia daedalea* received on loan from herbaria were recent enough to be suitable for DNA analysis, and so the placement of this species within the *Resupinateae* is uncertain. However, based on morphology, it does belong within the group (see section 3.4 "Taxonomy").
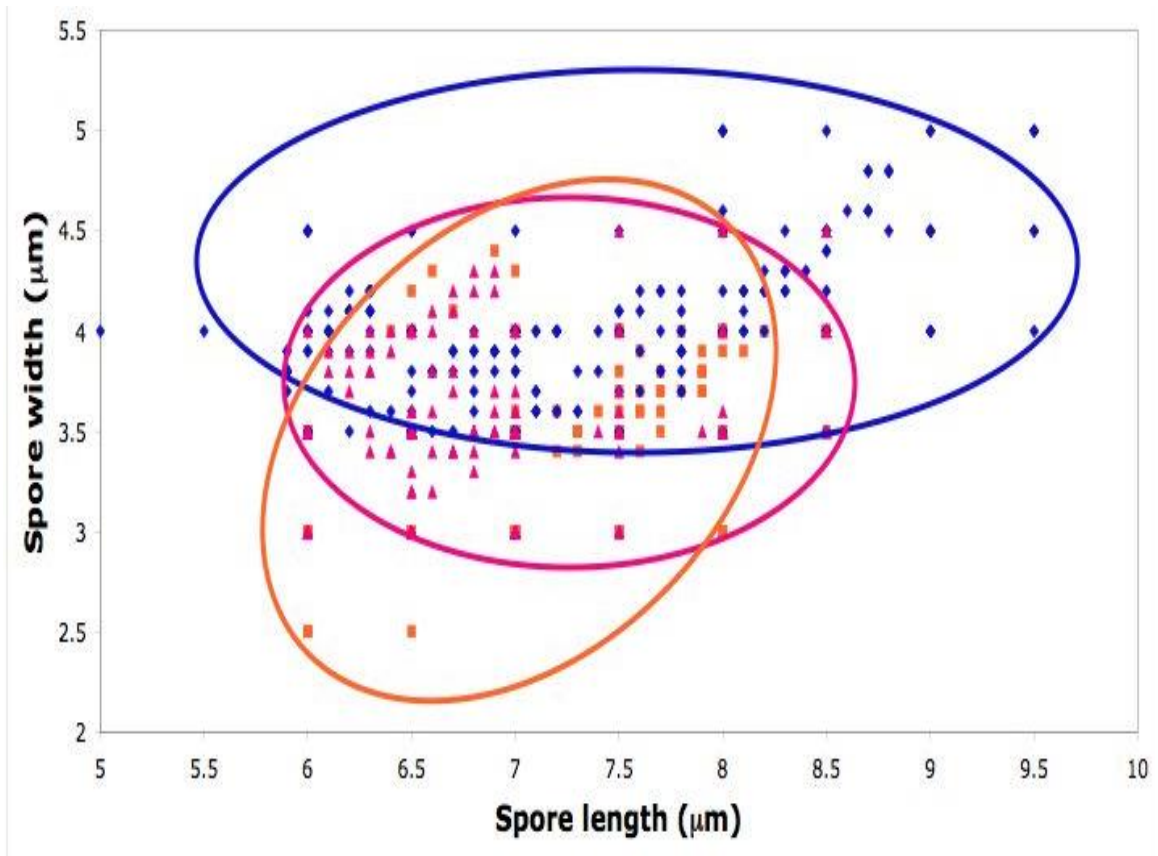
Figure 3.1 Spore distribution graph showing the length and width (in μm) of spores of all collections of *Resupinatus conspersus* (orange squares, n = 204 spores), *Porotheleum cinereum* (blue diamonds, n = 261 spores) and *Tapesia daedalea* (pink triangles, n = 324 spores) found in herbarium loans. Orange, blue and pink outlines contain data points that represent 95% of the spore distribution data for each species. These spore size distributions, while overlapping, correspond to different species based on geographical distribution.

3.3.2   *Resupinatus poriaeformis* and *Resupinatus urceolatus*

The phylogenetic analysis of these two species is presented in Chapter 2, Figure 2.1, and Chapter 4, Figure 4.3. Some collections from both Europe and North America have a thin, wispy subiculum and would be named *R. urceolatus,* and other collections have a dense subiculum and would be named *R. poriaeformis* (following Donk, 1962 and Thorn et al., 2005), but these are not resolved as separate by spore size (Figures 3.2 and 3.3) nor sequence analyses (Chapter 2, Figure 2.1; Chapter 4, Figure 4.3). Instead, molecular analyses distinguish the sequences of North American and European cultures or collections as well-supported clades. Since subiculum density cannot be used to distinguish these taxa, and since both *R. urceolatus* and *R. poriaeformis* are synonyms, the North American clade requires a new name.
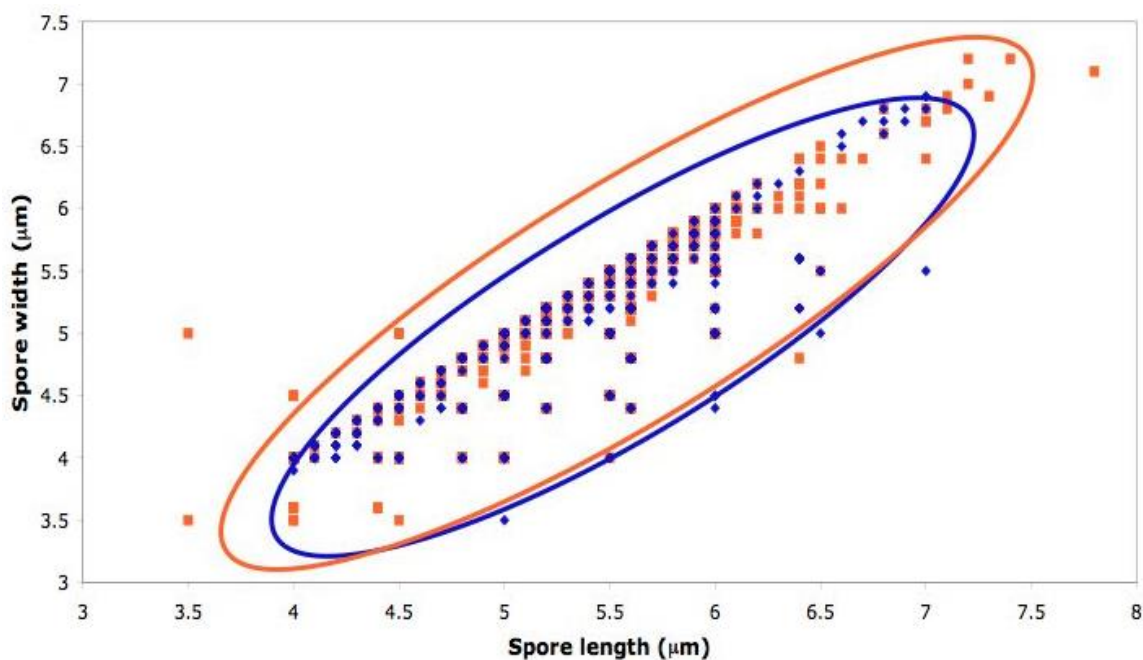
Figure 3.2 Spore distribution graph showing the length and width (in μm) of spores of all collections of *Resupinatus poriaeformis* (orange squares, n = 1528 spores) and *Resupinatus urceolatus* (blue diamonds, n = 1461 spores) from herbarium loans defined by thickness and density of subiculum. Orange and blue outlines represent 95% of the spore distribution data for each species. Species were defined on the basis of thickness and density of the subiculum; thick and dense in *R. poriaeformis* and thin and wispy in *R. urceolatus*.

Since subiculum density does not define species, all collections were plotted based on geographic location of the collection. To determine if geographic distribution correlates with spore size, spore width was plotted against spore length by continent of origin. The result of this analysis can be seen in Figure 3.3.
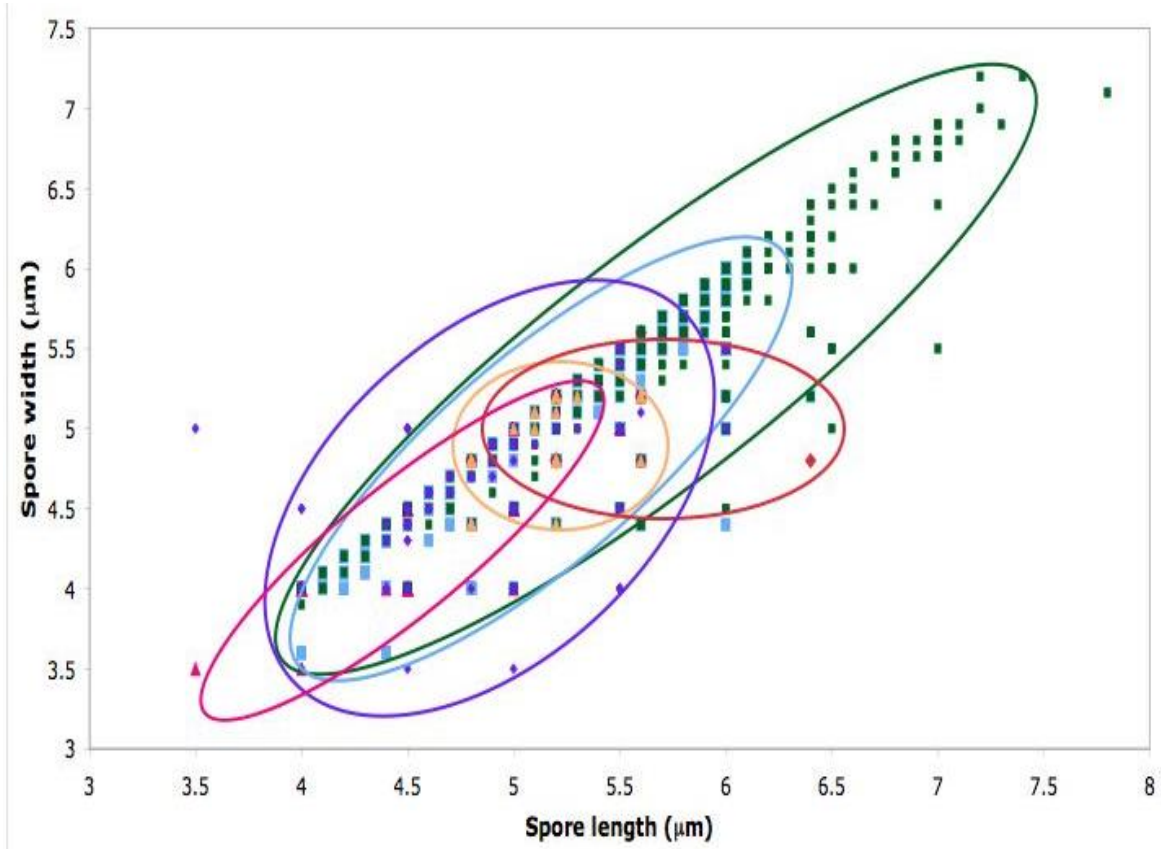
Figure 3.3 Spore distribution graph showing the length and width (in μm) of spores of all collections of the *Resupinatus poriaeformis/Resupinatus urceolatus* species complex based on herbarium collection location. Collections from Europe (green squares, n = 1742 spores) represent the most broad distribution of spore size, followed by North America (blue squares, n = 911 spores), Australia (purple diamonds, n = 254 spores), South America (pink triangles, n = 66 spores), Central America (red diamonds, n = 34 spores of a single collection), and "Other" (cream triangles, n = 43 spores of two collections). The distribution of spores is strongly dependent on the number of collections. Outlines represent 95% (Europe in green, South America in pink, the Australian continent in purple, North America in blue, and "Other" in cream) or 100% (Central America in red) of the spore distribution data for all collections from that continent.

The results of all of the morphological analyses suggest that determination of species membership based on morphology is not possible for these two species, but that purely a geographic approach may be taken. *Resupinatus poriaeformis* and *R. urceolatus* are synonyms and, since both species were "sanctioned" by Fries (1823 and 1828), the name that must be applied to all of these collections is *Resupinatus poriaeformis* as its basionym was published first (McNeill et al., 2012, Art. 13.1(d) and 15). North American collections requiring a new name are referred to as *Resupinatus poriaeformis* in molecular analyses (see Chapter 2 and Chapter 4), but are referred to as North American cyphelloid *Resupinatus* in section 3.4 (Taxonomy) below. Further analyses using molecular data need to be performed to determine if Central American, South American, Australasian, and other collections (Sri Lanka and the Canary Islands) represent either of these species or require their own species name.

3.4   Taxonomy

3.4.1   *Resupinatus conspersus, Porotheleum cinereum* and *Tapesia daedalea*

Resupinatus conspersus (Pers.: Fr.) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo, Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006.

≡ *Thelebolus hirsutus* DC, in Lam. & DC., Fl. franc. 2: 272. 1805.

≡ *Peziza conspersa* Pers., Myc. eur. (Erlanga) 1: 271. 1822.

≡ *Peziza conspersa* Pers.: Fr., Syst. Mycol. II: 108. 1823.

≡ *Tapesia conspersa* (Pers.: Fr.) Sacc., Syll. fung. (Abellini) 8: 379. 1889.

≡ *Stigmatolemma conspersum* (Pers.: Fr.) Donk, Persoonia 2(3): 339. 1962.

= *Solenia grisella* Quél., Bull. Soc. bot. Fr. 24: 329. 1878. (according to Donk, 1962)

    ≡ *Henningsomyces grisellus* (Quél.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 483. 1898.

    ≡ *Cyphella grisella* (Quél.) Bourdot & Galzin, Hyménomyc. de France (Sceaux): 163. 1928.

Fruit Bodies: hemispherical cups 0.2-0.4 mm across, densely packed in groups of 10-150 on a common stroma (subiculum) which is raised at the edges, becoming tomentose, dark grey to black, 3-10 mm across. When dry, fruit bodies are dark grey with dense

white surface hairs, hymenium dark (almost black) and smooth. Upon rehydration, fruit bodies a dark grey, surface hairs becoming hyaline. Subhymenium dark brown in KOH, hymenium hyaline. Hyphae strongly gelatinized in outer trama, incrusting brown pigment, 2.0-4.0 μm in diameter. Hyphae of inner trama running parallel to hymenium, slightly gelatinized, 1.0-3.0 μm in diameter. All hyphae smooth, thin-walled (monomitic), with clamps and are branching. Hyphae on the cup surface incrusted with fine crystals, hyaline, branching.

Basidia: 4-spored, clavate, hyaline to brown in KOH, 21-24(-25) x (4.5-)5.0-6.0 μm.

Cystidia: none seen.

Spores: hyaline, inamyloid, smooth-walled, angular, oblong or cylindric-elliptic, 6.0-8.0 x (2.5-)2.7-3.5(-4.0) μm.

Substrate ecology: on bark and rotting wood of coniferous trees (*Abies*).

Distribution: Czech Republic, France, Switzerland

Specimens examined: BPI (258346), K (166163), PC (0084526, 0084528, 0084529, 0084530), PRM (690529, 709534, 869189, 902024).

Comments and observations: *Resupinatus conspersus* is very rarely seen, due to its habitat. It grows high up in trees, making it difficult to spot. It is inconspicuous, indistinguishable to the naked eye from lichens that also grow on *Abies* spp. (see Figure 3.5). It is easiest to find on recently felled trees (Breitenbach & Kranzlin, 1986). It can easily be distinguished from *Porotheleum cinereum* due to its habitat and substrate, *P. cinereum* being a tropical species growing on hardwood trees.

The name *Resupinatus conspersus* has been misapplied many times in the past. First, the species was described by de Candolle (in Lamarck & de Candolle, 1805) after he received material from Chaillet. The description was not very detailed, but de Candolle stated that the cups were globe-shaped bodies opening at the top with pores that were seated in a common membrane (de Lamarck & de Candolle, 1805). From this pore

escaped spores (which de Candolle called seeds). Persoon was the one to recognize that the "pores" were the openings of the cups and that each cup was an individual fruit body, and renamed the species *Peziza conspersa* (Persoon, 1822). Fries was the next to describe the fungus, which he did in more detail, and described a fungus very similar to *Resupinatus poriaeformis* (which he did not know at the time; Fries, 1822). *Resupinatus conspersus* was also distributed by Fuckel as *Solenia porioides*, but *S. porioides* is a synonym of *Porotheleum fimbriatum*, an unrelated and morphologically distinct species.

I attempted to sequence material from a collection in the Prague herbarium (PRM 869189) on *Abies* from Switzerland. Unfortunately, the sequence generated from this collection was unusual and not very useful: there was a clean read for only about 60 base pairs, then the sequence trace disappeared for the rest of the ITS region for the forward read (using ITS1 as a sequencing primer), and had zero signal strength for all but the last 60 base pairs using the reverse read (using LS1R as a sequencing primer). These 60 base pairs put the collection in the *Resupinateae*, most closely related to the European *Resupinatus applicatus* collections (96% identity based on BLAST results), but 60 base pairs is not enough to build an alignment or construct a reliable tree. For this reason, this sequence was omitted from all analyses. Further efforts have been made to produce a cleaner sequence for this collection, but so far have not yielded any results. Despite this, the transfer of this species into *Resupinatus* by Thorn et al. (2005) is supported by morphological and phylogenetic data in this study.
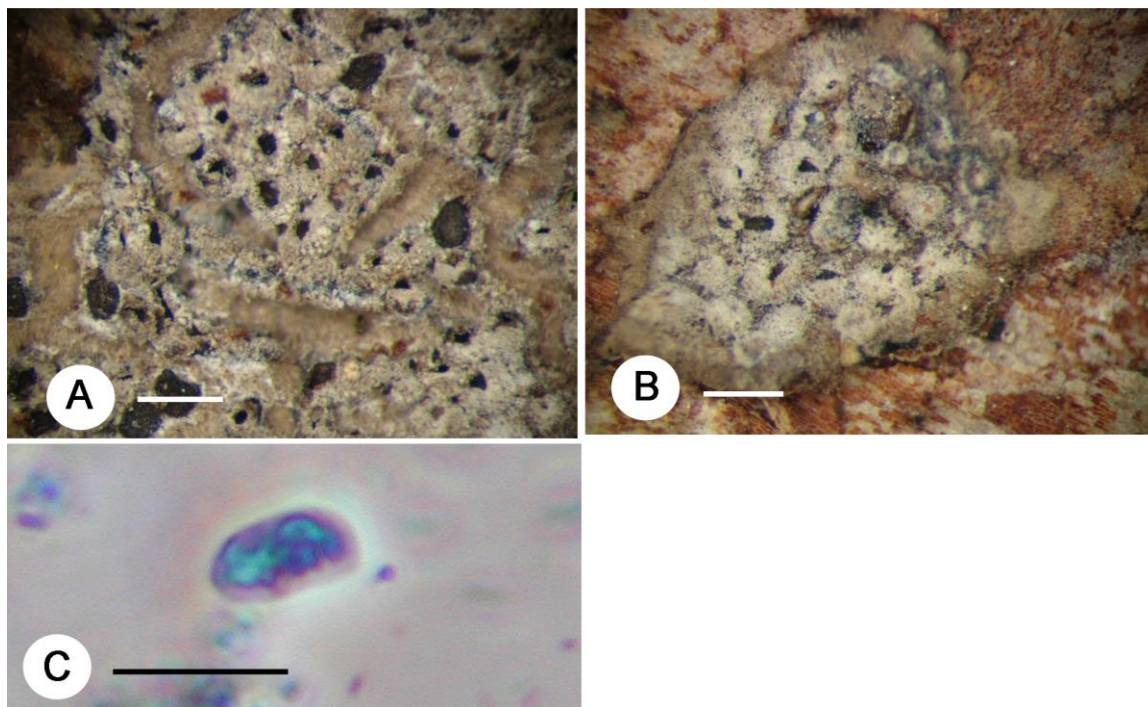
Figure 3.4 *Resupinatus conspersus*. A. Fruit body macromorphology from a collection with mature cups on *Abies* bark (Bar = 1.0 mm; BPI 258346). B. Fruit body macromorphology from a collection with less mature cups on *Abies* (Bar = 0.5 mm; K 166163). C. Basidiospore (Bar = 10 μm; PC 0084530).

Porotheleum cinereum Pat., Bull. Soc. mycol. Fr. 9: 130. 1893.

Fruit bodies: cupulate, densely packed in groups of 50-150 cups, black-brown to nearly blackened, 150-250 μm in diameter, seated in a thick and dense white to light grey subiculum, curling upwards and becoming detached from the substrate near the edges. Fruit bodies up to 5 cm in length, 2-3 cm wide. Cups covered in white (hyaline, inamyloid) diverticulate surface hairs with crystal encrustations, up to 150 μm long and 3-5 μm across, finger-like projections 2-4 μm long. Pileal trama composed of gelatinized hyaline hyphae 1.5-3.5 μm in diameter, thin-walled, loosely woven. Hymenial trama composed of gelatinized dark brown hyphae, more densely packed, 2-3.5 μm in diameter, thin-walled. Hymenium smooth, appearing nearly black macroscopically but composed of hyaline to clear-brown tightly packed basidia and basidioles. Some basidioles

appearing elongated and smaller in diameter than others, could be sterile cells separating the maturing basidioles (most noted near the margin of the cup).

Basidia: 4-spored, clavate, hyaline to brown in KOH, (25-)26-30 x (6.5-)7.5-8.5 μm.

Cystidia: none seen, but surface hairs become shorter and more densely packed near the margin of each cup.

Spores: hyaline, inamyloid, smooth-walled, oblong, (5.0-)6.0-8.0(-9.5) x (3.2-)3.5-4.5(-5.0) μm. Most spores are curved in the middle, giving the spore a slight "jelly bean" shape.

Substrate ecology: on rotting wood and bark of unidentified deciduous trees in tropical or sub-tropical areas.

Distribution: Brazil, Colombia, Dominica, Ecuador, El Salvador, Guadeloupe, Panama, Venezuela.

Holotype: FH 258745 (!); collected at Cratère de Pululahua in Ecuador in March 1892 by G. de Lagerheim.

Specimens examined: BPI (258368), FH (258746), ISC (371973), NYBG (886, 3591, 4454, 5149, 5183, 6332, 414548, 414549).

Comments and observations: this species differs from *Resupinatus conspersus* by substrate (deciduous trees for this species versus coniferous trees with *R. conspersus*) and distribution (tropical and sub-tropical areas for this species versus European mountainous regions for *R. conspersus*). One sequence deposited in Genbank as *Resupinatus conspersus* was from material collected on rotting logs in Ecuador (Bodensteiner et al., 2004); based on its distribution it is named *P. cinereum* in this thesis (Figures 2.1 and 4.3). Unfortunately, the collection associated with this sequence was not available for study, and so it could not be analyzed morphologically for this study.

Porotheleum cinereum is much more common than previously thought (at the outset of this study it was only known from two collections in FH, one in BPI, and one in ISC, all

collected prior to 1900). Based on collections in the New York Botanical Gardens herbarium, this species is commonly misidentified as *Porotheleum poriaeforme* or identified simply as "*Porotheleum* sp." or "*Cyphella* sp.", after expeditions to the tropics to document fungal diversity. It is presumed that if such a modern undertaking were to occur, this species would be commonly found today in the rainforest habitat that remains.

Porotheleum cinereum was placed in synonymy with *Porotheleum poriaeforme* by W.B. Cooke, as his concept of this latter species was exceptionally broad (Cooke, 1957). However, based on the morphological characteristics of this species, combined with the phylogenetic analysis of ribosomal DNA sequences, this species is distinct and belongs in the *Resupinateae*, where it is the closest relative of *Stromatocyphella conglobata*, and requires a new combination in the genus *Resupinatus*.
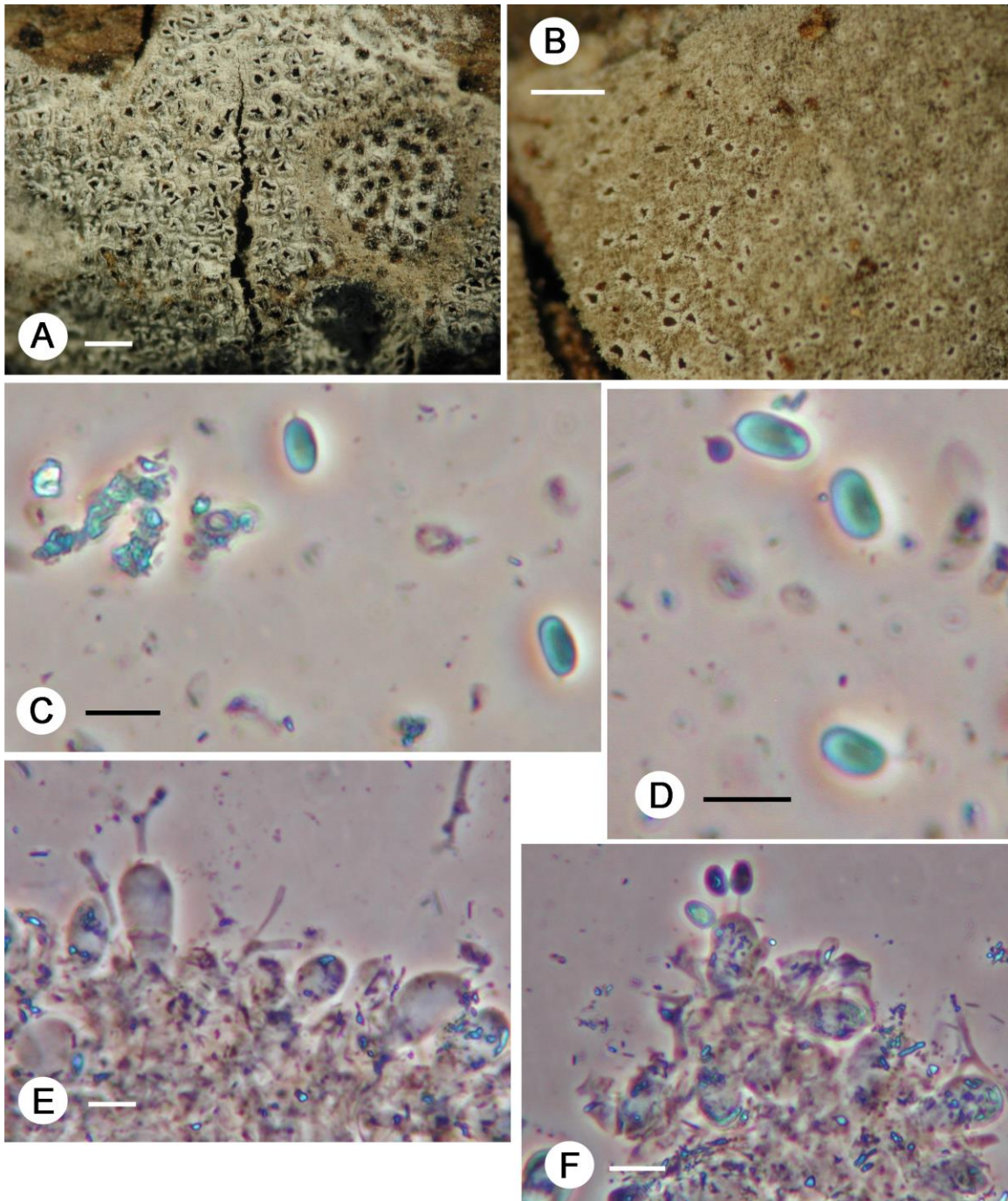
Figure 3.5 *Porotheleum cinereum*. A. Fruit body macromorphology of older cups, with the subiculum rolling up at the edge and encrusted surface hairs losing their crystal coating with age (Bar = 1.0 mm; NYBG 886). B. Fruit body macromorphology of young cups, showing cup colour darkens with age (Bar = 1.0 mm; NYBG 886). C. Basidiospores and a fragment of a surface hair with crystal encrustation (Bar = 10 μm; NYBG 886). D. Basidiospores with apiculus clearly visible (Bar = 10 μm; NYBG 886). E. Hymenium with immature basidia, one starting to produce spores at far right (Bar = 10 μm; NYBG 886). F. Basidium and mature basidiospores (Bar = 10 μm ; NYBG 886).

Tapesia daedalea (Schwein.) Sacc., Syll. fung. (Abellini) 8: 379. 1889.

≡ *Peziza daedalea* Schwein., Trans. Am. phil. Soc., Ser. 2 4(2): 174. 1832

= *Peziza tela* Berk. & Curt., in Berkeley, Grevillea 3(no. 28): 156. 1875.

      ≡ *Tapesia tela* (Berk. & Curt.) Sacc., Syll. fung. (Abellini) 8: 373. 1889.

      ≡ *Cyphella tela* (Berk. & Curt.) Massee, J. Linn. Soc., Bot. 35: 117. 1901.

Fruit bodies: cups gregarious, in groups of 15-60, blackened, 150-200 μm in diameter, margin incurved when fresh and when dry, pileus covered with hyaline diverticulate surface hairs up to 75 μm long. Subiculum pure white, very thick and dense, effused, occupying patches on the substrate approximately 1.5 x 0.5 cm, curling upwards towards the edges of fruitifications. Pileal trama gelatinized, composed of hyaline hyphae 1.5-4 μm in diameter that are loosely packed. Hymenial trama gelatinized, dark brown, hyphae 1.5-4.5 μm in diameter, more densely packed than in pileal trama. Hymenium hyaline in KOH, slightly brownish in Melzer's, made up of basidia and basidioles. All hyphae with clamps and branching from clamps.

Basidia: 4-spored, clavate, hyaline to brown in KOH, (14-)17-24(-25) x (4.5-)5.0-6.0(-6.5) μm

Cystidia: diverticulate cystidia present around the outer rim of the fruit bodies, hyaline, with clamp connections, 16-25 x 3.5-5.0 μm.

Spores: hyaline, inamyloid, smooth-walled, oblong, (6.0-)6.3-8.0(-8.5) x 3.0-4.5 μm.

Substrate ecology: on bark or rotting wood of dicotyledonous deciduous trees in warm-temperate eastern North America, observed on *Acer, Magnolia, Monis, Quercus, Tecoma*, and the rotting wood of various other unidentified tree species.

Distribution: United States (AL, IA, NJ, SC, VA).

Type: FH 258739 (!); "*in cortice ramulorum,*" Fungi Carolinae Exsiccati Ravenel; no date, collector or location information on collection packet

Specimens examined: BPI (258317, 258323), FH (258741, 258742, 258744, 258752, 258759, 258760), K (166164 [holotype of *Cyphella tela*]), NYBG (853, 2317(2)b), PH (1074202, 1074203)

Observations: *Tapesia daedalea* was originally believed to be a new species in the *Resupinateae*, discovered in herbarium collections from North America. It is nearly identical in all respects to both *Resupinatus conspersus* and *Porotheleum cinereum* (see above for a complete discussion and description of these species) with the exception of the substrate and geographic distribution. The species is found on the rotting wood of deciduous trees, and is found exclusively in the southeastern United States. At first glance it appears to be rare, but many older specimens were incorrectly named; for instance, Ellis and Everhart distributed this species in their exsiccati as *Solenia poriaeformis*. More effort should be put into collecting cyphelloid fungi in the southeastern United States in order to to rediscover this species (the most recent collection of this species was made in 1889) so that a proper phylogenetic analysis using molecular data can be performed. Based on morphological evidence gathered in this study, this species belongs in the *Resupinateae*, and could be considered the North American counterpart of *Resupinatus conspersus*.

It is possible that this species is a synonym of *Porotheleum cinereum* (and that this species is much more widely distributed than first thought), but until a sequence is generated of this species they are not treated as synonyms. One notable difference between *Porotheleum cinereum* and *Tapesia daedalea* is the texture of the substrate: the wood on which *Porotheleum cinereum* is found is always too decomposed to determine species identity (even to genus), whereas *Tapesia daedalea* is found on substrates with much less decomposition and the substrate can often be identified to the genus level.
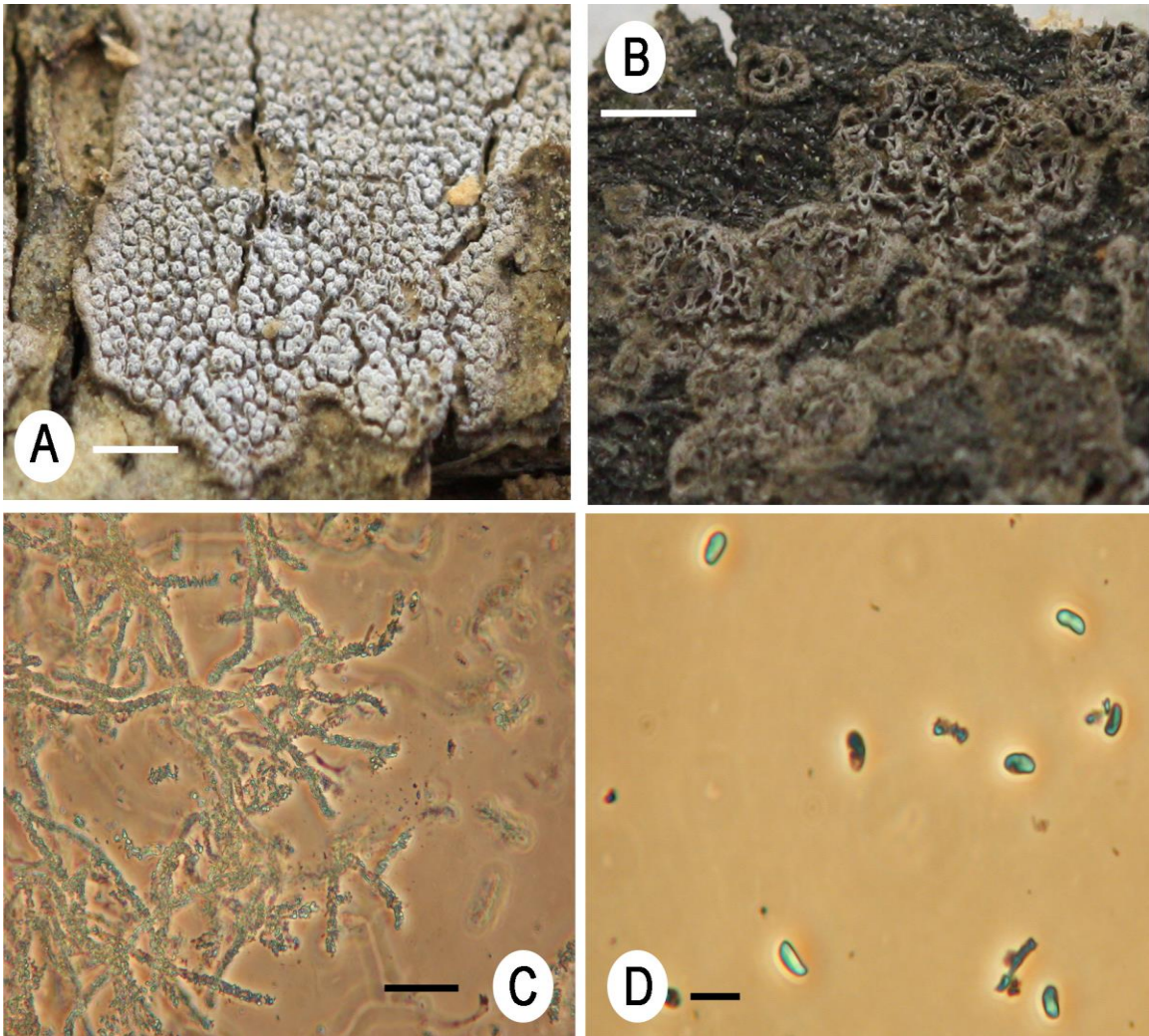
Figure 3.6 *Tapesia daedalea*. A. Macromorphology of young fruit bodies (Bar = 1.5 mm; BPI 258323). B. Macromorphology of old fruit bodies (Bar = 1.5 mm; BPI 258317). C. Crystal-encrusted surface hairs (Bar = 20 μm; FH 258742). D. Basidiospores (Bar = 10 μm; FH 258744).

3.4.2 *Resupinatus poriaeformis, Resupinatus urceolatus* and North American cyphelloid *Resupinatus*

Resupinatus poriaeformis (Pers.: Fr.) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo, Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006.

≡ *Peziza anomala ? poriaeformis* Pers., Syn. meth. fung. (Gottingen) 2: 656. 1801.

≡ *Peziza poriaeformis* (Pers.) DC, in Lam. & DC., Fl. franc., Edn 3 (Paris) 2: 36. 1805.

≡ *Peziza poriaeformis* (Pers.: Fr.) Fr., Syst. Mycol. II: 106. 1823.

≡ *Tapesia poriaeformis* (Pers.: Fr.) Fuckel, Jb. nassau. Ver. Naturk. 23-24: 301. 1870.

≡ *Solenia poriaeformis* (Pers.: Fr.) Fuckel, Jb. nassau. Ver. Naturk. 27-28: 290. 1874.

≡ *Henningsomyces poriaeformis* (Pers.: Fr.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 483. 1898.

≡ *Cyphella poriaeformis* (Pers.: Fr.) Bourdot & Galzin, Hymenomyc. de France (Sceaux): 163. 1927.

≡ *Stigmatolemma poriaeforme* (Pers.: Fr.) W.B. Cooke, Beih. Sydowia 4: 128. 1961.

≡ *Stromatoscypha poriaeformis* (Pers.: Fr.) G. Cunn., Bull. N.Z. Dept. Sci. Industr. Res., Pl. Dis. Div. 145: 305. 1963.

= *Solenia tephrosia* Pers., Myc. Euro. Erl.: 271. 1822.

= *Solenia urceolata* Wallr. ex Fr., Elench. fung. (Greifswald) 2: 28. 1828. (this study)

   ≡ *Henningsomyces urceolatus* (Wallr. ex Fr.) O.K., Rev. Gen. Pl. 3(2): 483. 1898.

   ≡ *Solenia poriaeformis* var. *urceolatus* (Wallr. ex Fr.) Pilát in Ann. mycol., Berl. 23: 168. 1925.

   ≡ *Cyphella urceolata* (Wallr. ex Fr.) Bourd. & Galz., Hym. France 162. 1928.

   ≡ *Stigmatolemma urceolatum* (Wallr. ex Fr.) Donk, Persoonia 2(3): 341. 1962.

   ≡ *Resupinatus urceolatus* (Wallr. ex Fr.) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo, Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006.

= *Peziza aleuritica* Wallr., Fl. crypt. Germ. 2: 488. 1833. (according to Donk, 1962)

= *Cyphella brunnea* W. Phillips, Grevillea 13(no. 66): 49. 1884. (according to Donk, 1962)

   ≡ *Chaetocypha brunnea* (W. Phillips) Kuntze, Revis. gen. pl. (Leipzig) 2: 847. 1891.

=? *Porotheleum reticulatum* Petch, Ann. R. bot. Gdns Peradeniya 7(4): 289. 1922. (this study; see "Observations", below)

Fruit Bodies: cupulate or goblet-shaped, 150-280 μm in diameter, crowded in groups of 30 to 1000s of cups on a common subiculum. Subiculum thick and dense, or absent or nearly absent, creamy-white. Cups tan to dark brown or grey, covered in hyaline diverticulate or irregularly warted surface hairs up to 75 μm long, heavily encrusted with hyaline or pale brown crystals. Pileal trama hyaline to subhyaline (appearing faintly brown or yellow-brown in thick cross-sections in Melzer's), strongly gelatinized, composed of loosely woven hyphae 2.5-4.5 μm in diameter. Hymenial trama dark brown, also gelatinized but less conspicuous than in the pileal trama, composed of more densely

packed hyphae 3-5 mm in diameter. Macroscopically, hymenium darker or the same colour as the exterior of the cup (medium to dark brown), smooth; microscopically hyaline, composed of tightly packed basidia and basidioles.

Basidia: 4-spored, clavate, hyaline to faintly brown in KOH, (14-)18-20(-25) x (4.5-)5.5-6.8(-7.5) µm

Cystidia: present along the margin of the cup; diverticulate, hyaline, (11-)13-18 x 3.0-5.0 µm.

Spores: hyaline, inamyloid, smooth-walled, globose to subglobose, often with a prominent apiculus, (4.0-)4.5-5.8(-6.0) x (4.0-)4.3-5.7(-6.0) µm

Substrate ecology: on rotting wood of dicot trees in Europe; rarely on bark and on standing trunks; one instance on the bark of a dicotyledonous vine. Observed from *Acer, Betula, Carpinus, Clematis, Corylus, Fagus, Fraxinus, Populus, Quercus, Salix,* and *Tilia*

Distribution: Czech Republic, France, Germany, Great Britain (England, Wales), Norway, Slovakia, Sweden

Specimens Examined: BPI (258320, 323716, 323719, 323720), FH (258762, 258764, 258768), K (13501, 23193, 31487, 57502, 62514, 77430, 88532, 91345, 113838, 129953), L (0796996, 0796997, 0796998), NYBG (4, 43, 56, 57, 78, 1930), O (64265, 65566, 65603, 65625, 91124, 100001, 100044, 146746, 146747, 146751, 146752), PRM (171919, 171920, 171921, 171922, 171923, 171924, 171928, 497463, 497464, 497465, 497466, 618452, 714999, 843392, 845243, 848090, 882505, 882507, 894656), STR (F.x. 197 [although indicated as type material of *R. urceolatus*, the holotype if it exists would be at S], P.656, 3 collections with no accession numbers)

Observations: *Resupinatus poriaeformis* and *R. urceolatus* have been synonymized by some authors (e.g. Cooke, 1961) and separated by others (e.g. Donk, 1959; Thorn et al., 2005) based on the morphology of the subiculum: thick and dense in *R. poriaeformis* versus thin and wispy in *R. urceolatus*. Based on the results of this study, this comparison is inappropriate in the light of a molecular analysis, as collections with thin and wispy

subicula and thick and dense subicula are present in the same clade in both the LSU-only and the ITS/LSU combination trees (see Figure 2.1 and Figure 4.3). However, two distinct clades can be separated based on geography: European collections carrying the name *Resupinatus poriaeformis*, and North American collections that require a new name (discussed in the next species description, "North American cyphelloid *Resupinatus*"). Collections of morphologically indistinguishable cyphelloid *Resupinatus* have been found in Australia and New Zealand (see Chapter 4), the Canary Islands (Chapter 5), Brazil (Chapter 5), Panama (Chapter 5), Mayotte (Chapter 5), and Sri Lanka (Chapter 5, as *Porotheleum reticulatum*) but they are not discussed here.
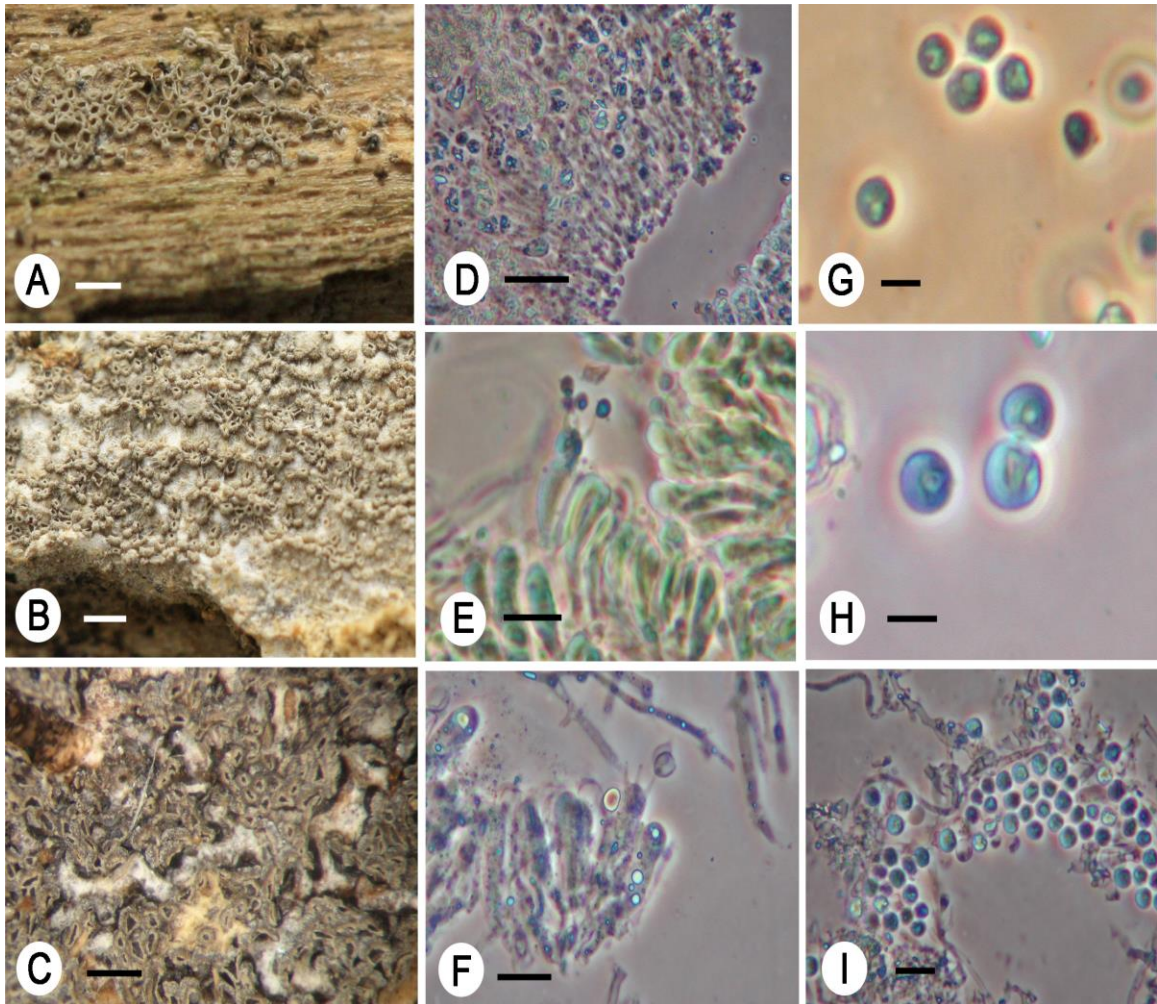
Figure 3.7 *Resupinatus poriaeformis*. A. Mature fruit bodies on a substrate with a thin, wispy subiculum (Bar = 1.0 mm; K 77430). B. Mature fruit bodies on a substrate with a dense, thick subiculum (Bar = 1.0 mm; K 31487). C. Old, decaying fruit bodies on a substrate with a dense, thick subiculum (Bar = 1.0 mm; PRM 497465). D. Branching cystidia found along the rim of the cup of each fruit body (Bar = 20 μm; K 31487). E. Basidium with immature basidiospores (Bar = 10 μm; K 23193). F. Basidium with mature basidiospores (Bar = 10 μm; K 113838). G. Basidiospores (Bar = 5 μm; PRM 497465). H. Basidiospores of the type collection of *Resupinatus urceolatus* (Bar = 5 μm; STR F.x. 197). I. Basidiospores of a particularly fertile collection (Bar = 10 μm; K 23193).

North American cyphelloid *Resupinatus*

Fruit Bodies: cupulate, large compared to other species in the group (up to 1.5 mm across; most 300-600 μm), sessile, dark grey to dark brown, farinose on exterior, margin inrolled when dry. Subiculum thick and dense, or absent or nearly absent, few hyphae strongly crystal-encrusted with thousands of cuboid hyaline crystals, grey. Surface hairs hyaline, nearly impossible to measure and distinguish due to presence of crystals but appearing diverticulate and 20-45 μm long. Trama composed of slightly gelatinized hyphae 1.5-3.5 mm in diameter, branching from clamps, loosely woven and becoming more densely packed nearer to hymenium. Hymenium brown to grey-brown, hyaline in cross-section, composed of tightly packed basidia and basidioles. Subhymenium brown in cross-section, slightly gelatinized, composed of tightly packed hyphae 2-4 μm in diameter.

Basidia: 4-spored, clavate, hyaline in KOH or slightly yellow-brown (clear-brown in Melzer's), 22-30 x 5.0-7.0 μm.

Cystidia: present along the margin of the cup; diverticulate, hyaline, (11-)13-18 x 3.0-5.0 μm.

Spores: hyaline, inamyloid, smooth-walled, globose to subglobose, (4.4-)4.8-5.5(-6.4) x (4.0-)4.4-5.2(-5.6) μm

Substrate ecology: on rotting wood of deciduous trees in North America. On *Acer, Platanus, Populus, Quercus, Salix,* and *Tilia*

Distribution: Canada (BC, ON), United States (DE, IA, LA, MA, ME, MI, MN, MO, MT, NJ, NY, PA, VA, WI)

Specimens examined: BPI (257860, 257861, 257996, 258314, 258315, 258316, 258318, 258319, 258321, 258322, 258324, 258325, 258326, 258369, 258370, 323717, 323718, 323721), FH (258753, 258754, 258755, 258756, 258758, 258760b, 258769c, 258765, 258767), L (0796999), NYBG (36, 37, 67, 204(1), 204(2), 364, 636, 872, 2317(1), 2317(2)a, 2317(2)b, 2317(3), 2317(4), 3172, 4958, 13778, 24721, 30140, 292116), RGT080820/01 and RGT100622/01 (UWO).

Observations: North American cyphelloid *Resupinatus* requires a new name but is very closely related (both based on morphology and based on phylogenetic analysis) to the previous species, *Resupinatus poriaeformis*. It is restricted to North America in distribution. This may be a sampling artifact, as very little effort has been made to collect this species recently, which contributes to a lack of sequence data. A more intensive sampling effort in both Europe and North America (as well as on other continents) might show that the distribution of the species is more cosmopolitan, or that there might even be more than one species present in North America. This trend is repeated in the *Resupinateae*, and is often seen general in the mycological literature (for example, Frohlich & Hyde, 1999; Taylor, 2002; Whitcomb & Stutz, 2007; Buee et al., 2009).

North American cyphelloid *Resupinatus* displays culture characters consistent with the ability to trap nematodes (hyphal pegs with adhesive droplets on vegetative hyphae; Thorn & Barron, 1986), however this characteristic was not observed in this study. Hyphal pegs have never been shown to be in contact with nematodes, unlike the adhesive pegs of known nematode-trapping species (Drechsler, 1950; Barron, 1975; Barron, 1977; Friman, 1993), or initiate hyphal growth after contact with a passing nematode, unlike the microdroplets of *Pleurotus ostreatus* (Thorn & Barron, 1984; Barron & Thorn, 1987; Barron, 2003).
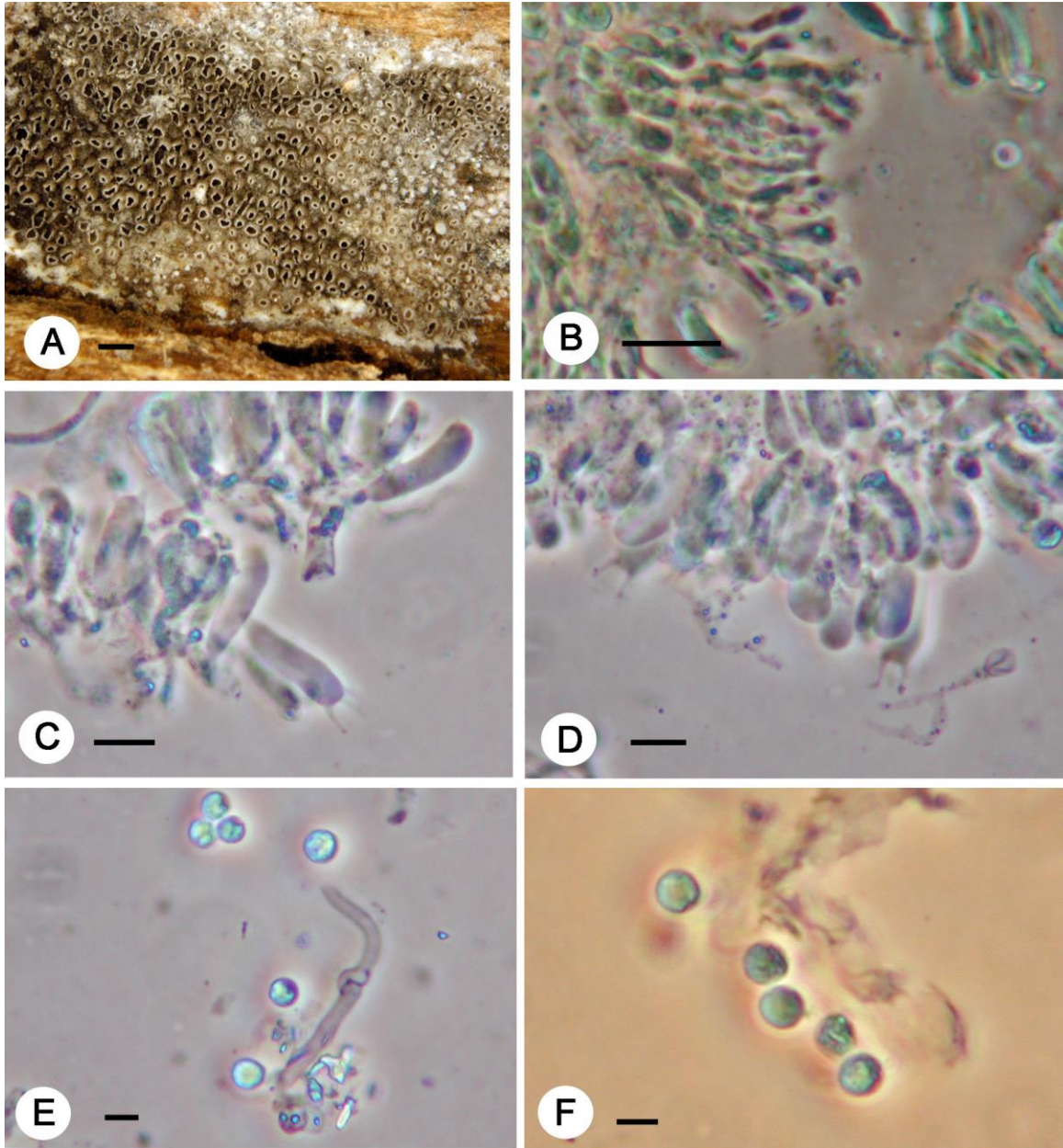
Figure 3.8 North American cyphelloid *Resupinatus*. A. Fresh fruit bodies, taken the day of collection (Bar = 1.0 mm; RGT080820/01). B. Cystidia found around the edge of the cup that are functionally equivalent to cheilocystidia in gilled *Resupinateae* (Bar = 20 μm; NYBG 24721). C. A mature basidium with three sterigma visible (Bar = 10 μm; BPI 258314). D. Two mature basidia and one cystidium with a branching projection (Bar = 10 μm; BPI 258315). E. Basidiospores and a fragmented surface hair with crystal encrustations (Bar = 5 μm; BPI 258325). F. Basidiospores (Bar = 5 μm; FH 258758).

3.5   Discussion

Based on the collections observed throughout this study of *Resupinatus conspersus*, *Porotheleum cinereum*, *Tapesia daedalea, Resupinatus poriaeformis,* and a North American cyphelloid *Resupinatus* (which requires a new name), no generalizations can be made about the patterns of species distribution in the *Resupinateae*. Morphologically identical species such as *Resupinatus poriaeformis* and the North American cyphelloid *Resupinatus* are not genetically identical and, based on a small sample size, can be distinguished based on geographic location. Other species, such as *Resupinatus conspersus* and *Porotheleum cinereum*, are not necessarily distinguished based on geography, but rather based on substrate.

The species illustrated in this chapter have traditionally been underrepresented in collection records in herbaria due to two factors: a lack of collection effort (fungi with small fruit bodies are difficult to find unless one is specifically looking for them) and a lack of effort in proper identification of herbarium collections. With the exception of North American cyphelloid *Resupinatus* (called either *Resupinatus poriaeformis* or *R. urceolatus* in herbarium collections, as well as previous taxonomic combinations of both of these species), none of these species were represented in more than five herbarium collections prior to this study. After examining many misidentified and "underidentified" (collections identified to the genus level only, and only based on superficial characters not a thorough morphological analysis) herbarium collections, it is clear that these species are far more common than originally believed. With a renewed effort to collect them based on information gathered from previous herbarium collections (time of year collected, collection location, substrate, etc.), it is likely that they will be found increasingly frequently.

Host or substrate specificity in the *Resupinateae* can be seen in some species but not others. In this study the distinction was made between *Resupinatus conspersus* and *Porotheleum cinereum* based on host: the first occurs only on *Abies*, while the second can be found across a wide variety of hardwood species (and never on gymnosperms). For other species, there is no discernable pattern of substrate specificity between morphologically identical species: *Resupinatus poriaeformis* and North American

cyphelloid *Resupinatus* are both found on diverse hardwood species (both on *Quercus* and *Salix*, for example).

Morphological characters used to delineate species in the *Resupinateae* have been shown here to be useful in some cases (spore size and shape, for example, used in combination with cup size, shape and colour) while others are indicative of some unknown external factor and are not diagnostic for the species. The subiculum characters, for example density and thickness, traditionally used to delimit *Resupinatus poriaeformis* and *Reuspinatus urceolatus* do not hold up to molecular analyses. Instead, subiculum thickness and density are likely reflective of weather conditions (dry conditions perhaps resulting in a thicker, denser subiculum to protect against desiccation). More work needs to be done in this area to determine if weather conditions play a role in the development of morphological traits in different species of *Resupinatus*.

3.6   References

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Chapter 4

4 The *Resupinateae* of Australia and New Zealand

This chapter examines the species of *Resupinateae* from Australia and New Zealand, including those already known as well as new species discovered through DNA and microscopic analysis of herbarium samples.

4.1 Introduction

Fungi of Australia and New Zealand were first collected by botanical explorers in the 18th and 19th centuries and were sent back to experts in Britain for description. Local efforts to collect and describe them were led predominantly by Sir John Burton Cleland (1878-1971) in the early 20th century (Cleland, 1918, 1919a, 1919b, 1923, 1924, 1927, 1928, 1931). Unfortunately, most publications by Cleland contained information only about the superficial characteristics of fruit bodies along with spore sizes, which is not enough information to distinguish species in the *Resupinateae* or many other fungal groups (Wood, 1986). Since Cleland, the five most important mycologists who have contributed to the knowledge of Australian *Resupinateae* are G.H. Cunningham (the cyphelloid species), and G. Stevenson, E. Horak, B.P. Segedin, and C.A. Grgurinovic (the lamellate species).

Gordon Herriot Cunningham (1892-1962) was the very first mycologist and plant pathologist in New Zealand. He established the New Zealand Fungal Herbarium and is regarded as the father of New Zealand mycology (Dingley, 2013). He was well known for his meticulous drawings and very detailed species descriptions, which illustrate the differences in different layers of the fruit bodies, something many other mycologists failed to do at the time (Cunningham, 1963). Unfortunately, he did not make any connections between the cyphelloid species he was describing (*Resupinatus huia* and *Resupinatus poriaeformis*, both at the time classified in *Stromatoscypha*) and lamellate species described in Australia and New Zealand with similar micromorphology, or with works such as Singer's *Agaricales in Modern Taxonomy* (1951; 1962) that might have allowed him to place his new cyphelloids in their correct context.

Greta Stevenson (1911-1990) published a series of five monographs of the *Agaricales* of New Zealand, of which the last monograph treated members of the *Resupinateae* (Stevenson, 1964). The genus *Resupinatus* covered six species and was separated into two sections; Section A contained species with smooth spores, and Section B contained species with rough spores; cyphelloid relatives were not considered (Stephenson, 1964). The other five species are now treated in various genera: the smooth-spored species in Section A are *Resupinatus purpureo-olivaceus* (now in *Pleurotus*; Segedin et al., 1995), *Resupinatus crawfordii* (now in *Panellus*; Segedin et al., 1995), *Resupinatus tristis* (transferred first to *Marasmiellus*, now in *Campanella*; Horak, 1971; Segedin, 1993), and the rough-spored species in Section B are *Resupinatus dorotheae* (now in *Delicatula*; Horak, 1971) and *Resupinatus sordulentus* (now known as *Conchomyces bursiformis*; Horak, 1981). As a result only her *Resupinatus violaceogriseus* (a smooth-spored species from Section A) is included in this study.

Egon Horak (1937-) is a retired mycologist and former curator of the Herbarium of the Swiss Federal Institute who specialized in the mushroom-forming fungi. He named and described over 1,000 species from 30 countries, with emphasis on species originating from South America and Australasia (Landcare Research, 2014). He regularly made trips to New Zealand for mushroom collection, and has deposited 164 types and over 570 collections in the Landcare Research Herbarium in Auckland (PDD; Landcare Research, 2014). In all publications discussing the *Resupinateae*, Horak maintained that *Marasmiellus* has ovate spores while *Resupinatus* has spherical spores, which meant that he placed *Resupinatus violaceogriseus* in *Marasmiellus* (Horak, 1971).

Barbara P. Segedin (1923-2004) was a mycologist at the University of Auckland who studied the agarics of New Zealand. She described many new species, only one of which is treated in this study: *Campanella* (now *Resupinatus*) *vinosolividus* (Segedin, 1993).

Cheryl Grgurinovic (1953-) revisited Cleland's monographs of the Fungi of Australia which culminated in the publication of the text *The Larger Fungi of Australia* (Grgurinovic, 1997). This included two species of *Resupinatus* and contained drawings of microscopic characters of each of the 96 new species she described in the book, as well

as nearly 100 drawings and water-colours by notable Australian female artists who painted and drew mushrooms for J.B. Cleland (Ratkowsky, 1998). Her species descriptions are much more detailed than Cleland's, and many of his species were placed in modern genera. Grgurinovic, like Cleland and Cunningham before her, did not make the connection between cyphelloid and lamellate species in the *Resupinateae*.

Collections of *Resupinateae* from Australia and New Zealand are well represented in herbaria in these countries and around the world. This provides an excellent basis from which to examine the phylogenetic relationships within the group, especially between cyphelloid and lamellate members. This chapter will examine the molecular and morphological relationships between previously described species in *Stigmatolemma* and *Resupinatus*, as well as providing the descriptions of four new species of fungi discovered in herbarium collections in Australia and New Zealand.

4.2 Materials and Methods

4.2.1 Herbarium samples

Dried specimens of the *Resupinateae* and candidates that might belong to that group were requested for microscopic study through letters sent by the late Dr. Jane Bowles (UWO Herbarium) to herbaria around the world (AD, CANB, DAR, HO, MEL, PDD; herbarium acronyms following Holmgren et al., 1990, updated at http://sciweb.nybg.org/science2/IndexHerbariorum.asp). When there was sufficient material (and collections were 40 years old or less), a request was also sent for DNA analysis. Herbarium collections were then analyzed for taxonomic characters (see section 4.2.2 Herbarium collection analysis) and, when possible, DNA was extracted (see section 4.2.4 DNA extraction and amplification).

4.2.2 Herbarium collection analysis

All species of the *Resupinateae* possess many taxonomic characters that are useful in identification. Among the most important characters for use in identification are the colour, size and shape of the fruit body; the colour, shape (including ornamentation) and size of surface hairs; the presence, colour and thickness of a gelatinous layer in a vertical

section of the fruit body tissues; basidiospore shape, size and ornamentation; the size and shape of basidia and the presence, shape and size of any other characteristic cells in the hymenium such as cheilocystidia, pleurocystidia, or metuloids.

Notes and measurements were taken of dried collections for fruit body size (in μm), colour and shape; location of attachment to the substrate; presence and distribution of surface hairs; and presence or absence of a subiculum or subiculum-like structure. Small portions of fruit bodies of dried collections were rehydrated, and changes in colour of the fruit body and surface hairs were noted (often, fruit bodies are much darker in colour with surface hairs more visible when dry than when fresh). Photographs of the dried collections and rehydrated portions were taken, then the rehydrated portions of the fruit body were sectioned by hand using a razor blade and squash-mounted on a microscope slide.

Two mounts were made on each microscope slide, in different mountants to emphasize different microscopic characters (Melzer's reagent for spore, surface hair, and hyphal characteristics, and KOH for basidia and cystidia characteristics; Largent, 1977). Basidiospore, basidium, cystidia and surface hair measurements are represented as a range, with values in parentheses representing the smallest and largest values, and the size range representing values between the tenth and ninetieth percentiles (as per Thorn and Barron, 1986). Other measurements (for example the diameter of hyphae, or the length and width of sterigmata) are represented as a range of values, the smallest and largest observed. A full description of microscopic methods can be found in Chapter 2, section 2.2.2.

4.2.3   Media and cultures

Cultures were obtained from the ICMP culture collection in New Zealand and were maintained in 60 mm Petri dishes of Malt Extract Agar (MEA, 12.5 g malt extract and 15 g agar per liter distilled water; Nobles 1965) and Potato Dextrose Agar (PDA, EMD Chemicals, Inc.). Liquid cultures for DNA extraction were made in malt extract broth (5 g malt extract per liter distilled water). These cultures were allowed to grow to produce

enough biomass for harvesting for DNA extraction (see section 4.2.4 DNA extraction and amplification).

4.2.4   DNA extraction and amplification

DNA was extracted from dried herbarium collections and fresh collections in the same way. Portions of the fruit body were placed on a microscope slide and rehydrated in sterile distilled water. Once the small portions were rehydrated, they were finely chopped using a sterilized razor blade. Fifty milligrams of tissue was put into a micro-bead tube from the PowerLyzer UltraClean Microbial DNA Isolation Kit (MO BIO Laboratories, Carlsbad, California), and processed according to the manufacturer's protocol. DNA was extracted from liquid cultures using the same kit with the following modifications. Mycelium was removed from liquid medium, excess media removed and 50 mg transferred into the micro-bead tube. DNA extracts were quantified using a Nanodrop 2000 Spectrophotometer (Thermo Scientific, Wilmington, Delaware) and kept at 4 °C (overnight) or at -20 °C (for extended periods).

The DNA extract was amplified using a PCR protocol in a Biometra T1 Thermocycler (Montreal Biotech) according to Koziak et al. (2007) and the fungal primers ITS1 (5'—TCCGTAGGTGAACCTGCGG—3'; White et al., 1990) and LR5 (5'—ATCCTGAGGGAAACTTC—3'; Vilgalys and Hester, 1990). This primer pair amplifies ribosomal DNA from the 3' end of the small ribosomal subunit (SSU) through the ITS1, 5.8S, ITS2, and the 5' end of the large ribosomal subunit (LSU; including the D1/D2 variable domains). Presence or absence of a PCR product was determined using gel electrophoresis in a 1.5% Agar gel made with TAE electrophoresis buffer containing 0.5 μg/mL ethidium bromide.

Once the presence of the desired size of PCR product was confirmed, the PCR products were cleaned using the QIAquick PCR purification kit (Qiagen, Mississauga, Ontario) or the BioBasic PCR purification kit (Bio Basic Canada Inc., Markham, Ontario). Each DNA extract was amplified in four PCR reactions of 30 μL to ensure a large amount of PCR product was obtained, and these four PCR tubes were pooled into one cleaned PCR

product. The cleaned PCR product was quantified on the Nanodrop 2000 machine and sent for sequencing.

4.2.5   Sequencing of PCR products

Cleaned PCR products were sent for sequencing at the Robarts Research Insitute at Western University using sequencing primers ITS1, LS1 (5'—ACTACCCGCTGAACTTAAG—3'; Hausner et al., 1993) and LR3R (5'—GTCTTGAAACACGGACC—3'; Vilgalys and Hester, 1990) on the coding strand and LR5, LR3 (5'—GGTCCGTGTTTCAAGAC—3'; Vilgalys and Hester, 1990) and LS1R (5'—CTTAAGTTCAGCGGGTA—3'; Hausner et al., 1993) on the complementary strand. Once all six regions were sequenced, the sequences were cleaned and assembled in SeqEd v1.03 (Applied Biosystems Software, Foster City, California) for phylogenetic analysis.

4.2.6   Phylogenetic analysis

The sequences generated in this study were aligned with those already available in GenBank (see Appendix B for a full list of sequences used throughout this thesis) using MEGA5 v5.05 or MEGA6 v6.01 for Mac (Tamura et al., 2011 & 2013). When applicable, alignments were edited to improve the alignment. Species of *Calyptella* and *Hemimycena* were chosen to root the tree, as per Thorn et al. (2005). The ingroup used to construct the tree consisted of 45 sequences of 25 different taxa, resulting in an alignment of 1875 characters. The dataset was trimmed to 1213 characters so all sequences were of the same length in the alignment, and the resulting alignment file was exported for further analysis.

Phylogenetic analyses according to maximum likelihood methods were performed in MEGA5/6. Node support was assessed using bootstrapping, with 1000 replicates. The tree was generated using the combined dataset of ITS and LSU sequences and is presented in Figure 4.3.

4.3 Results

4.3.1 Herbarium Collections and Microscopy

A total of 109 collections representing 16 species of Australian and New Zealand *Resupinateae* were obtained from seven herbaria. Of these, 13 species (47 collections) proved to be exclusively Australasian *Resupinateae* and are reported on here. The remaining 62 collections represent one species hypothesized to be new to science (the Australian equivalent of *Resupinatus poriaeformis*, restricted to Europe, and the unnamed North American cyphelloid *Resupinatus*, both of which are discussed in Chapter 3), two species of lamellate *Resupinatus* that are known from other parts of the world, discussed briefly here and in more detail in Chapter 5, and two species that are not in the *Resupinateae* and are treated in more detail in Chapter 6.

To determine species circumscription, spore sizes were plotted on graphs to generate a visual representation of the distribution of the length and width of all of the spores measured per species. Spores of species that are otherwise morphologically similar were plotted on together (e.g., Figure 4.1). *Resupinatus huia* was originally collected in New Zealand (specifically, Huia and hence the name) and is morphologically very similar to the type of *Stigmatolemma*, *Resupinatus incanus* from South Africa. A spore scatter plot was made to compare the spore size ranges for both of these species to determine if this would be useful in species identification. It was determined for *Resupinatus huia* that there was sufficient overlap with spores of the older, morphologically similar species *R. incanus* that these two taxa cannot be distinguished on spore size alone. Unfortunately, *Resupinatus incanus* has not been collected recently, so a sequence-based analysis is not possible between these species.
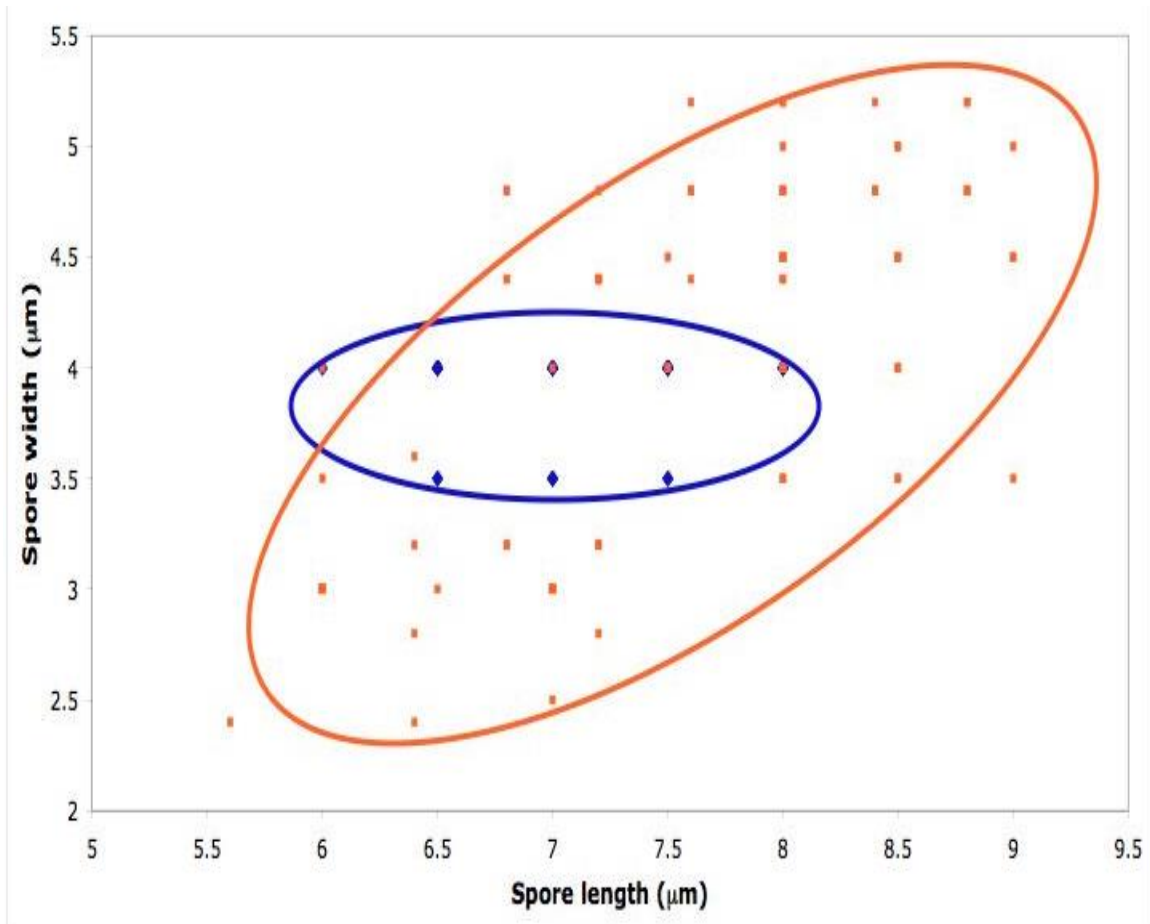
Figure 4.1 Spore distribution graph showing the difference in size and shape of
***Resupinatus incanus* and *Resupinatus huia* spores.** The length and width (in μm) of
spores of all collections identified as *R. incanus* (blue diamonds, n = 34 spores) and *R.
huia* (orange squares, n = 102 spores). Ellipses contain the data points that represent 95%
of the spore distribution data for *R. huia* (orange outline) and 100% of the spore
distribution data for *R. incanus* (blue outline). Since the blue ellipse is found within the
larger orange one, it is impossible to determine if these taxa are separate species based on
spore morphology, and other morphological characteristics are too similar to distinguish
them.

There has been confusion between *Resupinatus applicatus* and *R. subapplicatus* (Cleland, 1927; Grgurinovic, 1997; Cooper, 2012b). Specimens to which the name *Resupinatus subapplicatus* has been applied recently (Grgurinovic, 1997; Cooper, 2012b) represent a potentially distinct species with elliptical spores (see "Notable Collections", below), whereas the type specimen of *R. subapplicatus* has subglobose to globose spores. Six collections from AD-C reported in Grgurinovic (1997) have elliptical spores, but this was not observed when the six specimens were obtained for analysis: two of the six collections had globose to subglobose spores with a dense mat of black hairs at the point of attachment and so are treated as *Resupinatus trichotis* (AD-C 10962 and 10964), three were morphologically identical to the type of *Resupinatus subapplicatus* with globose to subglobose spores and a light covering of white surface hairs (and so are treated as this species in this study; AD-C 10961, 10963 and 10965), and the did have truly ovate to elliptical spores (AD-C 10960, treated below as a notable collection allied to *R. cinerascens*). Molecular data (Figure 4.3) indicate that there are three species within the globose-spored group: *Resupinatus applicatus* 4, *R. applicatus* 5, and *R. subapplicatus* (for more discussion of these taxa, see below under Taxonomy).

Resupinatus cinerascens and *Resupinatus violaceogriseus* share similar morphologies and recently Cooper (2012b) suggested that until they are found to be different species, they should be treated as synonyms. Using spore size and shape, it appears that they are indeed separate species (Figure 4.2); this difference is supported by molecular data (Figure 4.3). Two collections, named *R. cinerascens* or *R. violaceogriseus,* do not fit within these boundaries (red outlines in Figure 4.2); unfortunately, both collections were too old with too little material to obtain sequence data.

See below, section 4.4 "Taxonomy", for a full discussion of the species represented in this study.
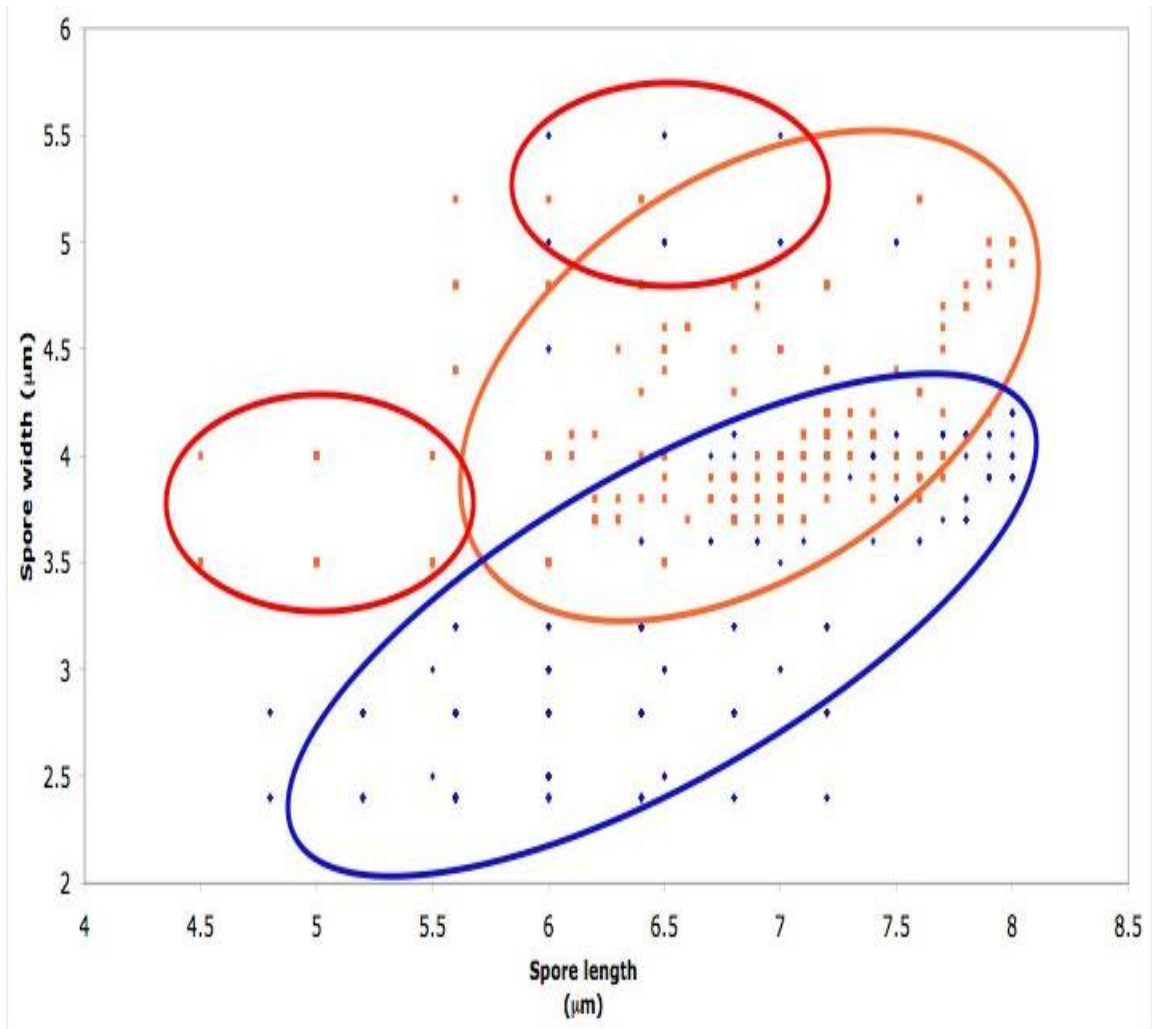
Figure 4.2 Spore distribution graph of *Resupinatus cinerascens* and *Resupinatus violaceogriseus*. The length and width (in μm) of spores of all collections identified as *R. cinerascens* (orange squares, n = 319 spores) and *R. violaceogriseus* (blue diamonds, n = 464 spores)*,* surrounded by outlines that contain 90% of the spore data for each species, and red ellipses represent single collections that are outliers. The lower left red ellipse is Australian lamellate *Resupinatus* 2, while the other red ellipse is a collection misidentified as *Resupinatus violaceogriseus* and should instead be referred to as *R. cinerascens*.

4.3.2   Sequence Data

The molecular dataset of the ingroup of this study consisted of 45 sequences representing 25 taxa. The outgroup was selected based on Thorn et al. (2005).The data presented here in Figure 4.3 are a combination of the ITS and LSU datasets in a Maximum Likelihood analysis, with bootstrap support above 70% indicated above the nodes. For a full list of sequences used in this study, refer to Appendix B.

Of the 25 taxa represented, eight are represented exclusively by collections from Australia and/or New Zealand: "Australian cyphelloid *Resupinatus*," *Resupinatus applicatus* 4, *Resupinatus subapplicatus*, *Resupinatus applicatus* 5, Australian lamellate *Resupinatus* 1, *Resupinatus cinerascens*, *Resupinatus violaceogriseus* 1, and *Resupinatus violaceogriseus* 2. Of these species, *Resupinatus applicatus* 4 and 5 are morphologically identical, as well as morphologically identical to *Resupinatus subapplicatus* (see Taxonomy, below, for the difference between *Resupinatus subapplicatus* and *R. applicatus*). Only a small fragment of *Resupinatus applicatus* 5 was received from Dr. Neal Bougher (E 9139) and was nearly completely used for molecular analysis, but a very small fragment, insufficient for a full morphological analysis, was left over and was enough to determine spore size and shape. *Resupinatus applicatus* 4 was not observed by me, but morphological data presented in J.A. Cooper's "Mycological Notes 7" (2012) coincide with what was found for Australian, European and North American *Resupinatus applicatus* collections. In order to determine if there are indeed morphological differences between these three species (*R. applicatus* 4 and 5, and *R. subapplicatus*), a more thorough morphological analysis needs to be performed.

Resupinatus violaceogriseus is also represented by a species complex of two sister species. Based on morphological analysis done in this study (for sample PDD 87379), by J.A. Cooper (for sample HQ533014 [PDD 95788]; Cooper, 2012), and by R.H. Petersen (for sample TENN 2674; pers. comm.), these two species are identical. A more thorough morphological analysis needs to be performed on these three samples to determine slight morphological differences, now that genetic differences are known. This study does confirm that this species is indeed a member of the *Resupinateae* and belongs in *Resupinatus*, not *Marasmiellus* as stated by Horak (1971).

Figure 4.3 rDNA ITS and LSU Maximum Likelihood tree showing the phylogeny of the *Resupinateae*. Bootstrap values (1000 replicates) are only shown if above 70%. Scientific names in bold font indicate that sequences were obtained from GenBank (represented by their GenBank accession number, species name, and strain information if known). Scientific names in regular font indicate that sequences were generated in this study from dry or fresh material (represented by strain number or herbarium accession number and species name resulting from a morphological analysis). Red lines in the ingroup designate sequences derived from taxa with cyphelloid fruit bodies (showing that the cyphelloid habit is multiply derived), and the blue line in the ingroup designates the sequence derived from the taxon with poroid fruit bodies. Sequences generated from taxa with green text are only known from sequence data (as indicated with bold font) or culture data (as indicated with regular font). As taxa were identified morphologically prior to the sequence analysis, when a single morphospecies is present multiple times in a tree the first number (i.e. *Resupinatus applicatus* 1) is assigned based on the sequence derived from the collection most representative of the type (same collection location, substrate of the type, or both) and the rest are numbered as they appear in the tree from top to bottom. Coloured arrows are for reference only between pages; arrows of the same colour join two lines together across pages (e.g. the red arrow down in the first panel connects the line with the red arrow up in the middle panel). Coloured boxes represent geographical information with respect to where the collection was made: red squares for North American collections, orange squares for South American collections, yellow squares for Asian collections, green squares for European collections, blue squares for Australian collections, and purple squares for collections from Central America and the Caribbean. One collection, TENN 8870, is known from the Caucasus Mountains (more specific information is not provided) which is widely regarded as one of the points where the European and Asian continents are divided. Thus, this collection is indicated with a square that is half yellow, half green.

RGT100622/01 NA cyphelloid *Resupinatus* ■
92 ⌐ T-244 NA cyphelloid *Resupinatus* ■
99 └─ RGT080820/01 NA cyphelloid *Resupinatus* ■
98 ⌐ O 65625 *Resupinatus poriaeformis* ■
└─ O 65603 *Resupinatus poriaeformis* ■
TENN 4102 *Resupinatus applicatus* 1 ■
98 ⌐ T-099 *Resupinatus applicatus* 1 ■
└─ TENN 2417 *Resupinatus applicatus* 1 ■
97 ⌐ AN 012974 *Rhodocyphella cupuliformis* ■
└─ ICMP 16593 Australian cyphelloid *Resupinatus* 1 ■
GQ142021 ***Resupinatus* sp. 1 (HMJAU 7036)** ■
T-236 *Resupinatus striatulus* ■
HQ533025 *Resupinatus applicatus* 4 (PDD 95777) ■
99 ⌐ TENN 4403 *Resupinatus applicatus* 2 ■
└─ **AY571059 *Resupinatus applicatus* 2 (PB 335)** ■
77 ⌐ E 8427 *Resupinatus subapplicatus* ■
76 ⌐ TENN 3547 *Resupinatus subapplicatus* ■
└─ PDD 87473 *Resupinatus subapplicatus* ■
DQ017063 *Resupinatus porosus* (PR 5832) ■
E 9139 *Resupinatus applicatus* 5 ■
99 ⌐ **GQ142022 *Resupinatus trichotis* (HMJAU 2150)** ■
91 ⌐ RGT100622/02 *Resupinatus applicatus* 3 ■
95 ⌐ Silver_Box *Resupinatus applicatus* 3 ■
└─ FP102486Sp *Resupinatus applicatus* 3 ■

4.4   Taxonomy

Resupinatus applicatus 4 and 5 (undescribed species)

≠ *Resupinatus applicatus* (Batsch: Fr.) Gray, Nat. Arr. Brit. Pl. (London) 1: 617. 1821.

For a full morphological description of this species complex, refer to Chapter 2, section 2.4 "Taxonomy". The information presented below pertains specifically to collections of *Resupinatus applicatus* 4 and 5 from Australia and New Zealand.

Substrate ecology: on rotting wood of hardwood trees, observed on *Kunzea, Nothofagus, Pseudowintera, Quercus, Ripogonum, Ulex,* and other unidentified species.

Distribution: Australia (mainland Australia, Tasmania and Norfolk Island), New Zealand

Specimens examined: AD-C (55542, 55544, 55546, 55846), CANB (574876, 574880, 574881, 742140, 742279), DAR (14206), MEL (261051, 2096593, 2231620, 2300677), PDD (70479, 79793, 86842, 86862, 87025, 87046, 87121, 87196, 87307, 87325); sequences are of the two taxa were derived from two collections not observed in this study (GenBank sequence of PDD 95777 and a small fragment of a fruit body from the personal collection of Neal Bougher, E9139).

Observations: Sequence data indicate that two different Australasian species in this morphological species complex are unrelated to each other. Based on morphological evidence, all these species are identical but DNA sequence data indicate otherwise (see Figure 4.3). These species differ from the other three species in the *Resupinatus applicatus* species complex by their geographic distribution; they are only found in Australia and New Zealand based on information gathered thus far. *Resupinatus applicatus* 1 is distributed in North America, *Resupinatus applicatus* 2 in North America and Europe, and *Resupinatus applicatus* 3 in North America. Based on a map of collection information of all collections identified as *Resupinatus applicatus* 4 or 5, or *Resupinatus subapplicatus* distinctions between species can be made based on either geography or substrate, but not both. *Resupinatus applicatus* 4 is represented by collections on various species of hardwoods and is only found in New Zealand.

Resupinatus applicatus 5 is represented by collections on various species of hardwoods and is only found in Australia. *Resupinatus subapplicatus* is only found on *Eucalyptus* (and one collection where the substrate is *Pseudopanax*), but is present in Australia and New Zealand. Five collections of the *Resupinatus applicatus* species complex are of undetermined membership: two from Norfolk Island, and three from Tasmania. These collections are presumed to be *Resupinatus applicatus* 5 until they (or more recent collections from the same locations on the same substrates) are sequenced. The geographic distribution of these three morphologically identical species can be seen in Figure 4.5 below.
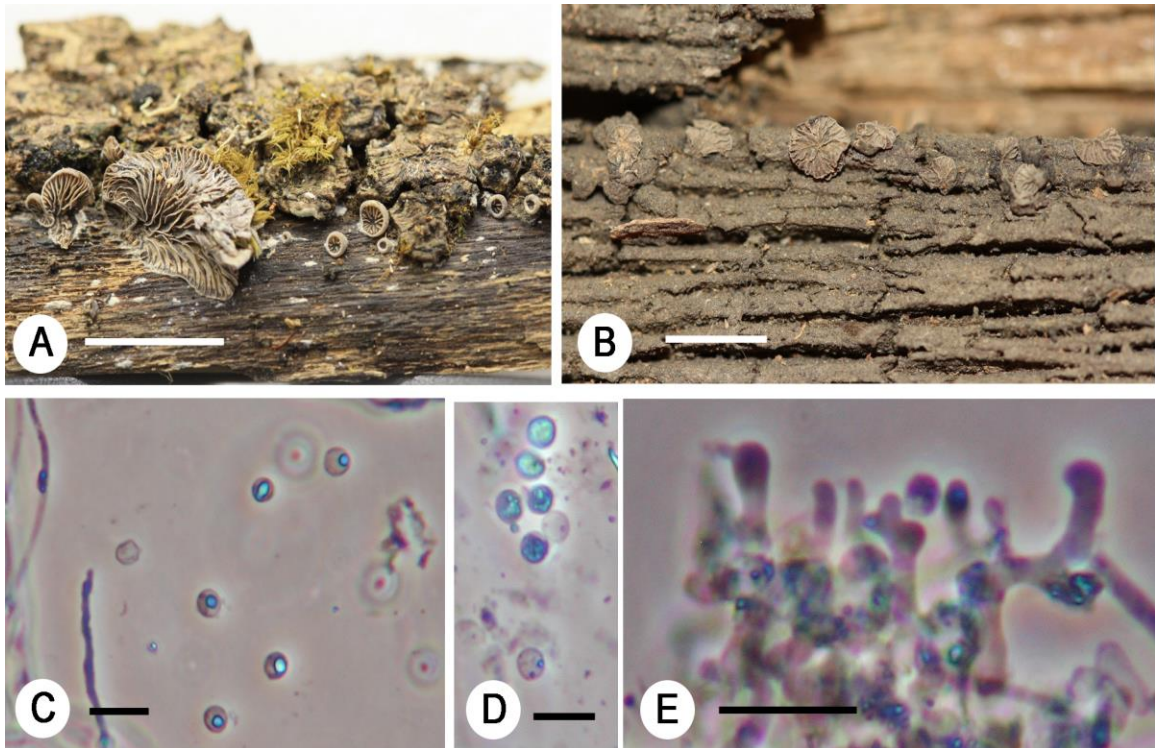
Figure 4.4 *Resupinatus applicatus* 4 and 5. A. Dried fruit bodies (MEL 2300677; Bar = 20 mm). B. Very small dried fruit bodies (DAR 14206; Bar = 10 mm). C. Basidiospores (MEL 2300677; Bar = 10 μm). D. Basidiospores (DAR 14206; Bar = 10 μm). E. Cheilocystidia (DAR 14206; Bar = 20 μm).

Figure 4.5 Map of the distribution of collections identified as *Resupinatus applicatus* 4 and 5, and *Resupinatus subapplicatus*. *Resupinatus subapplicatus* collections that have not been sequenced (black squares) and that have been sequenced (red squares) are found on both Australia and New Zealand but are restricted to *Eucalyptus* as a substrate. *Resupinatus applicatus* 4 (collections that have not been sequenced represented by black triangles, and the one collection that has been sequenced represented by a light blue triangle) is restricted to New Zealand, and *Resupinatus applicatus* 5 (collections that have not been sequenced represented by black circles, and the one collection that has been sequenced represented by a dark blue circle) is restricted to Australia. The three collections in Tasmania and the two on Norfolk Island are presumed to represent collections of *Resupinatus applicatus* 5 until molecular evidence suggests otherwise.

Resupinatus cinerascens (Cleland) Grgur., Larger Fungi of South Australia 47: 47. 1997.

≡ *Pleurotus cinerascens* Cleland in Trans. R. Soc. South Aust. 51: 301. 1927.

Fruit Bodies: up to 15 mm in diameter, cupulate or convex in shape, laterally attached at the apex. Fruit bodies are grayish black when fresh, drying darker (almost black), with dense hairs around the margin. Surface hairs much more dense and prominent when fruit bodies are young, with surface hairs creating a dense white mat on the surface of the cup. Lamellae radiating from a central point, close and numerous with many short lamellulae at the margin. Edge of lamellae appearing frosted by the presence of numerous cheilocystidia. Pileal surface containing cylindric hyphae, 1.6-5.5 μm in diameter with short projections and numerous encrusting crystals. Pileal flesh filamentous, hyphae smooth-walled, gelatinized, hyaline. Trama of the hymenophore filamentous, gelatinized, parallel to the surface of the hymenium. Clamp connections present on all hyphae.

Basidia: 4-spored, clavate, brownish in KOH, (22-)24-26 x (4.5-)5.0-6.0 μm.

Cystidia: abundant; 19-35.5 x 2.5-6 μm, with diverticulate branching.

Spores: hyaline, inamyloid, smooth-walled, ovate to elliptical, not oblong or cylindric, (5.8-)6.1-7.1(-7.5) x (3.5-)3.8-4.6(-5.0) μm

Substrate ecology: on rotting wood and bark of living deciduous and coniferous trees; one specimen on *Banksia* cone scales; also observed on *Eucalyptus,* and *Pinus*

Distribution: Australia, New Zealand

Holotype: AD 10959 (!); collected on *Eucalyptus viminalis* in Belair National Park, in South Australia, Australia in August 1927 by J.B. Cleland.

Specimens Examined: AD-C (51358, 51359, 53231, 54471, 55199, 55262), MEL (1053061, 2031421, 2031422, 2313581), PDD (80649), personal herbarium of N. Bougher (E8202, E8238)

Observations: *Resupinatus violaceogriseus* can be distinguished by having much larger fruit bodies (up to 25 mm across) tinged violet towards the margin and by its oblong to

cylindrical spores 5.6-7 x 2.6-2.8 μm (Figure 4.3). One notable collection of this species is on cones of *Banksia marginata* (*Proteaceae*). As far as collections of *Resupinateae* are concerned, no other specimens were collected on cones of any kind.
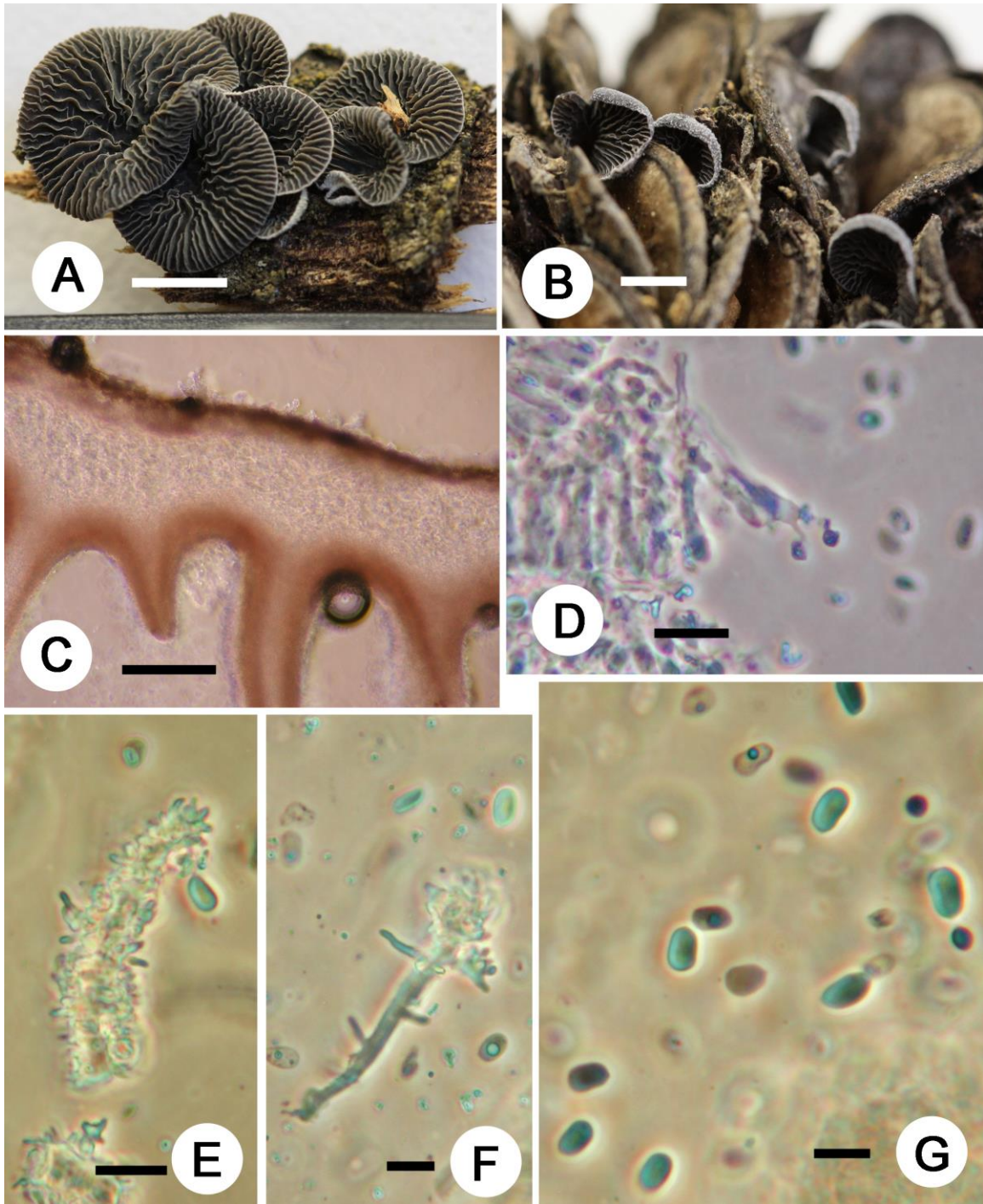
Figure 4.6 *Resupinatus cinerascens*. A. dried fruit bodies on rotting wood (bar = 20 mm; AD 51359); B. dried fruit bodies on *Banksia marginata* cones (bar = 1.0 cm; AD 55199); C. cross-section showing location of pigmentation in this species, with long, branching surface hairs visible at the top (bar = 350 mm; AD 55262); D. basidium with spores attached (bar = 15 mm; AD 53231); E. surface hair fragment and spore (bar = 20 mm; AD 54471); F. cheilocystidium that would have been located on the top gill edge (bar = 10 mm; AD 51359); G. spores (bar = 10 mm; AD 55262).

Resupinatus huia (G. Cunn.) Thorn, Moncalvo & Redhead, in Thorn Moncalvo, Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006.
≡ *Solenia huia* G. Cunn., Trans. Roy. Soc. N.Z. 81: 179. 1953.
≡ *Porotheleum huia* (G. Cunn.) W.B. Cooke, Mycologia 49(5): 691. 1957.
≡ *Stigmatolemma huia* (G. Cunn.) W.B. Cooke, Beih. Sydowia 4: 128. 1961.
≡ *Stromatoscypha huia* (G. Cunn.) G. Cunn., Bull. N.Z. Dept. Sci. Industr. Res., Pl. Dis. Div. 145: 305. 1963.

Fruit Bodies: cyphelloid, globose or depressed-globose, small (250-550 µm in diameter), aggregated in groups of up to 80 on a common white subiculum. Subiculum made of felty, white hyphae that are loosely attached to the substrate and densely packed, up to 160 µm thick. Cups in individual depressions in the subiculum, separated by a wall of dense, loosely-woven hyphae. Cups almost black when dry, covered in a dense mat of white hairs, becoming less distinct with age. When rehydrated, cups a dark brown-black (almost black) with surface hairs much less pronounced. Pileal surface containing cylindrical hyphae with short finger-like projections at the tips and encrusting crystals. Pileal flesh gelatinous, hyaline, hyphae with clamp connections. Hymenophoral trama gelatinous with hyphae running parallel to the hymenium, light yellow-brown to brown. Hymenium hyaline, composed of branching hyphae and a dense layer of basidia, basidioles, and paraphyses.

Basidia: 4-spored, clavate, hyaline in KOH, (19-)20.2-24(-25) x (6.0-)6.5-7.5(-8.0) µm

Cystidia: none observed.

Spores: hyaline, inamyloid, smooth-walled, oblong, (5.5-)6.2-8.6(-9.1) x (2.5-)3.0-5.0(-5.3) µm

Substrate ecology: on rotting wood of dicot trees; observed on *Leptospermum* and *Nothofagus*

Distribution: New Zealand

Holotype: PDD 4392 (!); collected on *Leptospermum ericoides* in Auckland, New Zealand in November 1945 by G.H. Cunningham.

Specimens Examined: BPI (257953), PDD (92596)

Observations*: Resupinatus huia* is strikingly similar to the type of the genus *Stigmatolemma*, *Stigmatolemma incanum* (see Chapter 2). Only the difference in collection location (South Africa versus New Zealand) distinguishes these species. Since there have been recent collections of this species in New Zealand but no recent collections of *Stigmatolemma incanum*, it is impossible to do a molecular comparison, although it is expected that they would be closely related.
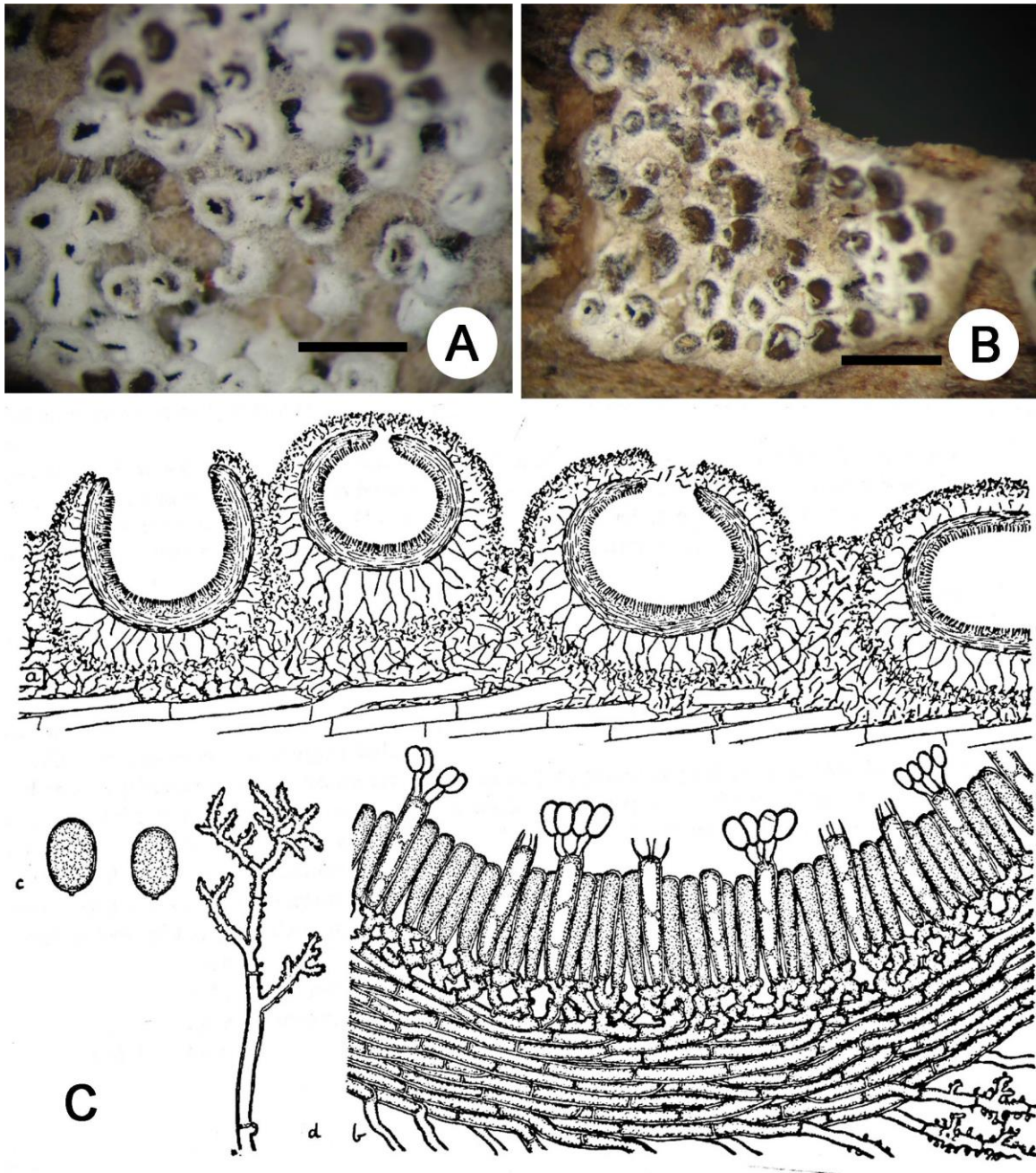
Figure 4.7 *Resupinatus huia*. A. Dried young fruit bodies, with a dense covering of surface hairs, with the creamy-white subiculum visible between cups (bar = 1.0 mm; BPI 257953). B. Dried older fruit bodies, showing the dense covering of surface hairs is lost with age (bar = 1.0 mm; BPI 257953). C. Drawings of this species by G.H. Cunningham, showing cross-sections of the fruit bodies (a), a magnified view of the hymenium showing basidia with spores attached and surface hair structure visible in the bottom right (b), spores (c), and the structure of some crystal encrusted branched hyphae on the cuticle of the fruit bodies (d) (Cunningham, 1963).

Resupinatus merulioides Redhead & Nagas., Can. J. Bot. 65(5): 973. 1987.

Fruit Bodies: pileus 2-19 mm in diameter, attached directly to the substrate via the back of the cap (lacking a stipe). Fruit bodies brownish-grey when fresh, appearing smooth on the pileus and slightly wrinkled (surface hairs only visible under the compound microscope when fresh). When dry, the surface hairs are much more easily visible as a white coating on the back of the cap, fruit bodies a darker grey-brown. With reticulated gills, primary gills radiating outwards from a central point and many gill-like connections between them, with some immature fruit bodies almost appearing poroid. Pileal trama gelatinized, hyaline, with loosely woven hyphae 2-5 μm in diameter. Hymenial trama similar to that of the pileus; hyphae gelatinized, 2-4.5 μm in diameter, hyaline to faintly brownish. Hymenial layer of loosely packed basidia and basidioles, brown, with cheilocystidia along the top surface of the lamellae. All hyphae with clamp connections.

Basidia: 4-spored, clavate, yellow-brown in KOH, 20-22(-35) x 4.5-5.5 μm

Cystidia: cheilocystidia along the top edge of the lamellae, usually only in mature fruit bodies (rarely seen in younger specimens). Clavate or cylindrical cells, 15-18 x 4.8-6.2 μm, with 1-2 finger-like projections at the apex (up to 15 μm long).

Spores: hyaline, inamyloid, smooth-walled, subglobose, (4.0-)4.4-5.6(-6.4) x (3.6-)4.0-4.8 μm

Substrate ecology: on fallen rotting wood of dicot trees, rarely lignified monocotyledons

Distribution: Australia, Japan, New Zealand.

Type: DAOM 187819 (not observed); collected in the Kanaya Hotel gardens near Lake Chuzenji in the Gumma prefecture, Honshu, Japan in August 1983 by J. Ginns.

Specimens Examined: CANB (9218803), PDD (89882)

Observations: *Resupinatus merulioides* has been collected once in New Zealand and once in Australia since its description in Japan. Morphologically similar species have been collected in other locales (for example, an unidentified fungus collected by Mr.

Pablo Sandoval in Chile, see Chapter 6), but these can be eliminated from the genus *Resupinatus* by their lack of a coralloid pileipellis with the characteristic surface hairs. Other morphologically similar species belong in *Campanella* and *Marasmiellus* (Redhead & Nagasawa, 1987).
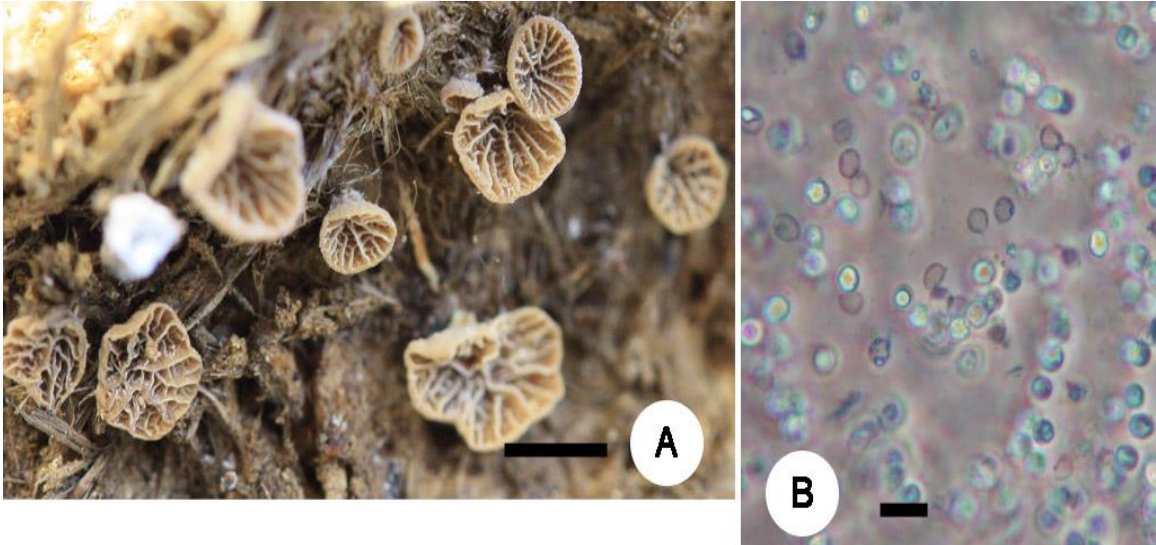
Figure 4.8 *Resupinatus merulioides*. A. Dried fruit bodies showing the reticulated gill network (bar = 15 mm; CANB 9218803). B. Spores (bar = 10 μm; CANB 9218803).

Resupinatus subapplicatus (Cleland) Grgur., Larger Fungi of South Australia 47: 47. 1997 (sensu Cleland non Grgurinovic).

≡ *Pleurotus subapplicatus* Cleland, Trans. Roy. Soc. South Australia 51: 301. 1927.

Fruit Bodies: pileus 6-16 mm in diameter, attached directly to the substrate (lacking a stipe). Grey to dark grey-black when fresh, with a tomentose covering when fresh. When dry, grey with a matted covering of surface hairs, becoming almost white near the point of attachment. Hyphae of pileal surface densely packed, with coralloid-diverticulate surface hairs, dark brown to grey, 12.5-25 x 2.5-5 μm. Pileal trama gelatinized, with filamentous hyphae 1.5-5.5 μm in diameter, hyaline. Hymenial trama gelatinized, hyphae running parallel to the hymenium, hyaline. Lamellae densely packed, radiating outwards from a central point, grey to grey-black with a frosting of cheilocystidia along the top edge. Hymenium composed of basidia and basidioles, hyaline to brown. All hyphae with clamp connections.

Basidia: 4-spored, clavate, yellow-brown in KOH, (16.5-)18-28(-30) x (4.5-)5.5-6.5(-7) μm

Cystidia: cheilocystidia along the edge of the lamellae, diverticulate, hyaline, 10-20 x 3-6 μm.

Spores: hyaline, inamyloid, smooth-walled, globose to subglobose, (4.5-)5-6(-6.2) x (4.4-)4.8-5.9 μm

Substrate ecology: on rotting wood of dicot trees; on *Eucalyptus* and *Pseudopanax.*

Distribution: Australia, New Zealand

Holotype: AD-C 10963 (!); collected from an upright rotting support post of a glasshouse in Blackwood, Australia on April 9 1925 by J.B. Cleland.

Specimens examined: AD-C (10961, 10965, 55258), MEL (269113, 1052588, 2090235, 2305275), PDD (87473)

Observations: Originally, *Resupinatus subapplicatus* was believed in this study to represent a synonym of *Resupinatus applicatus*. Cleland was misled by the description of

Resupinatus applicatus by Carleton Rea in "British Basidiomycetae" (Rea, 1922), in which the name was misapplied to *Hohenbuehelia reniformis* (Meyer: Fr.) Singer (Watling & Gregory, 1989). The species described by Rea (1922, i.e., *H. reniformis*) had ovate to elliptical spores, whereas Cleland's specimens have globose to subglobose spores. Cleland (1927) then based his new species, *Resupinatus subapplicatus*, on the collections with globose spores, which in fact match the true *Resupinatus applicatus*. Grgurinovic (1997) noted this mistake and stated that *Resupinatus applicatus* has globose to subglobose spores, but then misapplied the name *Resupinatus subapplicatus* to a taxon with subglobose to elliptical spores (the collections observed by Grgurinovic were also observed in this study, and the measurements provided by her do not agree with the measurements provided here). In this study, the name *Resupinatus subapplicatus* is applied to collections on *Eucalyptus* (as was a paratype of *R. subapplicatus*, not seen) and *Pseudopanax* (determined to belong in this group based on DNA sequence analysis), while collections on other substrates are referred to as part of the *Resupinatus applicatus* species complex (for a distinction between *R. applicatus* 4 and 5, see observations under that species name and Figure 4.5).
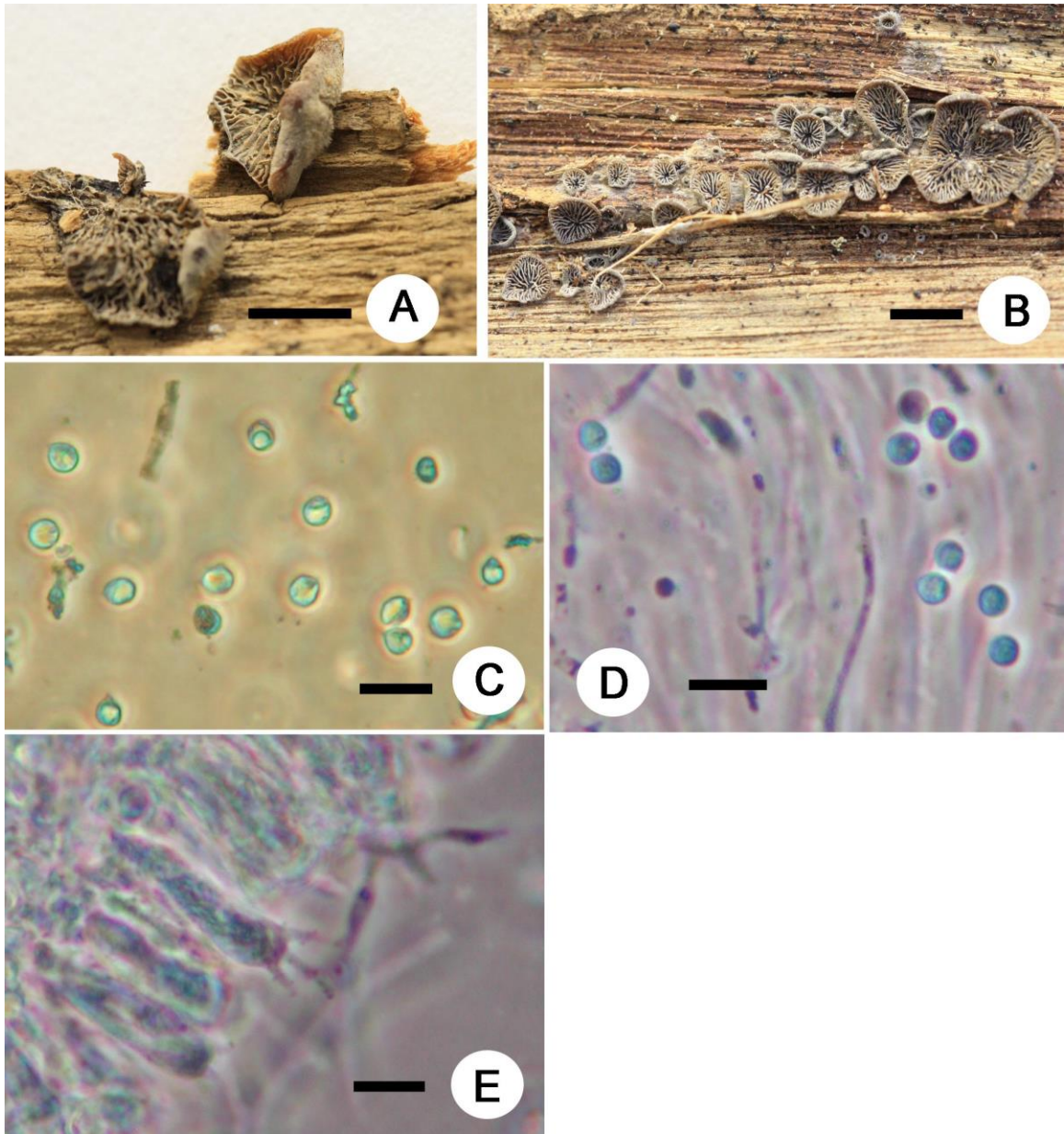
Figure 4.9 *Resupinatus subapplicatus*. A. Fruit bodies of a Cleland collection (bar = 20 mm; AD 10963). B. Fruit bodies of a recent collection (bar = 15 mm; AD 55258). C. Spores of the same collection (bar = 10 μm; AD 10963). D. Spores of a recent collection (bar = 10 μm; AD 55258). E. Basidium with two sterigmata visible (bar = 10 μm; AD 10963).

Resupinatus vinosolividus (Segedin) J.A. Cooper, Index Fungorum 3: 1 (2012a).
≡ *Campanella vinosolivida* Segedin, N.Z. J. Bot. 31(4): 382 (1993).

Fruit Bodies: pileus attached dorsally directly to the substrate (lacking a stipe), orbicular in shape, 3-30 mm across, gelatinous when fresh and drying tough. When fresh, the back of the pileus appears hairless and is a purple-brown but when dry is a very dark grey-brown and the surface hairs are much more apparent. Diverticulate to asterostromelloid elements in the cuticle, hyaline, up to 65 μm long. Pileal trama strongly gelatinized, hyphae hyaline to faintly brown, 2-4.5 μm in diameter. Hymenial trama made up of very narrow hyphae, hyaline, gelatinized, 1.5-2.5 μm in diameter, running parallel to the hymenium. Hymenium faintly brown, composed of very densely packed basidia and basidioles with cheilocystidia along gill edges. Lamellae radiate outwards from the point of attachment to the substrate with cross-veins that are throughout the fruit body when young and only in the centre of the hymenium when more mature. Hymenium where there are reticulated gills much darker than where there are only radial primary gills.

Basidia: 4-spored, very tightly packed in hymenium, 15-20 x 5.5-6.5 μm

Cystidia: cheilocystidia seen only at edge of fruit bodies on top surface of gills; hyaline, digitate to diverticulate, up to 25 μm long (5-6 μm wide)

Spores: hyaline, inamyloid, smooth-walled, globose to subglobose (a few nearly elliptical), 6.7-7.1(-7.5) x (5.5-)6.7-7.1 μm; material examined not very fertile and had few spores.

Substrate ecology: on fallen rotting wood of unidentified dicotyledonous trees (too decomposed to determine species)

Distribution: Australia, New Zealand

Holotype: PDD 29270 (not examined); collected on fallen rotting wood in Laingholm, New Zealand in May 1971 by D.W. Dye.

Specimen examined: AD-C (10966)

Observations: *Resupinatus vinosolividus* is remarkably similar to *Resupinatus merulioides* with a few notable differences. First, the gills are not fully cross-veined at maturity in this species as in *R. merulioides* but rather only reticulated when the fruit bodies are young. Second, the basidiospores of *R. merulioides* are more consistently globose to subglobose and much smaller than those of this species. *R. vinosolividus* was not targeted in this project since it was only very recently transferred to *Resupinatus* from *Campanella* (Segedin, 1993; Cooper, 2012b). The herbarium specimen observed was distributed as a collection of *Resupinatus subapplicatus*. The collection observed in this study (AD-C 10966) has some unusual hyphae not reported from other collections or reported from the type collection of this species. These hyphae are very broad, with monilioid swellings (Fig. 4.10c-d). An unpublished ITS sequence of this species (PDD 72876, New Zealand) placed it as a sister group to *R. violaceogriseus* (Cooper, 2012b).
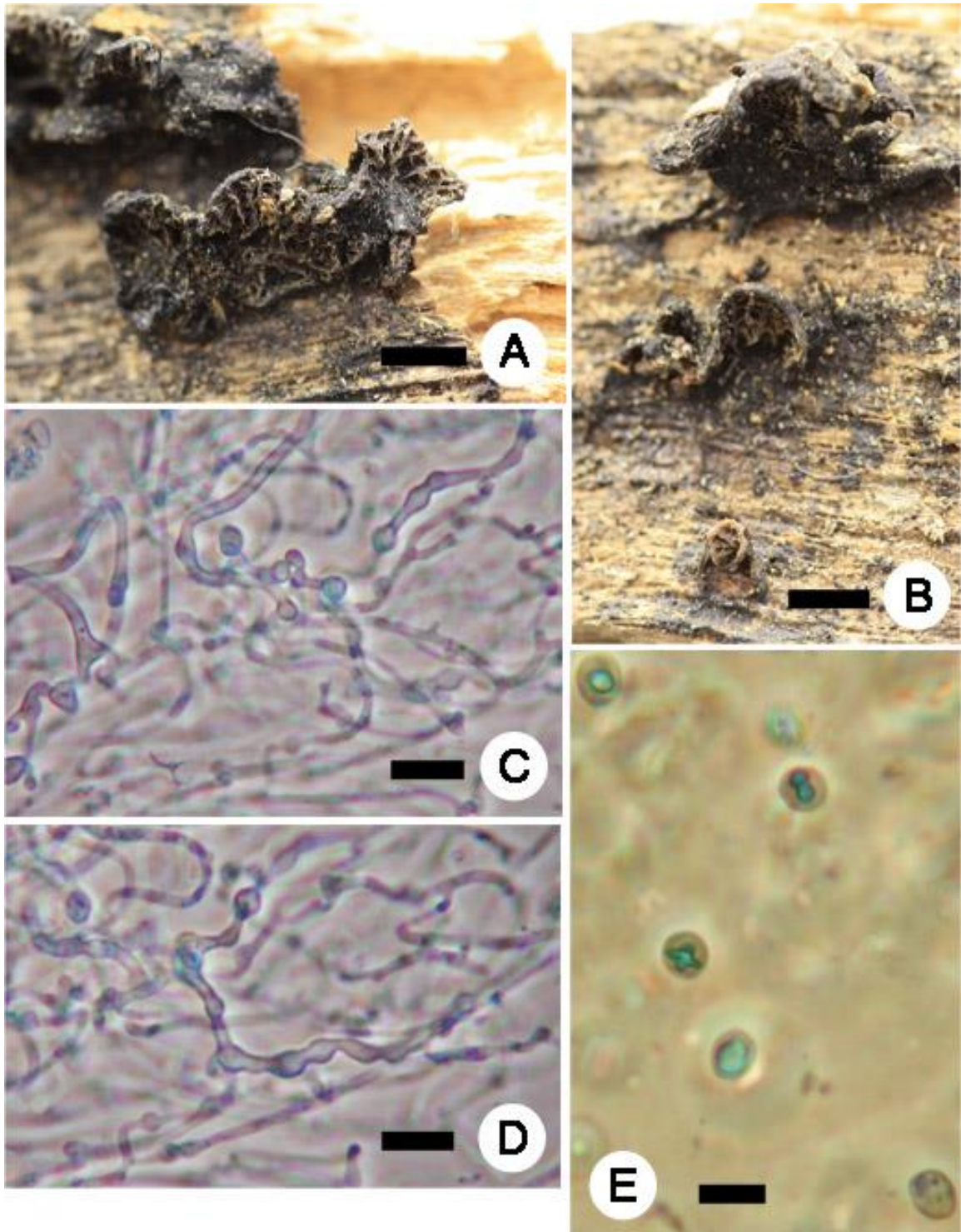
Figure 4.10 *Resupinatus vinosolividus*. A. Dried fruit bodies, with reticulated gills visible at the top right (bar = 10 mm). B. Dried fruit bodies, with reticulated gills visible in the middle (bar = 10 mm). C-D. Unusual bulbous swellings of hyphae in the pileal trama (bars = 15 μm). E. Spores (bar = 10 μm). All photographs from AD 10966.

Resupinatus violaceogriseus G. Stev., Kew Bull. 19(1): 22. 1964.
≡ *Marasmiellus violaceogriseus* (G. Stev.) E. Horak, N.Z. J. Bot. 9(3): 459. 1971.
Fruit Bodies: pileus 10-25 mm in diameter, young fruit bodies violet at the margin, older fruit bodies entirely violet-grey, attached to substrate directly by the back of the fruit body (lacking a stipe). Margin of cups inrolled when young, becoming bell-shaped or broadly flattened when more mature. Outer surface of the pileus covered with a thick white tomentose covering when mature, made up of the unique thick-walled, long surface hairs with pegs. Pileal trama gelatinized, made up of loosely woven hyphae 1.5-5 μm in diameter, grey-brown. Hymenophoral trama containing hyphae parallel to the hymenium, with gelatinized hyphae up to 4 mm in diameter. Hymenium composed of tightly packed basidia and basidioles, with cheilocystidia along edges of lamellae. Lamellae radiating from point of attachment (slightly off-centre), tightly packed, violet-grey, frosted along gill edges, with many lamellulae extending from the margin.

Basidia: 4-spored, clavate, brown in KOH, (19-)20.5-22.5(-25) x (3.5-)4-5(-6) μm

Cystidia: cheilocystidia along gill edges, highly branching finger-like projections from the apex with unbranched projections further down the cell, 13-19 x 2.0-4.5 μm.

Spores: hyaline, inamyloid, smooth-walled, oblong to cylindric, (5.2-)5.6-7(-7.2) x (-2.4)2.6-2.8(-3.5) μm

Substrate ecology: on rotting wood and bark of deciduous and coniferous trees; observed on *Kunzea*, *Nothofagus*, *Polyscias*, *Pomaderris, Ripogonum*, and other unidentified species.

Distribution: Australia, New Zealand

Holotype: collected on fallen *Nothofagus menziesii* in Nelson, New Zealand in July 1949 by A. Crawford (in K, not observed).

Specimens examined: MEL (269121, 1052586, 2059634, 2063505, 2119132, 2231606, 2292301), PDD (59254, 70489, 75559, 79820, 80153, 83794, 87197, 87379, 91781)

Observations: The *Resupinatus violaceogriseus* species complex, once believed to be a member of *Marasmiellus* when the generic concept of *Resupinatus* was restricted to species with globose spores (Horak, 1971), has been demonstrated using sequence data to belong to the genus *Resupinatus* (Cooper, 2012b) and is confirmed with this study. This is one of the only species that can be reliably identified to the species complex in the field based on the large size of the fruit bodies, the very hairy surface of immature fruit bodies, and the slightly violet tint to the surface of the pileus.

There are two different species to which this name has been applied, based on DNA sequence data. Morphologically, these two species are identical and there are no other characteristics which distinguish these species (ecology, geography, host, etc.). More collections of these species need to be sequenced in order to discern if limits to species can be made. In terms of host and known sequences, *R. violaceogriseus* 1 was found on an unidentified rotting hardwood as well as on *Nothofagus solandri*, and *R. violaceogriseus* 2 was found on *Ripogonum scandens* (*Liliales*). This could be a good start to limits between sister species within this complex, but would require a larger sample size.
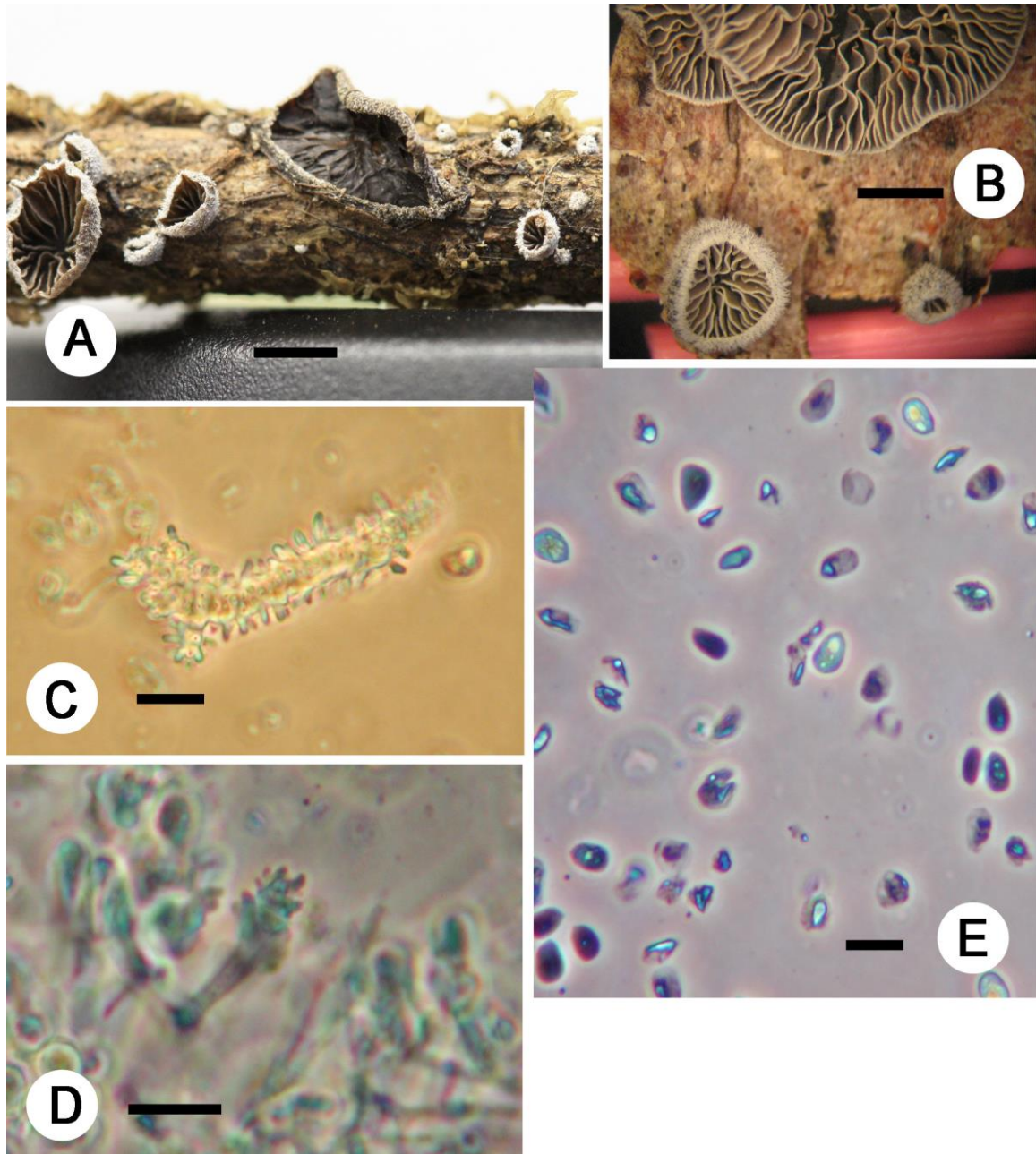
Figure 4.11 *Resupinatus violaceogriseus*. A. Dried fruit bodies in various stages of development (bar = 15 mm; MEL 2119132). B. Magnified view of the surface of young fruit bodies, showing the dense surface hairs that thin with age (bar = 5 mm; PDD 91781). C. Microscopic structure of a surface hair (bar = 15 μm; MEL 2059634). D. A cheilocystidium (bar = 10 μm; MEL 2119132). E. Spores (bar = 10 μm; MEL 2231606).

Australian lamellate *Resupinatus* 1 (unpublished new species, 2014).
Fruit Bodies: pileus semi-circular to ligulate or fan-shaped, 5-20 mm across, curving upwards from eccentric point of attachment to the substrate via a pseudostipe. Pileus dark brown when young to almost black when more mature, cuticle velvety with a covering of hyaline hairs. Margin of the fruit body scalloped, almost transparent. Lamellae radiate out to the margin from the point of attachment and continue down the pseudostipe. Numerous lamellulae present along the margin. Pileus covered in asterostromelloid to diverticulate surface hairs in a Rameales-structure. Cuticular hyphae nearly black, slightly gelatinized, up to 5 μm in diameter. Pileal trama hyaline, strongly gelatinized, clamped hyphae up to 6 μm in diameter. Hymenial trama made up of tightly packed gelatinized clamped hyphae running parallel to the hymenium, hyaline to brown. Hymenium composed of basidia, basidioles and cheilocystidia.

Basidia: with clamps, 2- to 4-spored, clavate to subclavate, hyaline in KOH, yellow-brown in Melzer's, 26-35(-45) x 5.5-6.5(-7.0) μm

Cystidia: numerous on gill edge of most collections, diverticulate, hyaline, 32-44 x 5-7 μm

Spores: hyaline, inamyloid, smooth-walled, elliptical to cylindrical, (6.0-)6.5-7.6 x (3.8-)4.1-4.9(-6.0) μm

Substrate ecology: rotting wood of dicotyledonous trees, predominantly in *Eucalyptus* mixed woodlands; observed on *Acacia, Eucalyptus,* and *Xanthorrhoea*

Distribution: Australia

Specimens examined: AD-C (55348, 55601, 56856, 57163, 57180, 57542)

Observations: the new species provisionally designated as Australian lamellate *Resupinatus* 1 was discovered amongst herbarium packets sent from the Adelaide National Herbarium in Australia. Upon microscopic analysis of the herbarium specimen, further samples were requested and sent by Pam Catcheside that were deposited in AD

since the time of the original herbarium loan request. Sequence analysis of these collections places this species within *Resupinatus* (Figure 4.3), where it is easily distinguished by its thick, gelatinous pileus, maturing into a spoon-shaped or funnel-shaped fruit body (Figure 4.12 a, b and d), and the nearly cyphelloid immature fruit bodies (Figure 4.12 c).
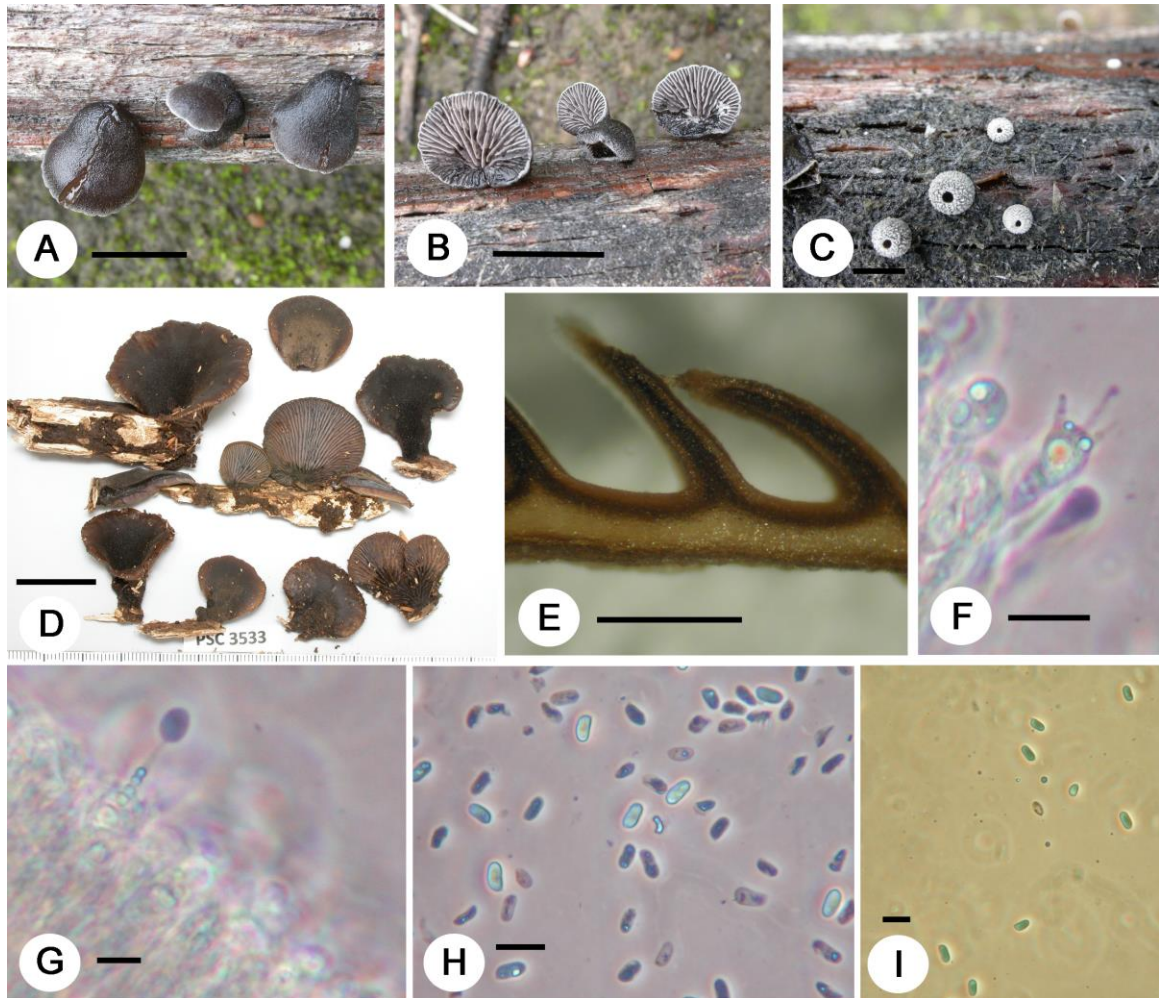
Figure 4.12 Australian lamellate *Resupinatus* 1. A. Fresh fruit bodies, pileal surface (AD-C 57163; Bar = 10 mm). B. Fresh fruit bodies, hymenial surface (AD-C 57163; Bar = 10 mm). C. Fresh primordial fruit bodies, hymenial surface (AD-C 57163; Bar = 5 mm). D. Fresh fruit bodies in various stages of development (AD-C 56856; Bar = 20 mm). E. Cross-section showing locations of pigmentation, in the pileal and gill trama hyphae (AD-C 55601; Bar = 100 μm). F. Basidium (AD-C 55601; Bar = 10 μm). G. Mature basidium with immature spore attached (AD-C 55601; Bar = 5 μm). H. Basidiospores (AD-C 55601; Bar = 10 μm). I. Basidiospores (AD-C 55601; Bar = 10 μm). Photographs of fresh fruit bodies (Panels A-D) by P.S. Catcheside.

Australian cyphelloid *Resupinatus* 1, (unpublished new species, 2014)
Fruit Bodies: cups scattered, rarely in groups of three to seven cups, heavily crystal encrusted, no subiculum. Cups 0.5-1.0 mm (rarely to 1.5 mm) across, approximately 0.5 mm high. Margin inrolling when dry. Exterior grey-brown, slightly greenish when visibly high numbers of algae are present on the substrate (as evidenced by the substrate taking on a greenish tint), with heavily encrusted diverticulate surface hairs up to 50 μm long, 2-3.5 μm in diameter. Pileal trama slightly gelatinized, composed of loosely-woven hyaline hyphae 2-3.5 μm in diameter. Hymenial trama brown, also slightly gelatinized but much more densely packed than the previous layer, running parallel to the hymenium, 2-4 μm in diameter. Hymenium appearing slightly darker than the exterior of the cup when dry (dark brown to dark grey-brown), but microscopically composed of tightly packed hyaline basidia and basidioles. All hyphae with clamps, and branching from clamps.

Basidia: clavate to subclavate, hyaline in KOH, 4-spored, 20-25 x 4-6 μm.

Cystidia: none seen.

Spores: hyaline, inamyloid, jack-shaped with six large spines 1.5-2(-3) μm long, 3.8-4.0 x 3.8-4.0 μm (spore measurement excluding spines). Few ovate or elliptical, hyaline, inamyloid, smooth-walled spores also present; 5-7 x 3.5-5 μm.

Substrate ecology: on rotting *Dacrycarpus* wood in New Zealand

Distribution: New Zealand

Specimen examined: PDD 88932

Observations: the species provisionally designated as Australian cyphelloid *Resupinatus* 1 is macroscopically identical to both *Rhodocyphella cupuliformis* from North America (see Chapter 2) and *Resupinatus griseopallida* from Europe (see Chapter 5), although the latter differs in its smooth, ovate spores. A culture of Australian cyphelloid *Resupinatus* 1 (as *Rhodocyphella cupuliformis*) was obtained from the New Zealand national culture collection (ICMP) that was generated from the herbarium collection listed above. It was

successfully sequenced and is a sister species to the North American *Rhodocyphella cupuliformis*, and unrelated to the European *Resupinatus griseopallida*.

The species also shares the notable characteristic of always being associated with algae on the surface of the substrate (like both identical morphospecies listed above). Unfortunately, the idea that it could be an algal associate wasn't arrived at until after the loan from PDD was returned, and consequently further morphological studies were not possible. Before conclusions can be drawn on the possible relationship between the surface alga and the fungus (whether a lichen, algal parasite, or some other relationship between fungus and algae), this collection needs to be examined morphologically in more detail. The algal cells could also be identified by sequencing, which could also provide a clue for whether or not this is a basidiolichen. Indeed, the observation that the algal species is one that is already known to form relationships with fungi would increase our confidence that this species of *Resupinatus* is also a basidiolichen.

Unfortunately, only macroscopic photographs of this collection are available as all microscopic images of spores and basidia were lost in 2008 due to a computer hard drive failure. Photographs of the fruit bodies are presented below, as well as a photograph of drawings done by B. Paulus (included in the herbarium packet) of microscopic characteristics observed after collection.
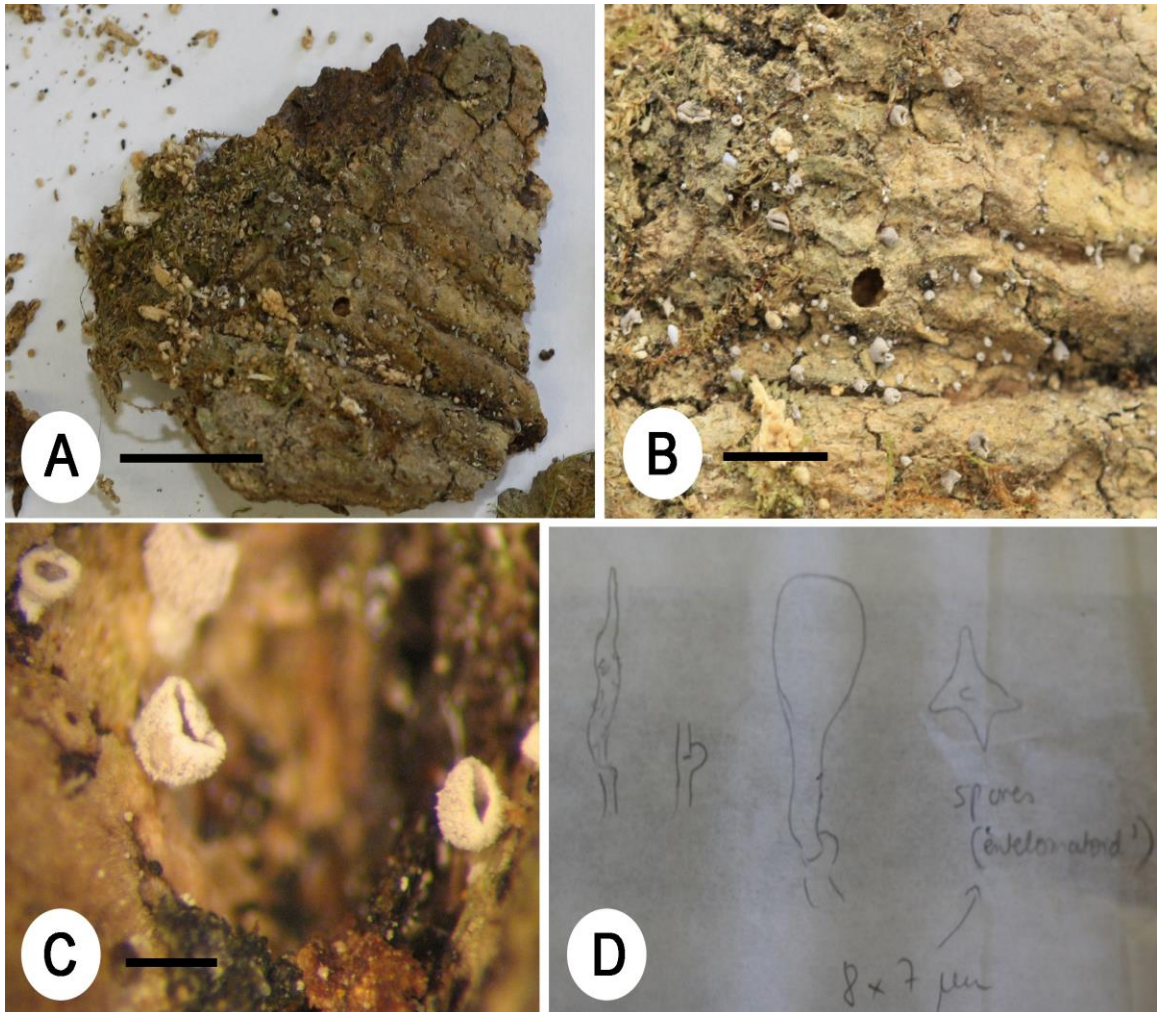
Figure 4.13 Australian cyphelloid *Resupinatus* 1. A. Portion of substrate with fruit bodies, showing the faint green colouring of the surface of the wood (becoming more vibrant after rehydrating), and insect emergence holes for scale (Bar = 10 mm). B. Same portion of the substrate but more magnified, with fruit bodies on the surface (Bar = 5 mm). C. Macroscopic image of the fruit bodies, showing the outer surface of the fruit body that is densely covered in surface hairs (Bar = 200 μm). D. Drawings of microscopic features of the collection; from left to right: crystal-encrusted hyphal tips, clamp connections, basidioles, and spores (by B. Paulus). All photographs of collection PDD 88932.

Australian cyphelloid *Resupinatus* 2, (unpublished new species, 2014)
Fruit Bodies: cupulate or goblet-shaped, 150-280 µm in diameter, crowded in groups of 30 to 1000s of cups on a common subiculum. Subiculum thick and dense, or absent or nearly absent, creamy-white. Cups tan to dark brown or grey, covered in hyaline diverticulate or irregularly warted surface hairs up to 75 µm long, heavily encrusted with hyaline or pale brown crystals. Pileal trama hyaline to subhyaline (appearing faintly brown or yellow-brown in thick cross-sections in Melzer's), strongly gelatinized, composed of loosely woven hyphae 2.5-4.5 µm in diameter. Hymenial trama dark brown, also gelatinized but less conspicuous than in the pileal trama, composed of more densely packed hyphae 3-5 mm in diameter. Macroscopically, hymenium darker or the same colour as the exterior of the cup (medium to dark brown), smooth; microscopically hyaline, composed of tightly packed basidia and basidioles.

Basidia: clamped, 4-spored, clavate, hyaline to faintly brown in KOH, (14-)18-20(-25) x (4.5-)5.5-6.8(-7.5) µm

Cystidia: present along the margin of the cup; diverticulate, hyaline, (18-)19-24(-26) x 5.5-7 µm.

Spores: hyaline, inamyloid, smooth-walled, globose to subglobose with apiculus, (4.4-)5-5.8(-6) x (4.2-)4.5-5.7(-6) µm

Substrate ecology: on rotting wood of dicot trees in Australia and New Zealand; rarely on bark and on standing trunks; observed on *Brachyglottis, Eucalyptus, Metrosideros,* and *Prosanthera.*

Distribution: Australia, New Zealand

Specimens examined: BPI (257954), CANB (751987), MEL (2308212, 2308228), PDD (7138, 11162, 12963, 24323)

Observations: the species known here as Australian cyphelloid *Resupinatus* 2 is morphologically identical to *Resupinatus poriaeformis*, discussed in Chapter 3. Major

differences are in substrate and geographic range: this species is found exclusively on tree species endemic to Australia and New Zealand, and the distribution is within these two countries. It is likely that it would also be found on other South Pacific islands where the tree species and forest diversity is similar to that of Australia and New Zealand, but due to a lack of sampling effort it has never been found.

The attempt was made to extract and amplify ribosomal DNA of this species but has so far been unsuccessful. The conclusion that this is a separate species from *Resupinatus poriaeformis* is therefore only an assumption, based on the difference in substrate and geography from both the European *R. poriaeformis* and the North American cyphelloid *R. poriaeformis*-like species.
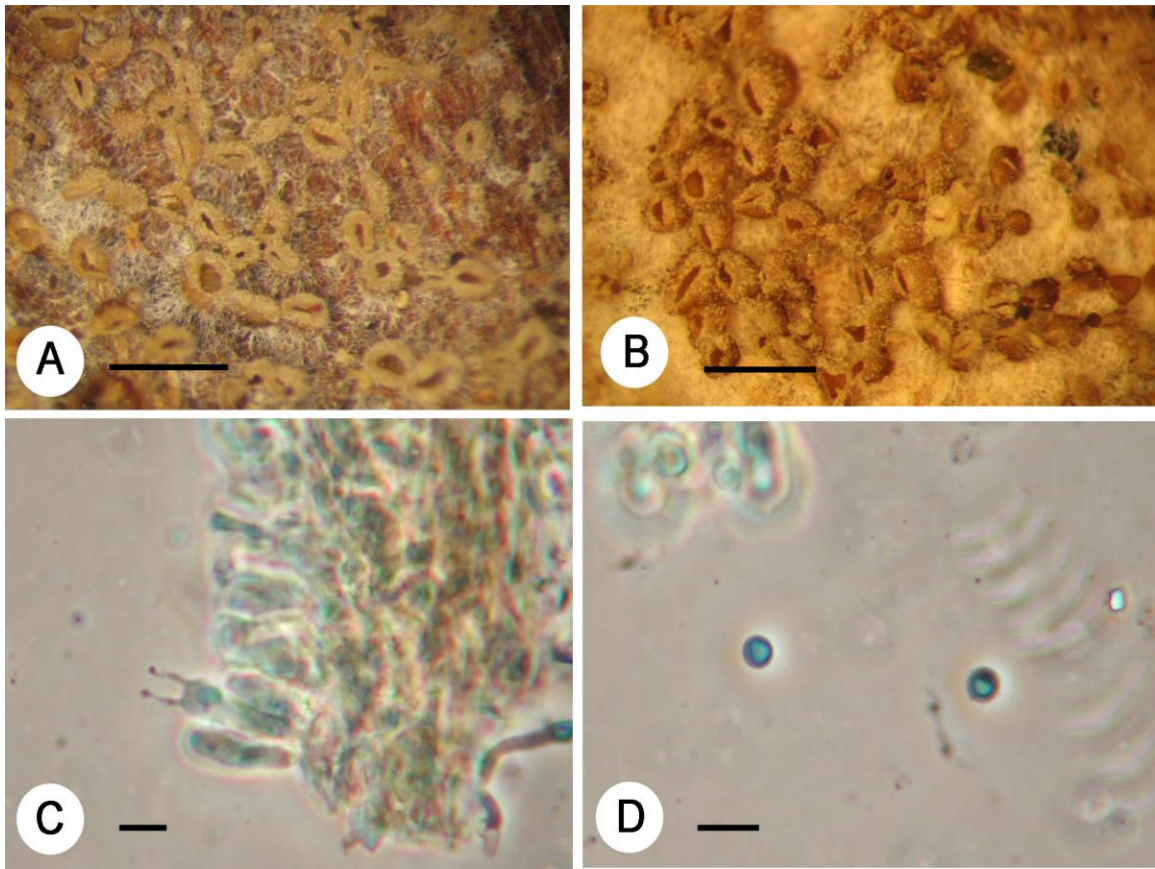
Figure 4.14 Australian cyphelloid *Resupinatus* 2. A. Mature fruit bodies with a nearly absent subiculum (similar to the species concept for the former *Resupinatus urceolatus*; see Chapter 3), and substrate clearly visible through the thin, wispy mat of hyphae (Bar = 1.0 mm; PDD 12963). B. Mature fruit bodies with a thick, dense subiculum (similar to the species concept of *Resupinatus poriaeformis* before it was synonymized with *Resupinatus urceolatus*; see Chapter 3) covering the substrate (Bar = 1.0 mm; PDD 24323). C. Basidium with basidiospores in a very early stage of development (Bar = 10 μm; CANB 751987). D. Basidiospores (Bar = 10 μm; CANB 751987).

Resupinatus trichotis (Pers.) Singer, Persoonia 2(1): 48. 1961.
≡ *Agaricus trichotis* Pers., Mycol. eur. (Erlanga) 3: 18. 1828.
≡ *Resupinatus applicatus* var. *trichotis* (Pers.) Krieglst., Beitr. Kenntn. Pilze Mitteleur. 8: 177. 1992.
= *Agaricus rhacodius* Berk. & M.A. Curtis, Ann. Mag. nat. Hist., Ser. 3 4(no. 22): 288. 1859.
≡ *Pleurotus rhacodium* (Berk. & M.A. Curtis) Sacc., Syll. fung. (Abellini) 5: 380. 1887.
≡ *Dendrosarcus rhacodium* (Berk. & M.A. Curtis) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 464. 1898.
≡ *Pleurotus applicatus* f. *rhacodium* (Berk. & M.A. Curtis) Pilát, Atlas Champ. l'Europe, II: *Pleurotus* Fries (Praha): 67. 1935.
≡ *Resupinatus rhacodium* (Berk. & M.A. Curtis) Singer, Lilloa 22: 253. 1951.
≡ *Geopetalum rhacodium* (Berk. & M.A. Curtis) Kühner & Romagn., Fl. Analyt. Champ. Supér. (Paris): 68. 1953.

For a full description of this species, see Thorn & Barron, 1986.

Ecology: on rotting wood of dicot trees.

Distribution: Australia

Hosts: unidentified rotting wood

Specimens examined: AD-C (10962, 10964), MEL (2292300)

Observations: *Resupinatus trichotis* is known from the tropics as well as southern North America, but unknown until now on the Australian mainland. All three of these collections have identical coarse, dense, black surface hairs near the point of attachment on the pileal surface of the fruit body, characteristic of this species. All other morphological characters match the descriptions provided in Thorn & Barron (1986) as well as Singer (1951 & 1961). Unfortunately, none of the collections observed above were good candidates for DNA extraction and sequencing (due to the age of two collections, AD-C 10962 and 10964, and the lack of material of the third) so it cannot be determined if the Australian collections are the same species as those found in North and South America.

Resupinatus cf. striatulus (Pers.) Murrill, N. Amer. Fl. (New York) 9(4): 242. 1915.
≡ *Agaricus striatulus* Pers., Syn. meth. fung. (Göttingen) 2: 485. 1801.
≡ *Pleurotus striatulus* (Pers.) P. Kumm., Führ. Pilzk. (Zerbst): 105. 1871.
≡ *Calathinus striatulus* (Pers.) Pat., Cat. Rais. Pl. Cellul. Tunisie (Paris): 28. 1897.
≡ *Acanthocystis striatula* (Pers.) Kühner, Botaniste 17: 112. 1926.
≡ *Geopetalum striatulum* (Pers.) Kühner & Romagn., Fl. Analyt. Champ. Supér. (Paris): 68. 1953.
≡ *Urosporellina striatula* (Pers.) E. Horak, Beitr. Kryptfl. Schweiz 13: 609. 1968.

For a full description of this species, see Thorn & Barron, 1986.

Substrate ecology: on unidentified rotting wood of dicot trees.

Distribution: Australia

Specimen examined: CANB 574872

Observations: this collection fits all descriptions published of *Resupinatus striatulus* but with one exception: it was not found on rotting coniferous wood. If the strict sense of the definition is taken, as is used in this study, *Resupinatus striatulus* is essentially identical to *Resupinatus applicatus* but differentiated by occurring on conifers (whereas *R. applicatus* is on hardwoods), as well as the texture and transparency of the pileus. *Resupinatus striatulus* has nearly transparent fruit bodies when fresh, especially at the margins of the pileus, and the gills are clearly visible through the surface of the pileus. The margin of the pileus is also crisped (the edge is wavy or scalloped, but the scalloped pattern follows the spacing of the gills), which is not found in any other species with tan fruit bodies. Unfortunately, the only collection observed was not suitable for DNA extraction and sequencing, so it is impossible to determine if this species has the same sequences as the sequence generated from a collection on a conifer in Europe that has been deposited in GenBank.

4.4.1   Notable Collections

The following collections are listed here as examples of possible additional diversity, although not enough information is available to describe new species. Until these collections are re-examined and sequences are obtained from new material, they are discussed here as notable collections that are atypical of species delineations discussed elsewhere in this chapter.

AD-C 55538 and AD-C 55545: these two collections are macromorphologically similar to *Resupinatus applicatus*, but have ovate spores as opposed to globose to subglobose spores. The two collections are also micromorphologically nearly identical to *Resupinatus cinerascens*, but lack the dense covering of surface hairs on the fruit bodies. The collections also have very unusual large, presumably sterile, cells similar to the metuloids of *Hohenbuehelia*, which are not seen in any other collection of either *Resupinatus applicatus* or *Resupinatus cinerascens*. More recent collections of this species need to be found and sequenced before one can determine whether it represents a new species. See Figure 4.15, below, for photographs of these two collections.

AD-C 10960, CANB 605135, MEL 1053060, and MEL 2318047: these three collections are macromorphologically similar to *Resupinatus cinerascens* (very dark, nearly black fruit bodies with a dense covering of surface hairs), but with globose spores as opposed to the ovate or elliptical spores that *R. cinerascens* has. I attempted to sequence MEL 1053060 (as well as a work-study student under my mentorship in the lab, T. D. Kim; see statement of co-authorship), but was unsuccessful (likely due to the specimen age). Sequencing of MEL 2318047 was also unsuccessful due to surface contamination of the dried material. More recent collections need to be found and sequenced. before proceeding further.
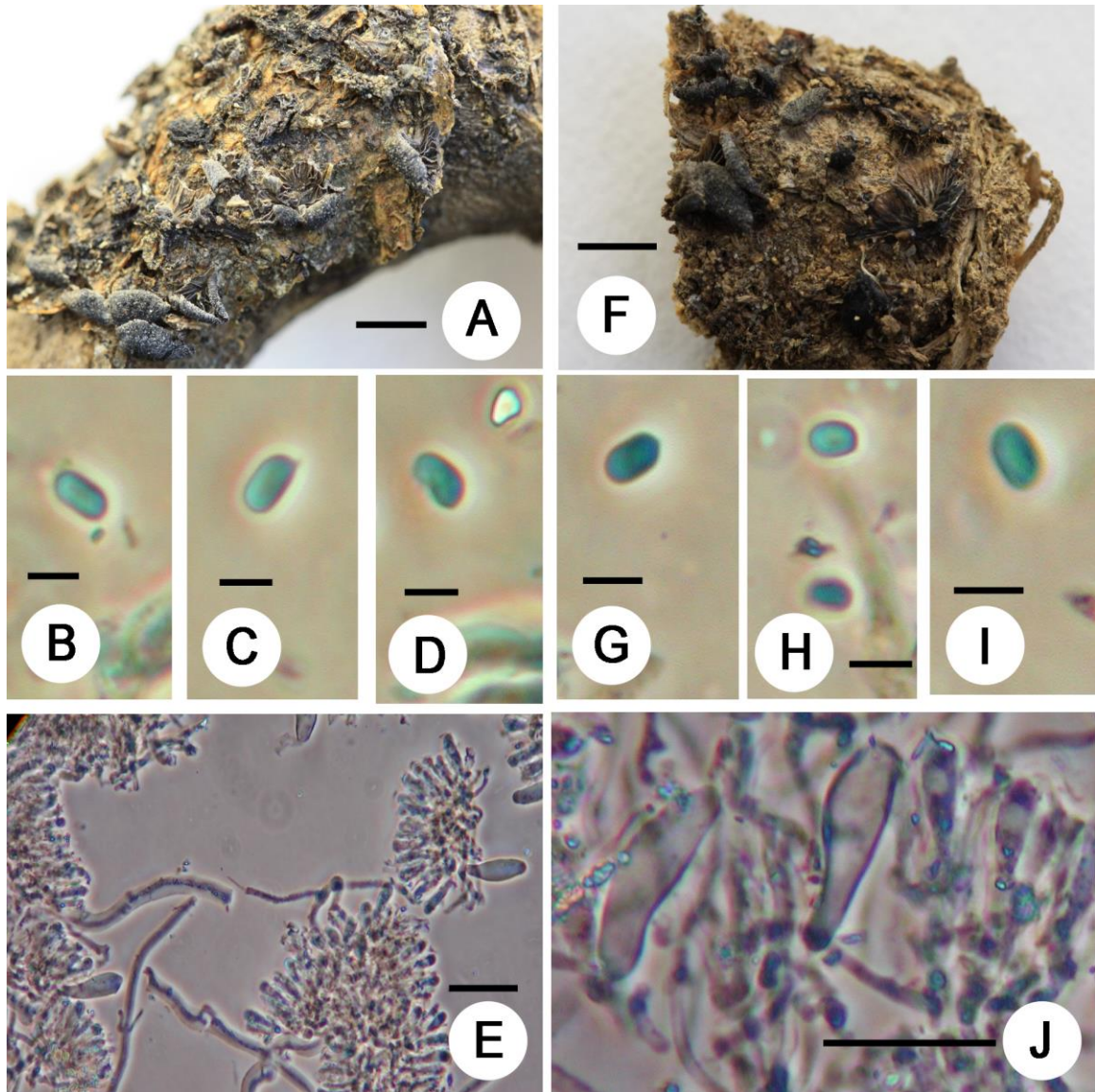
Figure 4.15 AD-C 55538 and AD-C 55545, two notable collections from Australia similar to both *Resupinatus applicatus* and *Resupinatus cinerascens*. A. Fruit bodies (AD-C 55538; Bar = 20 mm). B-D. Basidiospores (AD-C 55538; Bar = 5 μm). E. Cystidia and strongly gelatinized hyphae (AD-C 55538; Bar = 30 μm). F. Fruit bodies (AD-C 55545; Bar = 20 mm). G-I. Basidiospores (AD-C 55545; Bar = 5 μm). J. Cystidia and basidioles (AD-C 55545; Bar = 30 μm).

PDD 7139 and 16951: these two collections do not fit the species concept of *Resupinatus poriaeformis* (and Australian cyphelloid *Resupinatus* 2) and do not appear to belong to any previously described species from Australia or New Zealand. The collections do match the description of the type of *Resupinatus hyalinus* (Singer, 1989), and so they are treated as collections of this species. Until a successful sequence is generated from these collections and a non-type collection of *Resupinatus hyalinus* is found, it cannot be determined if these represent a new species or a new record of *R. hyalinus* in New Zealand. For a more thorough discussion of this species, see Chapter 5.

4.5   Discussion

This study recorded 14 species of *Resupinatus* from Australia and New Zealand, including the seven species recorded previously (*Resupinatus cinerascens*, *R. huia, R. meruliodes, R. subapplicatus, R. trichotis, R. vinosolividus,* and *R. violaceogriseus*), plus one new record (*Resupinatus hyalinus*) and six apparently new species (*Resupinatus applicatus* 4 and 5, Australian lamellate *Resupinatus* 1, Australian cyphelloid *Resupinatus* 1 and 2, and *Resupinatus "striatulus"* on hardwood). Ten species are lamellate or lamellate-merulioid and four species are cyphelloid. Australia and New Zealand are rich in diversity of various groups of macrofungi; for example, boletes (Watling & Gregory, 1988), *Amanita* (Miller, 1992), generalist ectomycorrhizae (Castellano & Bougher, 1994), *Eucalyptus*-associated fungi (May & Wood, 1997), hypogeous fungi (Bougher & Lebel, 2001), and *Xerula* (Petersen, 2008). This is the first study to document the diversity of the *Resupinateae* in Australia and New Zealand.

The internal transcribed spacer region of the ribosomal DNA (ITS-rDNA) is a phylogenetically informative region for this group. It demonstrates the multiple derivations of the cyphelloid fruit body morphology within the *Resupinateae*, and also highlights the extreme phenotypic plasticity displayed within the group; members of the group that are lamellate and cyphelloid often appear on the same major branches of the

tree. This sequence also reveals multiple lineages within groups that would be considered one species on the basis of macro- and micromorphology: two lineages within *Resupinatus violaceogriseus* and three lineages within the globose-spored *Resupinatus applicatus* complex (including *R. subapplicatus*).

4.5.1 Cyphelloid *Resupinateae*

Among the four cyphelloid species of *Resupinatus* recorded from Australia and New Zealand, *R. huia* (described from New Zealand) may not be distinct from *R. incanus* (described from South Africa), but is kept separate here based on geographic distribution. Until a new collection of *R. incanus* is found to enable sequence comparison, it is impossible to determine if it and *R. huia* are distinct. Morphological evidence suggests, based on spore size distribution diagrams, that *Resupinatus huia* is perhaps a geographic race within *Resupinatus incanus*, as the distribution of spore sizes of the former is found within the distribution of the latter. A member of the *R. poriaeformis* group has been reported from Australia and New Zealand, and is regarded here as a distinct species since sequences of this group from Europe and North America form separate clades (see Figure 4.3 and Chapter 2). Similarly, the Australasian counterpart of *Rhodocyphella cupuliformis* shows sufficient sequence difference from the North American representative to be considered a separate species. This is an unusual cyphelloid species in the *Resupinateae* in that it does not produce a subiculum and is only slightly gelatinized (unlike the thick layer of strongly gelatinized hyphae in the trama of other species in the *Resupinateae*, both cyphelloid and lamellate species). It has only been reported once from New Zealand from *Dacrycarpus dacrydioides*. Finally, two herbarium collections deposited in the Landcare Research herbarium in New Zealand (PDD) and named *Resupinatus poriaeformis* do not correspond to any species currently described in *Resupinatus* (or the former *Stigmatolemma*) except possibly *Resupinatus hyalinus.* That species has been collected just once, in Brazil, and is deposited in INPA (Singer, 1989). Unfortunately, the description of *Resupinatus hyalinus* is insufficient to make a conclusive identification of the New Zealand material, and INPA does not loan specimens; however, the spore sizes do match (6-6.5 x 3.3-4 μm). A more thorough discussion of this species can be found in Chapter 6.

4.5.2   Lamellate *Resupinateae*

Of the gilled members of the *Resupinateae* in Australia and New Zealand, the most common are *Resupinatus cinerascens* and *Resupinatus violaceogriseus*. *Resupinatus cinerascens* is the most commonly collected lamellate species of the *Resupinateae* collected in Australia, while the same can be said for *Resupinatus violaceogriseus* in New Zealand. These species could be mistaken for each other but the fruit bodies of *Resupinatus violaceogriseus* have a violet hue around the margin while those of *Resupinatus cinerascens* do not. The spores of these two species are also different, with the spores of *Resupinatus violaceogriseus* being much narrower (Figure 4.2).

Resupinatus merulioides and *Resupinatus vinosolividus* have lamellate-merulioid fruit bodies, the latter with the characteristic reticulated lamellae when the fruit bodies are young, but as the fruit bodies grow outwards the reticulation only remains between the gills in the middle of the fruit body. Microscopically, these species are very different and can be distinguished by their differing spore shape and size. A sequence of *Resupinatus vinosolividus* was generated by J.A. Cooper confirms assignment to *Resupinatus* (Cooper, 2012b), but it was not deposited in GenBank and so was unavailable for study. Two attempts were made during this study to sequence the collection of *Resupinatus merulioides* in PDD, but both attempts returned sequences of contaminants.

This study has confirmed the shortcomings of using only morphological characters to distinguish species: three morphologically identical, independently evolved, species historically would have all been referred to as *Resupinatus applicatus* sensu stricto. The these species are genetically distinct from any European collection of *Resupinatus applicatus* sequenced thus far, and so are referred to here as *Resupinatus applicatus* 4 and 5 (when the substrate is not *Eucalyptus* or *Pseudopanax*) and *Resupinatus subapplicatus* (on either *Eucalyptus* or *Pseudopanax*). This further illustrates that morphology is not a good predictor of phylogeny, as all three species evolved independently (they constitute a polyphyletic group).

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Chapter 5

5 Systematics of the remaining species in the *Resupinateae* and species lost in the literature

This study will examine the species in the *Resupinateae* not covered in previous chapters. Most of these species have been not adequately described previously in the literature in order to compare them with better-known species, and DNA sequences for phylogenetic analysis are lacking. Many species were published once as three- or four-line descriptions in the 19th century, and then never reported again. Such species are said to have been "lost" in the literature and may represent up to 50,000 fungal species in total (Hawksworth & Rossman, 1997).

5.1 Introduction

5.1.1 Remaining species previously classified in the *Resupinateae*

Thirty-five species are currently classified in *Resupinatus*, one in *Stromatocyphella*, and one in *Aphyllotus*. Three *Stigmatolemma* species have been left in in that genus because too little is known about them to transfer them confidently to *Resupinatus* (Thorn et al., 2005). Many of these species have already been covered in previous chapters, but some, unlike their relatives, do not fit into neat categories. These species will be covered in greater depth here. They include gilled members *Resupinatus alboniger*, *Resupinatus dealbatus, Resupinatus kavinii*, *Resupinatus striatulus*, and *Resupinatus trichotis*, as well as the cyphelloid member *Resupinatus griseopallidus* (*Resupinatus taxi*). The two remaining cyphelloid members previously classified in *Stigmatolemma*, *Resupinatus hyalinus* and *Stigmatolemma farinaceum*, will be covered in Chapter 6 as "Excluded and Understudied Species".

5.1.2 Species lost in the literature

Since the initial description of the *Resupinateae* (Singer, 1948), many species have been hypothesized to be closely related to *Resupinatus, Stigmatolemma, Stromatocyphella* or *Asterotus* based on morphological evidence, but they have not been transferred into the

Resupinateae (e.g., by Burt, 1914; Cooke, 1957; Cooke, 1961). Prior to Singer's description of the *Resupinateae*, some species were thought to be closely related to members of the *Resupinateae*, but they have not been included in the *Resupinateae* or examined morphologically since their description (by Rick, 1906; Petch 1922; Burt, 1924; Burt, 1926). Yet more species with descriptions similar to those in the *Resupinateae* were described once in the 19th and early 20th centuries and then forgotten (Schweinitz, 1822; Berkeley, 1873; Phillips & Plowright, 1884; Saccardo, 1889a; Saccardo, 1889b; Patouillard & de Lagerheim, 1893). I examined the literature from the time of Linnaeus (1753) and Fries (1821) to discover such lost members of the *Resupinateae*, with a focus on the cyphelloid species. A morphological analysis based on type material (or, when unavailable, other suitable material of the same species) is provided here for *Cellypha subgelatinosa, Cyphella brunnea*, *Maireina pseudurceolata*, *Peziza pruinata*, *Porotheleum reticulatum*, *Rhodocyphella grisea, Solenia subporiaeformis,* and *Tapesia tela*.

5.2   Materials and Methods

5.2.1   Literature Search for Lost Species

While other species known to belong to the *Resupinateae* were being researched, care was put into searching for similar species in the literature. Online databases (indexfungorum.org) and repositories such as CYBERLIBER (www.cybertruffle.org.uk/cyberliber), the Biodiversity Heritage Library (www.biodiversitylibrary.org), and Libri Fungorum (www.librifungorum.org) were searched for species hypothesized to belong to the *Resupinateae* based on keywords in Latin species descriptions: the presence of a whitish subiculum in conjunction with hyaline spores, cup-shaped tan, brown or nearly black fruit bodies aggregated on the substrate, living on unidentified (or identified) rotting wood or bark, and being gelatinized. Once a species description was found that matched that of a species belonging to the *Resupinateae*, the location of the type of the species, if it still exists, was determined and a herbarium loan request sent.

5.2.2   Herbarium samples

Known or suspected members of the *Resupinateae* were requested for microscopy, specifically targeting type specimens and any other collections under names of species lost in the literature and species suggested to be close relatives of members of the *Resupinateae.* Loan requests were sent by the late Dr. Jane Bowles (UWO Herbarium) to herbaria around the world (AD, ARIZ, B, BPI, CANB, C, FH, GBIF, GJO, HO, INPA, K, L, MEL, NCU, NYBG, O, PC, PDD, PH, PRC, PRM, S, STR, TENN, UPS; herbarium acronyms following Holmgren et al., 1990, updated at http://sciweb.nybg.org/science2/IndexHerbariorum.asp). Herbarium collections were analyzed for taxonomic characters (see section 5.2.3 Herbarium collection analysis).

5.2.3   Herbarium collection analysis

All species of the *Resupinateae* possess many taxonomic characters that are useful in identification. Among the most important are the colour, size and shape of the fruit body, the colour, shape (including ornamentation) and size of surface hairs, the presence, colour and thickness of a gelatinous layer in a vertical section of the fruit body tissues, basidiospore shape, size and ornamentation, the size and shape of basidia, and the presence, shape and size of any other characteristic cells in the hymenium, such as cheilocystidia, pleurocystidia, or metuloids.

Notes and measurements were taken of dried collections for fruit body size (in μm; a range from smallest mature fruit bodies to largest mature fruit bodies that show no signs of decomposition), colour and shape, location of attachment to the substrate, presence and distribution of surface hairs, and presence or absence of a subiculum or subiculum-like structure (a mat of hyphae on the surface of the substrate at the base of the fruit bodies). Small portions of fruit bodies of dried collections were rehydrated, and changes in colour of the fruit body and surface hairs were noted (often, fruit bodies are much darker in colour with surface hairs more visible when dry than when fresh). Photographs of the dried collections and rehydrated portions were taken using a Canon Rebel XS 10.0 MP camera and either an EF 50 mm 1:1.8 lens (photographs of the entire dried collection) or an EF 100mm 1:2.8 macro lens (macrophotographs of fruit bodies). The

rehydrated portions of the fruit body were sectioned by hand using a razor blade and squash-mounted on a microscope slide.

Two mounts were made on each microscope slide, in different mountants to emphasize different microscopic characters. One group of sections were mounted in Melzer's reagent (containing potassium iodide and iodine to stain starch, and dextrin, chloral hydrate as a clearing agent to better visualize darkly pigmented fungal structures, and sterile distilled water; Largent, 1977), and the other in 2% potassium hydroxide solution (KOH; Largent, 1977). Melzer's reagent was used to visualize spore characteristics (shape, size, colour changes and spore ornamentation), hyphal characteristics (size, shape, colour, presence or absence of clamps, presence or absence of septa), and surface hair characteristics (size, shape, colour). Due to the difficulty of spreading cells in Melzer's even with application of light pressure to the coverslip, basidia and cystidia are difficult to observe and measure in this mountant. Separation of cells in these tissues is much more effective in potassium hydroxide, and so this solution was used to visualize characteristics of basidia (size, shape, and colour) and cheilocystidia (size, shape, colour, ornamentation). Spore colour was determined in KOH. Due to the tendency of KOH to over-inflate cells, spore measurements were not taken in this mountant as this would change the average spore size range, potentially quite dramatically for some species.

All microscopic measurements are represented in micrometers (μm). Basidiospore, basidium, cystidia, and surface hair measurements are represented as a range, with values in parentheses representing the smallest and largest values, and the size range representing values between the tenth and ninetieth percentiles (as per Thorn and Barron, 1986). Other measurements (for example the diameter of hyphae, or the length and width of sterigmata) are represented as a range of values, the smallest and largest observed. Microscopic characters were photographed using a Nikon Coolpix camera.

5.3   Taxonomy

5.3.1   Remaining members currently classified in the *Resupinateae*

Resupinatus alboniger (Pat.) Singer, Beih. Nov. Hedw. 51: 17. 1977
≡ *Pleurotus alboniger* Patouillard, Bull. Soc. Mycol. Fr. 9: 126. 1893
≡ *Hohenbuehelia albonigra* (Pat.) Noordeloos, Doc. Myc. (23)91: 9-11. 1993.
Fruit Bodies: cupulate, sessile, up to 7 mm across, very dark brown in colour when

mature and pruinose grey-brown when young, drying nearly black. Lamellae radiate from

point of attachment and are grey-brown to black (nearly black when dry and frosty along

gill edges).

Basidia: with clamps, 4-spored, hyaline in KOH, clavate, (16-)19-21 x 5-6 μm

Cystidia: along gill edges, with irregular finger-like projections (digitate), thin-walled,

23-35 x 8-10 μm.

Spores: hyaline, inamyloid, smooth-walled, cylindrical, some slightly wider on end with

apiculus, (5.5-)6.2-7.5 x (2.5-)3.0-3.4 μm

Substrate ecology: on dead wood of dicots; observed on *Fagus* and *Morus*, reported

from diverse hardwoods (Singer, 1973).

Distribution: Australia, Ecuador (Singer, 1973), Greece (Gonou-Zagou et al., 2011),
        Holland, United States (ME, MS), Venezuela (Singer, 1973), France, Tanzania
        (Thorn & Barron, 1986).

Type: in FH, collected in a ravine near Quito, Ecuaor in February 1892 by De
        Lagerheim.

Specimens examined: AD-C (55538), one collection from Michael Kuo

Observations: *Resupinatus alboniger* has been alternately placed in *Hohenbuehelia* (a

genus of strongly gelatinized, white-spored fungi) and *Resupinatus* based on

cheilocystidia characteristics. Nuclear ribosomal DNA analysis places this species within

the *Resupinateae* (Thorn et al., 2005; Chapter 2, Figure 2.1), as suggested originally by

Singer (1977). Other characters that place it morphologically within *Resupinatus* and not

in *Hohenbuehelia* include the lack of asexual nematode-trapping state (previously called *Nematoctonus*), the lack of metuloids along the gill surface, and the digitate cheilocystidia. Unfortunately, photographs of this species were lost as the result of a hard drive failure in 2008, but excellent photographs by Michael Kuo can be seen on his online mushroom identification key website Mushroom Expert (www.mushroomexpert.com/resupinatus_alboniger.html). Based on molecular analysis, *R. alboniger* is a sister species to the clade of Australian species of the *Resupinatus violaceogriseus* species complex and *Resupinatus cinerascens* (see Chapter 2, Figure 2.1, and Chapter 4, Figure 4.3). In previous analyses (Thorn et al., 2005), the closest relative was *Resupinatus dealbatus*, a relationship that was not corroborated in this study. There appear to be two distinct geographic and host-related races of this species. The first, represented by a single collection (T-129.7), is from an unknown location in the United States, while the second consists of several collections (including one GenBank reference sequence) found exclusively throughout the Great Smokey Mountains National Park in North Carolina and Tennessee (USA; Figure 4.3). The separation of these two clades has high bootstrap support. This suggests that these populations are in the process of undergoing evolutionary divergence. Unfortunately, additional single-spore isolates, used to test mating compatibility, could not be obtained as no recent collections were made during this study. Sequences were generated from cultures propagated in culture collections (TENN).

Resupinatus dealbatus (Berk.) Singer, Beih. Sydowia 7:30. 1973.
≡ *Panus dealbatus* Berk., London J. Bot. 6: 317. 1847.
≡ *Panellus dealbatus* (Berk.) Murrill, N. Amer. Fl. (New York) 9(4): 245. 1915.
≡ *Pleurotus dealbatus* (Berk.) Pilát, Atlas Champ. l'Europe, II: *Pleurotus* Fries (Praha): 178. 1935.
≡ *Asterotus dealbatus* (Berk.) Singer, Mycologia 35(2): 161. 1943.

For a description of this species, see Thorn & Barron (1986).

Observations: *Resupinatus dealbatus* was not examined in this study, but a sequence in GenBank was used in the phylogenetic analysis of the group. The analysis again supports placement of the species in *Resupinatus* (Thorn et al., 2005; see Figure 2.1). Many

Resupinatus species grow on the underside of rotting wood, and this one is an exception: it grows supine on the top surface of the substrate, with the hymenium facing down. Recent collections made by Jan Thornhill near Havelock, Ontario, were reported too late to borrow for morphological and sequence analysis. These collection are now in the lab (UWO), and morphological and molecular analysis ongoing.

Resupinatus kavinii (Pilát) M.M. Moser, in Gams, Kl. Krypt.-Fl., Bd II b/2, ed. 4 (Stuttgart) 2b/2: 153. 1978.
≡ *Pleurotus kavinii* Pilát, Hyphomycetes 8: 23. 1931.
≡ *Resupinatus applicatus* f. *kavinii* (Pilát) Pilát, Micologia Veneta (Padova): 66. 1935.
≡ *Urospora kavinii* (Pilát) Singer, Beih. Botan. Centralbl., Abt. B 56: 145. 1936.
≡ *Geopetalum kavinii* (Pilát) Kühner & Romagn., Fl. Analyt. Champ. Supér. (Paris): 68. 1953.

Fruit Bodies: cupulate, 0.2-3 mm in diameter, with a central pseudostipe. Grey when dry and non-striate, tan to brown and non-striate when fresh. Hymenium smooth when fruit bodies are very small, and folded into gills when larger that radiate from location of pseudostipe, macroscopically brown to dark brown when fresh with white gill margins, composed of hyaline to pale brown basidia and basidioles with hyaline cheilocystidia. Cuticle slightly striate when dry or fresh in the largest fruit bodies, nonstriate in smaller ones, with a grey coarse tomentum at the point of attachment in older fruit bodies, a dense covering in grey to white surface hairs in younger fruit bodies, all becoming more glabrous at the margin. Flesh gelatinous between epicutis and gill trama, hyphae in gelatinous zone a light brown and 2-4.5 μm in diameter. Subhymenium dark brown, composed of gelatinized tightly packed hyphae 2.5-4.5 μm in diameter. All hyphae with clamps, and branching from clamps. Cuticle covered in hyaline, inamyloid, diverticulate hairs up to 50 μm long, 4-6 μm wide, with irregular finger-like projections up to 4 μm long.

Basidia: 4-spored, clavate, faintly brown in Melzer's, hyaline in KOH, 15-22 x (4.0-)4.5-5 μm

Cystidia: cheilocystidia along gill edges, diverticulate, (12-)13.5-18(-20) x (5.0-)5.5-7.5 μm, projections rounded, with encrusting crystals at the tips of the projections.

Spores: hyaline, inamyloid, smooth-walled, globose to subglobose, (4.0-)4.2-5.0(-5.2) x (4.0-)4.2-4.9(-5.1) μm

Substrate ecology: on decorticated rotting trunks of hardwood trees; observed on *Fagus* and also reported from *Ulmus* (Dämon, 2001)

Observed Distribution: Ukraine, also reported from Austria (Dämon, 2001), Poland (Gumińska, 2000), and the United Kingdom (Watling & Gregory, 1989; Legon & Henrici, 2005).

Holotype: PRM 497293 (!); "USSR, Ucraina Transcarpatica, in fagetis supra Kobylecka Polana", collected in July, 1929 by A. Pilát

Specimen examined: only the type was examined in this study.

Observations: *Resupinatus kavinii* is morphologically very similar to *Resupinatus applicatus*, but has fruit bodies that are much smaller than observed in any collection of *R. applicatus* (0.2-3.0 mm across on average in *R. kavinii*, compared to 3-10 mm across in *R. applicatus*). The fruit bodies are so small, in fact, that a few do not have any gills at all and are cyphelloid rather than lamellate. As the fruit bodies grow larger, the hymenium folds into gills (with the largest of the fruit bodies on the substrate having only ten gills; most have two to five gills). This is unusual in that no other species known in *Resupinatus* can have two different fruit body morphologies, depending on the stage of development. Even the smallest fruit bodies of *Resupinatus applicatus* (or any other species with lamellate or poroid fruit bodies in the group) have gills, and no gills were ever observed in species with large cyphelloid fruit bodies (such as *Rhodocyphella cupuliformis* and *Resupinatus griseopallidus*). As *R. kavinii* lacks sequence data from any collection, confirming that it is a distinct species from *Resupinatus applicatus*, despite morphological convergences, is not possible at this time. Due to the unusual duality in types of fruit bodies produced in this collection, it is considered a separate species until molecular evidence suggests otherwise. A concerted effort is needed to sequence European collections of *R. applicatus* with very small fruit bodies on *Fagus* (the substrate of the type collection) to compare with European collections of *R. kavinii*, as well as *R.*

appliatus with larger fruit bodies on other hardwood substrates, to determine if these are distinct species.
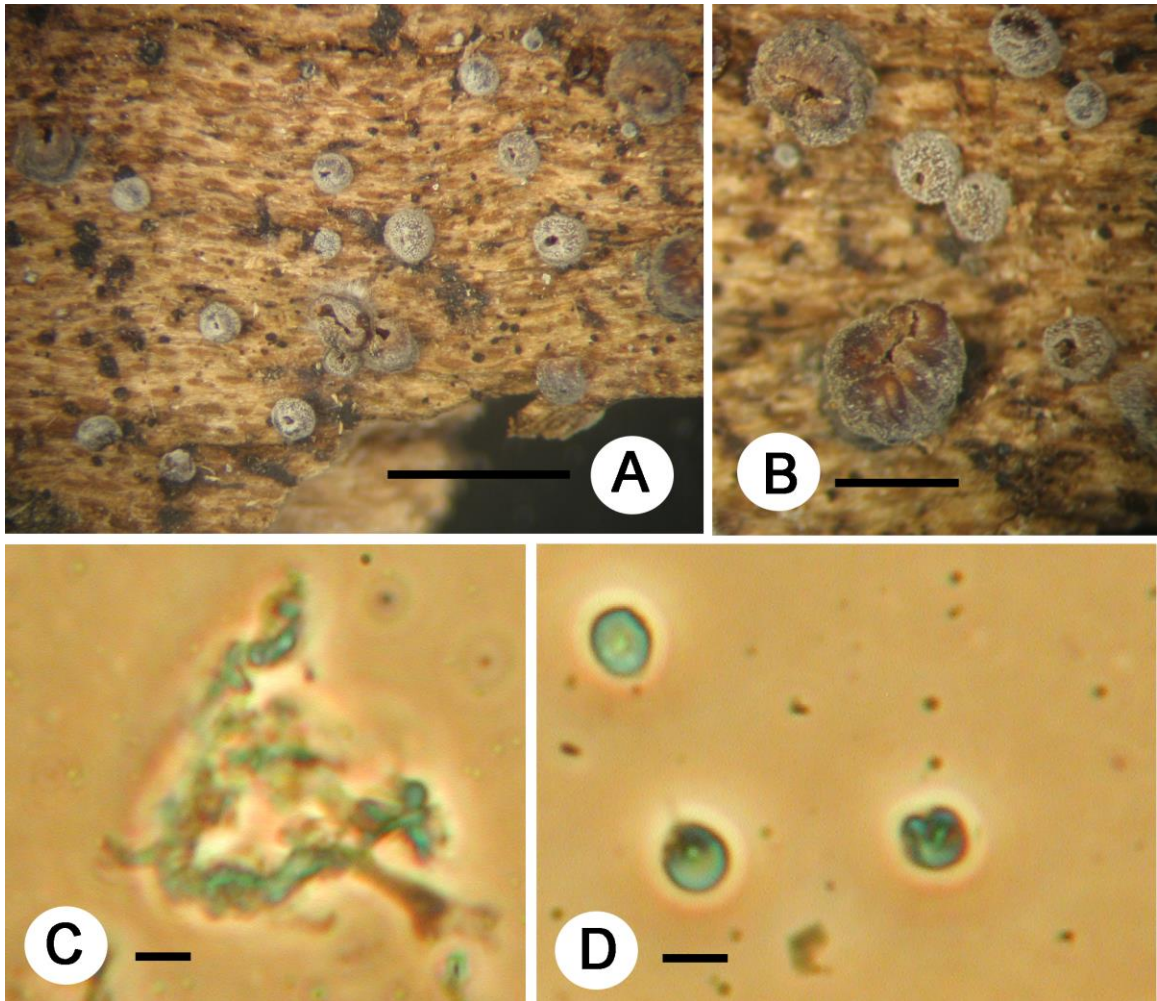
Figure 5.1 *Resupinatus kavinii*. A. Dried fruit bodies, many of which contain two or fewer gills due to their small size (Bar = 5 mm). B. The largest fruit body of the collection, with ten gills (Bar = 3 mm). C. A fragment of a surface hair (Bar = 10 µm). D. Basidiospores (Bar = 5 µm). All photographs are from the type collection, PRM 497293.

Resupinatus striatulus (Pers.) Murrill, N. Amer. Fl. (New York) 9(4): 242. 1915.
≡ *Agaricus striatulus* Pers., Syn. meth. fung. (Gottingen) 2: 485. 1801.
≡ *Pleurotus striatulus* (Pers.) P. Kumm., Fuhr. Pilzk. (Zwickau): 105. 1871.
≡ *Calathinus striatulus* (Pers.) Pat., Cat. Rais. Pl. Cellul. Tunisie (Paris): 28. 1897.
≡ *Acanthocystis striatula* (Pers.) Kühner, Botaniste 17: 112. 1926.
≡ *Geopetalum striatulum* (Pers.) Kühner & Romagn., Fl. Analyt. Champ. Supér. (Paris): 68. 1953.

Fruit Bodies: sessile, attached dorsally (occasionally laterally), 2-7 mm in diameter, grey-brown to black when fresh and becoming darker when dried. Cap finely pruinose; pileus appearing translucent-striate due to the folding of the hymenium, more noticeable near the margin. Margin entire or crisped (crenulate), in some fruit bodies nearly transparent, in others a lighter brown than the rest of the pileus. Gills radiate outwards from central or eccentric point, moderately narrow, same colour as the cap or slightly lighter in colour with a paler margin; gill margin entire. Cuticle made up of tangled hyphae with many incrusting crystals, yellow-brown in colour, 1.5-4 μm in diameter. Pileal trama strongly gelatinized, hyaline, hyphae 1.5-4 μm in diameter. Gill trama gelatinized, hyaline, becoming brownish near the hymenium, hyphae 2-4 μm in diameter. Subhymenium dark brown, hyphae becoming gelatinized as they extend into the trama. All hyphae with clamps. Hymenium made up of basidia and basidioles, light brown in Melzer's but pigment bleeding out in KOH.

Basidia: 4-spored, clavate, faintly brown in Melzer's, hyaline in KOH, (20-)22-28.5(-30) x (5-)5.5-6.5(-7) μm

Cystidia: cheilocystidia along gill edges, diverticulate, (12-)15.5-25(-26) x (5-)5.5-7.5 μm, projections rounded or tapering to a needle-like point, with encrusting crystals at the tips of the projections, dislodging with light pressure on the coverslip during the squash mount process.

Spores: hyaline, inamyloid, smooth-walled, globose to subglobose, (4.2-)4.7-5.4(-5.7) x (4-)4.7-5.3(-5.6) μm

Substrate ecology: on undersides of downed rotting trunks of coniferous trees and very well-rotted hardwood trees; observed on *Pinus, Fagus*, and other unidentified coniferous trees and hardwood trees.

Distribution: reported from Canada (BC, MB, NB, ON, QC), United States ("New England", NY), England, Germany (Thorn & Barron, 1986); observed from Australia, Czech Republic, Norway.

Type: Unknown

Specimens examined: B (70 0014065), CANB (574872), UPS (510561)

Observations: *Resupinatus striatulus* is often synonymized with *Resupinatus applicatus*, but if the two extremes of these species are compared, there are significant differences, not the least of which is the size of the fruit bodies; the fruit bodies of *Resupinatus striatulus* can be up to twenty times smaller and have ten times fewer gills than that of the largest *Resupinatus applicatus*. Coloration of the fruit bodies can also be quite different; from a tawny-brown to tan in *Resupinatus striatulus* to dark grey and almost blackened in *Resupinatus applicatus*. The substrate for growth also differs. The first difference in substrate is the species of tree: *Resupinatus striatulus* grows predominantly on coniferous trees (but also on well-rotted hardwoods), and *Resupinatus applicatus* only on hardwood tree species. Fries (1821) noted that he had seen examples of this species on *Corylus* and *Betula*, and the distinction between *Resupinatus applicatus* and *Resupinatus striatulus* can be explained by a textural difference in substrate: the degree of decomposition of the wood. A difference between these two species may be that *Resupinatus striatulus* is found growing on very well-rotted (by white rot) and softened wood, whereas *Resupinatus applicatus* grows on much harder wood that has not been as severely degraded, often with rinds or crusts of other fungi on the surface (Thorn & Barron, 1986). The species delineations used in this study correspond to the texture and the type of substrate: *Resupinatus applicatus* grows only on hardwoods with the structure and integrity of the wood still intact (less rotted wood than the next species), and *Resupinatus striatulus* grows only on conifers (or sometimes hardwood species) that have been previously well rotted by other wood decay fungi. This species delineation is supported by molecular evidence (see Figure 2.1 and Figure 4.3).
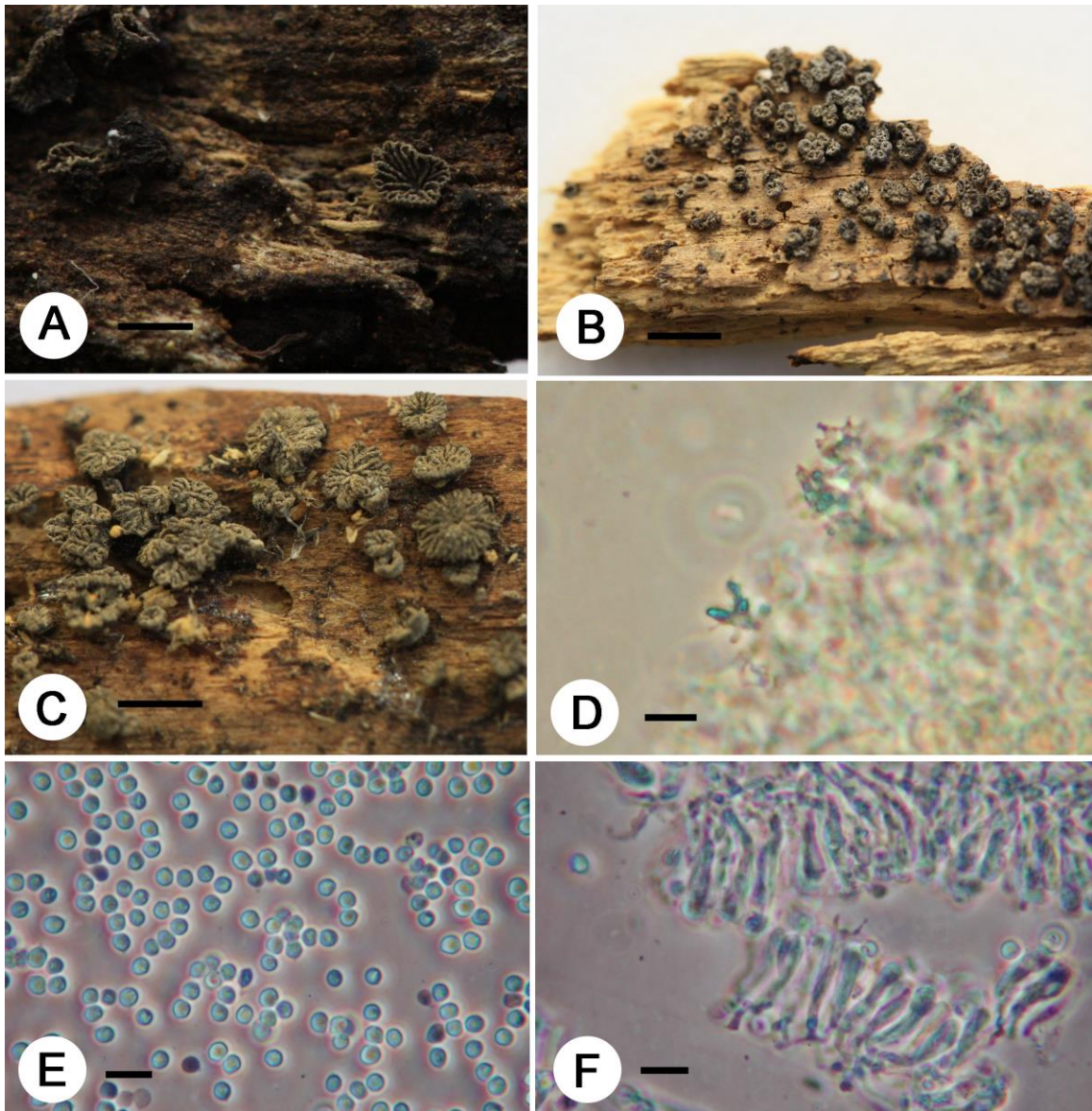
Figure 5.2 *Resupinatus striatulus*. A. Macromorphology of an Australian collection, showing the scalloped edges of the fruit body, reported from an unknown conifer species (CANB 574872; Bar = 5.0 mm). B. Macromorphology of the smallest fruit bodies observed of this species, from pine (B 70 0014065; Bar = 5.0 mm). C. Fruit bodies of a European collection on pine, with the same scalloped edges as the Australian collection (B 70 0014065; Bar = 5.0 mm). D. Cheilocystidia (CANB 574872; Bar = 10 μm). E. Basidiospores (UPS 510561; Bar = 10 μm). F. Basidium and basidioles (UPS 510561; Bar = 10 μm).

Resupinatus trichotis (Pers.) Singer, Persoonia 2(1): 48. 1961.
≡ *Agaricus trichotis* Pers., Mycol. eur. (Erlanga) 3: 18. 1928.
≡ *Resupinatus applicatus* var. *trichotis* (Pers.) Krieglst., Beitr. Kenntn. Pilze Mitteleur. 8: 177. 1992.

Fruit Bodies: cupulate to flattened in profile, 3-15 mm across (up to 20 mm across in one collection), nearly semi-circular (dimidate) to circular (orbicular) in face-view, sessile, grey or grey-black when fresh and drying slightly darker (almost blackened) with a raised area on the cuticle with shaggy black hairs (diverticulate under the microscope, dark brown, up to 500 μm long, 2-5 μm in diameter) near the point of attachment. Margin hairless when mature, pruinose when young. Gills radiate from a central point above the point of attachment to the substrate, narrow, grey-brown to nearly black with a light frosting on the margin. Pileal trama gelatinized, hyaline, made up of tangled hyphae 2-4 μm in diameter. Hymenial trama pale brown, gelatinized, with more densely packed hyphae of the same size. Subhymenium dark brown, made up of densely packed hyphae. Hymenium pale brown (in Melzer's) or hyaline (in KOH), made up of basidia and basidioles. All hyphae with clamps.

Basidia: 4-spored, clavate, hyaline in KOH, (16-)19-27(-30) x 5-6(-7) μm.

Cystidia: diverticulate cheilocystidia, 20-27 x 5-6 μm, with finger-like projections up to 2 μm long, hyaline.

Spores: hyaline, inamyloid, smooth-walled, subglobose to almost ovate (a few spores nearly globose), (4.5-)4.8-5.6(-6) x (4.1-)4.3-5.2(-5.5) μm.

Substrate ecology: on rotting wood of dicot trees; observed from *Acer, Fagus, Fraxinus,* and *Salix.*

Distribution: Reported from Great Britain, Hungary, Italy, Yugoslavia, Holland, Agentina, Brazil, Japan, Canada, and the United States (Thorn & Barron, 1986); observed from Australia, United States (PA, NJ, IL)

Type: Unknown

Specimens examined: AD-C (10962, 10964), DAR (64161), MEL (2292300)

Observations: *Resupinatus trichotis* is strikingly similar to *Resupinatus applicatus* (Pilát, 1935, for example, treated it as a form of *Resupinatus applicatus*, while Krieglsteiner, 1992, treated this species as a morphological variant of *Resupinatus applicatus*), but differs by the size and shape of its spores. As opposed to having the predominantly globose to subglobose spores, the species has predominantly subglobose to ovate spores. This, combined with the black tomentum of coarse hairs on the back of the pileus, makes it easy to recognize. Based on the molecular analyses presented in Chapters 2 and 4, *R. trichotis* is in a clade with *Resupinatus applicatus* 4from New Zealand and sister to the *Resupinatus applicatus* 3 clade from North America (LSU-only tree; Figure 2.1), or with *Resupinatus applicatus* 5 from Australia and *Resupinatus applicatus* 3 from North America (LSU and ITS combined dataset tree; Figure 4.3). Both trees have high bootstrap support for these clades.
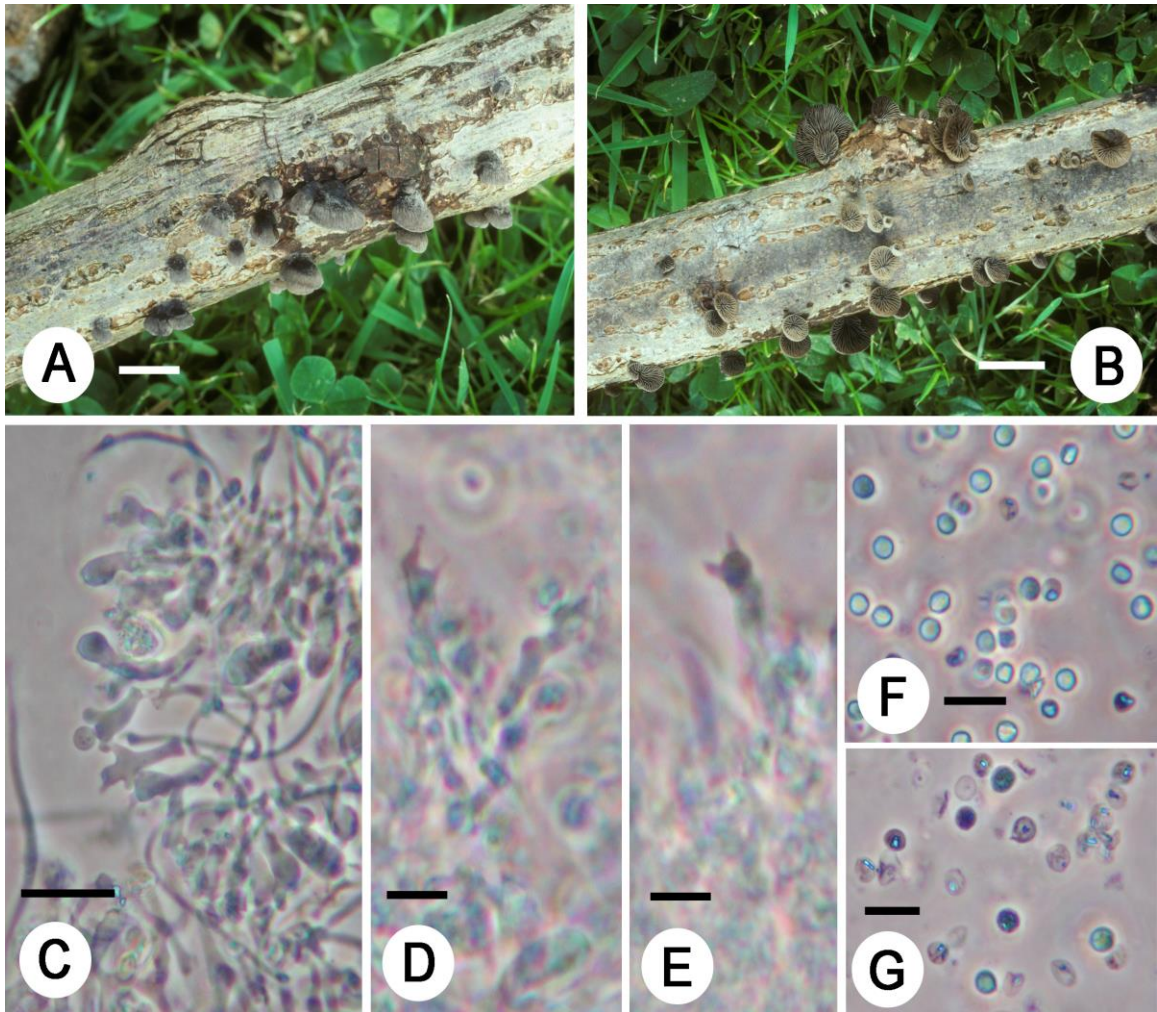
Figure 5.3 *Resupinatus trichotis*. A. Fresh fruit bodies, pileal surface (photo by R.G. Thorn, RGT860908/02; Bar = 15 mm). B. Fresh fruit bodies, hymenial surface (photo by R.G. Thorn, RGT860908/02; Bar = 15 mm). C. Cheilocystidia (DAR 64161; Bar = 25 μm). D. Cheilocystidia and a basidium (AD-C 10962; Bar = 10 μm). E. Basidium (AD-C 10964; Bar = 10 μm). F. Basidiospores (AD-C 10964; Bar = 10 μm). G. Basidiospores (MEL 2292300; Bar = 10 μm).

Resupinatus griseopallidus (Weinm.) Knudsen & Elborne, in Knudsen & Vesterholt, Funga Nordica, Agaricoid, Boletoid and Cyphelloid Genera (Gylling): 913. 2008.
≡ *Cyphella griseopallida* Weinm., Hymeno- et Gasteromycetes Florae Rossicae: 522. 1836.
≡ *Chaetocypha griseopallida* (Weinm.) Kuntze, Revis. Gen. Pl. (Leipzig) 2: 847. 1891.
≡ *Calyptella griseopallida* (Weinm.) Park.-Rhodes, Trans. Br. mycol. Soc. 37(4): 332. 1954.
≡ *Cellypha griseopallida* (Weinm.) W.B. Cooke, Beih. Sydowia 4: 54. 1961.
= *Lachnella myceliosa* W.B. Cooke, Beih. Sydowia 4: 74. 1961 (fide Knudsen & Vesterholt, 2008)
= *Cyphella taxi* Lév., Annls Sci. Nat., Bot., ser. 3 8: 336. 1841.
    ≡ *Chaetocypha taxi* (Lév.) Kuntze, Revis. gen. pl. (Leipzig) 2: 847. 1891.
    ≡ *Stigmatolemma taxi* (Lév.) Donk, Persoonia 2(3): 342. 1962.
    ≡ *Resupinatus taxi* (Lév.) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo, Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006. (per Knudsen & Vesterholt, 2008)
≠ *Rhodocyphella cupuliformis* (Berk. & Ravenel) W.B. Cooke, Beih. Sydowia: 105. 1961. (this study, see Chapter 2)

The description of this species has been reproduced from Knudsen & Vesterholt (2008) appended with data gathered in this study, which is indicated in italics.

Fruit Bodies: cup-shaped, solitary or in small groups, not seated in a subiculum. Cap 0.5-1.5 mm wide, 0.5-1 mm high, with incurved to straight, slightly wavy, entire margin, micaceous, pale grey; hymenium on inside smooth, dark grey brown; flesh tough, somewhat gelatinous. Cap surface with branched dendrohyphidia covered with pale yellowish crystals.

Basidia: (2-)4-spored. Clavate, hyaline or slightly clear-brown, 20-22.5 x 4.4-7 μm.

Cystidia: absent.

Spores: *asexual spores (borne on cuticular hyphae near the base of the fruit bodies) 5-5.5 x 4.5-5 μm, subglobose, slightly angular in outline from 3-4 low warts, apiculus short, hyaline. Sexual* spores subglobose to broadly elliptical, smooth-walled, inamyloid, hyaline, 4.5-5.5 x 4-5 μm.

Substrate ecology: scattered on wood and bark of dicotyledonous and coniferous trees in Europe; reported from *Clematis, Juniperus, Lonicera, Populus, Quercus, Salix, Syringa, Taxus, Vitis* (Knudsen & Vesterholt, 2008)

Observed distribution: Russia, France, Denmark, Czech Republic

Type: Unknown

Specimens examined: PRM 561126, and one personal collection sent as a gift from T. Lassøe (R 12489, Copenhagen).

Observations: the European species *Resupinatus griseopallidus* has been confused with the North American taxon *Rhodocyphella cupuliformis*, which has also gone under the names *Cyphella taxi* (Coker, 1921) or *Stigmatolemma taxi* (Gilbertson & Blackwell, 1986). However, the European taxon has smooth, ovate spores, as illustrated by Léveillé (1837, 1841), in contrast to the angular-spinose spores of *Rh. cupuliformis* (see Chapter 2, Figure 2.6). The European *R. griseopallida* occurs on eutrophic wood or bark of hardwood or coniferous hosts, often associated with green algae. Based on the phylogenetic analysis presented in Figure 4.3, this species does belong in *Resupinatus*. It has a similar morphology to other members of the *Resupinateae* (similar in morphology to lamellate members, but is too small to have the hymenium folded into gills), and is basal in the tree. Based on morphological and molecular analysis of several collections from North America (Figure 2.1 as "*Resupinatus taxi*" and Figure 4.3 as "*Rhodocyphella cupuliformis*") and a collection from Europe (Figure 4.3 as "*Resupinatus griseopallidus*"), three different species are part of this species complex: the North American *Rhodocyphella cupuliformis* on *Juniperus* (Chapter 2), the Australasian cyphelloid (a new species requiring a new name) on *Dacrycarpus* (Chapter 4), and the European *Resupinatus griseopallidus*.
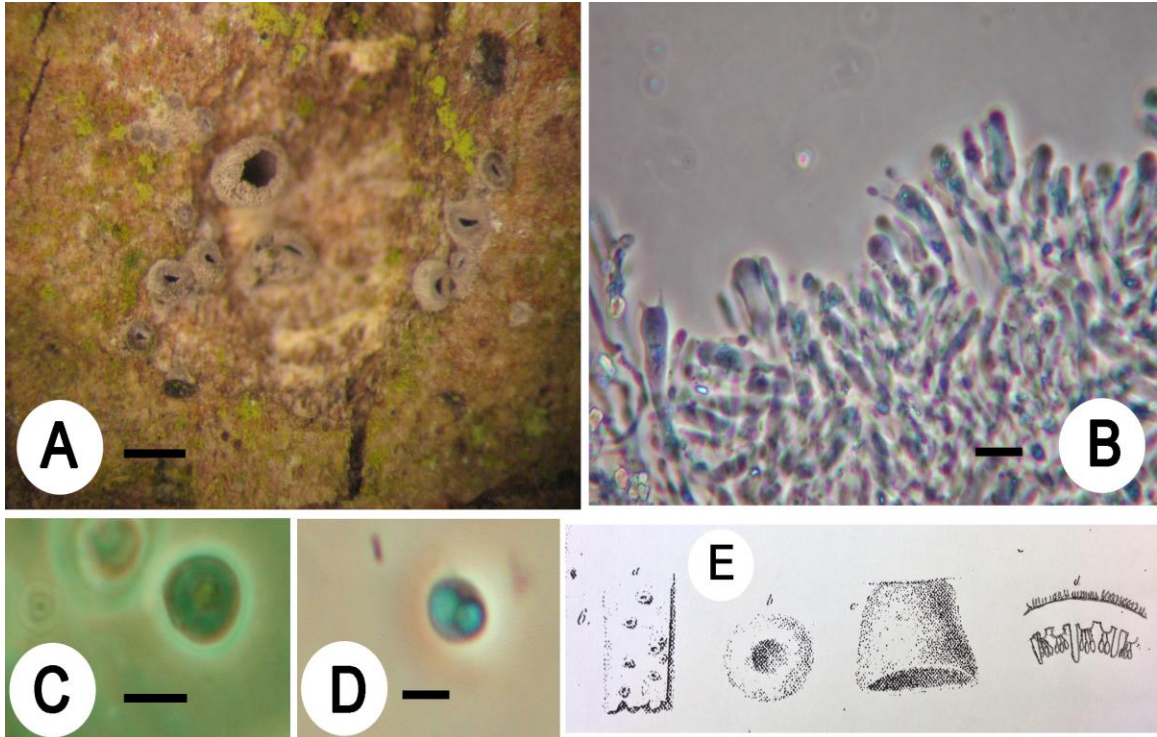
Figure 5.4 *Resupinatus griseopallidus*. A. Fruit bodies on the substrate (R 12489; Bar = 1.0 mm). B. Basidia (with attached immature basidiospores) and basidioles (R 12489; Bar = 10 µm). C. Basidiospore (PRM 561126; Bar = 5 µm). D. Basidiospore (R 12489; Bar = 5 µm). E. Original drawings by Léveillé, in original description of *Cyphella taxi*, of the fruit bodies on the substrate, a single fruit body from the top and from the side, and the hymenium with basidia and smooth, ovate basidiospores attached (no scale of drawings provided; Léveillé, 1841).

Resupinatus hyalinus (Singer) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo,
Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006.
≡ *Stigmatolemma hyalinum* Singer, Fieldiana, Bot. 21: 43. 1989.
Fruit Bodies: cupulate, light tan to brown when dried, nearly transparent when
rehydrated in distilled water; 0.5-1.0 mm in diameter, 0.3-0.5 mm high. Cups sessile in a
thickened subiculum (or a very dense coating of surface hairs, spreading onto the
substrate), creamy-white. When dry, margins of cups inrolling and cups becoming
flattened, exterior pruinose to granulose; when fresh cups broadly cupulate with inrolled
frosted margins, pileus pruinose. Cuticle with diverticulate Rameales-like surface hairs,
hyaline, up to 50 μm long, 3-6 μm in diameter, with finger-like projections up to 4 μm.
Pileal trama gelatinized, hyphae loosely tangled, 1.5-4 μm in diameter, hyaline.
Hymenial trama light brown in Melzer's and KOH, gelatinized, made up of densely
packed hyphae of the same size, but hyphae coiled in a "bedspring trama". Hymenium
smooth, made up of densely packed basidia and basidioles, pale brown in Melzer's,
hyaline in KOH. All hyphae with clamps.

Basidia: 4-spored, brown in Melzer's, hyaline in KOH, clavate, (18-)22-26 x 6-8 μm.

Cystidia: found around the top edge of each fruit body; similar to surface hairs with
finger-like projections (some more atypical cystidia with bulbous swellings and a single
projection from the top of the cell), up to 50 μm long.

Spores: hyaline, inamyloid, smooth-walled, oblong to elliptical, (5.5-)6-7.5(-8) x (3-)3.5-
4.5(-4.9) μm

Substrate ecology: on rotting wood of deciduous trees; observed on *Coprosma* and other
unidentified species.

Distribution: New Zealand, Brazil

Holotype: INPA 10565 (not seen); on wood of dead hardwood tree north of Manaus,
Brazil on January 30 1978 by R. Singer.

Specimens examined: PDD (7139, 16951)

Observations: *Resupinatus hyalinus* has only been reported once from the literature prior to this study (the type specimen in Brazil). Based on the morphology of the collections from New Zealand they are representative of this species, although this conclusion can only be based on the description of the type, as INPA does not loan herbarium specimens (type or non-type) outside Brazil. Singer (1989) provided a description (16 lines) and no accompanying drawings or photographs of the specimen. Without seeing the type specimen it is difficult to judge if the collections in New Zealand are, in fact, conspecific to *R. hyalinus*. Should examination of the type show that the New Zealand collections and the species Singer described from Brazil are not the same morphologically, the two collections from New Zealand will require a new species name in *Resupinatus*. Based on the type description, Thorn et al. (2005) felt confident in transferring this species into the genus *Resupinatus* where it is currently classified.
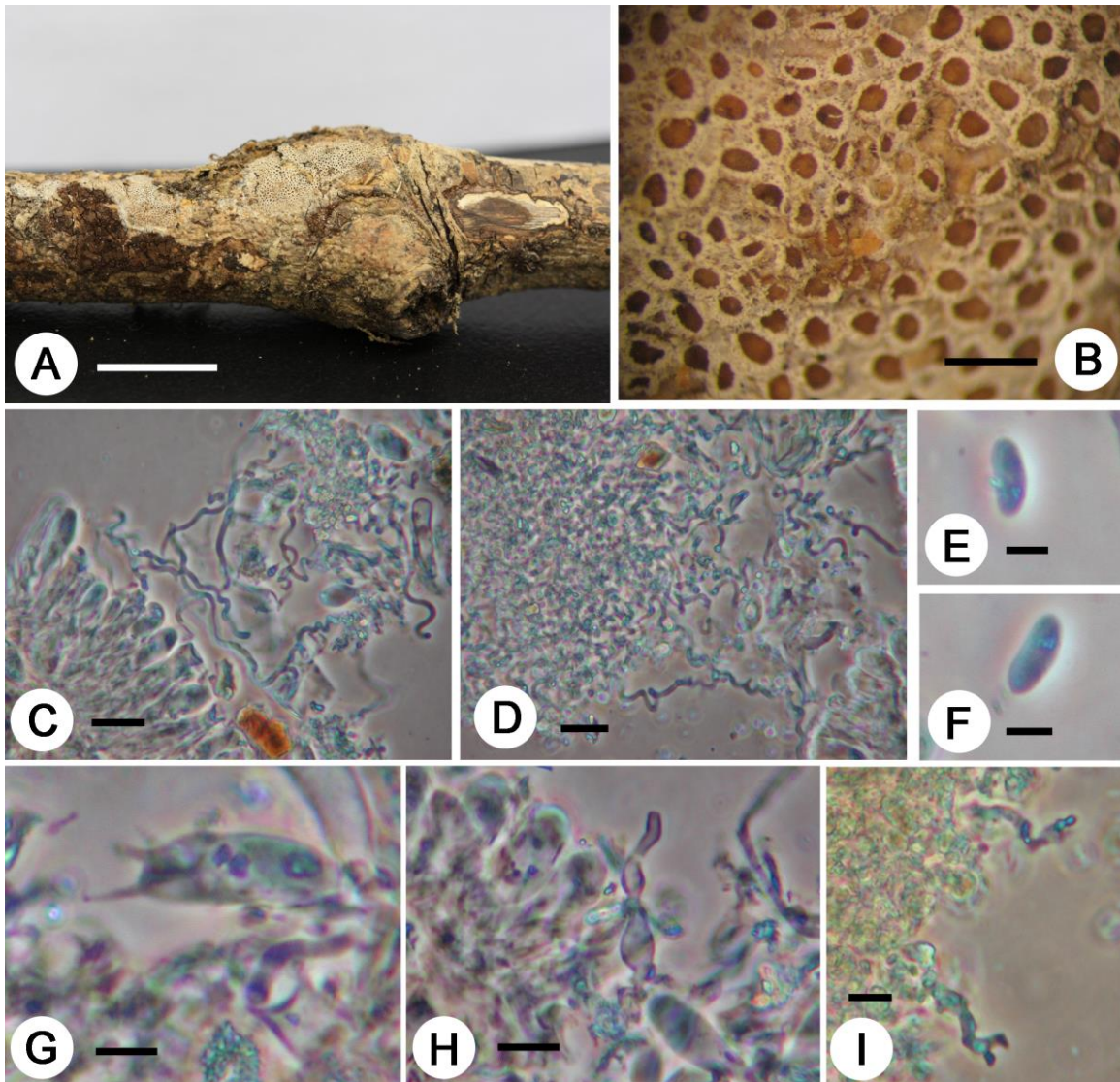
Figure 5.5 *Resupinatus hyalinus*. A. Substrate with an aggregation of fruit bodies (Bar = 20 mm). B. Macroscopic dried fruit bodies (Bar = 200 µm). C. Coiled hymenophoral trama hyphae with a portion of the hymenium (Bar = 10 µm). D. Coiled hyphae of the hymenophoral trama (Bar = 10 µm). E. Basidiospore (Bar = 5 µm). F. Basidiospore (Bar = 5 µm). G. Basidium with two sterimata visible (Bar = 10 µm). H. Atypical "bulbous" cystidium (Bar = 10 µm). I. Typical branching cystidia (Bar = 10 µm). All photographs from PDD 16951.

Stigmatolemma farinaceum (Kalchbr. & Cooke) D.A. Reid, Contr. Bolus Herb. 7: 22.
1975.

≡ *Cyphella farinacea* Kalchbr. & Cooke, Grevillea 9(49): 18. 1880

≡ *Chaetocypha farinacea* (Kalchbr. & Cooke) Kuntze, Revis. gen. pl. (Leipzig) 2: 847.
1891.

≡ *Phaeoglabrotricha farinacea* (Kalchbr. & Cooke) W.B. Cooke, Beih. Sydowia 4: 116.
1961.

Fruit Bodies: cups sessile, very dark in colour (nearly black), margins inrolling when dry, 0.3-1 mm in diameter. Surface of cups encrusted with mineral encrustations, "subiculum" made up of mineral matter, not hyphae, greyish-white. Pileal trama slightly gelatinized, hyphae 1.5-3 μm in diameter, hyaline, with large clamps. Gelatinization most prominent at point of attachment to the substrate. Subhymenium dark brown-black to olivaceous, giving the appearance of the hymenium being of the same colour, hyphae 1.5-3.5 μm in diameter. Hymenium made up of densely packed basidia and basidioles. Characteristics of the surface hairs indistinguishable due to the heavy incrustation of mineral matter on the exterior of all of the fruit bodies of the type collection examined.

Basidia: hyaline, 4-spored, clavate, slightly brown in Melzer's, hyaline in KOH, (15-)16-20 x (6-)6.5-7.5(-8) μm

Cystidia: none seen.

Spores: hyaline, inamyloid, smooth-walled, appearing granular on the interior, subglobose, (5.5-)6-8 x 5-6(-7) μm

Substrate ecology: on rotting wood of deciduous trees.

Distribution: South Africa

Type: K 166168 (!); on rotting wood, collected at the Cape of Good Hope, South Africa in September 1883 by Rev. C. Kalchbrenner

Specimens Examined: only the type collection exists under this name

Observations: *Stigmatolemma farinaceum* is currently treated (on IndexFungorum) as a synonym of *Resupinatus urceolatus* (so therefore a synonym of *R. poriaeformis* as these

two species are now synonymized and *R. poriaeformis* takes priority; see Chapter 3). Based on examination of the types of both species, this is incorrect. *Stigmatolemma farinaceum* (the last treatment of the species prior to its synonymization with *Resupinatus urceolatus*) can be distinguished from *Resupinatus poriaeformis* by its complete lack of subiculum, the fact that the trama is only weakly gelatinized, the subglobose (as opposed to globose) spores, and the colour of the fruit bodies. The type collection is the only known specimen, and it is in poor condition with very little material left on the substrate. Based on the morphological characteristics that could be discerned from the type collection, it is doubtful that it belongs in the *Resupinateae* at all, other than the fruit bodies being cyphelloid and there being gelatinization in the pileal and hymenial trama (which are characters that many species have converged on in different groups).
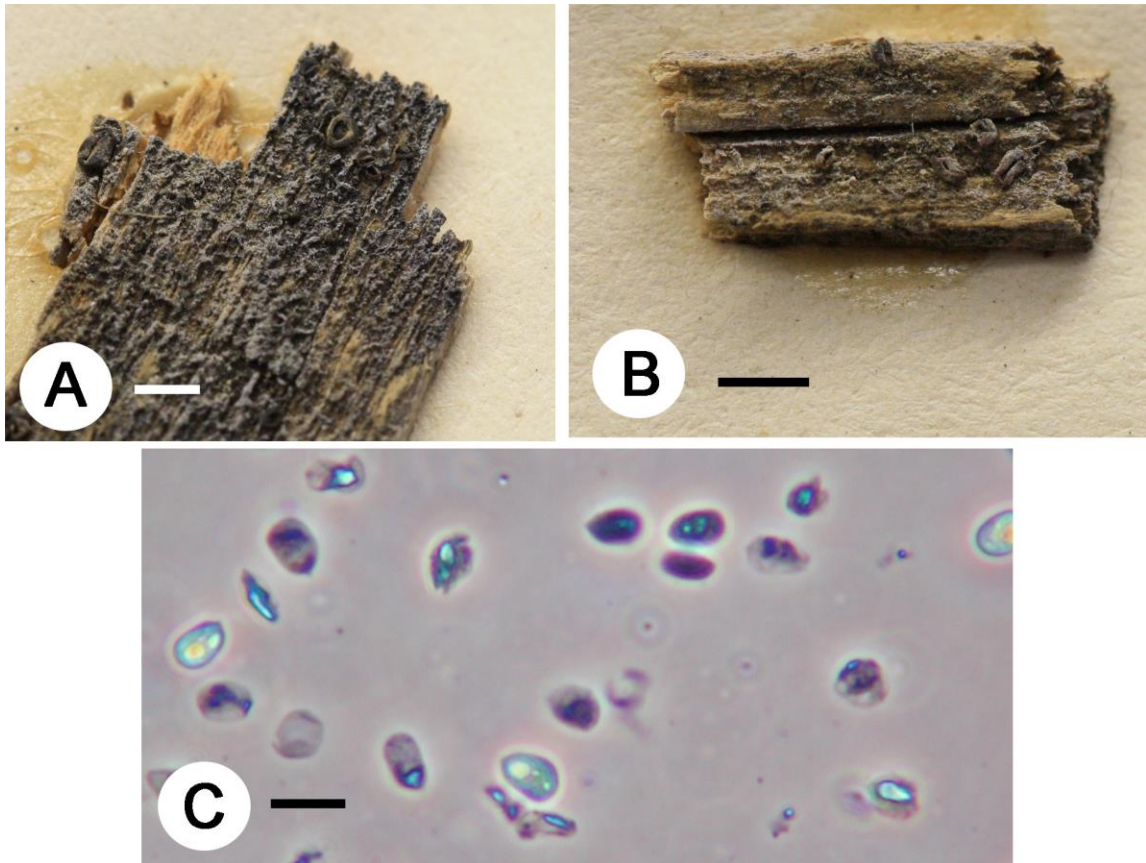
Figure 5.6 *Stigmatolemma farinaceum*. A. The largest two fruit bodies, with the mineral matter coating on the substrate clearly visible (Bar = 2 mm). B. One large and several smaller fruit bodies (Bar = 2 mm). C. Basidiospores (Bar = 10 μm). All photographs of the type collection, K 166168.

5.3.2   Lost species discovered in the literature

Cyphella brunnea W. Phillips, Grevillea 13(no. 66): 49. 1884.
≡ *Chaetocypha brunnea* (W. Phillips) Kuntze, Revis. gen. pl. (Leipzig) 2: 847. 1891.
= *Resupinatus poriaeformis* (Pers.) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo,
    Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006. (according to Donk, 1962)

Fruit Bodies: "sessile, scattered or crowded, cupulate, dirty-brown, clothed near the margin with a grey pruina; margin incurved, lacerated, mouth oblique; hymenium smooth, discoloured-brown; flesh paler, subgelatinous. Cups 0.5 mm across, 0.8 mm high" (from Phillips & Plowright, 1884)

Basidia: "clavate, two to four spicules" (from Phillips & Plowright, 1884)

Cystidia: none noted in the description.

Spores: "colourless, globose, 5-6 μm" (from Phillips & Plowright, 1884)

Substrate ecology: on bark and wood *of Sambucus* trees.

Distribution: United Kingdom (England)

Type: K (not seen); on wood and bark of elder trees, collected in Shrewsbury, England at an unknown date by W. Phillips.

Specimens examined: none; only the type collection exists under this name

Observations: based on the description of *Cyphella brunnea* provided in Phillips & Plowright (1884) and the expanded discussion of this species by Donk (1962), the species is a further synonym of *Resupinatus poriaeformis*. A subiculum is not mentioned in the description by Phillips, although Donk mentions that the subiculum is thin, nearly absent, crystal encrusted, and made up of clamped hyphae. The rest of the description, from the colour and size of the fruit bodies to the size and shape of the spores is consistent with all collections seen of *Resupinatus poriaeformis*. The type collection of this species was requested from the Kew herbarium but it was not received.

Peziza pruinata Schwein., Schr. naturf. Ges. Leipzig 1: 120. 1822.

≡ *Tapesia pruinata* (Schwein.) Sacc., Syll. fung. (Abellini) 8: 379. 1889.

≡ *Porotheleum pruinatum* (Schwein.) Pat., Essai Tax. Hyménomyc. (Lons-le-Saunier): 57. 1900.

Fruit Bodies: cups gregarious, in groups of 15-30, nearly black with a whitened exterior due to the dense surface hairs, 125-200 μm in diameter, margin incurved when fresh and when dry, pileus covered with hyaline diverticulate surface hairs up to 75 μm long. Subiculum pure white, very thick and dense, effused, occupying patches on the substrate approximately 0.5-1.5 cm long and 0.3-0.5 cm wide. Pileal trama gelatinized, hyaline, hyphae 1.5-4 μm in diameter. Hymenial trama gelatinized, dark brown, hyphae 1.5-4.5 μm in diameter. Hymenium smooth, hyaline in KOH, slightly brownish in Melzer's, made up of basidia and basidioles. All hyphae with clamps.

Basidia: 4-spored, clavate, hyaline in KOH, 17-20(-24) x 5-6(-6.5) μm

Cystidia: none seen but surface hairs extend all the way to the margin of the cup and could act as cystidia.

Spores: hyaline, inamyloid, smooth-walled, oblong to cylindrical, (5.5-)6-7 x 3-3.5(-4) μm

Substrate ecology: on bark of old *Vitis* vines.

Distribution: United States (MD, NC)

Specimens examined: BPI (258312, 258313, 798457), FH (258740, 258741, 258757), NYBG (38(1), 38(2), 805)

Observations: *Peziza pruinata* is morphologically identical to *Tapesia daedalea* (Chapter 3) with the exception of substrate (this species is exclusively on grape vine), as well morphologically very similar to the type of the former genus *Stigmatolemma*, *Resupinatus incanus* (from which it differs by geographic distribution). A slight

difference in subiculum micromorphology can be observed between *T. daedalea* and *P. pruinatum*: under the dissecting microscope the subiculum of *P. pruinatum* appears to be grainy (a characteristic that cannot be quantified by a measurement) and when examined microscopically a large number of very small cuboid crystals are seen to originate from the hyphae that make up the subiculum (the cuboid crystals are not present in *T. daedalea*). Unfortunately, DNA extraction and amplification from this species is not possible as it has not been collected or documented since the 1880s. Prior to that date the species was thought to be rare, although it turns up often in herbaria, mislabeled as *Solenia poriaeformis* or *Porotheleum poriaeforme* (as annotated by W.B. Cooke). The lack of collections of this species after 1900 reflects poor conservation practices in old growth forests as well as forests managed for the lumber trade; grape vines require support for growth and smother the plants under it, thus decreasing the potential value of lumber (Smith, 1984; Callow & Parikh, 2012). Grape vines were evidently removed from forests, such that old growth grape vine (very large vines estimated to be 50 years of age or older) is becoming exceedingly rare. Currently, grape vines are only managed in forests actively used to produce lumber and no longer in natural areas in Canada or the United States, and as a result, the vine populations are maturing. Unfortunately, the fungal biota that once inhabited vines may never return as chemical herbicides (with ingredients known to be toxic to many species of fungi) were heavily employed to control grape populations in the 1970s and 1980s (Smith, 1977; Hamel, 1983).

Grape bark is a unique substrate due to the phenolic compounds present in the stem (Souquet et al., 2000). These phenolic compounds can be toxic to many species of fungi and are likely to select in favour of fungi capable of breaking them down (Guiraud et al., 1995). For this reason, despite the morphological similarities between the collections examined of this species and those of *Tapesia daedalea*, the ability of *Peziza pruinata* to grow on a substrate with such high concentrations of potentially toxic phenolics, it should be considered a separate species from *T. daedalea* until further genetic comparisons (using recent collections of both species) can be made.
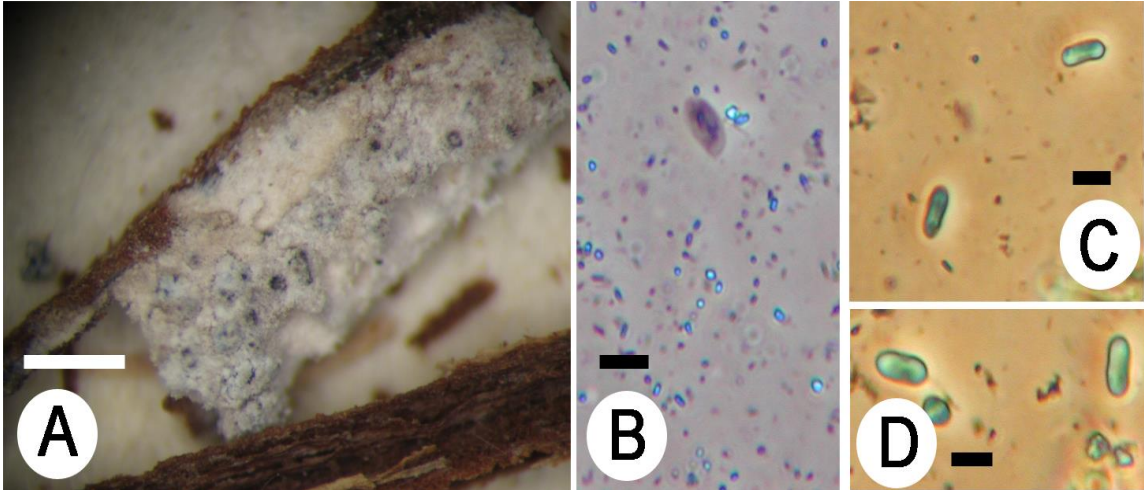
Figure 5.7 *Peziza pruinata*. A. Fruit bodies and grainy subiculum on the substrate (Bar = 500 μm; BPI 258313). B. Cuboid crystals characteristic of the hyphae that make up the subiculum, giving it the grainy appearance (Bar = 5.0 μm; BPI 258312). C. Basidiospores (Bar = 5.0 μm; BPI 258312). D. Basidiospores (Bar = 5.0 μm; FH 258741).

5.3.3   Possible species of *Resupinateae*

Porotheleum reticulatum Petch, Ann. Roy. bot. gard. Peradeniya 7(4): 289. 1922.
=? *Resupinatus poriaeformis* (Pers.) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo, Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006. (this study)
Fruit Bodies: cupulate, 250-750 μm in diameter, sessile, scattered, 50-150 in a group (drying in smaller groups within a patch; each dried group containing 25-40 cups). Subiculum very thin and wispy, almost absent in areas, heavily encrusted. Cups brown when fresh, drying lighter brown to almost tan with white surface hairs, heavily encrusted with small (2-3 μm across) cuboid white crystals. Hairs highly branched, up to 50 μm long, branches finger-like, up to 3 μm long. Trama made up of gelatinized hyphae, loosely packed, 1.5-3.5 μm in diameter, becoming more densely packed in subhymenium. Trama hyaline, subhymenium dark brown. Hymenium smooth, made up of tightly packed basidia and basidioles, hyaline. All hyphae with clamps, branching points originate from clamps.

Basidia: clavate, 4-spored, very thin and straight, hyaline in KOH, 22-30 x 5-7 μm.

Cystidia: none.

Spores: hyaline, inamyloid, smooth-walled, contents appearing granular at times, globose to subglobose, 5.0-5.3 x 5.0-5.2 μm.

Substrate ecology: on dead, rotting wood of dicot trees.

Distribution: Sri Lanka

Holotype: K 166169 (!); on dead wood, collected in Hakgala, Sri Lanka (Ceylon) in April 1919 by T. Petch.

Observations: based on morphology, *Porotheleum reticulatum* may be a synonym of *Resupinatus poriaeformis*. The species should not be confused with *Cyphella reticulata* Berk. & Broome (1875). Should a more recent collection of *Porotheleum reticulatum* be found, a comparison should be made of the ITS sequences of this species and *Resupinatus poriaeformis* to ensure they are indeed conspecific, especially since the morphologically inseparable North American and European taxa apparently represent separate species (Chapter 2).
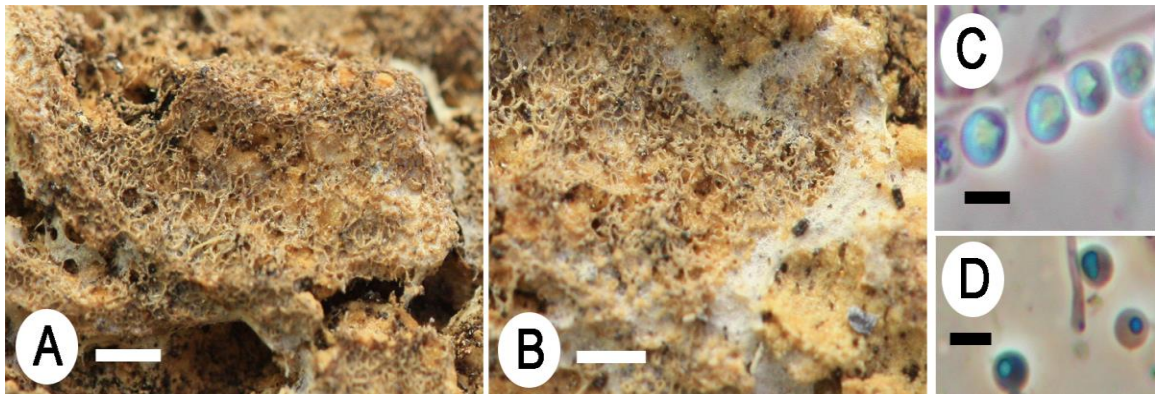
Figure 5.8 *Porotheleum reticulatum*. A. Mature fruit bodies (Bar = 1.0 mm). B. Younger fruit bodies and the white edge of the subiculum (Bar = 1.0 mm). C. Basidiospores (Bar = 5.0 μm). D. Basidiospores (Bar = 5.0 μm). All images are of the type collection, K 166169.

Solenia subporiaeformis Burt, Ann. Mo. bot. Gdn. 11: 24. 1924.
Fruit Bodies: sphaerical to cupulate, 150-250 µm in diameter, appearing embedded in a very thick, dense grayish subiculum. Cups dark brown when fresh, drying darker (nearly black), covered in a dense mat of white hairs (diverticulate, up to 80 µm long with projections 2-4 µm long, hyaline under the microscope). Trama gelatinized, made up of loosely woven hyaline hyphae 1.5-4 µm in diameter, branching from clamps. Subhymenium nearly black, made up of tightly packed gelatinized hyphae, 1.5-3.5 µm in diameter. Hymenium hyaline in KOH, slightly brownish in Melzer's, made up of tightly packed basidia and basidioles. All hyphae with clamps.

Basidia: 4-spored, clavate, hyaline in KOH, brownish in Melzer's, characteristically short compared to other species in the group, (9-)12-20 x (6-)6.5-7 µm.

Cystidia: none seen; surface hairs extend nearly to the mouth of the cup and become shorter as they near the margin.

Spores: hyaline, inamyloid, smooth-walled, oblong, (5.6-)6.4-7.2 x (2.4-)2.8-3.5(-4) µm

Substrate ecology: on rotting wood of decorticated dicot trees

Distribution: Venezuela

Holotype: BPI 258361 (!); collected on Margarita Island, Venezuela on July 11, 1903 by A.F. Blakeslee

Specimen examined: only the type exists.

Observations: *Solenia subporiaeformis* appears appears superficially identical to *Resupinatus poriaeformis* but can be distinguished by its ovate to oblong spores as opposed to the globose spores that *R. poriaeformis* has. Based on morphological characters of the collection examined, this species belongs in the *Resupinateae.*

A number of similarities exist between this species and some of Rick's collections of *Theleporus griseus*, especially those which he annotated as *Solenia grisella* var.

theleporea (FH 258750, FH 258751), an unpublished name, and one of the two Farlow collections of *Theleporus griseus* (FH 258748). Without having seen the type of *Theleporus griseus* it is impossible to determine if *T. griseus* and *S. subporiaeformis* are synonyms (in which case *T. griseus* has priority). The habitats are the same (tropical forest) and macroscopic and microscopic characters are very similar, and slight differences in morphology could be attributed to age of fruit bodies when collected, amount of moisture present during fruit, or amount of care taken during the drying process.
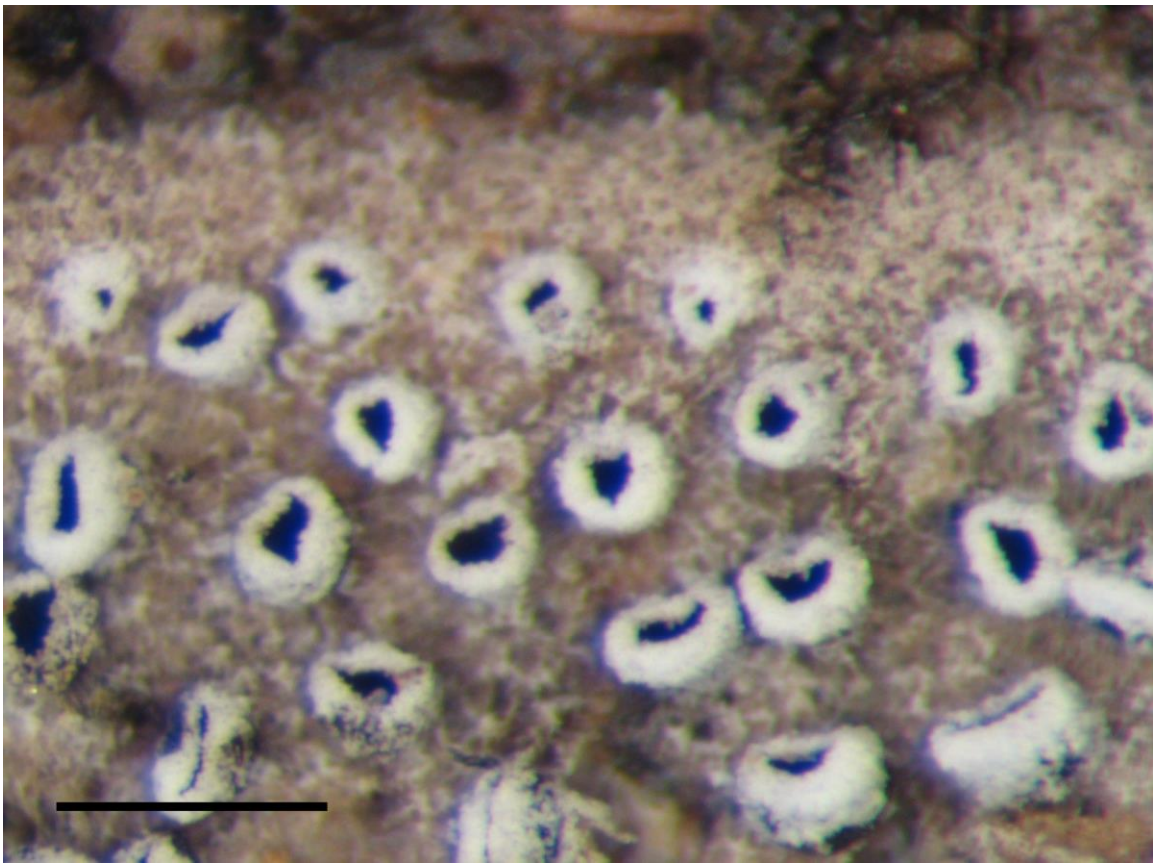
Figure 5.9 *Solenia subporiaeformis*. Macroscopic image of the fruit bodies and the edge of the subiculum (Bar = 500 μm; BPI 258361). Microscopic images of the spores and a basidium were lost in a computer hard drive failure in 2008.

Tapesia tela (Berk. & Curtis) Sacc., Syll. fung. 8: 373. 1889.

≡ *Peziza tela* Berk. & Curtis, Grevillea 3: 156. 1875.

≡ *Cyphella tela* (Berk. & Curtis) Massee, Jour. Myc. 6: 179. 1891.

= *Peziza daedalea* Schwein., Trans. Am. phil. Soc., Ser. 2 4(2): 174. 1832. (this study, Chapter 3)

Type: K 166164 (!); on wood, collected in South Carolina, USA prior to 1875 by M.J. Berkeley.

Additional specimen examined: FH (258744; co-type)

Observations: *Cyphella tela* was first described by Berkeley and Curtis, and transferred to *Tapesia* by Saccardo, who remarked that it was nearly identical to *Peziza* (*Tapesia*) *pruinata*, but did not synonymize them (Saccardo, 1889). Massee also thought that the species could be distinguished from *Peziza pruinata* based on spore colour: *Tapesia tela* has brown spores and *Peziza pruinata* has hyaline spores (a finding not supported in this study; Massee, 1891). Burt (1926) did not note the similarity of the two species, but did remark that *Tapesia tela* is nearly identical to *Peziza daedalea*, which he did personally observe. Having viewed the type collections (portions in K and FH), I conclude that *Tapesia tela* is the same as *Peziza daedalea* and should be considered a synonym. The two co-type collections are compared against the type of *Peziza daedalea* in Figure 5.10, which clearly shows that one cannot distinguish the spores of the species from those of *Peziza daedalea*, and all other morphological characteristics are identical. *Peziza daedalea* differs from *Peziza pruinata* by growing on hardwood species, not grape vine.
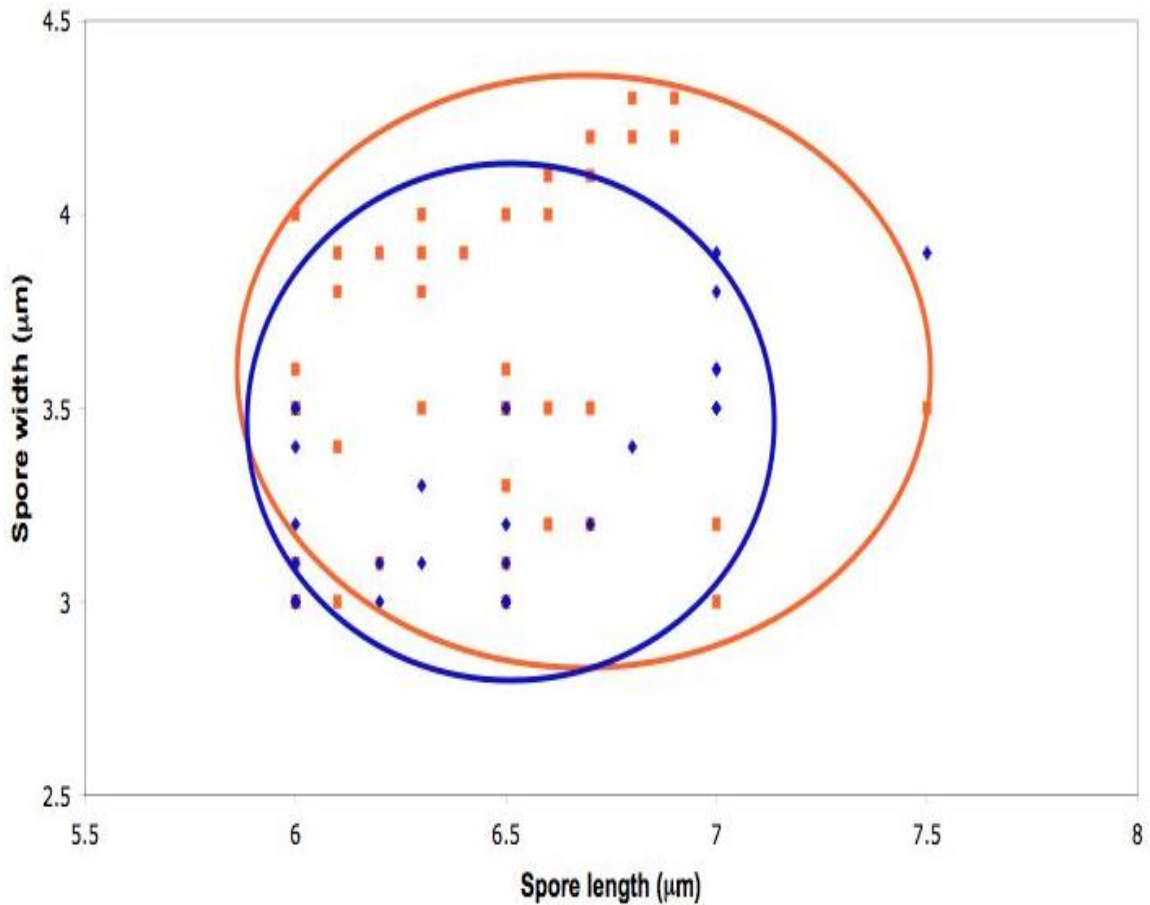
Figure 5.10 Spore distribution graph showing the spore length and width (measured in μm) of the type collections of *Cyphella tela* (orange squares, n = 50 spores) and the type collection of *Peziza daedalea* (blue diamonds, n = 34 spores). These names represent three collections of the same species as evidenced by their overlapping spore size distributions. The collections are identical in all other respects, including collection location (South Carolina). Outlines represent the spore distribution for 99% of the data for *Cyphella tela* and 95% of the data for *Peziza daedalea*.

Rhodocyphella grisea (Petch) W.B. Cooke, Beih. Sydowia ser II: 106. 1961.
≡ *Cyphella grisea* Petch, Ann. R. bot. Gdns. Peradeniya 7(4): 289. 1922.
Fruit Bodies: scattered, at most 5-10 close together on the substrate, no subiculum, heavily crystal-encrusted, cup-shaped, 0.5-1.5 mm in diameter, margin inrolling when dry. Exterior grey to grey-brown in older fruit bodies, cream-ish in younger fruit bodies, hymenium smooth and darker than the exterior (brown to darker grey-brown in older fruit bodies, tan to brown in younger fruit bodies), made up of basidia and basidioles. Trama slightly gelatinized, made up of loosely-woven hyaline hyphae 1.5-3.5 μm in diameter. Hymenial trama brown, slightly gelatinized, made up of more tightly packed hyphae 1.5-4.0 μm in diameter. Surface hairs few, appearing more pronounced when dry, tightly packed near the point of attachment to the substrate; diverticulate, 20-50 x 4.5-5.5 μm. All hyphae clamped, branching from clamps.

Basidia: clavate to subclavate, hyaline in KOH, faintly brown in Melzer's, 4-spored, 18-25 x 4-6 μm.

Cystidia: none seen.

Spores: sexual spores hyaline, inamyloid, smooth-walled, appearing granular on the interior, shortly ovoid to elliptical, 6-7 x (5-)6-6.5 μm; asexual spores hyaline, inamyloid, jack-shaped with six long spines 2-3 μm long, 3.8-4.1 x 3.8-4.0 μm.

Substrate ecology: on fibrous bark of a *Rubus*-like tree (Petch, 1922)

Distribution: Sri Lanka

Type: K 166165 (!); collected on *Rubus*-like fibrous bark in Hakgala, Sri Lanka in December 1917 by T. Petch.

Specimen examined: only the type exists

Observations: *Rhodocyphella grisea* is nearly identical in all respects to *Resupinatus griseopallida* with the exception of the substrate, which could not be determined with certainty, and the distribution (where *Resupinatus griseopallida* is a European species; see Chapter 5). More recent collections from Sri Lanka are desirable for sequence

comparisons with *R. griseopallida*. This taxon also shows the unusual characteristic of having two different spore types produced from two different locations within the fruit body: smooth, ovate spores are produced on basidia, and jack-shaped spores produced from somewhere near the base of the fruit body (only apparent in squash-mounts, which make it difficult to determine where these spores originate).
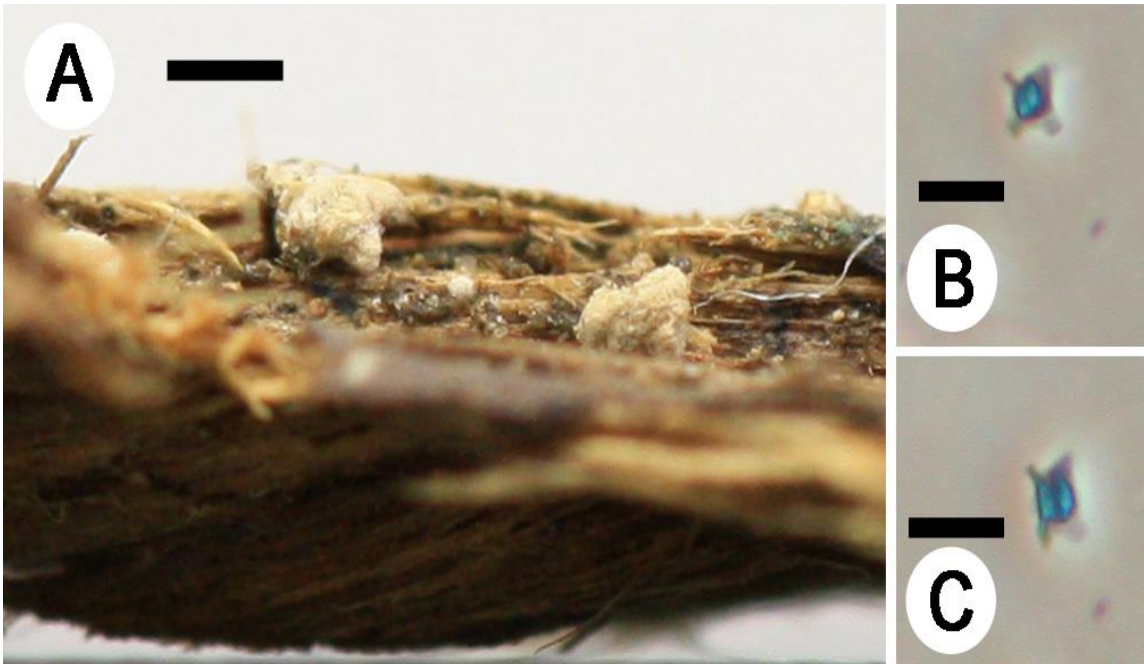
Figure 5.11 *Rhodocyphella grisea*. A. Immature fruit bodies, prior to the pigment in the pileus darkening (the darker pseudostipe can be seen in the fruit body at the top left of the image; Bar = 1.0 mm). B. Asexual spore produced from hyphae near the base of the fruit body (Bar = 10 μm). C. Asexual spore (Bar = 10 μm). All images are from the type collection, K 166165.

Maireina pseudurceolata W.B. Cooke, Beih. Sydowia ser. II: 92. 1961.
= *Resupinatus poriaeformis* (Pers.) Thorn, Moncalvo & Redhead, in Thorn, Moncalvo,
   Redhead, Lodge & Martin, Mycologia 97(5): 1148. 2006. (this study)

Type: PRM 171929; collected in Aveyron, France in November 1905 by Galzin (not
seen).

Observations: based on the description by Cooke (1961), *Maireina pseudurceolata* is
probably a synonym of *Resupinatus poriaeformis*.

Cellypha subgelatinosa (Berk. & Ravenel) W.B. Cooke, Beih. Sydowia 4: 58. 1961.
≡ *Cyphella subgelatinosa* Berk. & Ravenel, Grevillea 2(no. 13): 5. 1873.
≡ *Chaetocypha subgelatinosa* (Berk. & Ravenel) Kuntze, Revis. gen. pl. (Leipzig) 2: 847.
   1891.
Fruit Bodies: sessile, cupulate, brown to almost dark olive-green when dry (brown to
grey-brown when fresh), found in groups of 1-4 cups on the substrate. Exterior of cups
appearing fused together, margins inrolling and becoming frosted white when dry,
opening 150-300 μm in diameter, becoming larger (250-400 μm in diameter) when
rehydrated. Fruit bodies embedded in a brown to grey-brown subiculum raised off the
substrate, 0.5-1.5 mm across, erupting out of lenticels or other bark wounds or cracks.
Pileal trama strongly gelatinized, composed of hyaline hyphae loosely packed, 1.5-4 μm
in diameter. Hymenial trama composed of brown to yellow-brown hyphae more tightly
packed, also strongly gelatinized, 2-4.5 μm in diameter. Hymenium appearing dark
brown but hyaline in cross-section, smooth, composed of basidia and basidioles. Surface
hairs present along exterior of the frutification (not present in the dense subiculum that
appears to fuse the cups together), diverticulate with branches finger-like (up to 2 μm
long), hyaline, up to 100 μm long. All hyphae with clamps and branching from clamps.

Basidia: 2- or 4-spored, clavate, hyaline in KOH, 26-28 x 6-8 μm.

Cystidia: present along the margin of each cup (giving the frosty-white appearance when
dry), hyaline, with clamps at base, diverticulate, asterostromelloid or Rameales-like, with
finger-like projections up to 2 μm long, 15-25 x 4.5-6 μm.

Spores: hyaline, inamyloid, smooth-walled, cylindrical to elongate, 7.8-9.5 x 3.0-3.5 µm.

Substrate ecology: erupting from lenticels (or other wounds or cracks) in bark of rotting wood; observed on *Alnus.*

Distribution: United States (SC)

Holotype: K 166170 (!); on bark of *Alnus serrulata*, collected in Aiken, South Carolina in 1870 by H.W. Ravenel.

Specimen examined: only the type exists.

Observations: *Cellypha subgelatinosa* is similar in many respects to *Stromatocyphella conglobata* (see Chapter 2 for a description of this species). It differs in the colour of the fruitifications (olive-green or brown when dry versus the dark grey to nearly black of *Stromatocyphella conglobata*), and the number of fruit bodies in a single fruitification (very few in *C. subgelatinosa* versus 10-30 cups, never single cups, in *S. conglobata*). The type specimen was examined by Cooke (1961) before the species was transferred to *Cellypha*, but his description doesn't match the collection, the type description (Berkeley & Ravenel in Berkeley, 1873), or the expanded description of the type by Burt (1914). Cooke (1961) describes the fruit bodies as olive-green (as opposed to the brown to black or tan colouring in Berkeley (1873) or brown to tan in Burt (1914)), and the basidia nearly two times smaller than descriptions previous to his, and 4-spored instead of 2-spored as noted by Burt, and the surface hairs as being brown, when Burt notes that these are hyaline (a feature observed in this study).

Should *C. subgelatinosa* be collected again, DNA analysis would likely show that it is closely related to *Stromatocyphella conglobata*, based on their morphological similarity. This might, however, simply be an example of convergent evolution as is so often seen in the *Resupinateae* and the species might be most closely related to a lamellate member of *Resupinatus*. Based on the morphological analysis performed on the type collection of *Cellypha subgelatinosa*, it belongs in the *Resupinateae*.
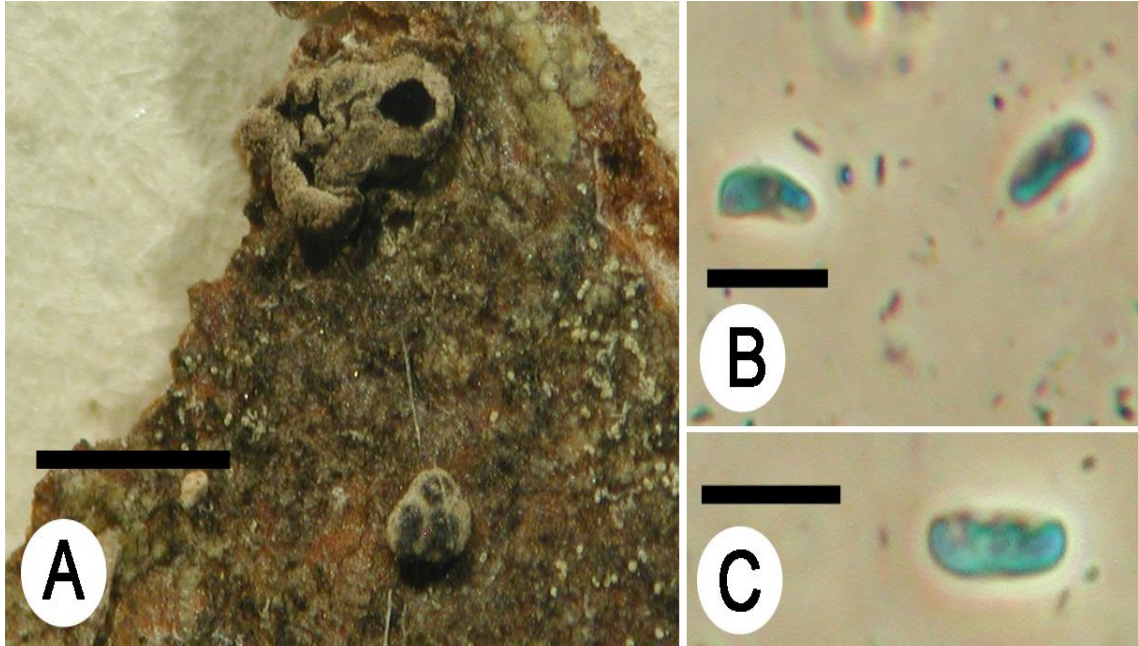
Figure 5.12 *Cellypha subgelatinosa.* A. Fruit bodies (Bar = 1.0 mm). B. Basidiospores (Bar = 10 μm). C. Basidiospore (Bar = 10 μm). All images are from the type collection, K 166170.

5.3.4   Notable collections

Three collections that are morphologically identical to *Resupinatus poriaeformis* require further examination using molecular sequence analysis. The three collections would expand the known range and habitat of *R. poriaeformis* should they be members of the same species, having been recovered in tropical Brazil (FH 258749), the Canary Islands (O 12606), and the tropical island of Mayotte, near Madagascar (PC 85422). Due to the fact that the name *Resupinatus poriaeformis* has traditionally been applied to at least two different species, it can be assumed that the three collections represent a single new tropical species of *Resupinatus* with cyphelloid fruit bodies (or potentially up to three new species).

5.4   Conclusion

As a result of literature searches for this study, six new species names can now be added as synonyms of species that are already recognized as members of *Resupinatus* or are in the *Resupinateae*: *Cyphella brunnea, Maireina pseudurceolata, Porotheleum reticulatum*, and *Solenia tephrosia* are synonyms of *Resupinatus poriaeformis*, *Rhodocyphella grisea* is a synonym of *Rhodocyphella cupuliformis* (in *Resupinatus*), and *Cyphella tela* is a synonym of *Tapesia daedalea* (a species that belongs in *Resupinatus*). Five species discovered in the literature are new to *Resupinatus* as a result of this study: *Tapesia daedalea, Peziza pruinata, Solenia subporiaeformis,* and *Cellypha subgelatinosa.* Since all of the new species added to the group based on this analysis are species with cyphelloid fruit bodies, it stands to reason that the number of times the cyphelloid fruit body morphology has evolved has also increased in number, but until recent collections of these species are found, that is merely an assumption.

This study echoes the need of reevaluating species published with very short type descriptions and then lost to science. This is not a new idea; it was brought up as far back as 1896 when Erwin F. Smith stated that mycologists of the future would be better off and their jobs would be easier if half the fungal species descriptions at the time had never been written (Smith, 1896).

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Chapter 6

6 Excluded and Understudied Species

6.1 Introduction

The *Resupinateae* are a group of fungi that have been largely ignored in the recent mycological literature. Sequences of a few taxa have been included in recent molecular studies of the *Agaricales* (Thorn et al., 2000; Moncalvo et al., 2000; Moncalvo et al., 2002; Hibbett & Binder, 2002; Bodensteiner et al., 2004; Binder et al., 2005; Thorn et al., 2005), but many species that are or may be members of this group have not been treated since the time of their description in other genera and families. A goal of this project was to rediscover some of these "lost" species in the literature and assign them names according to current classification systems (see Chapter 5) and, along the way, to provide better identifications for the many collections of *Resupinateae* that have been deposited in herbaria identified only to the genus or family level. Type and other specimens of lost species were requested on loan, along with underidentified collections that might belong to the *Resupinateae*. Collections and species that did belong in the *Resupinateae* are discussed in the previous chapters, and those that were unavailable for study, unrelated to the *Resupinateae*, or unidentifiable are presented here.

6.2 Materials and Methods

6.2.1 Herbarium samples

Letters were sent by the late Dr. Jane Bowles (UWO Herbarium) to herbaria around the world, requesting dried specimens for use in microscopic analyses of species thought to belong to *the Resupinateae* and fungi with cyphelloid fruit bodies that are "under identified" according to their herbarium labels (AD, ARIZ, B, BPI, CANB, C, FH, GBIF, GJO, HO, INPA, K, L, MEL, NCU, NYBG, O, PC, PDD, PH, PRC, PRM, S, STR, TENN, UPS; herbarium acronyms following Holmgren et al., 1990, updated at http://sciweb.nybg.org/science2/IndexHerbariorum.asp).

6.2.2   Herbarium collection analysis

Notes and measurements were taken of dried collections for fruit body size (in mm), colour and shape; location of attachment to the substrate; presence and characteristics of surface hairs; average number of gills (if present); presence of cheilocystidia; and presence or absence of a subiculum or subiculum-like structure. Small portions of dried fruit bodies were rehydrated, and changes in colour of the fruit body and surface hairs were noted. Photographs of the dried collections and rehydrated portions were taken. The rehydrated portions of the fruit body were sectioned by hand using a razor blade and squash-mounted on a microscope slide.

Two mounts were made on each microscope slide, each one being stained differently to emphasize different microscopic characters. The first group of sections were stained using Melzer's reagent, and the second group with a 2% potassium hydroxide (KOH) solution (Largent, 1977). Melzer's reagent is used to visualize spore characteristics, hyphal characteristics, and surface hair characteristics. Separation of cells in these tissues is much more effective in KOH, so this solution is used to visualize characteristics of basidia and cheilocystidia. Spore colour is also sometimes difficult to discern in Melzer's so basidiospore colour is confirmed in KOH.

All microscopic measurements are represented in micrometers (μm). Basidiospore, basidium, cystidia and surface hair measurements are represented as a range, with values in parentheses representing the smallest and largest values, and the size range representing values between the tenth and ninetieth percentiles (as per Thorn and Barron, 1986). The range of ratios of spore length to width is reported as Q. Other measurements (for example the diameter of hyphae, or the sterigma length and width) are represented as a range of values (smallest and largest measurements) based on observed collections.

Specimens outside the scope of this thesis (*Resupinateae*) were studied microscopically by Dr. R.G. Thorn for identification; his determinations are reported here. For a full description of the methods involved in microscopic analyses, refer to Chapter 2.

6.2.3   Molecular methods

DNA was extracted from dried collections using portions of the rehydrated fruit body. The material was finely chopped using a sterilized razor blade and 50 mg of tissue was put into a micro-bead tube from the MoBio Bacterial DNA Isolation Kit (MO BIO Laboratories, Carlsbad, California), or the Thermo Scientific GeneJET Plant Genomic DNA Purification Mini Kit (Thermo Fisher Scientific Inc., Waltham, Massachusetts) with added garnet beads to provide additional mechanical disruption. Other steps followed the manufacturers' protocols.

The DNA in the extraction product was amplified in a Biometra T1 Thermocycler (Montreal Biotech) according to Koziak et al. (2007) and the fungal primers ITS1 (5'—TCCGTAGGTGAACCTGCGG—3'; White et al., 1990) and LR5 (5'—ATCCTGAGGGAAACTTC—3'; Vilgalys & Hester, 1990), amplifying the 3' end of the small ribosomal subunit (SSU) through the ITS1, 5.8S, ITS2, and the 5' end of the large ribosomal subunit (LSU; including the D1/D2 variable domains). Presence or absence of a PCR product was determined using gel electrophoresis in a 1.5% agar gel made in TAE electrophoresis buffer containing 0.5 µg/mL ethidium bromide (EtBr).

Once the presence of the desired size of PCR product was confirmed, the PCR products were cleaned using the QIAquick PCR purification kit (Qiagen, Mississauga, Ontario) or the BioBasic PCR purification kit (Bio Basic Canada Inc, Markham, Ontario) and quantified using a Nanodrop 2000 machine. Cleaned PCR products were sent for sequencing at the Robarts Research Institute at Western University on an ABI Illumina sequencing platform (Applied Biosystems). Sequences were cleaned and assembled in SeqEd v1.03 (Applied Biosystems Software, Foster City, California).

The sequences generated in this study (see Appendix B for a full list of sequences used) were aligned with those already available in GenBank using MEGA5 v5.05 for Mac (Tamura et al., 2011), and then MEGA6 v6.06 once released (Tamura et al., 2013). The ingroup used to construct the Patagonian campanelloid tree consisted of 72 sequences of 62 different taxa (five *Omphalotus* sequences of five taxa were represented in the outgroup), resulting in an alignment of 1254 characters. The dataset was trimmed to 828

characters so all sequences were of the same length in the alignment, and the resulting alignment file was exported for further analysis. The ingroup used to construct the Chilean *Hohenbuehelia* tree consisted of 36 sequences of 20 taxa (six *Pleurotus* sequences of six different taxa, and five *Cortinarius* sequences of five different taxa were chosen as outgroups), resulting in an alignment of 1345 characters. The dataset was trimmed to 1218 characters so all sequences were of the same length, and the alignment file was exported for analysis.

Phylogenetic analyses using maximum likelihood and maximum parsimony methods were performed in MEGA5/6 using LSU sequence data. Node support in both analyses was assessed using bootstrapping, with 1000 replicates (only values greater than 70% are shown). The model of nucleotide substitution chosen for all maximum likelihood trees in this chapter was the General Time Reversible (GTR) model, and it was assumed that the rate of substitution was uniform across all sites and taxa. Gapped positions were deleted.

The heuristic model used for tree inference was the Nearest-Neighbour-Interchange (NNI) model with a strong branch swap filter, and the initial tree was constructed using BioNJ. Since maximum likelihood and maximum parsimony trees were identical with only minor differences in boostrap values, only the maximum likelihood trees are shown. Full descriptions of molecular methods used are in Chapter 2.

6.3   Results and Discussion

6.3.1   Chilean collections believed to belong in the *Resupinateae*

Six collections thought to represent two novel species of Patagonian *Resupinateae* were received from Pablo Sandoval, Universidad de Chile, Santiago. The first species belongs in a group with *Gymnopus* and *Marasmius* (the /marasmioid clade; Wilson & Desjardin, 2005), but is on its own branch and is also a monotypic genus. The Maximum Likelihood ITS-LSU tree including two sequences of this species (P79 and 007) is shown in Figure 6.1. The second is a new species of *Hohenbuehelia*. The Maximum Likelihood ITS-LSU tree including a sequence of this new species of *Hohenbuehelia* (P80), as well as other species of *Hohenbuehelia* sequenced as part of this study, is shown in Figure 6.2.

Figure 6.1 Maximum Likelihood (ML) phylogeny of the marasmioid-gymnopoid clades based on the ITS-LSU gene regions of the nuclear-encoded rDNA gene. Statistical support was calculated from 1000 bootstrap replicates; only values higher than 70% are shown. The placement of P79 and 007, the new Patagonian species, is in a new clade and represents a new genus. Taxon names in bolded text are GenBank reference sequences (GenBank accession numbers before the name, and strain or collection numbers, if known, after the name), and taxon names in regular font were sequences generated in this study (with strain or collection numbers before the name). Clades and taxa are labelled according to Wilson & Desjardin (2005).

AY207236 *Marasmiellus ramealis* (GLM 45958)
AY639407 *Campanella eberhardtii* (DEH465-SFSU)
AY639422 *Gymnopus melanopus* (AWW54-SFSU)
99 AF223173 *Gymnopus peronatus* (CBS 426.79)
FJ750262 *Gymnopus subnudus* (TENN 61138)
AY639429 *Gymnopus subpruinosus* (DED6674-SFSU)
98 AY639417 *Gymnopus gibbosus* (AWW112-SFSU)
AY639421 *Gymnopus luxurians* (DEH1304-SFSU)
AY639412 *Gymnopus brunneigracilis* (AWW01-SFSU)
AY639413 *Gymnopus diminutus* var. *attenuatus* (AR099-SFSU)
AY639426 *Gymnopus nonnullis* var. *attenuatus* (AWW05-SFSU)
AY639435 *Marasmiellus synodicus* (DED5258-SFSU)
78 KJ189590 *Gymnopus eneficola* (TENN 69122)
KJ189578 *Gymnopus confluens* (TENN 67865)
84 KJ189570 *Gymnopus biformis* (TENN 65586)
AY639425 *Gymnopus menehune* (AWW87-SFSU)
AY639418 *Gymnopus indoctus* (AWW03-SFSU)

/marasmiellus

AF356165 *Lentinula lateritia* (STCL149)
99 AF261557 *Lentinula edodes* (TMI1941)
AF261561 *Lentinula novaezelandiae* (TMI1172)
77 AF261558 *Lentinula boryana* (RGT960624)
97 AF356147 *Lentinula raphanica* (Duke HN 2002)
99 AF261559 *Lentinula raphanica* [as *L. boryana* (HN2002)]

Lentinula

AY639439 *Rhodocollybia badiialba* (D.L.Largent 9199-SFSU)
AY639880 *Rhodocollybia maculata* (AFTOL-ID #540)
72 FJ750251 *Gymnopus incarnatus* (TENN 61089)
FJ750252 *Rhodocollybia butyracea* (TENN 60927)
90 GU369967 *Rhodocollybia unakensis* (TENN 58545)
93 GU369966 *Rhodocollybia lignitilis* (TENN 56628)
AY639441 *Rhodocollybia laulaha* (DED5873-SFSU)

Rhodocollybia

99 P79 Patagonian campanelloid
007 Patagonian campanelloid

/"gymnopanelloid" (new clade)

AY639438 *Marasmius copelandii* (DED5607-SFSU)
92 AF261329 *Marasmiellus opacus* (JEJ.574)
AY635776 *Marasmius alliaceus* (AFTOL-ID #556)
AY639437 *Marasmius applanatipes* (DED6628-SFSU)

Mycetinis

93 AF042628 *Micromphale perforans* (RV83/67)

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The reference sequences to place the new Patagonian *Hohenbuehelia* species (as well as other sequences belonging to species in *Hohenbuehelia* generated from cultures) were obtained using the phylogeny in Koziak et al. (2007). The outgroup was chosen based on a GenBank search where a *Pleurotus* sequence was queried and the closest non-*Hohenbuehelia* and non-*Pleurotus* match was used. TENN3003 is a culture sent as part of request for collections of *Resupinateae* in the University of Tennessee culture collection, and was originally misidentified by the collector as *Resupinatus alboniger*. As in Koziak et al. (2007), the top part of the tree still needs to be resolved, with three separate clades, denoting three different species, all named *Hohenbuehelia grisea* or *Nematoctonus robustus*.

6.3.2   Unidentified fungal culture T-919

One culture sequenced as a result of this study was originally identified as *Stigmatolemma taxi*, collected on *Juniperus* sp. from the Louisiana State University Campus by RG Thorn (T-919; see Appendix B for more information about this culture). Based on the ITS-LSU rDNA sequence obtained from this culture, this taxon cannot be assigned to any genus or family, as it has no close relatives in GenBank. The highest percent identity over the entire gene region, the partial ITS and/or LSU gene regions in GenBank was 82% to a species of *Nolanea*, but when sequences were aligned and put into a tree they did not group together in a clade (see Figure 2.1).

Figure 6.2 Maximum Likelihood (ML) phylogeny of *Hohenbuehelia* and *Pleurotus* species based on the ITS-LSU gene regions of the nuclear-encoded rDNA gene. Statistical support was calculated from 1000 bootstrap replicates; only values higher than 70% are shown. The placement of P80, the new Patagonian species, is in a clade with other species of *Hohenbuehelia* once believed to belong in *Resupinatus* due to the lack of conspicuous metuloids. Taxon names in bolded text are GenBank reference sequences (GenBank accession numbers before the name, and strain or collection numbers, if known, after the name), and taxon names in regular font were sequences generated in this study (with strain or collection numbers before the name). Sections of the tree unresolved in previous phylogenetic analyses of the group (i.e. the *Hohenbuehelia grisea* and *Nematoctonus robustus* clade at the top of the tree) were left with the names assigned to them in GenBank or in Koziak et al. (2007) as it was outside the depth of this study to deal with these taxonomic issues.

TENN 3003 *Hohenbuehelia grisea*
AF139952 *Hohenbuehelia grisea* (T-014a)
EF409760 *Hohenbuehelia grisea* (RGT010805/02)
EF546657 *Nematoctonus robustus* (ATCC MYA-4145)
EF409762 *Nematoctonus robustus* (01-RGTSN-526)
EF409759 *Nematoctonus robustus* (03-RGTSN-571)
EF409756 *Hohenbuehelia grisea* (RGT040611/01)
AF139959 *Hohenbuehelia portegna* (T-7)
EF409724 *Hohenbuehelia concurrens* (T-183b)
EF409765 *Hohenbuehelia subreniformis* (T-138b)
T-921.12 *Hohenbuehelia elegans*
AF139960 *Hohenbuehelia* sp. (RGT940206/01)
EF409753 *Nematoctonus pachysporus* (01-RGTSN-532)
EF409736 *Hohenbuehelia mastrucata* (T-025a)
EF409766 *Hohenbuehelia tylospora* (04-RGTSN-512)
EF409743 *Hohenbuehelia* sp. (RGT010810/02)
EF546659 *Hohenbuehelia leiospora* (ATCC MYA-4143)
EF409726 *Nematoctonus geogenius* (T-019a)
AF139956 *Hohenbuehelia petalodes* (T-104)
EF409720 *Hohenbuehelia angustata* (RGT020615/08)
EF409728 *Hohenbuehelia tremula* (T-083)
P80 *Hohenbuehelia* "patagonicus"
EF409722 *Hohenbuehelia pinacearum* (T-107)
EF409721 *Hohenbuehelia unguicularis* (T-047)
AY450342 *Pleurotus australis* (NZPR-215)
AY450348 *Pleurotus abieticola* (isolate 6554)
AY450347 *Pleurotus eryngii* (isolate 6690)
AY450346 *Pleurotus populinus* (isolate 9936)
AY450345 *Pleurotus ostreatus* (isolate 6689)
AY450349 *Pleurotus pulmonaris* (isolate 4203)
RGT010805/01 as "black *Hohenbuehelia*"
KJ635222 *Cortinarius carbonellus* (PDD:103685)
KJ635242 *Cortinarius* sp. (PDD:97543)
KJ635229 *Cortinarius xenosma* (PDD:88274)
KJ635245 *Cortinarius orixanthus* (PDD:97556)
KJ635240 *Cortinarius olivaceoniger* (PDD:97540)

0.02

6.4 Taxonomy

6.4.1 Species formerly placed in the *Resupinateae*

Aphyllotus campanelliformis Singer, Beih. Sydowia 7: 29. 1973.

Fruit Bodies: occurring singly on the substrate, cup shaped with a central pseudostipe, becoming more ear-shaped with age, up to 20 mm long and 15 mm wide, nearly transparent at the edge of the fruit body and becoming darker brown, almost black, towards the base. Surface hairs highly branched, some appearing nearly asterostromelloid (as in *Resupinatus dealbatus*), hyaline. Pileal trama weakly gelatinized, becoming more strongly gelatinized towards the pseudostipe, composed of hyaline hyphae 2.5-4 μm in diameter.

Basidia: 4-spored, clavate, brown in KOH, (19-)20.5-22.5(-25) x (3.5-)4-5(-6) μm .

Cystidia: none.

Spores: hyaline, inamyloid, smooth-walled, subglobose to ovate (few observed with the eccentric bulge described by Singer, 1989), (5.2-)5.6-7(-7.2) x (-2.4)2.6-2.8(-3.5) μm

Substrate ecology: on rotting wood and bark of deciduous trees in the tropics

Distribution: Colombia

Holotype: F B6034-1013515 (!); on bark of unidentified tropical tree species, collected in Futagasuga, Cundinamarca, Colombia in April 1968 by R. Singer.

Specimen examined: only the type was seen.

Observations: based on a morphological analysis of the type collection, there is no evidence to suggest that *Aphyllotus campanelliformis* belongs in the *Resupinateae*. The species was described by Singer using morphological characters consistent with members of the *Resupinateae*, but other groups show similar characteristics through convergent evolution (for example, the branched surface hairs that are typical in the *Resupinateae* can also be found in some members of the *Marasmiaceae*). Singer later stated himself

that morphological characters present in *A. campanelliformis* can also be found in *Campanella* and *Marasmius* (Singer, 1989), and *A. campanelliformis* is likely a close relative of the two genera. The collection observed, aside from being the type specimen, was not suitable for DNA analysis due to a paucity of material. A species described from Kenya, *Stipitocyphella keniensis* (Kost, 1998), is possibly a relative of *A. campanelliformis* in the *Marasmiaceae*, but without morphological evidence the transfer of *Stipitocyphella* to *Aphyllotus* is not appropriate.

Porotheleum fimbriatum (Pers.) Fr., Observ. Mycol. (Havniae) 2: 272. 1818.
≡ *Poria fimbriata* Pers., Neues Mag. Bot. 1: 109. 1794.
≡ *Boletus fimbriatus* (Pers.) Pers., Syn. Meth. Fung. (Gottingen) 2: 546. 1801.
≡ *Polyporus fimbriatus* (Pers.: Fr.) Fr., SM 1: 506. 1821. (non *Polyporus fimbriatus* Fr. (1830, Linnaea 5: 520)
≡ *Stromatoscypha fimbriata* (Pers.) Donk, Reinwardtia 1: 218. 1951.
≡ *Stigmatolemma fimbriatum* (Pers.) Pouzar, Ceska Mykol. 12(1): 27. 1958.

For a description of this widely distributed species, see Donk (1951).

Type: Unknown.

Specimens examined: PH 01074204, and one collection found during this study (JVM041009/02)

Observations: *Porotheleum fimbriatum* was formerly considered a member of the *Resupinateae* due to its thick, dense subiculum and small, cup-shaped fruit bodies. DNA analysis (not shown; Moncalvo et al., 2002) indicates that it belongs in the *Meripilaceae* (Kirk et al., 2008), not in the *Resupinateae*, and so it was excluded from study. *Porotheleum* is currently a monotypic genus (see IndexFungorum.org), but *Stromatoscypha defibulata*, described from Australia (Agerer, 2005), is likely a member as well.

6.4.2   Understudied species in the *Resupinateae*

Stigmatolemma poriforme (Henn.) W.B. Cooke, Beih. Sydowia 4: 128. 1961.
≡ *Cyphella poriformis* Henn., Bot. Jb. 22: 85. 1897

The description of this species is translated from the original source (Hennings, 1897).

Fruit Bodies: densely gregarious, subiculum pale, wispy-hairy, cupules membranous, sessile, concave, greyish yellow, externally hairy, margin ciliate, inrolled, hymenium smooth, becoming yellow, about 3 mm diameter.

Basidia: not mentioned

Cystidia: none mentioned

Spores: subglobose, hyaline, smooth, 1-1.5 µ. (very likely an error)

Substrate ecology: on rotting palm leaf sheaths in tropical Africa

Distribution: Cameroon

Holotype: collected in Itoki, Cameroon by P. Dusen in February 1891, believed to have been lost in the bombing of Berlin (Kohlmeyer, 1962).

Specimens examined: none

Observations: there is only one collection of *Stigmatolemma poriforme*, and from the Latin description it is not conspecific to *Resupinatus poriaeformis*. W.B. Cooke stated that he had observed the type collection of this species and described it in English (Cooke, 1961), but the description lacks detail (superficial character descriptions, such as the appearance of the fruit bodies and the subiculum, is partially copied from a description in Coker, 1921 of a different species, *Resupinatus poriaeformis*) and so the type collection – if it can be relocated – should be restudied to determine if the species is distinct and if it belongs in the *Resupinateae*. Providing that the measurements of the spores given in Cooke (1961) are correct and not just copied from someone else's description (they are not the same as Coker's *R. poriaeformis* spores), the spores are stated to be "broadly ovate to subglobose, apiculate, hyaline, slightly flattened on one

side, 8.4 x 6 μ" (Cooke, 1961). Cooke also states the cups are up to 0.5 mm across, have

a thin white subiculum, have a thin covering of surface hairs, basidia 4-spored and 14-18

x 7-9 μm.

Resupinatus stictoideus (Speg.) Nakasone, Crypt. Myc. 29(3): 242. 2008.
≡ *Cyphella stictoidea* Speg., Anales Soc. Ci. Argent. 17: 80. 1884.
= *Cytidia wettsteinii* Bres., in Hohnel, Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-
    Naturwiss. Kl. 83: 6. 1907. (fide Nakasone 2008)
        ≡ *Corticium wettsteinii* (Bres.) Sacc. & Trotter, Syll. fung. 21: 400. 1912.

The description of this species has been reproduced from Nakasone (2008).

Fruit Bodies: more or less discoid, up to 2 mm in diameter, often fusing together, up to

10 x 2 mm, brownish orange, sessile, shallowly embedded in substrate in small, ovoid

areas up to 1.5 x 0.75 mm, up to 150 μm thick, ceraceous to brittle in the dried state,

when hydrated becoming firm, ceraceous; hymenial surface smooth; margin entire.

Hyphal system monomitic with nodose-septate generative hyphae. Pileipellis a thin,

sparse, trichoderm of coralloid-diverticulate hyphae with a robust stalk and numerous

short, knobby branches. Trama a gelatinous matrix with a sparse network of hyphae;

tramal hyphae 2-3.5 μm in diameter, clamped, sparsely branched, walls 2-5 μm thick,

hyaline, gelatinous, acyanophilous. Subhymenium up to 10 μm thick, a dense,

agglutinated tissue. Hymenium a dense palisade of cystidia and basidia.

Basidia: clavate, 23-30 x 5.0-6.0 μm, clamped at base, 4-sterigmate, walls thin, hyaline,
smooth.

Cystidia: broadly fusiform 20-30 x 5.0-9.0 μm, clamped at base, walls thin, hyaline,
smooth.

Spores: broadly ellipsoid, 7.5-9.0(-10) x 4-5(-5.5) μm, Q = 1.8, walls thin, hyaline,
smooth, acyanophilous, not reacting in Melzer's reagent.

Substrate ecology: on rotting wood in the tropics.

Distribution: Brazil, Paraguay

Type: S F14701; "prope Fazenda bella vista in districtu urbis S. Cruz ad flumen Rio Pardo," collected in the province of Sao Paulo, Brazil, in July 1901 by Wettstein and Schiffner (isotype collections deposited in FH: FH 258371 and FH 258369).

Specimens examined: none.

Observations: Nakasone (2008) suggested that *Resupinatus stictoideus* might belong in the genus *Calyptella,* but at the same time rejected that possibility because *Calyptella* species have fruit bodies with stalks and do not have gelatinized hyphae. The presence of cystidia indicates that the species cannot belong to *Resupinatus* or the *Resupinateae*; its correct classification cannot be determined without fresh material since the known collections are too old for DNA analysis.

Chilean species #1 (Patagonian campanelloid), sp. nov.

Fruit Bodies: rounded flabelliform to reniform, applanate to convex or conchate, up to 3.6 cm wide and 2.0 cm long, gelatinous when fresh and brittle when dry. Light reddish brown to vinaceous red, lighter or nearly translucent at the margins. Surface rugulose, following the outline of the lamellae. Hymenophore concolorous or somewhat lighter, anastomosing (main veins with interconnecting cross veins at a lower level than the main veins). Stipe lateral, up to 3.7 x 2.4 mm, dark reddish brown, smooth (or rarely rough). Pileipellis a cutis of tubular, thick-walled hyphae 2.5-4 μm in diameter, branching, with clamps. Pileal trama composed of larger-diameter gelatinized, hyaline hyphae with radially thickened cell walls, 4.5-6 μm in diameter. Hymenium composed of densely-packed mature and immature basidia.

Basidia: clavate, 4-spored, hyaline to clear yellow-brown, 38-44 x 6.5-8.0 μm, clamped at base.

Cystidia: cheilocystidia present along gill edges, many with a long "hook" at the apex; hyaline, clavate to broadly fusiform 35-60 x 5.0-8.0 μm.

Spores: ellipsoid, (6.0-)6.8-8.0(-9.0) x (4.0-)4.5-5.2(-5.5) μm, walls thin, hyaline, smooth, inamyloid.

Substrate ecology: on rotting *Nothofagus* in Patagonia.

Distribution: Chile (Patagonia)

Specimens examined: 007, J14, J19, P79 (all deposited in the SGO herbarium, accession numbers 163626, 163622, 163624, and 163625); isotypes at UWO.

Observations: this Chilean gymnopanelloid was first tentatively identified as *Resupinatus merulioides* (known from Japan and Australia/New Zealand; see Chapter 4) because of morphological similarities or fruit body colour and the reticulated gill network on the surface of the hymenium. It is, however, new to science and constitutes a new clade within the larger marasmioid, gymnopoid and campanelloid tree (see Figure 6.1). It differs from *Resupinatus merulioides* and the *Resupinateae* by the very unusual hyphae in the pileal trama that have radially thickened cell walls (Figure 6.3 E), a character not present in any *Resupinatus* species. As this species appears to be restricted to *Nothofagus* forests in South America, more collection effort should be made in areas where this type of forest is prevalent to determine the actual species range.
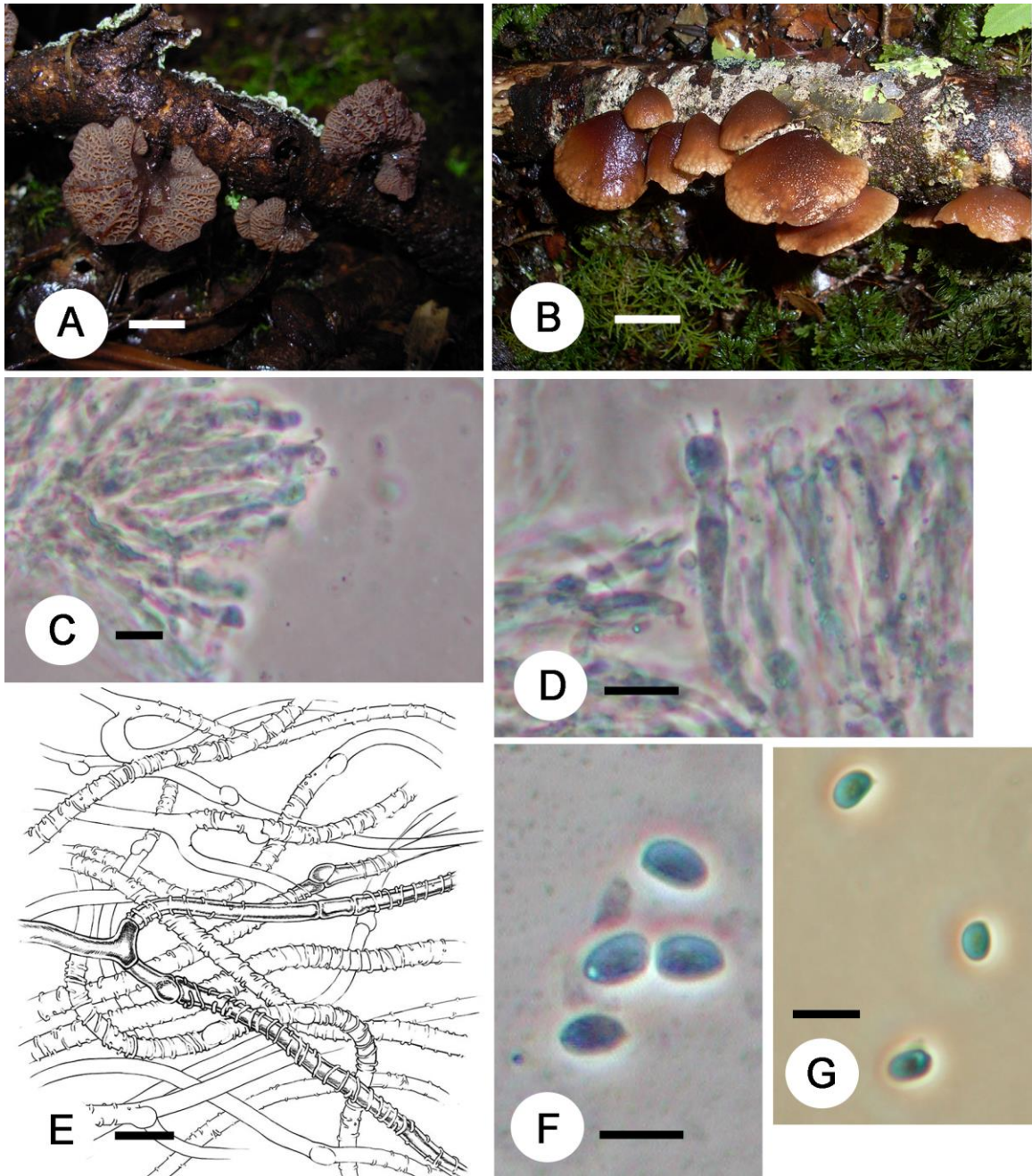
Figure 6.3 Chilean speices #1 (Patagonian campanelloid). A. Hymenial surface of the fresh fruit bodies, showing the reticulated gill network (photo by P. Sandoval-Lieva. Bar = 10 mm; J14). B. Pileal surface of the fresh fruit bodies (photo by P. Sandoval-Lieva. Bar = 10 mm; J14). C. Basidium and immature basidiospores (Bar = 10 μm; 007). D. Basidium with three sterigma visible (Bar = 10 μm; 007). E. Hyphae of the pileal trama showing radially-thickened cell walls (drawing by P. Sandoval-Lieva. Bar = 10 μm; J19). F. Basidiospores (Bar = 10 μm; 007). G. Basidiospores (Bar = 10 μm; P79).

Chilean *Hohenbuehelia*, sp. nov.

Fruit Bodies: rounded to funnel-shaped, applanate, up to 2.5 cm wide and 2.0 cm long, gelatinous when fresh and brittle when dry. Dark brown to dark black-brown when dry, nearly black when fresh, lighter in the middle of the fruit body near the stipe. Surface squamulose to pruinose, giving the appearance of a mat of grey hairs near the stipe. Hymenophore concolorous or somewhat lighter, gills radially arranged outwards from the stipe. Stipe central to eccentric, up to 2 x 2 mm, concolorous with the pileus, smooth (or rarely rough), nearly a hollow tube in some examples as to make the fruitbody appear funnel-shaped. Pileipellis a cutis of tubular, thick-walled hyphae 2.5-4 μm in diameter, branching, with clamps, clear yellow-brown to brown in colour. Pileal trama composed of similar gelatinized, hyaline hyphae, slightly larger in diameter, 3.5-5 μm, running vertically from hymenium to pileipellis, and secondarily septate (clamps present, but not at every cell division). Hymenium composed of densely-packed mature and immature basidia with metuloids.

Basidia: clavate, 2- or 4-spored, hyaline to clear yellow-brown, 28-36 x 5.0-6.5 μm, clamped at base.

Cystidia: metuloids present along gill surface, extending only marginally further than the layer of basidia in most examples (these structures are easily overlooked), with thickened walls at both the clamp end and the tip (tapering to a rounded point), hyaline to yellow-brown, approximately 30-45 μm long.

Spores: ovate to oblong, (6.0-)6.4-6.7(-6.8) x (2.1-)2.2-2.4(-2.5) μm, walls thin, hyaline, smooth, inamyloid.

Substrate ecology: on rotting *Nothofagus* in Patagonia.

Distribution: Chile (Patagonia)

Specimen examined: P80 (deposited in SGO and UWO)

Observations: collection P80 was sent with collections of Patagonian campanelloid species and labelled as "*Resupinatus* sp.", believed to be similar to *Resupinatus alboniger* or *Resupinatus trichotis*. The placement based on DNA sequence analysis prompted a re-examination and the observation of metuloids, which are easily overlooked. The presence of inconspicuous metuloids is not unusual in *Hohenbuehelia*, as other species once classified in *Resupinatus* were later reassigned after their *Nematoctonus* anamorphs were observed in culture. This appears to be the southern counterpart of the holarctic species *Hohenbuehelia unguicularis* (Thorn & Barron 1986). Unfortunately, the collection was already too dry when received to attempt to derive a culture, and so a description of the anamorph cannot be provided. The tramal hyphae are also unusual in that clamps are not present at every transverse cell wall. This had not been observed in any other collection throughout this study. In order to determine the range of the species (both host range and species distribution range), it is important to increase the collecting effort.
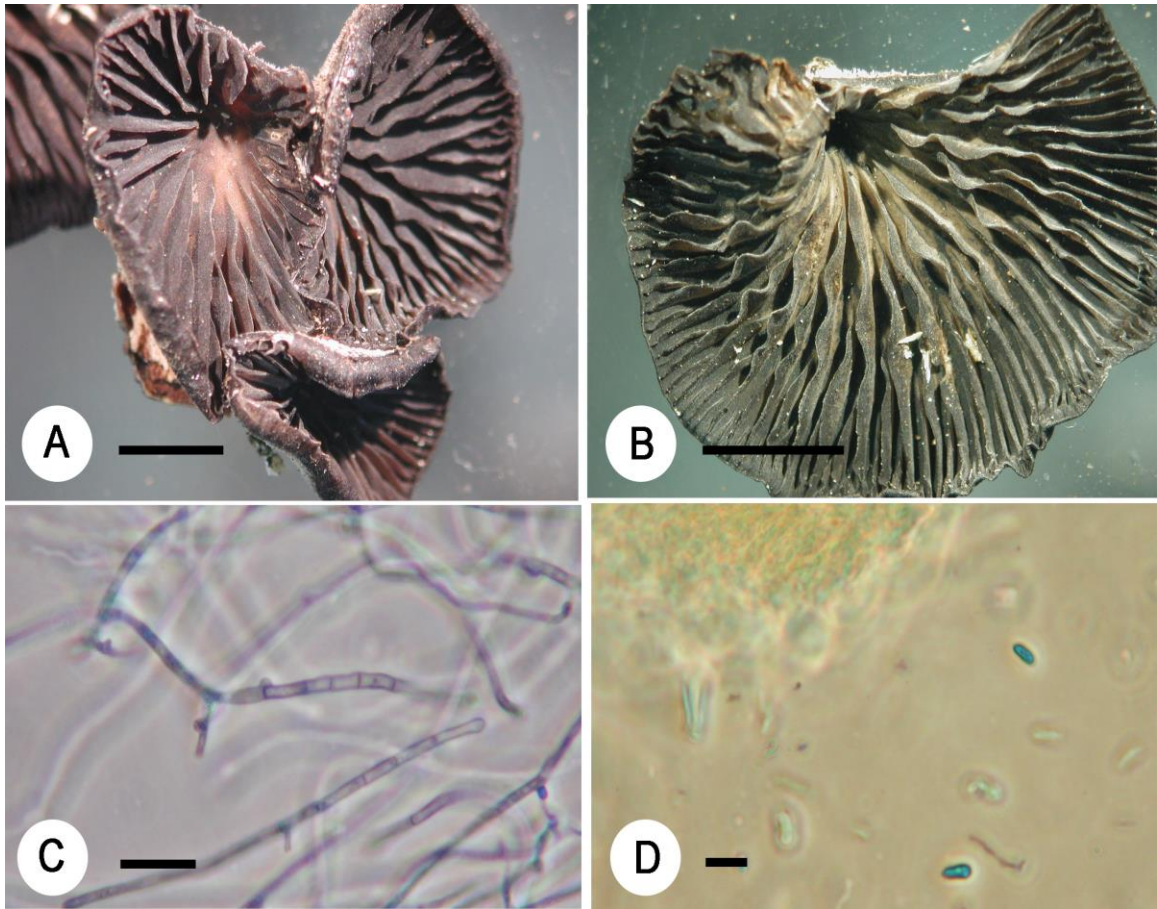
Figure 6.4 Chilean *Hohenbuehelia*. A. Dried small fruit bodies (Bar = 5.0 mm). B. Dried larger fruit body, showing the prominent funnel-like stipe (Bar = 5.0 mm). C. Secondarily septate hyphae present in the pileal trama of the fruit bodies (Bar = 20 μm). D. Basidiospores, and a metuloid that is out of focus (above the space between the "D" and the scale bar; Bar = 10 μm)

6.4.3　Species believed to belong in the *Resupinateae* based on a very short type description

Maireina cinerea (Burt) W.B. Cooke, Beih. Sydowia 4: 85. 1961.
≡ *Solenia cinerea* Burt, in Millspaugh & Nuttall, Publications of the Field Museum of Natural History, Botany Series 5(no. 212): 315. 1923.

Species description: see Bodensteiner (2006)

Specimen examined: BPI 258008 (the type collection of *Solenia cinerea*)

Observations: Although the descriptions of *Maireina cinerea* by Burt (in Millspaugh & Nuttall, 1923) and Cooke (1961) left room for doubt as to its correct classification, Bodensteiner (2006) provided a detailed description and illustration of the micromorphology, leaving no doubt that it is a species of *Merismodes*.

6.4.4　Misidentified herbarium collections

The following species are presented in alphabetical order (first by genus, then by species epithet) and the species determination of each herbarium collection was performed by Dr. R. Greg Thorn. The full description of each species is not presented as they represent an eclectic assemblage; a reference to a complete species description is presented with the taxonomy of each species. The herbarium accession numbers and the names originally associated with the accession numbers is also presented below. The full synonymy of each species listed below was obtained from Index Fungorum (www.indexfungorum.org/Names/Names.asp).

Peziza atrofusca Berk. & Curtis, Grevillea 3(no. 28): 156. 1875.
≡ *Tapesia atrofusca* (Berk. & Curtis) Sacc., Syll. fung. (Abellini) 8: 373. 1889.
≡ *Niptera atrofusca* (Berk & Curtis) Underw. & Earle, Bull. Alabama Agricultural Experiment Station 80: 203. 1897.
= *Catinella olivacea* (Batsch) Boud., Hist. Class. Discom. Eur. (Paris): 150. 1907.

Species description: see Greif et al., 2007.

Specimen examined: FH 258737 (syntype of *Peziza atrofusca* Berk. & Curtis)

Observations: We requested collections of many species of *Tapesia*, some of which have since proven to be members of *Resupinatus* (e.g., *Tapesia daedalea*, Chapter 3). At first glance the type collection of *Peziza atrofusca* appeared to be of a fungus with cyphelloid fruit bodies on a very dense subiculum, but actually consists of two separate fungi: the "subiculum" is a corticoid fungus, likely *Hyphodontia cineracea* (Bourd. & Galz.) J. Erikss. (as per the annotation slip by RGT). The name *Peziza atrofusca* is typified by the apothecia indicating that this name applies to an ascomycete, for which the correct name is *Catinella olivacea*, and not a basidiomycete.

Henningsomyces candidus (Pers.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 483. 1898.
≡ *Solenia candida* Pers., Ann. Bot. (Usteri) 1: 36. 1794.
≡ *Peziza candida* (Pers.) Pers., Syn. meth. fung. (Gottingen) 2: 676. 1801.
≡ *Calyptella candida* (Pers.) Pat., Essai Tax. Hymenomyc. (Lons-le-Saunier): 55. 1900.
≡ *Cyphella candida* (Pers.) Pat., Essai Tax. Hymenomyc. (Lons-le-Saunier): 55. 1900.
≡ *Lachnella candida* (Pers.) G. Cunn., Bull. N.Z. Dept. Sci. Industr. Res., Pl. Dis. Div. 145: 309. 1963.

Species description: Breitenbach & Kranzlin, 1986.

Specimens examined: AD-C 55602 (as *Henningsomyces candidus*), NYBG 48 (as *Cyphella* sp.), NYBG 404 (as *Solenia* sp.), NYBG 2082 (as *Henningsomyces* sp.).

Observations: this collection was sent from the Adelaide herbarium as part of a request including cyphelloid collections of Australian fungi. It was correctly identified by the original collector, and therefore does not belong in the *Resupinateae*.

Hydnopolyporus palmatus (Hook. in Kunth) O. Fidalgo, Mycologia 55(6): 715. 1963.
≡ *Polyporus fimbriatus* Fr., Linnea 5: 520. 1830, non *Polyporus (Porotheleum) fimbriatus* (Pers.:Fr.) Fr., Systema Mycologicum 1: 506. 1821. (treated above, in 6.4.1, as *Porotheleum fibriatum*)

Species description: Fidalgo, 1963.

Specimens examined: BPI 208456, 208457, 208458, 208459, 208460, 208461, 208462, 208463, 208464, 208465, 208466, 208467, 208468, 208469, 208470, 208471, 208472,

208473, 208474, 208475, 208560, 208577, 208593, 208596, 208598, 208600, 208601, 208602 (all collections as *Polyporus fimbriatus* Fr.)

Observations: multiple collections of this species arrived from the USDA herbarium (BPI) as part of a loan request for a different species, *Porotheleum fimbriatum*. Ryvarden (1991) treats this as *Hydnopolyporus fimbriatus* (Fr.) D. Reid (1962), but Fidalgo (1963) appears to be correct that the name *Polyporus fimbriatus* Fr. (1830) is an illegitimate later homonym (as per annotation slip by RGT).

Lachnella alboviolascens (Alb. & Schwein.) Fr., Summa veg. Scand., Section Post. (Stockholm): 365. 1849.
≡ *Peziza alboviolascens* Alb. & Schwein., Consp. fung. (Leipzig): 322. 1805.
≡ *Lachnella alboviolascens* (Alb. & Schwein.) Fr., Fl. Scan.: 343. 1836.
≡ *Cyphella alboviolascens* (Alb. & Schwein.) P. Karst., Not. Sallsk. Fauna et Fl. Fenn. Forh. 11: 221. 1870.
≡ *Chaetocypha alboviolascens* (Alb. & Schwein.) Kuntze, Revis. gen. pl. (Leipzig) 2: 847. 1891.
≡ *Cyphellopsis alboviolascens* (Alb. & Schwein.) Donk, Medded. Nedl. Mycol. Ver. 18-20: 129. 1931.

Species description: see Donk, 1931 and Cunningham, 1963.

Specimens examined: B (70 0014066; as *Cyphella pezizoides*), BPI (292977, 292978, 292979; all originally identified as *Cyphella pezizoides* Zopf.), ISC (352324, 352325, 366064, 378039, 378075, 378962; all originally identified as *Cyphella pezizoides* Zopf.)

Observations: specimens of *Cyphella pezizoides* Zopf. were requested on loan to determine the correct name for this species. The type was never received so no determination could be made of the synonymy of this species, but all of the collections received carrying this name belonged to the genus *Lachnella*.

Lachnella tiliae (Peck) Donk, Lilloa 22: 245. 1951.

≡ *Peziza tiliae* Peck, Ann. Rep. N.Y. St. Mus. 24: 96. 1872.
≡ *Trichopeziza tiliae* (Peck) Sacc., Syll. fung. (Abellini) 8: 428. 1889.
≡ *Cyphella tiliae* (Peck) Cooke, Grevillea 20(no. 93): 9. 1891.

Species description: see Agerer, 1983.

Specimens examined: BPI (297476, 297477; both originally identified as *Cyphella pezizoides* Zopf.), F (1004897; as *Cyphella pezizoides*)

Observations: *Lachnella tiliae* is distinguished from *Lachnella alboviolascens* via the substrate. *L. alboviolascens* occurs on hardwood but never on *Tilia*, whereas *L. tiliae* is only ever found on *Tilia* but superficially otherwise looks identical.

Lachnella villosa (Pers.) Donk, in Singer, Lilloa 22: 345. 1951.
≡ *Peziza villosa* Pers., Syn. meth. fung. (Gottingen) 2: 655. 1801.
≡ *Solenia villosa* (Pers.) Fr., Syst. mycol. (Lundae) 2(1): 200. 1822.
≡ *Cyphella villosa* (Pers.) P. Crouan & H. Crouan, Florule Finistere (Paris): 61. 1867.
≡ *Trichopeziza villosa* (Pers.) Fuckel, Jb. nassau. Ver. Naturk. 23-24: 296. 1870.
≡ *Lachnea villosa* (Pers.) Gillet, Champignons de France, Discom.(3): 80. 1880.
≡ *Chaetocypha villosa* (Pers.) Kuntze, Revis. gen. pl. (Leipzig) 2: 847. 1891.
≡ *Henningsomyces villosus* (Pers.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 483. 1898.

Species description: see Agerer, 1983.

Specimens examined: BPI 292806 (as *Cyphella cupuliformis* Berk. & Ravenel)

Observations: superficially, *Lachnella villosa* and *Cyphella cupulaeformis* (now classified in *Rhodocyphella* but belonging in *Resupinatus*) look similar but distinctions can be made even using a hand lens. The hairs on the exterior of the fruit bodies of this species are brown as opposed to the hyaline hairs of *Rh. cupuliformis*, and the hymenium of *L. villosa* is a cream or off-white as opposed to the nearly black hymenium of *Rh. cupuliformis* (see Chapter 2).

Lachnum papyraceum P. Karst., Bidr. Kann. Finl. Nat. Folk 19: 169. 1871.

≡ *Dasyscyphus papyraceus* (P. Karst.) Sacc., Syll. fung. (Abellini) 8: 434. 1889.

≡ *Atractobolus papyraceus* (P. Karst.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 446. 1898.

Species description: see Dennis, 1949.

Specimens examined: FH 258743 (as *Peziza pruinata* Schwein.), FH 258761 (as *Solenia poriaeformis* (Pers.) Fr.)

Observations: Both collections appear at first to consist of very small, mostly immature cyphelloid fruit bodies that lack a subiculum, but under even the dissecting microscope they do not at all resemble members of the *Resupinateae.*

Maireina monacha (Speg. in Roum. [sic]) W.B. Cooke, Beih. Sydowia 4: 90. 1961. (as per annotation slip by RGT)

≡ *Cyphella monacha* Speg., in Saccardo, Michelia 2(no. 7): 303. 1881.

≡ *Cyphellopsis monacha* (Speg.) D.A. Reid, Kew Bull. 17(2): 297. 1963.

= *Cyphella bresadolae* Grelet, Bull. Soc. mycol. Fr. 38: 174. 1922.

   ≡ *Merismodes bresadolae* (Grelet) Singer, Agaric. mod. Tax., Edn 3 (Vaduz): 665. 1975. (currently accepted name in Index Fungorum)

Species description: see Bodensteiner, 2006.

Specimens examined: BPI 292805 (as *Cyphella cupuliformis* Berk. & Ravenel), BPI 292937, 292938 (both as *Cyphella marginata* McAlpine), FH 258747 (as *Cyphella marginata* McAlpine)

Observations: Specimens of *Cyphella marginata* McAlpine were originally requested since this species was published as part of the flora of Australia and New Zealand and hasn't been examined since its description. The type of this species could not be located, so no conclusions could be made regarding its status.

Phaeosolenia ravenelii (Berk.) W.B. Cooke, Beih. Sydowia 4: 127. 1961.

≡ *Cyphella ravenelii* Berk., Grevillea 2(no. 13): 5. 1853.
≡ *Chaetocypha ravenelii* (Berk.) Kuntze, Revis. gen. pl. (Leipzig) 2: 847. 1891.

Species description: see Cooke, 1961.

Specimens examined: BPI (292983, 292984; both identified as *Cyphella ravenelii*)

Observations: this name has been applied to two different species. The two collections cited above were found on *Carya* sp. in North Carolina, and likely belong to the genus *Maireina*. The other collections carrying the name *Cyphella ravenelii* are not conspecific, and should be treated as *Merismodes fasciculatus*. The type collection was not observed as part of this study, but was found on the same substrate (*Carya*) as the collections observed. This suggests that the name *Phaeosolenia ravenelii* is not a synonym of *Merismodes fasciculatus* as has been considered in the past (Donk, in Singer, 1951; Bodensteiner, 2006).

Scytinotus longinquus (Berk.) Thorn, Index Fungorum 10: 1. 2012.
≡ *Agaricus longinquus* Berk., in Hooker, Bot. Antarct. Voy. Erebus Terror 1839-1843 2: 447. 1847.
≡ *Pleurotus longinquus* (Berk.) Sacc., Syll. fung. (Abellini) 11: 26. 1895.
≡ *Dendrosarcus longinquus* (Berk.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 464. 1898.
≡ *Panellus longinquus* (Berk.) Singer, Sydowia 5(3-6): 471. 1951.
≡ *Pleurotopsis longinqua* (Berk.) E. Horak, Aust. J. Bot., Suppl. Ser. 10: 7. 1983.

Species description: see Singer, 1951.

Specimens examined: AD-C 55543 (as *Resupinatus striatulus* (Pers.) Murrill)

Observations: *Scytinotus longinquus* has very pale fruit bodies (creamy-white, aging to a light brown), with amyloid, curved-cylindric basidiospores, characterisitcs that are not shared by any members of the *Resupinateae*.

6.4.5   Herbarium collections that could not be identified

AD-C 55539, 55540, 55541 (as *Resupinatus striatulus* (Pers.) Murrill) – there is no material left on the substrate in any of these collections.

BPI 292753 (as *Rhodocyphella cupuliformis* (B. & C.) W.B. Cooke) – there is no material left on the substrate.

HO 548042, 548043, 548044, 548045, 548046, 548047, 548048 (various identifications) – these collections were superficially examined to determine membership in the *Resupinateae*. None are members of the group (despite having been identified as *Resupinatus* (*Pleurotus*) *applicatus*), and none of could easily be identified. They will be identified at a later date.

NYBG 722 (as *Solenia* sp.) and **1160** (as *Rhodocyphella cupuliformis* (B. & C.) W.B. Cooke) – there is no material left on the substrate.

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Chapter 7

7　General Results and Discussion

7.1　"Cyphelloidism" in the *Resupinateae*

The cyphelloid fruit body morphology has evolved at least five separate times in the *Resupinateae*: once in the *Resupinatus urceolatus* and *Resupinatus poriaeformis* clade, once in the *Resupinatus conspersus* clade, once in the *Rhodocyphella cupulaeformis* and Australian cyphelloid *Resupinatus* 1 clade, once in the *Stromatocyphella conglobata* clade, and once in the *Porotheleum cinereum* clade (Figure 2.1 and Figure 4.4). However, all lamellate, poroid, and cyphelloid species of *Resupinateae* are part of the single genus, *Resupinatus*.

No habitat generalizations may be made about the likelihood of the cyphelloid fruit body morphology evolving in a clade. Clades of tropical species are no more or less likely to contain members with cyphelloid fruit bodies than those from temperate locations. There is also no correlation to substrate texture; species fruiting on well-rotted, spongy wood are no more or less likely to be cyphelloid than those growing on more dense wood. The growth rate of cyphelloid versus lamellate species was not altered on a range of media (full- or half-strength MEA or PDA, or more complex media such as Alphacel agar, modified Leonians agar, or liquid ME). These fungi grow extremely slowly in culture (rarely filling a 60 mm plate before the culture dies in 9-12 months), but a component of their natural environment may be missing in the laboratory. This may include a synergistic effect of other organisms (such as the digestive enzymes of other saprobic fungi that grow in rotting wood), bacteria that are naturally present in forests, or a compound present in rotting wood that cannot be mimicked *in vitro*.

A more thorough analysis of other *Resupinatus* species producing lamellate fruit bodies should be done to determine their phylogenetic relationships. Considering the pattern of evolution of the cyphelloid habit, it can no longer be presumed that species producing larger fruit bodies with more gills would group together in the tree. There are still at least 15 lamellate species in *Resupinatus* for which no DNA sequences are available.

7.2   Habitat and host specificity in the *Resupinateae*

Some *Resupinateae* species can be distinguished based on host substrate, but others cannot. For example, *Tapesia daedalea* and *Peziza pruinata* do not differ macromorphologically and occur throughout North America.. They are easily distinguished based on the host species, as *T. daedalea* only occurs on hardwoods, while *P. pruinata* occurs only on the bark of old grape vines. *Resupinatus conspersus* occurs only on *Abies* in the Alps, whereas the nearly identical *Porotheleum cinereum* occurs on hardwoods of tropical South America (Donk, 1962a; Patouillard & Lagerheim, 1893). Other species in the group are so-called generalists, occurring on many different substrates and have a broad host range. Morphological and substrate differences between collections labeled *Resupinatus urceolatus* or *Resupinatus poriaeformis* do not hold up with phylogenetic sequence analysis but can be differentiated based on geography (see Chapter 3 for a discussion of these species). Very few species, if any, can grow on both hardwoods and gymnosperms.

Ecological boundaries are often used as species boundaries (Case et al., 2004; Gaston, 2008; Sax, 2001; Thomas et al., 2006), in particular in the case of endophytes or plant pathogens, which are usually associated with only one or a few related host species (Collado et al., 1999; Higgins et al., 2007; Taylor et al., 1999; Taylor et al., 2006). For these, the geographic range of the fungi mirrors the geographic range (natural and/or introduced) of the host plants. Far less information is available about geographic ranges of other types of fungi such as saprobic or mycorrhizal fungi (for example, Bisby, 1943; Bissett & Parkinson, 1979; Redhead, 1989; Tedersoo et al., 2010; Vilgalys & Sun, 1994). Ecological or geographic boundaries can be used in the *Resupinateae* for some species (for example, *Resupinatus conspersus* in alpine Europe versus the morphologically similar *Porotheleum cinereum* in tropical South America), but not for others.

7.3   The *Resupinateae* of Australia and New Zealand

This study was the first comprehensive analysis of the smaller members of the *Resupinateae* of Australia and New Zealand, and it linked species with cyphelloid fruit bodies to those with lamellate fruit bodies. At least 25 species of *Resupinateae* occur in that part of the world, seven of which are new to science. Three species had previously been described from other countries and are now known also to exist in either Australia, New Zealand, or both.

Much of the remaining work needed to determine the membership of the *Resupinateae* concerns the amplification and sequencing of templates that are difficult to work with (either degraded samples due to their age or due to their earlier storage conditions) or that are type specimens (sequences of *Resupinatus huia* and *Resupinatus subapplicatus*). Additionally, work is required in more intensive sequencing and the naming of new species discovered in this study (Australian cyphelloid *Resupinatus* 2, the collections tentatively named *Resupinatus hyalinus*, a more intensive sampling of *Resupinatus applicatus* 4 and 5, and the notable collections similar in morphology to both *Resupinatus applicatus* and *Resupinatus cinerascens* but not quite fitting the species concept for either one). Most herbaria do not allow for the destructive sampling of their type specimens due to the value of the collection to the herbarium and to the scientific community. Forensic DNA kits are available that can be used to amplify degraded DNA from minute samples with no more destruction to collections than traditional microscopy. Unfortunately, the cost of the kits is prohibitive at this time. It is hoped that eventually sequences will become available for the type and historical collections of all of the fungi preserved in herbaria worldwide.

7.4   Additions to the *Resupinateae*: species discovered or misclassified among historic herbarium collections

Nine new species belonging in the *Resupinateae* were discovered among historic herbarium collections, under names that have not been subject to recent studies. Five of these, *Tapesia daedalea*, *Peziza pruinata, Solenia subporiaeformis, Cyphella grisea* and

Cellypha subgelatinosa require new combinations in *Resupinatus*: they are novel species within the genus. Unfortunately, the five new species are only known from their type collections, so none could be used for DNA analysis. They have been placed in the *Resupinateae* based on morphological characters. Four other species are synonyms of other species with names that have nomenclatural priority: *Cyphella brunnea*, *Maireina pseudurceolata*, and *Solenia tephrosia* are synonyms of *Resupinatus poriaeformis*, and *Cyphella tela* is a synonym of *Tapesia daedalea*. The membership of *Marasmiellus violaceogriseus* in *Resupinatus* (Cooper, 2012) was also confirmed in this study, bringing the total number of species in the genus to 72, from 58 prior to this study.

This emphasizes the usefulness and the importance of herbaria in mycological research: there are an estimated 1.5 million fungal species (Hawksworth, 2001) and only *ca*. 97,000 species have been formally described (DicFun10). Many "unknown" species will be found in misidentified herbarium collections. Of the 405 herbarium collections examined for this study, 87 (approximately 20%) represented new species in the *Resupinateae*.

7.5   Species excluded from the *Resupinateae*

Historically, many species once included in the *Resupinateae* due to morphological convergence are now excluded (sometimes entire genera; see Singer 1949, 1962, 1975, 1986; Thorn & Barron, 1986; Thorn et al., 2000, 2005; and Koziak et al., 2007). Convergence caused two species sent to Western for DNA sequencing from a collaborator in Chile to be morphologically assigned to *Resupinatus*, but analysis of their sequences showed them to be unrelated. One was morphologically similar to *Resupinatus merulioides* but is a member of a new clade within the *Gymnopus-Marasmius-Panellus* group, and the other was morphologically similar to *Resupinatus alboniger* but belongs to the genus *Hohenbuehelia*. These two examples further demonstrate that morphology does not always predict phylogeny.

Other species excluded from the *Resupinateae* based on data collected in this study were species with cyphelloid or small lamellate fruit bodies that had type descriptions lacking in enough detail to identify the species properly. This has been mentioned as a problem in the literature as far back as 1896, with regards to fungal pathogens of plants (Smith, 1896), insect pathogens (Petch, 1933), critiques of an author's work (such as Saccardo's infamously short species descriptions; Nannfeldt, 1936), critiques of entire genera (such as the insufficient detail describing species of *Zygodesmus*; Rogers, 1948), and descriptions of the type collections of resupinate *Hymenomycetes* (Donk, 1962b). Many of these species are still excluded from the group (a full list is presented in Chapter 6), which further emphasizes the need to go back through the literature and re-describe species based on examination of the type specimen, in much more detail. Without this level of detail, it is impossible to determine the proper membership of historical herbarium collections, and many species will likely be newly described (thus creating unnecessary synonyms) despite having an existing name that should be applied.

7.6 Implications of this study

Traditional morphological features used in identification to the species level in the fungi include cap size, colour and shape, hymenium shape and colour, spore size, shape, outer texture and colour, and habitat (amongst others; Largent, 1986 and Largent et al., 1977). These characters are all useful in identifying species in the *Resupinateae* to an extent; for some species a unique set of morphological characters irrefutably point to the proper identification of a single species, while for other species this same suite of morphological characters is not enough for proper identification and other characters must be considered. In the case of the latter, we resort to the sequencing of the ribosomal DNA, which so far has proven useful in this group at distinguishing morphologically identical species (and this gene region has good resolution for determining species relationships for phylogenetic tree construction) as well as species distinguished easily via morphological characters.

One question this study has attempted to answer is "are there rare fungi?" The answer seems to be that it depends on the circumstance, but likely yes. In some cases, such as with *Stromatocyphella conglobata* (found only a handful of times prior to the 1920s and very rarely since), rare species only appear to be rare because we aren't looking for them in the right place or at the right time of year. Once we realized that this was a winter-fruiting species on *Alder*, it is consistently found. In other cases, such as with *Peziza pruinata* (found only a handful of times in the mid-19th century and not since then), species do truly appear to be rare, as the substrate on which it grows (old growth grape) has been steadily eradicated in the 19th and 20th centuries. This reinforces the importance of habitat preservation, something not often considered for fungi. For example, wood decomposition may or may not be accelerated by climate change (Bradford et al., 2014), and preserving ideal habitat for all species to grow is essential.

Growing fungi in the *Resupinateae* in culture has shown to be difficult, as they do not grow nearly as well on artificial media as other fungal species. The growth rate of fungi in culture can be helpful for their identification, as well as culture characteristics like colour and morphological characters of asexual spores or spore-bearing structures that are produced (Nobles, 1965; St-Germain & Summerbell, 1996; Sharma & Pandey, 2010). Despite a variety of efforts used, the cultures of most members of the *Resupinateae* could not be encouraged to produce asexual or sexual spores. This suggests that a vital component required for the development of spores in members of the *Resupinateae* cannot be mimicked in artificial media. This has implications in other areas of fungal research, as many morphological characters of different species may be overlooked simply because the correct conditions are not provided in the laboratory.

Throughout this study, some fieldwork was done in an attempt to find recent collections of species in the *Resupinateae*, but with little success. Anecdotally, it was observed that the optimal habitat for these fungi to fruit is also suitable for many arthropods, particularly woodlice (isopods) in the suborder Oniscidea. This suggests that perhaps invasive arthropods are consuming the fruit bodies (or the mycelium) of wood rot fungi, leading to a decreased likelihood of finding them.

There is also anecdotal evidence for the discovery of new species of basidiolichens. These are lichens where the fungal symbiont is a basidiomycete as opposed to the typical ascomycete mycobiont (15,000-20,000 species of lichen have been described, and 98% have an ascomycete as the mycobiont; Oberwinkler, 2001). The species *Rhodocyphella cupuliformis*, Australian cyphelloid *Resupinatus* 1 and *Resupinatus griseopallida* are always found on wood with a thick layer of green algae on the surface. This is not necessarily indicative of these species being basidiolichens, but is a common morphological character of many of this type of lichens (Fisher et al., 2007; Lepp, 2014; Nelsen et al., 2007). Until more work is done, both morphological and molecular, the co-incidence of these organisms is best referred to as an associative relationship.

Based on the phylogenetic tree of all sequences obtained from members of the *Resupinateae* throughout this study, we can see that the cyphelloid fruit body morphology is probably derived, and that the ancestor of the group is most likely to be a lamellate basidiomycete. This study has furthered our understanding of the pattern of evolution of the morphology of fruit bodies in the *Agaricales*, as this study provides much finer resolution for this group than was achieved in Hibbett & Binder (2002) or Bodensteiner et al. (2004). This study further demonstrates that the development of a specific fruit body morphology from an ancestor with a different fruit body type is not unique (for example, cyphelloid fruit body from a lamellate ancestor as in this study), and this pattern of evolution of different fruit body morphologies has been shown in other groups of fungi as well: the corticioid fruit body has evolved in twelve separate clades in the homobasidiomycetes (Larsson et al., 2004; Larsson, 2007), gloeocystidia are multiply derived and are not good indicators of phylogenetic relationships (believed to have been derived twice, once in the russuloid fungi and once in the jelly fungi; Larsson & Larsson, 2003), and the poroid and lamellate fruit body morphologies are both multiply derived in the *Auriculariales* (Zhou & Dai, 2013). There are also multiple examples of the derivation of new fruit body morphologies in clades of lamellate fungi; within the genus *Panellus*, a genus of species mostly with lamellate fruit bodies, *P. pusillus* has a poroid fruit body (Burdsall & Miller, 1978; Jin et al., 2001).

7.7 Future studies

This study is the most inclusive phylogenetic analysis of this group to date, including 34 of 58 previously described members of the *Resupinateae* compared to the 13 in the most recent previous work (Thorn et al. 2005), and at least 14 new species were discovered in this study. However, not all species of *Resupinatus* were analyzed using molecular methods, for two reasons: 1) this study focused on the cyphelloid and smaller lamellate members of the group, and 2) no recent material was available for molecular studies of eight described species that have been included in *Resupinatus*. A more complete study that includes more of the lamellate representatives and makes a concerted effort to find recent material of species known only from historic collections would be in a better position to discern the species relationships and origins of the cyphelloid habit in the group.

Future studies should also attempt to culture all freshly collected material of *Resupinateae*, and engage in study of the biology of the group. There should be a focused study of their ecological role(s), whether as late-stage decomposers or as possible symbionts with green algae or cyanobacteria growing on the wood surface, or with microfauna or other microbes within the substrate.

This study has provided a snapshot of the diversity within a group of fungi in the *Agaricales*, and illustrates the point that we are losing critical habitat around the world for biodiversity. There is a real possibility that we have already lost some of these species and that ancient herbarium specimens are all that we have left.

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Appendix A: full list of herbarium specimens used

Table A-1: Full list of herbarium specimens used.

Type specimens are indicated with a "(T)". The following abbreviations may also be used if the specific type of type is known: "(HT)" (holotype), "(IT)" (isotype), "(LT)" (lectotype), "(NT)" (neotype), "(PT)" (paratype), or "(ST)" (syntype). For a description of these terms, please refer to "Terms and Abbreviations". If only the genus is provided in the column "Determined Identification", this indicates that the original identification was correct but a new genus must be used to refer to this species, as per current species identification in Index Fungorum (www.indexfungorum.org). This accepted combination is used in the "Taxonomy" section of each chapter. If there is no information entered in the "Determined Identification" box, it means that the herbarium specimen was correctly identified. If no collection information is listed below, the information is not available (either due to lack of information on the collection packet indicated by "N.R.", or due to illegible print indicated by "???"). Herbarium collections are arranged alphabetically by herbarium first, then numerically by accession number.

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
AD-C 10959	*Resupinatus cinerascens* (HT)		*Eucalyptus vimnalis*	Aug. 6 1927	Belair National Park, South Australia, Australia; J.B. Cleland	Chapter 4
AD-C 10960	*Resupinatus subapplicatus*	Undetermined	Pepper tree	Jun. 12 1921	Fullarton, Southern Lofty, South Australia, Australia; J.B. Cleland	Chapter 4
AD-C 10961	*Resupinatus subapplicatus*		N.R.	1924	Clare, Nothern Lofty, South Australia, Australia; J.B. Cleland	Chapter 4
AD-C 10962	*Resupinatus subapplicatus*	*Resupinatus trichotis*	N.R.	Sept. 15 1924	Willunga Hill, Southern Lofty, South Australia, Australia; J.B. Cleland	Chapter 4, Chapter 5
AD-C 10963	*Resupinatus subapplicatus* (T)		Rotting wood	Apr. 9 1925	Mr. Ashby's glasshouse, Wittunga Botanic Gardens, South Australia, Australia; J.B. Cleland	Chapter 4
AD-C 10964	*Resupinatus subapplicatus*	*Resupinatus trichotis*	N.R.	May 16 1925	Mount Lofty, Southern Lofty, South Australia, Australia; J.B. Cleland	Chapter 4, Chapter 5
AD-C 10965	*Resupinatus*		Bark	Apr. 25	Mount Lofty, Southern Lofty,	Chapter 4

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
	subapplicatus			1924	South Australia, Australia; J.B. Cleland	
AD-C 10966	*Resupinatus subapplicatus*	*Resupinatus vinosolividus*	Fallen trunk	Aug. 6 1927	Belair National Park, Southern Lofty, South Australia, Australia; J.B. Cleland	Chapter 4
AD-C 51358	*Resupinatus cinerascens*		*Eucalyptus orata*	Aug. 6 2002	Flinders Chase National Park, Ravine de Casoars, Kangaroo Island, Australia; P.S. Catcheside	Chapter 4
AD-C 51359	*Resupinatus cinerascens*		*Eucalyptus* branch	Jul. 10 1999	Grass Tree Conservation Park, South Australia, Australia; P.S. Catcheside	Chapter 4
AD-C 53231	*Resupinatus cinerascens*		*Eucalyptus*	July 1963	Belair National Park, Southern Lofty, South Australia, Australia; P.H.B. Talbot	Chapter 4
AD-C 54471	*Resupinatus cinerascens*		*Eucalyptus obliqua*	May 10 2008	Stringybark Walking Trail, Delamere, South Australia, Australia; P.S. Catcheside	Chapter 4
AD-C 55199	*Resupinatus cinerascens*		*Banksia marginata* cones	May 21 2003	South of Naracoorte, SE Joanna, South Australia, Australia; P.S. Catcheside	Chapter 4
AD-C 55258	*Resupinatus subapplicatus*		*Eucalyptus obliqua*	Oct. 27 1999	Stringybark Walking Trail. Delamere, South Australia, Australia; P.S. Catcheside	Chapter 4
AD-C 55262	*Resupinatus cinerascens*		Wood	May 29 1999	Grass Tree Conservation Park, South Australia, Australia; P.S. Catcheside	Chapter 4
AD-C 55538	*Resupinatus striatulus*	Undetermined	Mulberry	June 1913	Hawkesbury River, Milson Island, New South Wales, Australia; J.B. Cleland	Chapter 4, Chapter 5
AD-C 55539	*Resupinatus striatulus*	Undetermined	N.R.	June 1913	Milson Island, New South Wales, Australia; J.B. Cleland	Chapter 6

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
AD-C 55540	*Resupinatus striatulus*	Undetermined	Dead wood	June 1913	Milson Island, New South Wales, Australia; J.B. Cleland	Chapter 6
AD-C 55541	*Resupinatus striatulus*	Undetermined	N.R.	Apr. 5 1915	Manly, New South Wales, Australia; J.B. Cleland	Chapter 6
AD-C 55542	*Resupinatus striatulus*	*Resupinatus applicatus*	N.R.	May 5 1916	Sydney, New South Wales, Australia; J.B. Cleland	Chapter 2, Chapter 4
AD-C 55543	*Resupinatus striatulus*	*Scytinotus longinquus*	N.R.	Jun. 5 1916	Lisarow, New South Wales, Australia; J.B. Cleland	Chapter 6
AD-C 55544	*Resupinatus striatulus*	*Resupinatus applicatus*	N.R.	Jun. 29 1915	Mt. Wilson, New South Wales, Australia; J.B. Cleland	Chapter 2, Chapter 4
AD-C 55545	*Resupinatus striatulus*	Undetermined	Mulberry	June 1913	Milson Island, New South Wales, Australia; J.B. Cleland	Chapter 4
AD-C 55546	*Resupinatus striatulus?*	*Resupinatus applicatus*	N.R.	Jun. 5 1916	Lisarow, New South Wales, Australia; J.B. Cleland	Chapter 2, Chapter 4
AD-C 55601	*Resupinatus* sp.	Australian lamellate *Resupinatus* 1 (HT)	*Eucalyptus cladocalyx*	Jun. 5 2008	Near Flinders Chase Visitor Centre, Kangaroo Island, Australia; P.S. Catcheside	Chapter 4
AD-C 55602	*Henningsomyces candidus*		Rotten fallen timber	Jul. 19 2008	Mt. Panorama, Kuitpo, Southern Lofty, South Australia, Australia; P.S. Catcheside	Chapter 6
AD-C 55846	*Resupinatus applicatus*		N.R.	circa 1890	Provenance unknown, Tasmania, Australia; L. Rodway	Chapter 2, Chapter 4
ARIZ 012974	*Stigmatolemma taxi*	*Rhodocyphella cupuliformis*	*Juniperus virginiana*	Apr. 17 1986	St. Joseph Catholic Cemetary, North St., Baton Rouge, Louisiana, USA; M. Blackwell	Chapter 2
ARIZ 012975	*Stigmatolemma taxi*	*Rhodocyphella cupuliformis*	*Juniperus virginiana*	Aug. 16 1985	Defuniak Springs, Walton County, Florida, USA; M. Blackwell	Chapter 2
ARIZ 012976	*Stigmatolemma taxi*	*Rhodocyphella cupuliformis*	*Juniperus virginiana*	Aug. 16 1985	Defuniak Springs, Walton County, Florida, USA; M. Blackwell	Chapter 2
ARIZ 012977	*Stigmatolemma taxi*	*Rhodocyphella cupuliformis*	*Juniperus virginiana*	Aug. 16 1985	Defuniak Springs, Walton County, Florida, USA; R.L. Gilbertson	Chapter 2

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
ARIZ 012978	*Stigmatolemma taxi*	*Rhodocyphella cupuliformis*	*Juniperus virginiana*	Aug. 6 1985	Pensacola, Santa Rosa County, Florida, USA; R.L. Gilbertson	Chapter 2
B 70 0000333	*Resupinatus kavinii*	*Resupinatus applicatus*	N.R.	Jun. 2 1980	Kohlhasenbruck, Berlin, Germany; E. Ludwig	Chapter 2
B 70 0014065	*Pleurotus kavinae*	*Resupinatus striatulus*	auf Baumstrunk	August 1930	Mahrisch-Weisskirchen (Hranice), Podhorn, Czechoslovakia; F. Petrak	Chapter 5
B 70 0014066	*Cyphella pezizoides*	*Lachnella alboviolascens*	*Cytisus capitatus*	Dec. 20 1926	Tamsel, Baumschulen; P. Vogel	Chapter 6
BPI 208456	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	Palm roots	July 1929	Guantanamo, Cuba; B. Hioram	Chapter 6
BPI 208457	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	N.D.	Brazil; Dr. Spegazzini	Chapter 6
BPI 208458	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	1921	Montevideo, Uruguay; Dr. Felippone	Chapter 6
BPI 208459	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Sep. 23 1929	Poterno, at Pejivalle Farm, Costa Rica; C.W. Dodge & W.S. Thomas	Chapter 6
BPI 208460	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	Decayed stump	Jun. 28 1929	Dept. Junin, Pichis Trail, Yapas, Peru; E.P. Killip & A.C. Smith	Chapter 6
BPI 208461	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	August 1924	Mexico; Dampf	Chapter 6
BPI 208462	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Aug. 18 1935	Hacienda Cincinnati, Sierra Nevada de Santa Maria, Colombia; G.W. Martin	Chapter 6
BPI 208463	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	N.D.	Georgetown, Jamaica; Bartlett	Chapter 6
BPI 208464	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Oct. 18 1908	Near Cuernavaca, Morelos, Mexico; C.G. Pringle	Chapter 6
BPI 208465	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	October 1916	Caracas, Venezuela; Mr. & Mrs. J.N. Rose	Chapter 6

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
BPI 208466	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Feb. 8 1889	St. Martinsville P.O., Louisiana, USA; A.B. Langlois	Chapter 6
BPI 208467	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	May 3 1930	Cerro Guaca, Quebrada de Laja & Rio Nuevo, Puntarenas, Costa Rica; C.W. Dodge	Chapter 6
BPI 208468	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Aug. 31 1923	Santa Laura, Rio Maderia, Brazil; J.R. Weir	Chapter 6
BPI 208469	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	July 1925	Cuba; B. Hioram	Chapter 6
BPI 208470	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Oct. 27 1933	El Rubio, State of Tachira, Venezuela; J.I. Otero	Chapter 6
BPI 208471	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	February 1906	Annandale, Grenada; W.E. Broadway	Chapter 6
BPI 208472	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	July 1925	Cuba; B. Hioram	Chapter 6
BPI 208473	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	July 1925	Cuba; B. Hioram	Chapter 6
BPI 208474	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Sept. 9 1929	Vicinity of San Jose, Costa Rica; C.W. Dodge	Chapter 6
BPI 208475	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	Decaying wood	Apr. 24 1906	Rio Reventazon, Costa Rica; W.R. Maxon	Chapter 6
BPI 208557	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Aug. 10 1946	Tingo Maria, Peru; J.B. Carpenter	Chapter 6
BPI 208560	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Apr. 24 1930	Trail toward Corozal, Costa Rica; C.W. Dodge	Chapter 6
BPI 208593	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Jun. 26 1923	Guatemala; E.G. Smith	Chapter 6
BPI 208596	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	August 1950	Above Gomez Farias, Tamaulipas, Mexico; A.J. Sharp	Chapter 6
BPI 208598	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	1936	Alameda, Guatemala; J.R. Johnson	Chapter 6

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
BPI 208600	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	Jun. 2 1890	St. Martinsville P.O., Louisiana, USA; A.B. Langlois	Chapter 6
BPI 208601	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	February 1925	Brazil; J. Rick	Chapter 6
BPI 208602	*Polyporus fimbriatus*	*Hydnopolyporus palmatus*	N.R.	N.D.	Louisiana, USA; A.B. Langlois	Chapter 6
BPI 257859	*Theleporus griseus*	*Resupinatus poriaeformis*	Bark	1907	S. Leopoldo, Rio Grande do Sul, Brazil; J. Rick	Chapter 3, Chapter 5
BPI 257860	*Porotheleum poriaeforme*	North American cyphelloid *Resupinatus*	Rotting burnt log	Apr. 27 1971	Kelowna, British Columbia, Canada; S.A. Redhead	Chapter 3
BPI 257861	*Porotheleum poriaeforme*	North American cyphelloid *Resupinatus*	*Platanus wrightii*	Aug. 24 1967	Rucker Canyon Chiricahua Mtns, Coronado National Forest, USA; R.L. Gilbertson	Chapter 3
BPI 257953	*Stromatoscypha huia* (T)	*Resupinatus*	*Leptospermum ericoides*	November 1945	Huia, NZ; G.H. Cunningham (duplicate of PDD 4392)	Chapter 4
BPI 257954	*Stromatoscypha poriaeforme*	Australian cyphelloid *Resupinatus* 1	*Metrosideros perforata*	Feb. 20 1954	Ryan's Creek, Stewart Island, Otago, NZ; J.M. Dingley (duplicate of PDD 12963)	Chapter 4
BPI 257996	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	*Platanus occidentalis*	Aug. 8 1928	Elizabeth Furnace, Virginia, USA; C.L. Shear	Chapter 3
BPI 258008	*Solenia cinerea* (HT)	*Maireina*	*Quercus* bark	May 28 1920	Avalon, Los Angeles County, California, USA; L.W. Nuttall	Chapter 6
BPI 258312	*Solenia poriaeformis*	*Peziza pruinata*	Bark of grape vine	May 8 1938	Plummer's Island, in Potomac River near Cabin John, Maryland, USA; E.C. Leonard	Chapter 5
BPI 258313	*Solenia poriaeformis*	*Peziza pruinata*	Rotten tree trunk	Aug. 7 1938	Winston-Salem, North Carolina, USA; P.O. Schallert	Chapter 5
BPI 258314	*Solenia poriaeformis*	North American cyphelloid	N.R.	November 1911	Massachusetts, USA; A.P.D. Piguet	Chapter 3

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
		Resupinatus				
BPI 258315	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Jul. 26 1886	Vermillion Lake, Minnesota, USA; J.C. Arthur, L.H. Bailey, E.W.D. Holway	Chapter 3
BPI 258316	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten wood	N.D.	Newfield, New Jersey, USA, Ellis & Everhart #2317; J.B. Ellis	Chapter 3
BPI 258317	*Solenia poriaeformis*	*Tapesia daedalea*	N.R.	Aug. 6 1928	Elizabeth Furnace, Virginia, USA; C.L. Shear	Chapter 3
BPI 258318	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten wood	N.D.	Newfield, New Jersey, USA, Ellis & Everhart #2317; J.B. Ellis	Chapter 3
BPI 258319	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Decaying log	Jul. 26 1886	Vermillion Lake, Minnesota, USA; E.W.D. Holway	Chapter 3
BPI 258320	*Solenia poriaeformis*	*Resupinatus*	"in ligno pns…" ???	Apr. 25 1897	???, "Fungi Schemnitzienses"; "Andr. Kmet."	Chapter 3
BPI 258321	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Jul. 26 1886	Vermillion Lake, Minnesota, USA; E.W.D. Holway	Chapter 3
BPI 258322	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Jul. 30 1939	Iowa City, Iowa, USA; G.W. Martin	Chapter 3
BPI 258323	*Solenia poriaeformis*	*Tapesia daedalea*	Hanging oak branch	Apr. 14 1901	Auburn, Alabama, USA; F.S. Earle	Chapter 3
BPI 258324	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Jul. 26 1886	Vermillion Lake, Minnesota, USA; J.C. Arthur, L.H. Bailey, E.W.D. Holway	Chapter 3
BPI 258325	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Jun. 14 1929	Estherville, Iowa, USA; G.W. Martin	Chapter 3

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
BPI 258326	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten wood	Aug. 6 1935	Gull Lake Portage, Lake Temagami, T.F.R., Ontario, Canada; R. Biggs & J.W. Groves	Chapter 3
BPI 258346	*Solenia porioides*	*Resupinatus conspersus*	*Pinus picea*	N.D.	Neuchatel, Switzerland; N.R.	Chapter 3
BPI 258361	*Solenia subporiaeformis* (T)		Rotten wood	Jul. 11 1903	Margarita Island, Venezuela; A.F. Blakeslee	Chapter 5
BPI 258368	*Solenia grisella*	*Porotheleum cinereum*	Dead wood	N.D.	Brazil; J. Rick	Chapter 3
BPI 258369	*Solenia tephrosia*	North American cyphelloid *Resupinatus*	Decayed log	Jul. 25 1922	Kingston, Pensylvannia, USA; D.R. Sumstine	Chapter 3
BPI 258370	*Solenia tephrosia*	North American cyphelloid *Resupinatus*	Oak	Sept. 16 1934	Iowa City, Iowa, USA; G.W. Martin	Chapter 3
BPI 292753	*Cyphella cupulaeformis*	Undetermined	*Thuja occidentalis*	Nov. 10 1959	Cedar Swamp, Champaign County, Ohio, USA; W.B. & V.G. Cooke	Chapter 6
BPI 292797	*Cyphella conglobata*	*Stromatocyphella*	*Alder*	September (no year)	North Elba; C.H. Peck	Chapter 2
BPI 292799	*Cyphella conglobata*	*Stromatocyphella*	*Alder*	July (no year)	Adirondack Mountains; C.H. Peck	Chapter 2
BPI 292800	*Cyphella conglobata* (T)	*Stromatocyphella*	*Alnus*	July 1907	Lower Bartlett, New Hampshire, USA; R. Thaxter	Chapter 2
BPI 292803	*Cyphella conglobata*	*Stromatocyphella*	*Betula*	Jul. 14 1921	Stone Valley, Huntington County, Pensylvannia, USA; L.O. Overholts	Chapter 2
BPI 292805	*Cyphella cupulaeformis*	*Maireina monacha*	*Juniperus chinensis*	Sept. 5 1934	Newport, Rhode Island, USA; V.J. Vanicek	Chapter 6
BPI 292806	*Cyphella*	*Lachnella villosa*	*Robinia*	Aug. 20	Gatlinburg, Tennessee, USA;	Chapter 6

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
	cupulaeformis		*pseudoacacia*	1939	R.W. Davidson	
BPI 292807	*Cyphella cupulaeformis*	*Rhodocyphella*	*Juniperus* sp.	N.D.	Darien, Georgia, USA; H.W. Ravenel (Fungi Americani Exsiccati)	Chapter 2
BPI 292937	*Cyphella marginata*	*Maireina monacha*	Almond twigs	Jul. 28 1919	Corvallis, Oregon, USA; S.M. Zeller	Chapter 6
BPI 292938	*Cyphella marginata*	*Maireina monacha*	Peach twigs	Jul. 25 1919	Corvallis, Oregon, USA; S.M. Zeller	Chapter 6
BPI 292977	*Cyphella pezizoides*	*Lachnella alboviolascens*	N.R.	Jul. 31 1889	Clyde, New York, USA; J.B. Ellis	Chapter 6
BPI 292978	*Cyphella pezizoides*	*Lachnella alboviolascens*	*Genista florida*	Nov. 25 1903	Tamsel, Brandenburg; P. Vogel	Chapter 6
BPI 292979	*Cyphella pezizoides*	*Lachnella alboviolascens*	*Genista florida*	Sept. 10 1905	Tamsel, Brandenburg; P. Vogel	Chapter 6
BPI 292983	*Cyphella ravenelii*	*Phaeosolenia*	*Carya* sp.	N.D.	Aiken, South Carolina, USA; H.W. Ravenel	Chapter 6
BPI 292984	*Cyphella ravenelii*	*Phaeosolenia*	*Carya* sp.	N.D.	Aiken, South Carolina, USA; H.W. Ravenel	Chapter 6
BPI 297476	*Cyphella pezizoides*	*Lachnella tiliae*	*Tilia*	1887	Orano; F.L. Harvey	Chapter 6
BPI 297477	*Cyphella pezizoides*	*Lachnella tiliae*	*Tilia* bark	N.D.	London, Ontario, Canada; J. Dearness	Chapter 6
BPI 323656	*Porotheleum incanum* (T)	*Resupinatus*	N.R.	1881	Somerset East, South Africa; "Ex Karsten"	Chapter 2
BPI 323716	*Solenia tephrosia*	*Resupinatus poriaeformis*	Birch	N.D.	Stockholm, Sweden; L. Romell	Chapter 3
BPI 323717	*Solenia tephrosia*	North American cyphelloid *Resupinatus*	Rotten oak log	Aug. 25 1921	New Brunswick, New Jersey, USA; L.O. Overholts	Chapter 3
BPI 323718	*Solenia tephrosia*	North American cyphelloid	Old log	Oct. 30 1925	Parfrey's Glen, Wisconsin, USA; D.V. Baxter	Chapter 3

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		Resupinatus				
BPI 323719	*Solenia tephrosia*	*Resupinatus poriaeformis*	Dead wood	Jul. 11 1908	Allier, France; Rev. H. Bourdot (Herb. Bourdot #14631)	Chapter 3
BPI 323720	*Solenia tephrosia*	*Resupinatus poriaeformis*	*Salix*	November 1923	Bohemia; A. Pilat	Chapter 3
BPI 323721	*Solenia tephrosia*	North American cyphelloid *Resupinatus*	Rotten wood	N.D.	New Jersey, USA; J.B. Ellis (Ellis & Everhart #2317)	Chapter 3
BPI 332265	*Cyphella conglobata*	*Stromatocyphella*	*Betula*	Jul. 14 1921	Stone Valley, Huntington County, Pensylvannia, USA; L.O. Overholts	Chapter 2
BPI 798457	*Peziza pruinata*		*Vitis* sp.	N.D.	N.R.; Schweinitz (Schwein. Mtd. Coll. #855)	Chapter 5
CANB 574872	*Resupinatus* sp.	*Resupinatus striatulus*	Rotting wood	Jun. 13 1993	Sclerophyll forest, Australian Capital Territory, Canberra, Australia; H. Lepp	Chapter 4, Chapter 5
CANB 574876	*Resupinatus* sp.	*Resupinatus applicatus*	N.R.	Apr. 19 1995	Duncombe Bay Rd., Norfolk Island, Australia; H. Lepp	Chapter 2, Chapter 4
CANB 574880	*Resupinatus* sp.	*Resupinatus applicatus*	Dead wood	May 15 1997	Off Anson Bay Rd., Norfolk Island, Australia; H. Lepp	Chapter 2, Chapter 4
CANB 574881	*Resupinatus* sp.	*Resupinatus applicatus*	Underside of rotting log	Apr. 21 1992	Flowery Gully, 4 km S of Beaconsfield, Tasmania, Australia; H. Lepp	Chapter 2, Chapter 4
CANB 605135	*Pleurotus cinerascens*	Undetermined	*Eucalyptus*	Jun. 13 1976	Ferntree Gully National Park, Eastern Highlands, Victoria, Australia; N.H. & K.H. Sinnott	Chapter 4
CANB 742140	*Resupinatus* sp.	*Resupinatus applicatus*	*Quercus suber*	Oct. 26 2003	Glenloch Cork Oak Plantation, Australian Capital Territory, Canberra, Australia; H. Lepp	Chapter 2, Chapter 4
CANB 742279	*Resupinatus* sp.	*Resupinatus applicatus*	Twigs	Apr. 26 2004	Coolgardie District, 2 km N of Kintore, Western Australia,	Chatper 2, Chapter 4

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					Australia; H. Lepp	
CANB 751987	*Stigmatolemma* sp.	Australian cyphelloid *Resupinatus* 1	Well-rotted wood	May 4 2005	Boonoo Boonoo National Park, New South Wales, Australia; H. Lepp	Chapter 4
CBG 9218803	*Resupinatus* sp.	*Resupinatus merulioides*	Rotting palm trunk	Jun. 21 1992	Mutton Bird Pt. & Int. Hill, Lord Howe Island, New South Wales, Australia; H. Streimann & J.A. Elix	Chapter 4
DAR 14206	*Pleurotus applicatus*	*Resupinatus applicatus*	Rotting wood	Jul. 9 1965	Maltous Rd., Epping, Australia; J.K. McGechan	Chapter 2, Chapter 4
DAR 64161	*Pleurotus applicatus*	*Resupinatus trichotis*	*Acer rubrum*	November 1901	Newfield, New Jersey, USA; J.B. Ellis	Chapter 5
F B 6034-1013515	*Aphyllotus campanelliformis* (HT)		Ramules Boehemeriae	Apr. 11 1968	Near Futagasuga, Cundinamarca, Colombia; R. Singer	Chapter 6
F 1004897	*Cyphella pezizoides*	*Lachnella tiliae*	N.R.	Sept. 8 1904	Blue Mounds, Dane County, Wisconsin, USA; N.R.	Chapter 6
FH 258736	*Cyphella cupulaeformis* (IT)	*Rhodocyphella*	Dead bark	Before 1873	Aiken, South Carolina, USA; H.W. Ravenel	Chapter 2
FH 258737	*Peziza atrofusca*	*Catinella olivacea*	*Pinus*	October 1856	N.R.; Peters	Chapter 6
FH 258738	*Stigmatolemma taxi*	*Rhodocyphella cupuliformis*	*Juniperus* bark	N.D.	Darien, Georgia, USA; Ravenel F. Am. #224	Chapter 2
FH 258739	*Peziza daedalea* (T)		Bark	N.D.	Fungi Car. Exsic. Ravenel	Chapter 3, Chapter 5
FH 258740	*Peziza pruinata*		*Vitis*	N.D.	Fungi Car. Exsic. Ravenel	Chapter 5
FH 258741	*Peziza pruinata*	*Tapesia daedalea*	N.R.	N.D.	N.R.; J.B. Ellis	Chapter 3, Chapter 5
FH 258742	*Peziza pruinata*	*Tapesia daedalea*	*Monis* (?)	Nov. 6 1876	Malaga, New Jersey, USA; N.R.	Chapter 3, Chapter 5

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FH 258743	*Peziza pruinata*	*Lachnum ~papyraceum*	Bark	N.D.	Newfield, New Jersey, USA; J.B. Ellis	Chapter 6
FH 258744	*Peziza tela*	*Tapesia daedalea*	Damp rotten sticks	February 1848	Santee Canal, South Carolina, USA; H.W. Ravenel	Chapter 3, Chapter 5
FH 258745	*Porotheleum cinereum* (T)		N.R	March 1892	Cratere de Pululahua, Ecuador; Lagerheim	Chapter 3
FH 258746	*Porotheleum cinereum*		N.R.	N.D.	Pululahua, Ecuador; Lagerheim	Chapter 3
FH 258747	*Cyphella marginata*	*Maireina monacha*	Peach twigs	Jul. 25 1919	Corvallis, Oregon, USA; S.M. Zeller	Chapter 6
FH 258748	*Theleporus griseus*	Undetermined	N.R.	1908	Sao Leopoldo, Rio Grande do Sul, Brazil; J. Rick	Chapter 5
FH 258749	*Theleporus griseus*	*Resupinatus poriaeformis*	N.R.	1931	Sao Leopoldo, Rio Grande do Sul, Brazil; J. Rick	Chapter 5
FH 258750	*Solenia grisella* var. *theleporea*	Undetermined	N.R.	1907	Sao Leopoldo, Rio Grande do Sul, Brazil; J. Rick	Chapter 5
FH 258751	*Solenia grisella* var. *theleporea*	Undetermined	N.R.	1909	Sao Leopoldo, Rio Grande do Sul, Brazil; J. Rick	Chapter 5
FH 258752	*Cyphella grisella*	*Tapesia daedalea*	*Tecoma radicans*	Dec. 22 1936	Richmond, Virginia, USA; D.H. Linder	Chapter 3
FH 258753	*Cyphella poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	November 1931	Sharon, Massachusetts, USA; A.P.D. Piguet	Chapter 3
FH 258754	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten wood	Aug. 6 1935	Gull L.P., Lake Temagami, TFR, Ontario, Canada; R. Biggs & J.W. Groves	Chapter 3
FH 258755	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Oak bark	Jul. 30 1921	Kittery Point, Maine, USA; R. Thaxter	Chapter 3
FH 258756	*Solenia poriaeformis*	North American cyphelloid	Poplar wood	Oct. 8 1932	Canton, Massachusetts, USA; D.H. Linder	Chapter 3

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		Resupinatus				
FH 258757	*Solenia poriaeformis*	*Peziza pruinata*	Grape vine bark	Nov. 13 1920	Chapel Hill, North Carolina, USA; W.C. Coker	Chapter 5
FH 258758	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten log	Aug. 7 1892	Kittery Point, Maine, USA; R. Thaxter	Chapter 3
FH 258759	*Solenia poriaeformis*	*Tapesia daedalea*	*Magnolia*	Jan. 21 1889	St. Martinsville, Iowa, USA; A.B. Langlois	Chapter 3, Chapter 5
FH 258760a	*Solenia poriaeformis*	*Tapesia daedalea*	Various deciduous trees	N.D.	Newfield, New Jersey, USA; Ellis & Everhart #2317	Chapter 3, Chapter 5
FH 258760b	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Various deciduous trees	N.D.	Newfield, New Jersey, USA; Ellis & Everhart #2317	Chapter 3
FH 258760c	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Various deciduous trees	N.D.	Newfield, New Jersey, USA; Ellis & Everhart #2317	Chapter 3
FH 258761	*Solenia poriaeformis*	*Lachnum ~papyraceum*	N.R.	August 1907	"Chocaun" (?); W.G. Farlow	Chapter 6
FH 258762	*Solenia poriaeformis*	*Resupinatus*	*Salix*	Before 1894	Oestrich (Nassau); Fuckel	Chapter 3
FH 258763	*Solenia* sp.	*Stromatocyphella conglobata*	*Alnus*	September 1910	"Chocaun"; W.G. Farlow	Chapter 2
FH 258764	*Solenia poriaeformis*	*Resupinatus*	*Populus*	September 1908	"Cledi…?"; Illegible	Chapter 3
FH 258765	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	N.D.	N.R.; R. Thaxter	Chapter 3
FH 258767	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	November 1923	N.R.; N.R.	Chapter 3
FH 258768	*Solenia*	*Resupinatus*	*Fagus*	Sept. 22	Skane: Torekov parish, Hallands	Chapter 3

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	poriaeformis			1946	Vadero, Sweden; J. Eriksson	
FH 258769	*Cyphella conglobata*	*Stromatocyphella*	*Alnus incana*	Sept. 20 1934	Bell's Lake, North of Parry Sound, Ontario, Canada; H.S. Jackson	Chapter 2
HO 548042	*Solenia candida*	Undetermined	N.R.	N.D.	N.R.; Rodway (RH 191)	Chapter 6
HO 548043	*Solenia candida*	Undetermined	N.R.	August 1915	N.R.; Rodway (RH 191)	Chapter 6
HO 548044	*Solenia anomala*	Undetermined	Dead wood	August 1921	MC "Tholu" Gully; Rodway (RH 192)	Chapter 6
HO 548045	*Pleurotus applicatus*	Undetermined	Dead wood	N.D.	N.R.; Rodway (RH 26)	Chapter 6
HO 548046	*Pleurotus* sp.	Undetermined	Dead wood	N.D.	N.R.; Rodway	Chapter 6
HO 548047	*Pleurotus applicatus*	Undetermined	Dead wood	September 1919	N.R.; Rodway (RH 26)	Chapter 6
HO 548048	*Pleurotus diversipes*	Undetermined	Dead wood	N.D.	N.R.; Rodway (RH 27)	Chapter 6
K 13501	*Stigmatolemma poriiforme*	*Resupinatus*	*Fagus sylvatica*	Jan. 21 1990	Mickleham, Norbury Park, Surrey, England; N.W. Legon	Chapter 3
K 23193	*Stigmatolemma poriaeforme*	*Resupinatus*	*Salix*	Feb. 14 1993	The Causeway, Slapton, Devon, England; P.J. Roberts	Chapter 3
K 31487	*Stigmatolemma poriiforme*	*Resupinatus*	*Fagus sylvatica*	Oct. 9 1995	New Forest, Denny Wood, South Hampshire, England; N.W. Legon	Chapter 3
K 57502	*Stigmatolemma poriiforme*	*Resupinatus*	*Quercus petraea*	May 5 1998	Maentwrog, Plas Tan-y-Bwlch, Marionethshire, Wales; B. Ing	Chapter 3
K 62514	*Stigmatolemma poriaeforme*	*Resupinatus*	*Fagus sylvatica*	Sept. 25 1998	New Forest, Old Burley Inclosure, Hampshire, England; N.W. Legon	Chapter 3
K 77430	*Stigmatolemma poriaeforme*	*Resupinatus*	Deciduous wood	Jun. 4 2000	Esher Common, Below the Ledges, Surrey, England; P.J. Roberts	Chapter 3
K 88532	*Stigmatolemma poriiforme*	*Resupinatus*	Wood	Sept. 29 1984	Ockley, Vann Lake, Surrey, England; D.A. Reid & A. Thomas	Chapter 3
K 91345	*Stigmatolemma*	*Resupinatus*	Deciduous	Nov. 10	Durham, Raintonpark Wood,	Chapter 3

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	poriiforme		wood	2001	Durham County, England; A.W. Legg	
K 113838	*Stigmatolemma poriiforme*	*Resupinatus*	*Betula*	May 19 2003	Morrone Birchwoods, South Aberdeen, England; A. Henrici	Chapter 3
K 129953	*Stigmatolemma poriiforme*	*Resupinatus*	Hardwood	Apr. 12 2005	New Forest, Sims Wood, South Hampshire, England; D. Griffin	Chapter 3
K 166162	*Cyphella cupulaeformis* (HT)	*Rhodocyphella*	*Juniperus virginiana*	January, N.Y	South Carolina, USA; H.W. Ravenel #1403	Chapter 2
K 166163	*Solenia porioides*	*Resupinatus conspersus*	*Abies* sp.	N.D.	Neuchatel, Switzerland; L. Fuckel	Chapter 3
K 166164	*Cyphella tela* (HT)	*Tapesia daedalea*	Wood	N.D.	South Carolina, USA; M.J. Berkeley 1905/7724	Chapter 3, Chapter 5
K 166165	*Cyphella grisea* (IT)	*Rhodocyphella cupuliformis*	Fibrous wood and bark	December 1917	Hakgala, Sri Lanka; T. Petch	Chapter 5
K 166168	*Cyphella farinosa* (IT)	*Stigmatolemma farinaceum*	Wood	September 1883	Cape of Good Hope, South Africa; Comm. MacOwan 1221	Chapter 5
K 166169	*Porotheleum reticulatum* (HT)	*Resupinatus poriaeformis*	Dead wood	April 1919	Hakgala, Sri Lanka; T. Petch	Chapter 3, Chapter 5
K 166170	*Solenia subgelatinosa* (IT)	*Cellypha*	*Alnus serrulata*	Before 1873	Aiken, South Carolina, USA; H.W. Ravenel	Chapter 5
ISC 352324	*Cyphella pezizoides*	*Lachnella alboviolascens*	*Genista tinctoria*	June and July 1884	Mycotheca Marchica #3134, near Berlin, Prussia, P. Sydow	Chapter 6
ISC 352325	*Cyphella pezizoides*	*Lachnella alboviolascens*	*Genista tinctoria*	February 1884	Mycotheca Marchica #503, near Berlin, Prussia; P. Sydow	Chapter 6
ISC 366064	*Cyphella pezizoides*	*Lachnella alboviolascens*	*Genista tinctoria*	June 1884	Mycotheca Marchica #503, near Berlin, Prussia; P. Sydow	Chapter 6
ISC 371973	*Porotheleum cinereum*		N.R.	Aug. 22 1935	Sierra Nevada de Santa Marta, Colombia; G.W. Martin	Chapter 3
ISC 378039	*Cyphella*	*Lachnella*	*Genista florida*	Nov. 3	Tamsel, Baumschulen; P. Vogel	Chapter 6

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	pezizoides	*alboviolascens*		1936		
ISC 378075	*Cyphella pezizoides*	*Lachnella alboviolascens*	*Cytisus capitatus*	Dec. 20 1936	Tamsel, Baumschulen; P. Vogel	Chapter 6
ISC 378122	*Cyphella poriaeformis*	*Resupinatus*	N.R.	Aug. 1 1952	Prov. Chirique, Panama; G.W. Martin, A.L. Welden	Chapter 3
ISC 378862	*Cyphella pezizoides*	*Lachnella alboviolascens*	*Genista florida*	Jan. 25 1931	Tamsel, Baumschulen; P. Vogel	Chapter 6
L 0796996	*Stigmatolemma* cf. *poriaeforme*	*Resupinatus*	Oak branch	September 1952	Bois de Belleme (Sartres), France; M.A. Donk	Chapter 3
L 0796997	*Stigmatolemma poriaeforme*	*Resupinatus*	Oak wood	Dec. 20 1906	Aveyron, France; Galzin	Chapter 3
L 0796998	*Stigmatolemma poriaeforme*	*Resupinatus*	*Fagus*	Sept. 22 1946	Skane: Torekov parish, Hallands Vadero, Sweden; J. Eriksson	Chapter 3
L 0796999	*Stigmatolemma poriaeforme*	North American cyphelloid *Resupinatus*	*Tilia americana*	Jul. 5 1933	Estherville, Iowa, USA; A.M. Lovney & D.P. Rogers	Chapter 3
MEL 261051	*Resupinatus* sp.	*Resupinatus applicatus*	*Nothofagus cunninghamii*	Jun. 13 1994	Beeches Walking Track, Keppel Falls Scenic Reserve, Marysville, Australia; N.H. Sinnott	Chapter 2, Chapter 4
MEL 269113	*Resupinatus* sp.	*Resupinatus subapplicatus*	*Eucalyptus camaldulensis*	June 1995	Raymond Island, Gippsland Plain, Victoria, Australia; A. Bould	Chapter 4
MEL 269121	*Resupinatus* sp.	*Resupinatus violaceogriseus*	*Pomaclerris* sp.	Apr. 25 1996	Kinglake National Park, Eastern Highlands, Victoria, Australia; A.W. Thies	Chapter 4
MEL 1052586	*Resupinatus* sp.	*Resupinatus violaceogriseus*	N.R.	Between 1892-1895	Tarwin River, Gippsland Plain, Victoria, Australia; F. Mueller	Chapter 4
MEL 1052588	*Resupinatus applicatus*	*Resupinatus subapplicatus*	*Eucalyptus vimnalis*	June 1891	Gippsland Plain, Melbourne, Victoria, Australia; J. Minchin	Chapter 4
MEL 1053060	*Resupinatus cinerascens*	Undetermined	N.R.	Jul. 23 1967	Ellery Gorge, W. of Alice Springs, Central Australia South, Northern Territory, Australia; A.C.	Chapter 4

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					Beauglehole	
MEL 1053061	*Resupinatus cinerascens*		Bark and sticks	Jul. 5 1964	Far SW Lower Glenelg River, Princess Margaret Rose Cave area, Wannon, Victoria, Australia; A.C. Beauglehole	Chapter 4
MEL 2031421	*Resupinatus cinerascens*		Dead twigs	May 19 1936	Torimbuk, Eastern Highlands/Gippsland Plain, Victoria, Australia; J.H. Willis	Chapter 4
MEL 2031422	*Resupinatus cinerascens*		Fallen branchwood	May 7 1984	Lakes National Park, Rotamah Island, Gippsland Plain, Victoria, Australia; "Mrs. Thies"	Chapter 4
MEL 2059634	*Resupinatus applicatus*	*Resupinatus violaceogriseus*	*Polyscias sambucifolia*	Mar. 29 1999	Lyrebird Circuit Walk, Kinglake N.P., Eastern Highlands, Victoria, Australia; T.W. May	Chapter 4
MEL 2063505	*Resupinatus* sp.	*Resupinatus violaceogriseus*	Wood	Aug. 30 2003	Toolangi State Forest, Eastern Highlands, Victoria, Australia; T. Lebel	Chapter 4
MEL 2090235	*Resupinatus* sp.	*Resupinatus subapplicatus*	Mallee root	Jul. 31 1998	Beaumont-Howick Rd., Eyre, Western Australia, Australia; B. Archer	Chapter 4
MEL 2096593	*Resupinatus* sp.	*Resupinatus applicatus*	N.R.	N.D.	Grampians National Park, Grampians, Victoria, Australia; I.R. McCann	Chapter 2, Chapter 4
MEL 2119132	*Resupinatus* sp.	*Resupinatus violaceogriseus*	*Polyscias* sp.	Apr. 27 1998	Kinglake National Park, Eastern Highlands, Victoria, Australia; T.W. May	Chapter 4
MEL 2231606	*Resupinatus* sp.	*Resupinatus violaceogriseus*	On a stick	May 12 2003	Gembrook, Mortimer Reserve, Eastern Highlands, Victoria, Australia; S.H. & E.L. Lewis	Chapter 4
MEL 2231620	*Resupinatus* sp.	*Resupinatus applicatus*	Branch	May 1 2003	Wirriwilla Rainforest Walk, Eastern Highlands, Victoria,	Chapter 2, Chapter 4

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					Australia; S.H. Lewis, T. Lebel & T.W. May	
MEL 2292300	*Resupinatus* sp.	*Resupinatus trichotis*	Buried twigs	Jun. 30 2004	Derimark, William Bay National Park, Darling, Western Australia, Australia; K. Syme	Chapter 4, Chapter 5
MEL 2292301	*Resupinatus* sp.	*Resupinatus violaceogriseus*	N.R.	Jun. 23 2001	Grampians National Park, Grampians, Victoria, Australia; I.R. McCann & T.G. Argall	Chapter 4
MEL 2300677	*Resupinatus subapplicatus*	*Resupinatus applicatus*	N.R.	Nov. 1 2002	Base of Mt. Wellington, Tasmania, Australia; S.J. McMullan-Fisher	Chapter 2, Chapter 4
MEL 2305275	*Resupinatus* sp.	*Resupinatus subapplicatus*	*Eucalyptus polyanthemes*	Jul. 14 2001	Yarck, Henke Winery, Midlands, Victoria, Australia; N.H. Sinnott & C.H. Miller	Chapter 4
MEL 2308212	*Resupinatus poriaeformis*	Australian cyphelloid *Resupinatus* 1	*Eucalyptus* sp.	Aug. 1 1970	Haws Nest Road, Stoney Rises, Vic. Volcanic Plain, Victoria, Australia; G.W. Beaton & N.E.M. Walters	Chapter 4
MEL 2308228	*Resupinatus poriaeformis*	Australian cyphelloid *Resupinatus* 1	*Prosanthera lasianthos*	Aug. 5 1956	Tarra Valley, Gippsland Highlands, Victoria, Australia; K. Healey	Chapter 4
MEL 2313581	*Resupinatus cinerascens*		Wood	Sep. 9 1963	Top Mount Gower, Lord Howe Norfolk Island, Lord Howe Island, Australia; H.M & A.C. Geauglehole	Chapter 4
MEL 2318047	*Resupinatus* sp.	Australian lamellate *Resupinatus* 2	N.R.	Jul. 28 1996	Tidal River, Wilsons Promontory, Victoria, Australia; Field Naturalists Club of Victoria	Chapter 4
NYBG 4	*Solenia poriaeformis*	*Resupinatus*	*Salix* bark	November 1875	"In ripis rivulorum: 'Neckendorfer Thal pr. Islebiam (Sax. Bor.)"; J. Kunze	Chapter 3
NYBG 36	*Solenia*	North American	Old fence nails	N.D.	Missouri, USA; N.R.	Chapter 3

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	poriaeformis	cyphelloid *Resupinatus*				
NYBG 37	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Jul. 30 1939	Iowa City, Iowa, USA; G.W. Martin	Chapter 3
NYBG 38(1)	*Peziza pruinata*		*Vitis* bark	N.D.	N.R.; Schweinitz	Chapter 5
NYBG 38(2)	*Peziza pruinata*		*Vitis* bark	N.D.	N.R.; Schweinitz	Chapter 5
NYBG 43	*Solenia grisella*	*Resupinatus poriaeformis*	*Corylus* wood	1904	France; Bourdot	Chapter 3
NYBG 56	*Solenia poriaeformis*	*Resupinatus*	*Salix*	1897	???; N.R.	Chapter 3
NYBG 57	*Solenia poriaeformis*	*Resupinatus*	*Fagus* trunk	Sept. 22 1946	Skane: Torekov parish, Hallands, Vadero, Sweden; J. Eriksson	Chapter 3
NYBG 67	*Stigmatolemma poriaefrome*	North American cyphelloid *Resupinatus*	Wood	About 1886	Kittery Point, Maine, USA; N.R.	Chapter 3
NYBG 78	*Solenia poriaeformis*	*Resupinatus*	*Salix*	Apr. 4 1904	Prov. Brandenburg, "Triglitz in der Prignitz"; O. Jaap	Chapter 3
NYBG 152	*Cyphella cupulaeformis*	*Rhodocyphella ?cupuliformis*	*Juniperus bermudiana*	Dec. 8 1938	St. David's Islands, Bermuda; F.J. Seaver & J.M. Waterston	Chapter 2
NYBG 204(1)	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Jul. 26 1886	Vermillion Lake, Minnesota, USA; J.C. Arthur, L.H. Bailey Jr., E.W.D. Holway	Chapter 3
NYBG 204(2)	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Jul. 26 1886	Vermillion Lake, Minnesota, USA; J.C. Arthur, L.H. Bailey Jr., E.W.D. Holway	Chapter 3
NYBG 224(1)	*Cyphella cupulaeformis*	*Rhodocyphella*	*Juniperus*	N.D.	Darien, Georgia, USA; Fung. Amer. Exsic. #224	Chapter 2
NYBG 224(2)	*Cyphella cupulaeformis*	*Rhodocyphella*	*Juniperus*	N.D.	Darien, Georgia, USA; Fung. Amer. Exsic. #224	Chapter 2
NYBG 300	*Cyphella*	*Rhodocyphella*	*Junipersu*	Oct. 16	Paygi East, Bermuda; F.J. Seaver	Chapter 2

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
	cupulaeformis	*?cupuliformis*	*bermudiana*	1940	& J.M. Waterston	
NYBG 364	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	N.D.	New England, USA; A.P.D. Piguet	Chapter 3
NYBG 497	*Cyphella cupulaeformis*	*Rhodocyphella ?cupuliformis*	*Juniperus bermudiana*	Nov. 2 1942	Agricultural Station, Paget East, Bermuda; J.M. Waterston	Chapter 2
NYBG 511(1)	*Cyphella cupulaeformis*	*Rhodocyphella ?cupuliformis*	*Juniperus bermudiana*	Jun. 3 1943	Paygi East, Bermuda; J.M. Waterston	Chapter 2
NYBG 511(2)	*Cyphella cupulaeformis*	*Rhodocyphella ?cupuliformis*	*Juniperus bermudiana*	Jun. 3 1943	Agricultural Station, Bermuda; J.M. Waterston	Chapter 2
NYBG 636	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Decaying willow	Aug. 18 1897	Faulkland, Delaware, USA; A. Commons	Chapter 3
NYBG 722	*Cyphella* sp.	Undetermined	Palm frond	Jul. 6 1974	Aljibe, Providencia, Anori, above Rio Anori, Dpto. Antioquia, Colombia; K.P. Dumont, J.H. Haines, L.F. Velasquez, R. Fonnegra	Chapter 6
NYBG 805	*Peziza pruinata*		Grape vine	N.D.	Ohio, USA; Morgan	Chapter 5
NYBG 853	*Peziza pruinata*	*Tapesia daedalea*	Maple/oak bark	May 1874	Newfield, New Jersey, USA; J.B. Ellis	Chapter 3
NYBG 872	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotting wood	Dec. 11 1886	Howe Ave., banks of the Mississippi, Louisiana, USA; A.B. Langlois	Chapter 3
NYBG 886	*Cyphella* sp.	*Porotheleum cinereum*	Branch	Jun. 21 1975	Puerto Obaldia to Armila Indian Village, Prov. San Blas, Panama; K.P. Dumont, S.E. & S.M. Carpenter, S.A. Mori	Chapter 3
NYBG 1160	*Solenia* sp.	Undetermined	Wood	Nov. 25 1911	Palo Alto, Preston's Ravine, California, USA; W.A. Murrill & L.S. Abrams	Chapter 6

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
NYBG 1709	*Cyphella cupulaeformis*	*Rhodocyphella*	*Juniperus*	1873	Aiken, South Carolina, USA; H.W. Ravenel	Chapter 2
NYBG 1930	*Solenia poriaeformis*	*Resupinatus*	*Salix*	1894	Oestrich, Nassau; Fuckel	Chapter 3
NYBG 2317(1)	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten wood	N.D.	Newfield, New Jersey, USA; Ellis & Everhart's North American Fungi #2317	Chapter 3
NYBG 2317(2)a	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten wood	N.D.	Newfield, New Jersey, USA; Ellis & Everhart's North American Fungi #2317	Chapter 3
NYBG 2317(2)b	*Solenia poriaeformis*	*Tapesia daedalea*	Rotten wood	N.D.	Newfield, New Jersey, USA; Ellis & Everhart's North American Fungi #2317	Chapter 3
NYBG 2317(3)	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten wood	N.D.	Newfield, New Jersey, USA; Ellis & Everhart's North American Fungi #2317	Chapter 3
NYBG 2317(4)	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	Rotten wood	N.D.	Newfield, New Jersey, USA; Ellis & Everhart's North American Fungi #2317	Chapter 3
NYBG 3172	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Aug. 4 1933	Milford (Little Sioux River), Iowa, USA; D.P. Rogers	Chapter 3
NYBG 3591	*Porotheleum cinereum*		N.R.	Aug. 22 1935	Hacienda Cincinnati, Sierra Nevada de Santa Marta Dept. Magdalena, Colombia; G.W. Martin	Chapter 3
NYBG 4454	*Porotheleum poriaeforme*	*Porotheleum cinereum*	Branch	Jun. 9 1976	35 km from Zipaquira, on Zipaquira-Pacho Rd., Colombia; K.P. Dumont, S.E. Carpenter, M.A. Sherwood, L.A. Molina	Chapter 3
NYBG 4958	*Solenia*	North American	Rotten wood	Aug. 6	Lake Temagami, Ontario, Canada;	Chapter 3

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
	poriaeformis	cyphelloid *Resupinatus*		1935	R. Biggs & J.W. Groves	
NYBG 5149	*Stigmatolemma* sp.	*Porotheleum cinereum*	Wood	Jul. 27 1973	Finca Las Piletas, 1 km W of Santa Ana, El Salvador; G.A. Escobar	Chapter 3
NYBG 5183	*Stigmatolemma* sp.	*Porotheleum cinereum*	Wood	Jul. 27 1973	Finca Las Piletas, 1 km W of Santa Ana, El Salvador; G.A. Escobar	Chapter 3
NYBG 6332	*Porotheleum poriaeforme*	*Porotheleum cinereum*	Wood	Jul. 28 1972	Vicinity of El Arado, 12 km SW of Macarao, Edo. Miranda, Venezuela; K.P. Dumont, R.F. Cain, G.J. Samuels, G. Morillo	Chapter 3
NYBG 13778	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	N.R.	Aug. 18 1887	Faulkland, Delaware, USA; "S.G."	Chapter 3
NYBG 24721	*Porotheleum poriaeforme*	North American cyphelloid *Resupinatus*	Old log	Oct. 31 1957	Sandy woods, west edge of Albany, New York, USA; S.J. Smith, J.B. & R.D. Glasgow	Chapter 3
NYBG 30140	*Cyphella poriaeformis*	North American cyphelloid *Resupinatus*	Hardwood	Mar. 9 1955	Devil's Soup Bowl, Yankee Springs Recreation Area, Michigan, USA; D.P. Rogers	Chapter 3
NYBG 292116	*Solenia poriaeformis*	North American cyphelloid *Resupinatus*	*Quercus alba*	Nov. 3 1926	Merramac Highlands, Montana, USA; L.O. Overholts	Chapter 3
NYBG 414548	*Stigmatolemma poriaeformis*	*Porotheleum cinereum*	N.R.	Jun. 3 1961	Gombe Forest North of Pond Casse, Dominica; A.L. Welden	Chapter 3
NYBG 414549	*Stigmatolemma poriaeformis*	*Porotheleum cinereum*	Fallen wood	Jul. 3 1962	Ravine Blondeau, Guadeloupe; A.L. Welden	Chapter 3
O 12606	*Cyphella poriaeformis*	*Resupinatus*	*Laurus*	Jan. 9 1974	Tenerife, Monte de las Mercees, Canary Islands, Spain; L. Ryvarden	Chapter 5

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
O 64265	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Populus tremula*	Sept. 10 2000	Sogn Og Fjordane, Sogndal, Norway; L. Ryvarden	Chapter 3
O 65566	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Populus tremula*	Apr. 24 2002	Vest-Agder, Kristiansand, Norway; T.H. Dahl, I.J. Kittilsen	Chapter 3
O 65603	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Populus tremula*	Apr. 13 2002	Aust-Agder, Arendal, Norway; T.H. Dahl	Chapter 3
O 65625	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Tilia*	Apr. 21 2002	Aust-Agder, Arendal, Norway; T.H. Dahl	Chapter 3
O 91124	*Stigmatolemma poriiforme*	*Resupinatus*	*Quercus*	Oct. 13 1998	Rogaland, Hjelmeland, Norway; L. Ryvarden	Chapter 3
O 100001	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Populus*	Sept. 21 1998	Ostfold, Marker, Norway; M. Nunez	Chapter 3
O 100044	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Fraxinus*	Oct. 16 1998	Rogaland, Hjelmeland, Norway; J.N. Stokland	Chapter 3
O 146746	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Tilia*	November 1911	Oslo Fylke, Oslo, Norway; J. Egeland	Chapter 3
O 146747	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Tilia*	September 1911	Oslo Fylke, Oslo, Norway; J. Egeland	Chapter 3
O 146751	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	N.R.	Oct. 27 1918	Oslo Fylke, Oslo, Norway; J. Thomle	Chapter 3
O 146752	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Salix*	May 2 1915	Oslo Fylke, Oslo, Norway; J. Egeland	Chapter 3
PC 0084526	*Solenia porioides*	*Resupinatus conspersus*	*Abies*	March 1879	Neuchatel, Switzerland; P. Morthier	Chapter 3
PC 0084528	*Solenia grisella*	*Resupinatus conspersus*	Cut pine	Nov. 20 1877	Vauchamp sur Soulce, France; L. Quelet	Chapter 3
PC 0084529	*Solenia grisella*	*Resupinatus conspersus*	*Abies*	November 1878	N.R.; P. Morthier	Chapter 3
PC 0084530	*Solenia grisella*	*Resupinatus conspersus*	*Abies*	Nov. 13 1877	N.R.; L. Quelet	Chapter 3
PC 0085422	*Resupinatus*		N.R.	Jan. 18	Mayotte, Mont Sohoa Forest	Chapter 5

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
	poriaeformis			2010	Reserve, Chiconi; B. Buyck & V. Hofstetter	
PDD 4392	*Stromatoscypha huia* (T)	*Resupinatus*	*Leptospermum ericoides*	November 1945	Huia, NZ; G.H. Cunningham	Chapter 4
PDD 7138	*Stromatoscypha poriaeforme*	Australian cyphelloid *Resupinatus* 2	Rotten log	May 1948	Henderson, Auckland, NZ; J.M. Dingley	Chapter 4
PDD 7139	*Stromatoscypha poriaeforme*	*Resupinatus hyalinus*	Rotten branch	February 1931	Brooklyn, Maukau Harbor, Auckland, NZ; M. Hodgkins	Chapter 5
PDD 11162	*Stromatoscypha poriaeforme*	Australian cyphelloid *Resupinatus* 2	Dead wood	April 1946	Titirangi, Auckland, NZ; Myra Carter	Chapter 4
PDD 12963	*Stromatoscypha poriaeforme*	Australian cyphelloid *Resupinatus* 2	*Metrosideros perforata*	February 1954	Ryan's Creek, Stewart Island, Otago, NZ	Chapter 4
PDD 16951	*Stromatoscypha poriaeforme*	*Resupinatus hyalinus*	*Coprosma arborea*	June 1956	Little Barrier Island, Auckland, NZ; F.J. Newhook	Chapter 5
PDD 24323	*Stromatoscypha poriaeforme*	Australian cyphelloid *Resupinatus* 2	*Brachyglottis repandra*	Feb. 27 1965	Piha, Ngawharo Stream, Auckland, NZ; J.M. Dingley	Chapter 4
PDD 59254	*Resupinatus violaceogriseus*		Wood	Mar. 25 1991	Arthur's Pass National Park, North Canterbury, NZ; H. Neda	Chapter 4
PDD 70479	*Resupinatus trichotis*	*Resupinatus applicatus*	*Nothofagus solandri*	May 15 1996	Lyndon Saddle Track, Craigieburn Forest Park, Mid Canterbury, NZ; P.K. Buchannan, R.B. Allen, P.W. Clinton	Chapter 2, Chapter 4
PDD 70489	*Marasmiellus violaceogriseus*	*Resupinatus*	*Nothofagus solandri*	May 21 1996	Lyndon Saddle Track, Craigieburn Forest Park, Mid Canterbury, NZ; N.R.	Chapter 4
PDD 75559	*Resupinatus violaceogriseus*		Bark	May 9 2002	Haast Pass, Westland, NZ; P. Leonard	Chapter 4
PDD 79793	*Resupinatus applicatus*		Scrub	Mar. 20 2004	Kennedy's Bush, Mid Canterbury, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 79820	*Marasmiellus violaceogriseus*	*Resupinatus*	*Nothofagus solandri*	Mar. 14 2004	Bealy Chasm Track, North Canterbury, NZ; J.A. Cooper	Chapter 4

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
PDD 80153	*Marasmiellus violaceogriseus*	*Resupinatus*	*Nothofagus menziesii*	Nov. 24 2001	Lewis Pass, Buller, NZ; J.A. Cooper	Chapter 4
PDD 80649	*Marasmiellus violaceogriseus*	*Resupinatus cinerascens*	*Pinus radiata*	Aug. 29 2004	Kaiapoi Pines Beach, North Canterbury, NZ; J.A. Cooper	Chapter 4
PDD 83794	*Marasmiellus violaceogriseus*	*Resupinatus*	*Nothofagus solandri*	Oct. 25 2005	Oxford Forest, Eyre River, North Canterbury, NZ; J.A. Cooper	Chapter 4
PDD 86842	*Resupinatus applicatus*		Scrub	Dec. 26 2005	Sugarloaf Hill, Mid Canterbury, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 86862	*Resupinatus applicatus*		*Kunzea ericoides*	Jan. 6 2006	Hinewai Reserve, Akaroa, Mid Canterbury, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 87025	*Resupinatus applicatus*		*Ulex europaeus*	Sept. 12 2001	Banks Peninsula, Hinewai Reserve, Mid Canterbury, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 87046	*Resupinatus applicatus*		Dead wood, de-corticate	Apr. 30 2006	Montgomery Park, Banks Peninsula, Mid Canterbury, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 87121	*Resupinatus applicatus*		*Nothofagus menziesii*	May 12 2006	Nile River, Buller, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 87196	*Resupinatus applicatus*		*Kunzea ericoides*	Jun. 3 2006	Hinewai Reserve, Akaroa, Mid Canterbury, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 87197	*Marasmiellus violaceogriseus*	*Resupinatus*	*Kunzea ericoides*	Jun. 3 2006	Hinewai Reserve, Akaroa, Mid Canterbury, NZ; J.A. Cooper	Chapter 4
PDD 87307	*Resupinatus applicatus*		*Ripogonum scandens*	Feb. 11 2007	Kennedy's Bush, Mid Canterbury, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 87325	*Resupinatus applicatus*		*Pseudowintera colorata*	Feb. 24 2007	Ahuriri Reserve, Port Hills, Mid Canterbury, NZ; J.A. Cooper	Chapter 2, Chapter 4
PDD 87379	*Marasmiellus violaceogriseus*	*Resupinatus*	*Ripogonum scandens*	May 10 2007	Waiohine Gorge, Wairarapa, NZ; J.A. Cooper	Chapter 4
PDD 87473	*Resupinatus applicatus*	*Resupinatus subapplicatus*	*Pseudopanax crassifolius*	May 7 2007	Mt. Bruce, Wairarapa, NZ; J. A. Cooper	Chapter 4
PDD 88932	*Rhodocyphella*	Australian cyphelloid	*Dacrycarpus*	May 29	Pehitawa Reserve, Waikato, NZ;	Chapter 4

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
	cupuliformis	*Resupinatus* 1	*dacrydioides*	2006	B. Paulus	
PDD 89882	*Resupinatus merulioides*		Fallen dead wood	May 8 2006	Pororari River Walk, Punakaiki, Buller, NZ; P. & D. Catcheside	Chapter 4
PDD 91781	*Resupinatus violaceogriseus*		Bark	May 19 1990	Lake Monowai, Fiordland, NZ; B.P. Segedin	Chapter 4
PDD 92596	*Resupinatus huia*		*Nothofagus solandri*	May 8 2007	Featherston, Pigeon Bush Reserve, Wairarapa, NZ; B.C. Paulus, A.J. O'Donnell, J.P. Wilkie	Chapter 4
PH 01074202	*Peziza conspersa*	*Tapesia daedalea*	N.R.	N.D.	"Helv. Kze"	Chapter 3
PH 01074203	*Peziza poriaeformis*	*Tapesia daedalea*	N.R.	Before 1834	Bethlehem; Syn. Fung. #852, Schweinitz	Chapter 3
PH 01074204	*Porotheleum fimbriatum*		N.R.	N.D.	Salem, Bethlehem; Syn. Fung. #474-2	Chapter 6
PRM 38573	*Solenia grisella*	*Lachnella alboviolascens*	N.R.	Jul. 8 1936	N.R.; Sponheimer	Chapter 6
PRM 171919	*Porotheleum poriaeformis*	*Resupinatus*	*Salix* cf. *pentandra*	Aug. 10 1952	Prague, Czech Republic; Z. Pouzar	Chapter 3
PRM 171920	*Porotheleum poriaeformis*	*Resupinatus*	*Salix*	Apr. 2 1937	N.R.; Sponheimer	Chapter 3
PRM 171921	*Porotheleum poriaeformis*	*Resupinatus*	*Tilia*	Nov. 26 1934	N.R.; A. Pilat	Chapter 3
PRM 171922	*Porotheleum poriaeformis*	*Resupinatus*	*Salix*	Apr. 5 1932	"Praha-Daleji"; A. Pilat	Chapter 3
PRM 171923	*Porotheleum poriaeformis*	*Resupinatus*	*Salix*	November 1923	Praha-Kludorice; A. Pilat	Chapter 3
PRM 171924	*Porotheleum poriaeformis*	*Resupinatus*	Tremble, Causse Noir	Nov. 29 1912	France; M. Galzin	Chapter 3
PRM 171928	*Porotheleum poriaeformis*	*Resupinatus*	Dead wood	Jun. 10 1919	"Vastmanland: par. Vasteras-Barkaro Hogholmskar"; S. Lundell	Chapter 3
PRM 497250	*Pleurotus*	*Resupinatus*	*Quercus*	July 1933	Carpatorossia Kuzy prope Velky	Chapter 2

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
	applicatus				Boekov; A. Pilat	
PRM 497293	*Pleurotus kavinii* (HT)	*Resupinatus*	*Fagus sylvatica*	July 1929	"Ucrania Transcarpatica, in fagetis subra Kobylecka Polana", USSR; A. Pilat	Chapter 5
PRM 497463	*Porotheleum poriaeformis*	*Resupinatus*	*Quercus*	July 1933	Carpatorossiae, "Hab. in silvis ad rivum Kuzy supra Velky Bockov"; A. Pilat	Chapter 3
PRM 497464	*Porotheleum poriaeformis*	*Resupinatus*	N.R.	August 1930	???; A. Pilat	Chapter 3
PRM 497465	*Porotheleum poriaeformis*	*Resupinatus*	*Quercus*	July 1933	"in silvis ad rivum Kuzy supra Velky Bockov, Carpatorassiae"; A. Pilat	Chapter 3
PRM 497466	*Porotheleum poriaeformis*	*Resupinatus*	*Quercus*	July 1932	"in silvis supra Nemecka Mokra, distr. Tiacevo, Carpatorossiae"; A. Pilat	Chapter 3
PRM 560725	*Rhodocyphella cupulaeformis*		*Thuja occidentalis*	Oct. 10 1959	Cedar Swamp, Champaign County, Ohio, USA; W.B. & V.G. Cooke	Chapter 2
PRM 561126	*Cyphella taxi*	*Resupinatus griseopallidus*	*Juniperus communis*	Oct. 31 1953	"in declivitate montis Hradova prope Tahanove haud procul Kosice ad ligna"; F. Kotlaba	Chapter 5
PRM 561139	*Cyphella taxi*	*Resupinatus griseopallidus*	*Juniperus communis*	Jun. 18 1926	N.R.; A. Pilat	Chapter 5
PRM 618452	*Solenia poriaeformis*	*Resupinatus*	*Acer pseudoplatanus*	May 31 1947	"in silvis prope Krivoklat: Lansky luh prope Zbecnd"; M. Svrcek	Chapter 3
PRM 619826	*Pleurotus applicatus*	*Resupinatus*	N.R.	July 1909	N.R.; A. Pilat	Chapter 2
PRM 690529	*Solenia grisella*	*Resupinatus conspersus*	*Abies*	Jul. 17 195?	???; Z. Pouzar	Chapter 3
PRM 709534	*Solenia grisella*	*Resupinatus conspersus*	*Abies*	Jul. 17 1959	N.R.; Z. Pouzar	Chapter 3

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
PRM 714999	*Solenia poriaeformis*	*Resupinatus*	*Tilia*	Jul. 17 1970	"Smetanova Lhota haud procul Cimelice, in silvis versus piscina 'Jezero'"; M. Svrcek	Chapter 3
PRM 843392	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Tilia*	Jun. 26 1963	Slovensky; Z. Pouzar	Chapter 3
PRM 845243	*Solenia poriaeformis*	*Resupinatus*	*Fagus sylvatica*	Jul. 22 1969	"in valle Komarnicka dolina -------- Ninzy Komarnik"; Z. Pouzar	Chapter 3
PRM 848090	*Solenia poriaeformis*	*Resupinatus*	*Quercus cervis*	Jun. 7 1965	"area tata, Masiarsky bob----- Babina fr. Krafina"; Z. Pouzar	Chapter 3
PRM 869189	*Solenia grisella*	*Resupinatus conspersus*	*Abies*	Jul. 17 1959	???; Z. Pouzar	Chapter 3
PRM 882505	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Quercus*	Oct. 21 1992	"Moravia, area tuta Cahnor ap. Breclav"; Al. Vagner;	Chapter 3
PRM 882507	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Carpinus betulus*	Nov. 20 1992	"Moravia, Cizov pr. Vranov nad Dyji, SPR Podyji"; Al. Vagner	Chapter 3
PRM 894656	*Solenia poriaeformis*	*Resupinatus*	*Salix*	Oct. 25 2000	Praha, "kapaninsky les, in Alneto prope, Ruticky mlyn"; Z. Pouzar	Chapter 3
PRM 902024	*Solenia grisella*	*Resupinatus conspersus*	*Abies*	Jul. 18 1959	N.R.; Z. Pouzar	Chapter 3
STR F.x. 197	*Peziza urceolata* (T)	*Resupinatus poriaeformis*	*Clematis vitalba*	N.D.	Vahl. flor. dan. T. 1017. f. 3.; N.R.	Chapter 3
STR P. 656	*Peziza poriaeformis*	*Resupinatus*	*Salix fragilis*	N.D.	N.R.; N.R.	Chapter 3
STR (no #) 2	*Peziza poriaeformis*	*Resupinatus*	*Salix*	1814	Heringen; N.R.	Chapter 3
STR (no #) 3	*Peziza poriaeformis*	*Resupinatus*	N.R.	N.D.	N.R.; N.R.	Chapter 3
STR (no #) 4	*Peziza poriaeformis*	*Resupinatus*	N.R.	N.D.	N.R.; N.R.	Chapter 3
UPS 510561	*Pleurotus applicatus*	*Resupinatus striatulus*	*Pinus sylvestris*	Sept. 29 1932	Uppland: Bondykra par., Vardsatra, invid Naturparkens	Chapter 5

Herbarium Accession	Original Identification	Determined Identification	Substrate	Date collected	Collection Location; Collector	Chapter cited
					norra omrade, Sweden; M.A. Donk, S. Lundell & J.A. Nannfeldt	

Appendix B: full list of sequences used

Table B-1: Full list of sequences used.

Sequences generated in this study are arranged first in alphabetical order by accession number (herbarium accession number), then sequences obtained from GenBank are arranged alphabetically by accession number (GenBank accession number) in the column "Accession". Sequences obtained in this study are specified for whether they were obtained from dried herbarium specimens "(H)", fresh collections "(F)", or cultures "(C)". The "Determined Identification" column has been left blank when the ID based on this study agrees with the original ID of the collection. When the font in the "Determined Identification" column is bolded, this indicates that the identification is based on the top BLAST result. Collection information is given when known for GenBank sequences (when no collection information is given on GenBank, it is indicated here by "N.R.").

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
100426 av01 (C)	*Stromatocyphella conglobata*		*Alnus rugosa*	Behind 13 Maple, Humber Village, Newfoundland, Canada	Chapter 2
101129 av02 (C)	*Stromatocyphella conglobata*		Alder	Behind 13 Maple, Humber Village, Newfoundland, Canada	Chapter 2
ADC 55348 (H)	*Resupinatus* sp.	Australian *Resupinatus* 1	Well-decayed wood	Kelly Hill Caves Conservation Park, Kangaroo Island, Australia	Chapter 4
ADC 56856 (H)	*Resupinatus* sp.	Australian *Resupinatus* 1	*Eucalyptus cladocalyx*	Kelly Hill Caves Conservation Park, Kangaroo Island, Australia	Chapter 4
ADC 57180 (H)	*Resupinatus* sp.	Australian *Resupinatus* 1	*Eucalyptus cladocalyx*	Kelly Hill Caves Conservation Park, Kangaroo Island, Australia	Chapter 4
AN 012974 (H)	*Stigmatolemma taxi*	*Rhodocyphella cupuliformis*	*Juniperus virginiana*	East Baton Rouge Parish, Louisiana, USA	Chapter 2
FP 102486 (C)	*Resupinatus applicatus*	*Resupinatus appliatus 3*	Hardwood	Illinois, USA	Chapter 2
ICMP 16593 (C)	*Rhodocyphella cupuliformis*	Australian cyphelloid *Resupinatus* 1	*Dacrycarpus*	Waikato, New Zealand	Chapter 4

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
NZ9/E8202 (H)	*Resupinatus cinerascens*		N.R.	Paganoni Swamp, Karnup, Perth, Australia	Chapter 4
NZ10/E8238 (H)	*Resupinatus cinerascens*		N.R	Sir Frederick Samson Park, Samson, Perth, Australia	Chapter 4
NZ14/E8427 (H)	*Resupinatus* sp.	*Resupinatus subapplicatus*	N.R.	West Bay Bushland, Leeuwin-Naturaliste National Park, Augusta, Australia	Chapter 4
NZ18/E9139 (H)	*Resupinatus applicatus*	*Resupinatus applicatus* 5	N.R.	Donovan Street, Augusta, Australia	Chapter 4
O 65603 (H)	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	Aspen	Arendal, Norway	Chapter 2, Chapter 3
O 65625 (H)	*Stigmatolemma urceolatum*	*Resupinatus poriaeformis*	*Tilia*	Arendal, Norway	Chapter 2, Chapter 3
P80 (H)	*Resupinatus* sp.	*Hohenbuehelia* sp. nov.	*Nothofagus*	Patagonia, Chile	Chapter 6
PDD 87046 (H)	*Resupinatus applicatus*	*Resupinatus applicatus* 4	Dead wood	Banks Peninsula, Mid Canterbury, New Zealand	Chapter 2, Chapter 4
PDD 87197 (H)	*Marasmiellus violaceogriseus*	*Resupinatus violaceogriseus* 2	*Kunzea ericoides*	Hinewai Reserve, Akaroa, Mid Canterbury, New Zealand	Chapter 4
PDD 87379 (H)	*Marasmiellus violaceogriseus*	*Resupinatus violaceogriseus* 2	*Ripogonum scandens*	Waiohine Gorge, Wairarapa, New Zealand	Chapter 4
PDD 87473 (H)	*Resupinatus applicatus*	*Resupinatus subapplicatus*	*Pseudopanax crassifolius*	Mt. Bruce, Wairarapa, New Zealand	Chapter 4
RGT010805/01 (C)	Black *Hohenbuehelia*	[culture contaminant]	angiosperm twigs	QERC, San Gerardo de Dota, Costa Rica	Chapter 6
RGT010806/01 (C)	Cyphelloid	*Merismodes* sp.	angiosprem wood	QERC, San Gerardo de Dota, Costa Rica	Chapter 6
RGT080820/01 (F)	*Resupinatus urceolatus*	North American cyphelloid *Resupinatus*	*Acer saccharinum*	Remnant forest on UWO campus south of the former Ivey building, London, Ontario, Canada	Chapter 2, Chapter 3
RGT080909/07 (F)	*Mucronella calva*	*Scytinostroma* sp. (BLAST	Rotting conifer board	Notre Dame Provincial Park, Newfoundland, Canada	Chapter 6

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
		identification)			
RGT100622/01 (F)	*Resupinatus urceolatus*	North American cyphelloid *Resupinatus*	Rotting wood	Old Commissary woods, UWO campus, London, Ontario, Canada	Chapter 2, Chapter 3
RGT100622/02 (F)	*Resupinatus* sp.	*Resupinatus applicatus* 3	Rotting wood	Old Commissary woods, UWO campus, London, Ontario, Canada	Chapter 2
Silver Box (H)	*Resupinatus* sp.	*Resupinatus applicatus* 3	Dead hardwood	Woodson County, Kansas, USA	Chapter 2
T-001 (C)	*Resupinatus* sp.	*Resupinatus* sp. 1	*Quercus hypoleucoides*	Turkey Creek, Chiracahua Mountains, Colorado National Forest, Arizona, USA	Chapter 2
T-099 (C)	*Resupinatus applicatus*	*Resupinatus applicatus* 1	on hardwood - ?*Acer*	Ridge Road, Gatineau, Quebec, Canada	Chapter 2
T-114 (C)	*Resupinatus applicatus*	[culture mix-up; *Nematoctonus*]	on hardwood	New Hampshire, USA	Chapter 2
T-129.7 (C)	*Resupinatus alboniger*		N.R.	No data supplied: OK Miller, Jr. VT 1364	Chapter 2, Chapter 5
T-213 (C)	Cyphelloid	*Gloeocystidiellum* sp. (BLAST identification)	*Sorbus*	Point Lepreau on west side near tip, Lepreau Township, Charlotte County, New Brunswick, Canada	Chapter 2
T-236 (C)	*Resupinatus striatulus*		Underside of fallen beech	Chanterelle hill, Blomidon Provincial Park, Kings County, Nova Scotia, Canada	Chapter 2, Chapter 5
T-244 (C)	*Resupinatus urceolatus*	North American cyphelloid *Resupinatus*	*Acer saccharum*	Eramosa Township, Wellington County, Ontario, Canada	Chapter 2, Chapter 3
T-354 (C)	*Resupinatus trichotis*	[culture mix-up; Hymenochaetales]	Dead hardwood branch	Wolfville, Kings County, Nova Scotia, Canada	Chapter 2
T-919 (C)	*?Stigmatolemma taxi*	*Noleana* sp. (BLAST identification)	*Juniperus virginiana*	Oakley House, Audubon Estate off Hwy 965 near Baton Rouge, Louisiana, USA	Chapter 2, Chapter 6
T-921.12 (C)	*Hohenbuehelia*		on bark of	Raymond Gary State Park near Swink, Oklahoma,	Chapter 6

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
	elegans		living Juniperus	U.SA,	
TENN 2417 (C)	*Resupinatus applicatus*	*Resupinatus applicatus* 1	N.R.	Jackson County, Illinois, USA	Chapter 2
TENN 2674 (C)	*Resupinatus violaceogriseus*	*Resupinatus violaceogriseus* 1	N.R.	Fiordland Monowai Borland Lodge Track, New Zealand	Chapter 4
TENN 3003 (C)	*Resupinatus* sp.	*Hohenbuehelia grisea*	N.R.	Highlands, Macon County, North Carolina, USA	Chapter 6
TENN 3547 (C)	*Resupinatus* cf. *striatulus*	*Resupinatus subapplicatus*	N.R.	Mount Wilson, Blue Mountains, New South Wales, Australia	Chapter 4
TENN 4102 (C)	*Resupinatus alboniger*	*Resupinatus applicatus* 1	log and bark	Picklesiemer Falls Trail, Highlands, Macon County, North Carolina, USA	Chapter 2
TENN 4403 (C)	*Resupinatus striatulus*	*Resupinatus applicatus* 2	N.R.	Abrams Creek, Great Smoky Mountains Natinal Park, Anderson County, Tennessee, USA	Chapter 2
TENN 7918 (C)	*Resupinatus* sp.	*Mycoacia* sp. (BLAST identification)	N.R.	Gatlinburg, Sevier County, Tennessee, USA	Chapter 6
TENN 8870 (C)	*Resupinatus* sp.	*Resupinatus* sp. 2	on stick	Near Baranovka, Krasnodar Krai, Caucasia, Russia	Chapter 2
TENN 9124 (C)	*Cyphella* sp.	*Physalacria* sp. (BLAST identification)	on bark of *Juniperus virginiana*	East Baton Rouge Parish, Louisiana, USA	Chapter 6
TENN 10127 (C)	*Resupinatus* sp.	*Resupinatus alboniger*	on fallen sticks	Walland, Blount County, Tennessee, USA	Chapter 2, Chapter 5
TENN 10239 (C)	*Cyphellostereum* sp.	*Podoscypha* sp. (BLAST identification)	N.R.	Heredia Province, Costa Rica	Chapter 6
TENN 12070 (C)	*Resupinatus alboniger*		N.R.	University of Tennessee campus, Knoxville, Tennessee, USA	Chapter 2, Chapter 5
TENN 12406 (C)	*Resupinatus alboniger*	*Resupinatus* sp. 3	N.R.	Baxter Creek Trail, Great Smoky Mountains National Park, North Carolina, USA	Chapter 2

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
TENN 12417 (C)	*Resupinatus alboniger*		N.R.	Chimneys Picnic Area Trail, Great Smoky Mountains National Park, Tennessee, USA	Chapter 2, Chapter 5
TENN 12972 (C)	*Resupinatus alboniger*		N.R.	Jakes Creek Trail, Great Smoky Mountains National Park, Tennessee, USA	Chapter 2, Chapter 5
TENN 12990 (C)	*Resupinatus alboniger*		N.R.	Maddron Bald Trail, Great Smoky Mountains National Park, Tennessee, USA	Chapter 2, Chapter 5
AB158636	*Psilocybe merdaria*		N.R.	NBRC-30568	Chapter 2
AB777519	*Pleurotus eryngii*		N.R.	N.R.	Chapter 2
AF042595	*Collybia dryophila*	*Gymnopus dryophilus*	N.R.	RV83/180	Chapter 2, Chapter 6
AF042596	*Gymnopus polyphylla*		N.R.	RV182.01	Chapter 2
AF042597	*Rhodocollybia maculata*		N.R.	RV94/115	Chapter 2
AF042600	*Resupinatus alboniger*		N.R.	RV/JM s.n.	Chapter 2
AF042602	*Hohenbuehelia tristis*		N.R.	RV95/573	Chapter 2
AF042620	*Entoloma strictius*		N.R.	M96/10	Chapter 2
AF042621	*Omphalotus nidiformis*		N.R.	T1946.8	Chapter 2
AF042628	*Micromphale perforans*		N.R.	RV83/67	Chapter 2, Chapter 6
AF098404	*Omphalotus illudens*		N.R.	Strain 258	Chapter 6
AF139944	*Resupinatus dealbatus*		decaying hardwood	RM 930924/01, Aldo Leopold Preserve, Wisconsin, USA	Chapter 2, Chapter 5
AF139952	*Hohenbuehelia grisea*		Farmyard soil	T-014a, RGT840713/01, Ontario, Canada	Chapter 2, Chapter 6
AF139956	*Hohenbuehelia petalodes*		Soil in lawn	T-104a, ATCC 60597, Fungi Suecici 4656, Falun, Helmskogsvagen, Sweden	Chapter 2, Chapter 6

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
AF139959	*Hohenbuehelia portegna*		Dicot wood, ?Ulmus	T-7, J.E. Wright 1136 BAFC, Argentina	Chapter 6
AF139960	*Hohenbuehelia* sp.		Contaminant of fruit body of *Cortinarius*	T-454, RGT940206/01, Edson Forest, Alberta, Canada	Chapter 2, Chapter 6
AF223173	*Gymnopus peronatus*		N.R.	CBS 426.79; France, R. Kühner	Chapter 6
AF261325	*Omphalotus olivascens*		N.R.	VT645.7	Chapter 6
AF261327	*Caripia montagnei*		N.R.	JMCR.143	Chapter 2
AF261328	*Micromphale foetidum*		N.R.	JEJ.VA.567	Chapter 2, Chapter 6
AF261329	*Marasmiellus opacus*		N.R.	JEJ.574	Chapter 2, Chapter 6
AF261331	*Marasmius scorodonius*		N.R.	JEJ.586	Chapter 2
AF261336	*Gymnopus biformis*		N.R.	RV98/32	Chapter 2
AF261337	*Tetrapyrgos nigripes*		N.R.	AB777519	Chapter 6
AF261338	*Tetrapyrgos* sp.		N.R.	TENN 7373	Chapter 6
AF261372	*Resupinatus poriiformis*	North American cyphelloid *Resupinatus*	Populus tremuloides	RLG11556sp; Arizona, USA	Chapter 2, Chapter 3
AF261373	Cyphellaceae sp.	North American cyphelloid *Resupinatus*	Quercus	HHB3534sp, Michigan, USA	Chapter 2, Chapter 3
AF261475	*Lachnella alboviolascens*		N.R.	DAOM223321	Chapter 2
AF261557	*Lentinula edodes*		N.R.	TMI 1941	Chapter 6
AF261558	*Lentinula boryana*		*Quercus oleoides*	RGT960624, Volcan Cacao, Costa Rica	Chapter 6

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
AF261559	*Lentinula boryana*	*Lentinula raphanica*	N.R.	HN2002	Chapter 6
AF261561	*Lentinula novaezelandiae*		N.R.	TMI 1172	Chapter 6
AF261585	*Marasmius androsaceus*		N.R.	HN4730	Chapter 2
AF356147	*Lentinula raphanica*		N.R.	Duke HN2002	Chapter 6
AF356165	*Lentinula lateritia*		N.R.	STCL 149	Chapter 6
AJ406557	*Resupinatus trichotis*		N.R.	GEL4221	Chapter 2
AJ406561	*Campanella junghuhnii*		N.R.	GEL4720	Chapter 6
AJ406581	*Dendrothele acerina*		N.R.	GEL5350	Chapter 2
AM946450	*Gymnopus fusipes*		N.R.	C42389, Denmark	Chapter 6
AM946461	*Resupinatus appliatus*	*Resupinatus applicatus* 3	N.R.	TAA171569, Estonia	Chapter 2
AY204236	*Marasmiellus ramealis*		N.R.	GLM 45958, Bayer G 558, Germany	Chapter 6
AY207166	*Collybia hariolorum*		N.R.	GLM 45933, DSMZ 16155, Germany	Chapter 6
AY207167	*Collybia marasmioides*		N.R.	GLM 45932, DSMZ 15790, Germany	Chapter 6
AY207240	*Micromphale foetidum*		N.R.	GLM 45964, HKI ST 27334	Chapter 2
AY213567	*Armillaria sinapina*		N.R.	ST-13B, CF-2, Michigan, USA	Chapter 2
AY213568	*Armillaria gallica*		N.R.	M70, SP81-29, British Columbia, Canada	Chapter 2
AY213583	*Armillaria cepistipes*		N.R.	W113, Washington State, USA	Chapter 2
AY256708	*Marasmiellus*		*Juniperus*	TENN 59540, LSU Campus, Baton Rouge, East	Chapter 2

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
	juniperinus		*virginianus*	Baton Rouge, Louisiana, USA	
AY256709	*Gymnopus luxurians*		Standing *Quercus*	TENN 57910, Trail at Whitesides Church (Summer Chapel), Cashiers Jackson, North Carolina, USA	Chapter 2
AY256711	*Gymnopus fusipes*		N.R.	TENN 59300, South of Wolfstahl, Wangheimer Wald, Wolfstahl Bruck/Leitha, Lower Austria, Austria	Chapter 2
AY445115	*Campanella subdendrophora*		*Phalaris arundinacea*	Vancouver, British Columbia; ATCC 42449, type strain	Chapter 6
AY450342	*Pleurotus australis*		N.R.	NZPR-215, Australia	Chapter 2, Chapter 6
AY450345	*Pleurotus ostreatus*		*Sallix*	TENN 53662, Institute of Botany, Vienna Landstraße, Vienna, Austria, Epitype	Chapter 2, Chapter 6
AY450346	*Pleurotus populinus*		N.R.	TENN 56749, Crystal Springs, RTE 14 N. of Cedar City, Crystal Springs, Iron, Utah, USA	Chapter 2, Chapter 6
AY450347	*Pleurotus eryngii*		N.R.	WU13414, Austria	Chapter 2, Chapter 6
AY450348	*Pleurotus abieticola*		*Abies nephrolepis*	TENN 52359, Primorsky Krai, Russia, paratype	Chapter 2, Chapter 6
AY450349	*Pleurotus pulmonarius*		Dead *Fraxinus* trunk	TENN 50539, Kinnekulle Nature Reserve, Götene, Västra Götalands, Sweden	Chapter 2, Chapter 6
AY570998	*Cyphellopsis anomala*		N.R.	PB318, Germany	Chapter 2
AY571000	*Cyphellopsis anomala*		N.R.	PB333, Germany	Chapter 2
AY571006	*Flagelloscypha minutissima*		*Comarum palustre*	CBS 823.88, Srohnermarchen, near Daun, Germany	Chapter 2
AY571014	*Lachnella villosa*		N.R.	PB322, Germany	Chapter 2
AY571015	*Merismodes fasciculata*		*Alnus*	HHB-11894, Wisconsin, USA	Chapter 2
AY571016	*Merismodes*		N.R.	PB342, Switzerland	Chapter 2

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
	fasciculata				
AY571022	*Resupinatus applicatus*	*Resupinatus applicatus* 2	N.R.	PB335, France	Chapter 2
AY571024	*Resupinatus conspersus*	*Porotheleum cinereum*	N.R.	C61852, Ecuador	Chapter 2, Chapter 3
AY571031	*Calyptella capula*		N.R.	PB315, Norway	Chapter 4
AY571059	*Resupinatus applicatus*	*Resupinatus applicatus* 2	N.R.	PB335, France	Chapter 2
AY571061	*Resupinatus conspersus*	*Porotheleum cinereum*	N.R.	C61852, Ecuador	Chapter 3, Chapter 4
AY572005	*Calathella gayana*		N.R.	ZT8836, Chile	Chapter 2
AY635776	*Marasmius alliaceus*		Under *Abies*	AFTOL-ID #556, TENN 55620, Krasnaya Polyana, Sochi, Krasnodar Krai, Russia	Chapter 2, Chapter 6
AY639407	*Campanella eberhardtii*		N.R.	DEH465-SFSU, Hawaii, USA	Chapter 6
AY639411	*Gymnopus bicolor*		N.R.	AWW116_SFSU, holotype; Bali, Indonesia	Chapter 2
AY639412	*Gymnopus brunneigracilis*		N.R.	AWW01-SFSU; Java, Indonesia	Chapter 6
AY639413	*Gymnopus diminutus* var. *attenuatus*		N.R.	AR099_SFSU, holotype; Java, Indonesia	Chapter 2, Chapter 6
AY639417	*Gymnopus gibbosus*		N.R.	AWW112-SFSU; Java, Indonesia	Chapter 6
AY639418	*Gymnopus indoctus*		N.R.	AWW03-SFSU; Java, Indonesia	Chapter 6
AY639421	*Gymnopus luxurians*		N.R.	DEH1304-SFSU; Hawaii, USA	Chapter 6
AY639422	*Gymnopus melanopus*		N.R.	AWW54_SFSU; Java, Indonesia	Chapter 2, Chapter 6
AY639425	*Gymnopus menehune*		N.R.	AWW87-SFSU; Java, Indonesia	Chapter 6
AY639426	*Gymnopus nonnullis* var.		N.R.	AWW05-SFSU; Java, Indonesia	Chapter 6

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
	attenuatus				
AY639429	*Gymnopus subpruinosus*		N.R.	DED6674-SFSU; California, USA	Chapter 6
AY639432	*Gymnopus vitellinipes*		N.R.	AWW127_SFSU; Bali, Indonesia	Chapter 2, Chapter 6
AY639435	*Marasmius synodicus*		N.R.	DED5258_SFSU; Tennessee, USA	Chapter 2, Chapter 6
AY639436	*Marasmius alliaceus*		N.R.	BRNM568-Moravian Museum; Moravia, Czech Republic	Chapter 2
AY639437	*Marasmius applanatipes*		N.R.	DED6628_SFSU; California, USA	Chapter 2, Chapter 6
AY639438	*Marasmius copelandii*		N.R.	DED5607_SFSU; California, USA	Chapter 2, Chapter 6
AY639439	*Rhodocollybia badiialba*		N.R.	D.L.Largent9199-SFSU; California, USA	Chapter 6
AY639441	*Rhodocollybia laulaha*		N.R.	DED5873-SFSU; holotype; Hawaii, USA	Chapter 6
AY639880	*Rhodocollybia maculata*		N.R.	AFTOL-ID #540, PBM2481, Massachusetts, USA	Chapter 2, Chapter 6
AY640619	*Gymnopus dryophilus*		N.R.	AFTOL-ID #559, TENN 57012, Macon County, North Carolina, USA	Chapter 6
AY745709	*Anthracophyllum archeri*		on twigs	AFTOL-ID #973, PBM2201, Karri Valley, southwestern Wesern Australia	Chapter 2
DQ017063	*Resupinatus porosus*		Rotting wood	PR5832, Puerto Rico, USA	Chapter 4
DQ017064	*Resupinatus porosus*		Rotting wood	PR6198, Puerto Rico, USA	Chapter 2
DQ071700	*Phaeomarasmius rimulincola*		N.R.	FO 46666	Chapter 6
DQ112583	*Lycoperdon decipiens*		N.R.	MJ850902	Chapter 2

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
DQ112611	*Bovista cretacea*		N.R.	ANMH11622	Chapter 2
DQ112617	*Bovista minor*		N.R.	Steike951015	Chapter 2
DQ112620	*Bovista aestivalis*		N.R.	MJ1122	Chapter 2
DQ112621	*Bovista promontorii*		N.R.	MJ7070	Chapter 2
DQ112623	*Langermannia gigantean*		N.R.	MJ3566	Chapter 2
DQ112624	*Calvatia candida*		N.R.	MJ3514	Chapter 2
DQ112625	*Calvatia craniiformis*		N.R.	Steinke001017	Chapter 2
DQ156126	*Marasmius oreades*		N.R.	AFTOL-ID #1525, PBM2701	Chapter 6
DQ389734	*Tricholoma orirubens*		N.R.	RGC04-053	Chapter 2
DQ470816	*Omphalotus olearius*		N.R.	AFTOL-ID #1718, CBS 102282, Slovenia	Chapter 2, Chapter 6
EF160081	*Marasmius wynnei*		N.R.	BRNM 653619	Chapter 6
EF160087	*Marasmius mbalmayoensis*		N.R.	DMC 001c	Chapter 6
EF160088	*Marasmius megistus*		N.R.	DMC 002b	Chapter 6
EF160097	*Marasmius bekolacongoli*		N.R.	BRNM 695679	Chapter 6
EF409720	*Hohenbuehelia angustata*		Dicot log	RGT020615/08, Sector Montezuma, Parque Nacional Tenorio, Costa Rica	Chapter 6
EF409721	*Hohenbuehelia unguicularis*		*Populus*	T-047, Black Sturgeon Lake, Ontario, Canada	Chapter 6
EF409722	*Hohenbuehelia pinacearum*		*Abies balsamea*	T-107, RGT831015/04, Algonquin Provincial Park, Ontario, Canada	Chapter 6
EF409724	*Nematoctonus concurrens*	*Hohenbuehelia concurrens*	Isolated from a nematode	T-183=IMI 129985, United Kingdom	Chapter 6
EF409726	*Nematoctonus geogenius*		Isolated from a nematode	T-019, Ontario, Canada	Chapter 6

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
EF409728	*Hohenbuehelia tremula*		on soil	T-083, near Visoky Chlumec, Bohemia, Czech Republic	Chapter 6
EF409729	*Hohenbuehelia petalodes*		in a lawn	T-104, ATCC 60597, Fungi Suecici 4656, Falun, Helmskogsvagen, Sweden	Chapter 2
EF409736	*Hohenbuehelia mastrucata*		*Acer saccharum*	T-025a, West Gate, Algonquin Park, Ontario, Canada	Chapter 6
EF409743	*Hohenbuehelia* sp.		On dead liana	RGT010810/02, STR Trail, La Selva, Costa Rica	Chapter 6
EF409753	*Nematoctonus pachysporus*		Isolated from a nematode	01-RGTSN-532, Las Alturas Biological Station, Costa Rica	Chapter 6
EF409756	*Hohenbuehelia grisea*		on fallen dicot wood	RGT040611/01, Monumento Nacional Guayabo, Costa Rica	Chapter 6
EF409759	*Nematoctonus robustus*		Isolated from a nematode	03-RGTSN-571, Sirena Biological Station, Parque Nacional Corcovado, Costa Rica	Chapter 6
EF409760	*Hohenbuehelia grisea*		Dear dicot wood	RGT010805/02, San Gerardo de Dota, Costa Rica	Chapter 6
EF409762	*Nematoctonus robustus*		Isolated from a nematode	01-RGTSN-526, Las Alturas Biological Station, Costa Rica	Chapter 6
EF409765	*Nematoctonus subreniformis*	*Hohenbuehelia subreniformis*	Isolated from a nematode in *Acer*	T-138, West Gate, Algonquin Park, Ontario, Canada	Chapter 6
EF409766	*Nematoctonus tylosporus*	*Hohenbuehelia tylospora*	Isolated from a nematode	04-RGTSN-512, Monumento Nacional Guayabo, Costa Rica	Chapter 6
EF537889	*Phaeomarasmius erinaceellus*		N.R.	PBM 2598 (CUW), Tennessee, USA	Chapter 6
EF546657	*Nematoctonus robustus*		Isolated from a nematode	ATCC MYA-4145	Chapter 2, Chapter 6
EF546659	*Nematoctonus leiosporus*	*Hohenbuehelia leiospora*	Isolated from a nematode	ATCC MYA-4143	Chapter 2, Chapter 6
EU365662	*Omphalotus nidiformis*		*Pinus radiata*	CBS 323.49, Victoria, Australia	Chapter 6
FJ596893	*Resupinatus*		N.R.	TENN 62044, Great Smoky Mountains National	Chapter 4

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
	alboniger			Park, Gabes Mountain Trail, Cocke, Tennessee, USA	
FJ663209	*Neocampanella blastanos*		N.R.	K.K. Nakasone FP 150016 (CFMR), Luquillo, Puerto Rico	Chapter 6
FJ750251	*Gymnopus incarnatus*		N.R.	TENN 61089, Vic. Greymouth, Nelson Creek, Cow's Dam Loop Track, Greymouth, Buller, New Zealand	Chapter 6
FJ750252	*Rhodocollybia butyracea*		N.R.	TENN 60927, Great Smoky Mountains National Park, Albright Grove Entrance, Maddron Bald Trail, Cocke, Tennessee, USA	Chapter 2, Chapter 6
FJ750262	*Gymnopus subnudus*		N.R.	TENN 61138, Great Smoky Mountains National Park, Cades Cove, Primitive Baptist Church, Blount, Tennessee, USA	Chapter 6
FJ755224	*Clitocybe subditopoda*		N.R.	CZ482	Chapter 2
FJ904179	*Naucoria bohemica*		N.R.	EL71b_03	Chapter 2
FJ904945	*Marasmius aurantioferrugineus*		N.R.	HCCN GBDS-2861	Chapter 6
FJ904953	*Marasmius nivicola*		N.R.	BRNM 714574	Chapter 6
FJ904983	*Marasmius siccus*		N.R.	KG 119	Chapter 6
FJ917604	*Marasmius graminicola*		N.R.	BRNM 714697	Chapter 6
FJ917605	*Marasmius brunneoaurantiacus*		N.R.	BRNM 714700	Chapter 6
FJ917607	*Marasmius occultatus*		N.R.	BRNM 714699	Chapter 6
FJ917608	*Marasmius berteroi*		N.R.	BRNM 714698	Chapter 6
GQ142021	*Resupinatus* sp.	*Resupinatus* sp. 1	N.R.	HMJAU7036, China	Chapter 4
GQ142022	*Resupinatus trichotis*		N.R.	HMJAU2150, China	Chapter 4, Chapter 5
GQ142045	*Resupinatus* sp.	*Resupinatus* sp. 1	N.R.	HMJAU7036, China	Chapter 2

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
GQ289186	*Entoloma readiae*		N.R.	ME Noordeloos 2004050	Chapter 2
GQ289189	*Entoloma sericatum*		N.R.	ME Noordeloos 200328	Chapter 2
GQ289204	*Entoloma vezzenaense*		N.R.	WU 14588	Chapter 2
GU319117	*Marasmiellus koreanus*		N.R.	BRNM 714972, Korea	Chapter 6
GU319120	*Marasmiellus rhizomorphigenus*		N.R.	BRNM 715003	Chapter 6
GU369966	*Rhodocollybia lignitilis*		N.R.	TENN 56628, Cabinas Chacon-San Gerardo de Dota, Rio Savegre, San Jose, Costa Rica; Holotype	Chapter 6
GU369967	*Rhodocollybia unakensis*		N.R.	TENN 58545, Big Thicket Nature Preserve, Jack Gore Baygall Unit, Vic. Beaumont, Hardin, Texas, USA	Chapter 6
HM035072	*Psilocybe caerulescens*		N.R.	CBS 837.87; K.-D. Jahnke 014; DSM 902	Chapter 2
HM035073	*Psilocybe coprophila*		manure heap	CBS 417.82; Markham, Ontario, Canada	Chapter 2
HM035075	*Psilocybe cubensis*		N.R.	CBS 590.79; California, USA	Chapter 2
HM035077	*Psilocybe mexicana*		N.R.	CBS 831.87; Huautla, Mexico	Chapter 2
HM035076	*Psilocybe cyanensis*		soil	CBS 295.94; Baarn, The Netherlands	Chapter 2
HM035078	*Psilocybe montana*		poor gravelly soil	CBS 101791Ekkeroy, Finnmarken, Norway	Chapter 2
HM035080	*Psilocybe semilanceata*		partly decayed grasses	CBS 101868; Newtonmore, Perthshire, Scotland	Chapter 2
HQ533011	*Hemimycena tortuosa*		*Nothofagus solandri* var. *cliffortioides*	PDD:95759, North Canterbury, New Zealand	Chapter 4
HQ533014	*Marasmiellus violaceogriseus*	*Resupinatus violaceogriseus* 1	*Nothofagus solandri* var. *cliffortioides*	PDD:95788, North Canterbury, New Zealand	Chapter 4
HQ533025	*Resupinatus*	*Resupinatus*	*Nothofagus*	PDD:95777, Mid Canterbury, New Zealand	Chapter 4

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
	applicatus	*applicatus* 4	*solandri* var. *cliffortioides*		
JN649350	*Lepista sordida*		N.R.	EL4-03	Chapter 2
JQ320124	*Entoloma omiense*		N.R.	GDGM 27229, China	Chapter 2
JQ320127	*Entoloma incanum*		N.R.	HKAS 54614	Chapter 2
JQ320132	*Entoloma subtenuicystidiatum*		N.R.	GDGM 29246, China	Chapter 2
JQ320135	*Entoloma subclitocyboides*		N.R.	GDGM 26615, China	Chapter 2
JQ410327	*Entoloma caespitosum*		N.R.	GDGM 24025, China	Chapter 2
JQ654236	*Marasmiellus palmivorus*		N.R.	C6, Malaysia	Chapter 6
KC176278	*Hypholoma capnoides*		Mineral soil	T-773, Kellogg Biological Station LTER Conifer Forest #3 plot, near Gull Lake, Michigan, USA	Chapter 2
KC176282	*Clitopilus scyphoides*		Mineral soil	T-777, Kellogg Biological Station LTER T7R4, near Gull Lake, Michigan, USA	Chapter 2
KC176290	*Clitopilus* cf. *scyphoides*	*Clitopilus scyphoides*	Mineral soil	T-782, Kellogg Biological Station LTER Deciduous Forest #2 plot, near Gull Lake, Michigan, USA	Chapter 2
KC555559	*Entoloma sulcatum*		N.R.	GDGM 26543, China	Chapter 2
KF896249	*Marasmius ochroleucus*		N.R.	LE 295978, Russia	Chapter 6
KJ140596	*Porotheleum fimbriatum*		Rotting wood	CFMR:DLL2011-077, Wisconsin, USA	Chapter 4
KJ189570	*Gymnopus biformis*		N.R.	TENN 65586, Summer Chapel Trail, Highlands, Jackson, North Carolina, USA	Chapter 6
KJ189578	*Gymnopus confluens*		N.R.	TENN 67865, Vic. Potchen., Schlotheim, Thuringia, Germany	Chapter 6
KJ189590	*Gymnopus*		N.R	TENN 69122, Pasadena Ski Trails, Newfoundland,	Chapter 6

Accession	Original Identification	Determined Identification	Substrate	Collection Information	Chapter cited
	eneficola			Canada	
KJ395105	*Omphalotus japonicus*		N.R.	TNS Kasuya B817, Toyama, Toyama-shi, Jike, Japan	Chapter 6
KJ635222	*Cortinarius carbonellus*		Under *Nothofagus*	PDD:103685, Taupo, New Zealand	Chapter 6
KJ635229	*Cortinarius xenosma*		Under *Nothofagus*	PDD:88274, Otago Lakes, New Zealand	Chapter 6
KJ635240	*Cortinarius olivaceoniger*		Under *Nothofagus*	PDD:97540, Taupo, New Zealand	Chapter 6
KJ635242	*Cortinarius* sp.		Under *Nothofagus*	PDD:97543, Taupo, New Zealand	Chapter 6
KJ635245	*Cortinarius orixanthus*		Under *Nothofagus*	PDD:97556, Wellington, New Zealand	Chapter 6
KJ705190	*Mycena adonis*		N.R.	Isolate 916, St. Etienne, Quebec, Canada	Chapter 4

Appendix C: glossary

The definitions for this section are adapted from the Dictionary of the Fungi, 10th Edition (Kirk et al., 2008) unless otherwise indicated.

Agaricales: an order of fungi commonly known as the mushrooms or toadstools, which produce basidiospores on basidia, often on gills on the underside of umbrella-shaped fruit bodies.

Agaricomycotina: a subphylum within the *Basidiomycota* composed of macromycetes in three classes: *Agaricomycetes, Dacrymycetes, Tremellomycetes*.

Apothecium: generally cup-shaped fruit body of *Ascomycota* in which the asci form an exposed layer or hymenium; very similar in general appearance to the fruit body of cyphelloid *Basidiomycota*.

Ascomycota: phylum of the Kingdom *Fungi* with asci that produce internal ascospores through meiosis and have a restricted dikaryophase; commonly called the ascomycetes.

Ascomycotina: obsolete subphylum referring to what is now the **Ascomycota**.

Ascospore: a spore produced in an ascus; is the product of meiosis.

Ascus: the sac-like cell characteristic of the *Ascomycetes* that produces internal meiotic spores called ascospores (pl. **asci**).

Asterostromelloid hyphae: hyphae with swollen terminal cells with projections that are roughly perpendicular, and when viewed from the top appear star-shaped; characteristic of some members in the *Resupinateae.*

Basidiole: an immature basidium; may also be used to refer to a shape of cystidium that resembles an immature basidium.

*Basidiomycetes***:** obsolete former class name or, if uncapitalized, informal name of the **Basidiomycota**.

*Basidiomycota***:** phylum of the Kingdom *Fungi* with basidia that produce external basidiospores through meiosis and have an extended dikaryophase, commonly called basidiomycetes.

*Basidiomycotina***:** obsolete subphylum referring to what is now the *Basidiomycota*.

Basidiospore: a spore produced on a basidium; is the product of meiosis.

Basidium: the club-like cell characteristic of the basidiomycetes that produces external meiotic spores called basidiospores (pl. **basidia**).

Biological Species Concept: a species concept that states that two individuals are members of the same species if they can interbreed and produce fertile offspring (Mayr, 1942).

Cheilocystidium: a sterile cell (not bearing spores) projecting from the hymenium along gill edges.

Chlamydospore: a single-celled spore with a thickened cell wall, originating from the mycelium of a fungus.

Clade: a group of individuals that share one or more derived character states (synapomorphies); or, two or more extant taxa connected together by an internal node in a phylogenetic tree.

Clamp connection: a looping hyphal branch that bridges a septum in dikaryotic basidiomycetes to facilitate migration of one of the dikaryotic nuclei during cell division.

Clavate: club-shaped, or cylindrical with tapered base; used to describe the shape of basidia.

Cutis: A type of pileipellis composed of hyphae lying parallel to the surface.

Cyphelloid: derived from "*Cyphella*" (Greek: little cup) used to describe a basidiomycete fruit body that is cup-shaped (usually small) with a smooth hymenium, as in *Resupinatus poriaeformis*.

Dikaryon: a cell with two genetically distinct haploid nuclei.

Dimidate: used to refer to the shape of a fruit body; semi-circular and without a stipe.

*Discomycetes***:** an artificial class of ascomycetes with cup-shaped fruit bodies (apothecia); historically included cyphelloid fungi that had not been recognized as basidiomycetes.

DNA Barcoding: use of sequences from a short, diagnostic region of DNA that is universally present across all species to assign an individual to the level of species; the ITS region has been chosen in the *Fungi*.

Eccentric: referring to the stipe; off-centre (as opposed to central or lateral).

Epitype: a collection or illustration designated as a reference when the existing type material is not sufficient to be able to apply the name.

Evolutionary Species Concept: a species concept that states that a lineage is a species when it is evolving separately from other lineages and has its own evolutionary role and tendencies (Simpson, 1961).

Exsiccati: a collection of dried fungal material, often distributed as reference collections for a given geographic area (for example, Ellis and Everhart's Fungi of New Jersey).

Farinose: as if dusted with flour; used to describe the surface of a fruit body.

Fruit body: the spore-bearing organ of a fungus (both macrofungi and microfungi).

Glabrous: a smooth or hairless surface.

Globose: spherical; referring to the shape of spores with a Q value of 1.0 or nearly so

Granulose: a surface covered with small granules like a coating of salt.

Gregarious: used to describe aggregations of fruit bodies; in groups but not joined.

Holotype: the single collection, or one designated by the original author among several, upon which the author of a species based the name.

Hyaline: transluscent, transparent (syn. **colourless**).

Hymenium: an exposed layer of spore-bearing cells in a fruit body.

*Hymenomycetes***:** obsolete class of basidiomycetes with exposed hymenium.

Hypha: one of the filaments of a mycelium (pl. **hyphae**).

Iconotype: a type that is a photograph or painting of the actual specimen when the latter is missing.

Inamyloid: non-staining in Melzer's reagent (not containing starch, dextrin or cellulose).

Isotype: a duplicate or another part of the type material.

ITS Region: the region of ribosomal DNA known as the internal transcribed spacer region.

Lamella: a vertical plate in the hymenium of an agaric; commonly called a gill (pl. **lamellae**).

Lamellate: fruit bodies in which the hymenium is composed of lamellae.

Lamellula: small lamella that runs from the edge of the fruit body towards the stipe or centre, but do not reach the centre of the fruit body (pl. **lamellulae**).

Lectotype: a collection selected as a type in a later work using the original material used by the author to describe a species when no holotype was designated.

Ligulate: flat and narrow or tongue-shaped, used to refer to the shape of a fruit body.

Maximum Likelihood: a phylogenetic tree construction method that attempts to optimize a given model of evolution; each phylogenetic tree constructed is given a likelihood that represents the probability that such a tree could have resulted in the alignment being studied.

Maximum Parsimony: a phylogenetic tree construction method that attempts to minimize the number of steps required to explain a given alignment being studied.

Merulioid: used to describe a hymenium composed of reticulate ridges as in *Resupinatus merulioides*.

Monotypic: a taxon containing only one member.

Morphological Species Concept: a species concept in which species are defined by shared morphological characters, and other species identified by any morphological distinction (Cronquist, 1978).

Neotype: a collection of a species designated as the type when all the original type material is missing.

Paratype: any collection other than the holotype upon which the original description of a species is based.

Pellis, pileipellis: the covering of the fruit body surface opposite the hymenium; in agarics, usually the upper surface of the cap.

Phylogenetic Species Concept: a species concept that states that a species is the smallest diagnosable cluster of sexual organisms within which there is a parental pattern of ancestry and descent (Cracraft, 1983).

Polytomy: an internal node of a phylogenetic tree which has more than two immediate descending branches.

Poroid: used to describe a fruit body where the hymenium is composed of pores, as in *Resupinatus porosus*.

Posterior probability: a number assigned to a clade in a phylogenetic tree in Bayesian analyses that represents the fraction of sampled trees that support that clade. Also the probability that a tree is correct given the alignment.

Prior probability: an initial assumption as to the probability that a given phylogenetic tree is correct. In Bayesian analyses, all trees are assumed to be equally probable.

Pruinose: a surface that appears frosted or dusted with flour; usually used when referring to the surface of a fruit body (≈ farinose, but sometimes more reflective, as in frosty).

Pseudostipe: a usually lateral extension of the cap that serves as stipe or stem.

Q value: the ratio of length to width of elongate spores

Rameales-structure: a specific type of pellis where the terminal cells of hyphae are irregularly branched, asterostromelloid or diverticulate.

Resupinate: fruit bodies flat or dorsally attached on the substrate, with the hymenium exposed.

Sessile: lacking a stem.

Sterigma: prongs on the basidium that project the spores off the surface (pl. **sterigmata**).

Stroma: a mass of vegetative hyphae, on or in which fruit bodies or spores may be produced (a **subiculum** is a type of stroma present in the *Resupinateae*).

Subclavate: nearly cylindric, less tapered to the base than clavate (even-shaped); used to describe the shape of basidia.

Subglobose: not quite spherical,with a Q value of 1.1 to 1.2; referring to the shape of spores.

Subiculum: a fuzzy or felty growth of mycelium on the surface of the substrate under fruit bodies.

Sympleisiomorphy: shared ancestral character state.

Synapomorphy: shared derived character state.

Syntype: one of several collections cited by the author when proposing a species, when no holotype was designated.

Topotype: a collection of a species made from the same location as the original type material but at a later date.

Trama: flesh; the layer of hyphae between the hymenial layers of a gill (hymenial trama); also the layer of hyphae under the top surface of the pileus or cap (pileus trama).

Translucent-striate: usually referring to a pileal margin; a fruit body having flesh so thin that light passes through and the gills are visible as darker lines through the pileal surface.

Tribe: a taxon between the level of family and genus (e.g., *Resupinateae*).

Type: the collection upon which the description of a species is based or is considered to have been based (see also **epitype, holotype, iconotype, isotype, lectotype, neotype, paratype, syntype, topotype**)

Curriculum Vitae

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Post-secondary Education and Degrees:

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Honours and Awards:

Ruther Horner Arnold Fellowship in Plant Sciences
2008

Let's Talk Science Volunteer of the Year
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David E. Laudenbach Award in Plant Sciences
2009

Department of Biology Graduate Student Teaching Award
2011, 2013

Faculty of Science Graduate Thesis Research Award
2012

Learning Development Fellowship, Faculty of Science
2012

Related Work Experience

Teaching Assistant
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Let's Talk Science Teacher Partner
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Undergraduate Thesis Advisor
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Melissa Giamou (Dr. Sheila Macfie) 2010-2011
Kristina Race (Dr. Brock Fenton) 2011-2012

Guest Lecturer (Biology 2217)
The University of Western Ontario
2011-2013

Course Development (Biology 1001)
The University of Western Ontario
2015

Conference Oral Presentations:
McDonald, JV (2014). Blogging in Botany: what my blog has taught me about the way students learn. Technology in Education Symposium (TiES). London, Ontario.
McDonald, JV, Hollingsworth, L (2014). The importance of trees in London, Ontario. Earth Day Colloquium. London, Ontario.
McDonald, JV (2013). Gardening with native species. Earth Day Colloquium. London, Ontario (1st place best talk).
McDonald, JV, Thorn, RG (2012). Four exceptional cases in the *Resupinateae*. Great Lakes Mycology Meeting. London, Ontario.
McDonald, JV, Thorn, RG (2011). An introduction to the systematics of the *Resupinateae*. Mycological Society of America. Fairbanks, Alaska.
McDonald, JV, Thorn, RG (2011). An introduction to the systematics of the *Resupinateae*. Great Lakes Mycology Meeting. Peterborough, Ontario.
McDonald, JV (2010). What's in a name? Part Two – Concepts in Species Concepts. Western Research Forum. London, Ontario (3rd place best talk).
McDonald, JV, Thorn, RG (2009). An introduction to cyphelloid *Resupinateae*. Canadian Botanical Association. Wolfville, Nova Scotia.
McDonald, JV, Thorn, RG (2009). An introduction to cyphelloid *Resupinateae*. Great Lakes Mycology Meeting. Toronto, Ontario.
McDonald, JV (2009). What's in a name? A taxonomic approach to studying biological organisms. Western Research Forum. London, Ontario.

Invited Talks:
Strathroy-Caradoc Horticultural Society General Meeting (April 2016)
Nature in the City (January 2016)
Ministry of Natural Resources training week (May 2015)
London Garden Club General Meeting (March 2014)
Senior Alumni Group Arboretum Tour (October 2013, 2014, 2015)
London-Fanshawe Horticultural Society Arboretum Tour (June 2013)
Mycological Society of Toronto General Meeting (October 2012)