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Pfister, Donald H. and Healy, Rosanne (2021) Pezizomycetes. In: Zaragoza, O. (ed) Encyclopedia of Mycology. vol. 1, pp. 295–309. Oxford: Elsevier.

http://dx.doi.org/10.1016/B978-0-12-819990-9.00054-8

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# **Pezizomycetes**

**Donald H Pfister,** Harvard University, Cambridge, MA, United States **Rosanne Healy,** University of Florida, Gainesville, FL, United States

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## Introduction

The Pezizomycetes comprise a single order, Pezizales, with  $\geq$  22 families currently recognized. Along with the Orbiliomycetes, the class represents one of the basal lineages among the filamentous Ascomycota (Shen *et al.*, 2020). The class is thought to have originated between 400 and 540 mya (Beimforde *et al.*, 2014; Martin *et al.*, 2010; Murat *et al.*, 2018). The full diversity of the order has yet to be completely documented since previously undetected lineages continue to be found through application of molecular methods. There are approximately 200 genera and perhaps 2000 species. Ascomata are epigeous (above ground), or hypogeous (below ground). The truffles of commerce belong to this latter group. The epigeous ascomata are apothecial, cleistothecial or are highly reduced. The reduced forms are composed of only a few asci in clusters on vegetative hyphae with little or no sterile supporting tissue (excipulum). In the ep,lppigeous lineages, ascospores are generally forcibly released by an opening at the ascus apex resulting in the formation of an operculum, or lid. Hypogeous members occur in several of the families. There are at least 30 independent origins of truffle-like members (Alvarado *et al.*, 2011, 2016; Cabero *et al.*, 2016; Grupe *et al.*, 2019; Hansen *et al.*, 2013; Kraisitudomsook *et al.*, 2019; Kumar *et al.*, 2017; Læssøe and Hansen, 2007; Smith, 2014; Smith and Healy, 2009; Trappe *et al.*, 2010).

## **Distribution and Ecology**

Pezizomycetes can be found around the world but representatives are unevenly distributed. Members of certain families, especially those found in or on soil, show a particularly high diversity in temperate regions (Tedersoo *et al.*, 2014). These include the Pezizaceae, Morchellaceae, Helvellaceae, Rhizinaceae and many of the Pyronemataceae. Others are more abundant in tropical or subtropical regions, as exemplified by the Sarcosomataceae, Wynneaceae and Sarcoscyphaceae. Members of bryophilous Pyronemataceae are particularly common and diverse in the Arctic and Antarctic, but these fungi also occur in other regions (Olech and Mleczko, 2000; Schumacher, 1993). Although fieldwork and discovery in the Pezizomycetes is robust, recent work has shown that even in localities considered well studied, such as the Northern Hemisphere, new species have come to light. In the Southern Hemisphere, much remains to be documented.

Nutritionally Pezizomycetes are saprobic, mutualistic as mycorrhizae (Tedersoo *et al.*, 2006) or as endophytes (Arnold, 2007), or parasitic on bryophytes or vascular plants (Hansen and Pfister, 2006). An additional nutritional niche was recently discovered where some species were documented as bacterial farmers (Pion *et al.*, 2013), or otherwise mutualistic with certain bacteria (Benucci and Bonito, 2016; Giordano *et al.*, 2013; Splivallo *et al.*, 2015).

The plant parasitic species are scattered in various lineages. *Rhizina undulata* is reported as a root parasite of conifers (Ginns, 1968). *Pithya* species may cause branch dieback in conifers. *Caloscypha fulgens* is reported as a seed pathogen of conifers (Paden, 1972; Salt, 1974; Sutherland and Woods, 1978; Paden *et al.*, 1978). *Urnula craterium* has been implicated as the causal agent of strumella canker in oak (Davidson, 1950). *Phymatotrichopsis ominivora* is a serious root pathogen of cotton and other dicotyle-donous plants and is known only in its asexual state (Uppalapati *et al.*, 2010). Several Pyronemataceae are parasitic on bryophytes, including species of *Filicupula, Lamprospora, Moravecia, Neottiella, Octospora, Octosporella,* and *Octosporopsis* (Döbbeler, 1979; Egertová and Sochor, 2017; Hansen and Pfister, 2006; Sochorová *et al.*, 2019; Stenroos *et al.*, 2010). Apothecia occur directly on their moss or liverwort hosts or on surrounding soil. These often parasitize the rhizoids (Döbbeler, 1979; Stenroos *et al.*, 2019). There is evidence that species of *Wynnea* are parasitic on mushroom species in the genus *Armillaria* (Xu *et al.*, 2019).

With the advent of molecular approaches to studying fungal ecology, such as the sequencing of ectomycorrhizal root tips, a number of examples of mycorrhizal Pezizomycetes have been documented. Mycorrhizal Pezizomycetes most commonly form ectomycorrhizae with a broad range of angiosperm and coniferous tree species in boreal, temperate, and Mediterranean forests in the Northern Hemisphere and temperate forests of the Southern Hemisphere (Tedersoo and Smith, 2013; Tedersoo *et al.*, 2010), and with Cistaceae and some Rosaceae in arid shrub lands and deserts (Giovannetti and Fontana, 1982; McDonald *et al.*, 2010), but a few are also tropical (Tedersoo and Nara, 2010). Tedersoo and Smith (2013) hypothesized 20 independent origins of the ectomycorrhizal symbiosis in the Pezizomycetes although evidence is still equivocal for some lineages, such as *Sowerbyella*. *Sphaerosporella* species are ectomycorrhizal, but unusual in that they can grow saprobically as well (Danielson, 1984; Sánchez *et al.*, 2014). Some species of Tuberaceae and Pyronemataceae form orchid mycorrhizae with certain understory terrestrial orchids (Bidartondo and Read, 2008; Těšitelová *et al.*, 2012). Morphologically Pezizomycete ectomycorrhizae have a thin mantle, a well-developed Hartig net and they generally form short-distance or contact-type mycorrhizas without rhizomorphs (Agerer, 2001; Tedersoo *et al.*, 2010). Most of the mycorrhizal Pezizomycetes fruit in or on soil, particularly in disturbed areas or in soil with a neutral or elevated pH (Tedersoo *et al.*, 2014) and low content of organic matter. Petersen (1985) provides a review of the edaphic factors involved in growth and reproduction.

Truffle or truffle-like taxa are largely found within ectomycorrhizal lineages. However, truffles in the Tarzettaceae, Glaziellaceae, and some in the Pezizaceae such as *Carbomyces, Kalaharituber* and *Eremiomyces* are not known to be mycorrhizal. Their nutritional strategy is presumed to be saprobic (Hansen *et al.*, 2013; Kumar *et al.*, 2017). In some families, such as Chorioactidaceae, Sarcoscyphaceae and Sarcosomataceae, there are no truffle-like species and no mycorrhizal species are known.

Some non-ectomycorrhizal lineages of Pezizomycetes have been detected as a relatively small component of the endophytic community in healthy leaves, bark, branches and/or roots (Arnold, 2007). Lineages of endophytic Pezizomycetes include non-mycorrhizal Pezizaceae (Arnold, 2007), Sarcosomataceae (Wang *et al.*, 2005), Pyronemataceae and Tarzettaceae (Tedersoo *et al.*, 2013). *Sphaerosporella* species (in a complex of species under the name *S. brunnea*) are an exception to this observation as they have been reported as both endophytic and ectendo- or ectomycorrhizal with a broad range of hosts. However, endophytic and mycorrhizal *Sphaerosporella* are not usually detected on the same tree (Hughes *et al.*, 2020). Detected endophytic Pyronemataceae were mostly pyrophilous species (Raudabaugh *et al.*, 2020; Tedersoo *et al.*, 2013). Many lineages have also been found within lichen thalli (Tedersoo *et al.*, 2013).

The majority of Pezizomycetes are saprobic. They occur on organic material of various types – decaying wood, dung, leaf litter and twigs. The diversity of Pezizomycetes on dung is well documented with many studies and keys available (Bell, 1983; Doveri, 2004; Richardson and Watling, 1968). Some clades, such as the Ascobolaceae, are found almost exclusively on dung (Brummelen, 1967). Dung inhabiting species are also found in several clades of the Pseudombrophilaceae, Pyronemataceae and Pezizaceae (Hansen *et al.*, 2001; Hansen and Pfister, 2006; Perry *et al.*, 2007). In most cases little is specifically known of the biology of saprobic species in regard to nutrient requirements and utilization. Sarcoscyphaceae, Sarcosomataceae and Chorioactidaceae are found exclusively on wood, leaves and plant debris and are presumed to be saprobic.

There are a number of pyrophilous taxa for which fruiting is enhanced by fire or they fruit only after a burn. These are part of a succession of fungi colonizing burned areas, and these species are from various families including Morchellaceae, Pezizaceae, Pyronemataceae, Rhizinaceae, and Tarzettaceae. There is evidence that these fungi may persist in soil, the living tissues of bryophytes ferns, lichens and lycopods, woody debris and other substrates. Fire triggers the release of the fungus (Hughes *et al.*, 2020; Raudabaugh *et al.*, 2020). Certain species of the economically important morels (*Morchella* sp.) are stimulated to fruit prolifically after burns (Alexander *et al.*, 2002; Larson *et al.*, 2016; Pilz *et al.*, 2004).

## **Morphological Features**

#### Ascomata

Apothecia are the basic type of ascomata in the Pezizomycetes. These range in size from several millimeters to about 20 centimeters and they vary from sessile cups of small to large size to stalked cups to the stipitate-piliate structures found in the Helvellaceae, Discinaceae, and Morchellaceae. Some highly reduced members, such as species of *Ascodesmis*, produce little more than small fascicles of asci. More highly reduced forms are found in *Eleutherascus* and *Monascella* (Guarro and Arx, 1986) in which solitary asci are produced on hyphae or in clusters on unspecialized hyphae. Ascomata are often highly pigmented, particularly the hymenium. Carotenoid pigments have been characterized (Arpin, 1968). Other pigments may give the hymenium brown, orange, purple or black colors.

Variation in typical apothecial ascomata are found, some examples are presented in **Fig. 1**. On the one hand there are highly reduced types that are merely asci scattered on hyphae as mentioned above but also small cleistothecial (closed) ascomata are found in a few cases. In the case of *Orbicula parietina*, active discharge has been lost and spores are liberated in a powdery mass (Hansen *et al.*, 2005). *Heydenia alpina* forms stalked cleistothecial fruitbodies and is closely related to *O. parietina* (Leuchtmann and Clémençon, 2011). It is a small fungus that occurs on plant debris and mosses. It is stipitate with a dark stipe that is topped by a pale mass of hyaline spores and radiating hyphae. No asci are present in mature specimens. Molecular evidence confirms that this species belongs in the Pseudombrophilaceae along with *Orbicula*. The two genera share characteristics of a cleistothecial fruitbody and asci that disintegrate early in the development of the ascomata but they are different in important morphological features (Leuchtmann and Clémençon, 2011). These genera were often placed outside of the Pezizomycetes and, in the case of *Orbicula*, confused with Myxomycetes.

Truffle fruitbodies are found in a number of lineages. Following the terminology of Weber *et al.* (1997) these ascomata have been characterized by the position of the asci and the hymenia in relationship to the tissues of the ascomata. Stereothecia are ascomata that lack a hymenium, the asci being scattered individually or in chambers in the mass of sterile tissue. When the hymenium is located on the outside of an ascoma the term exothecium is used. In some cases the hymenium is present as a distinct layer but the ascoma is highly convoluted; this type of ascoma is termed a ptycothecium. All of these specialized types of ascomata are derived from apothecial forms. The literature on many of these taxa as a whole is reviewed in Ekanayaka *et al.* (2018), Læssøe and Hansen (2007) and O'Donnell *et al.* (1997).

Some highly reduced forms are found among the bryophyte parasites. The ascomata are partly closed and have only a few asci and are reminiscent of perithecia.

### The Hymenium

This is the layer composed of asci and paraphyses that line the surface of the apothecium. Asci are the structures in which karyogamy and meiosis occur in the life cycle of the Ascomycota. The asci arise from ascogenous hyphae, which in turn have formed after the process of plasmogamy between two receptive structures from compatible individuals. Ascogenous hyphae are



Fig. 1 Examples of ascoma morphologies in families of Pezizomycetes. A. Ascobolaceae: Ascobolus denudatus; B. Caloscyphaceae: Caloscypha fulgens; C. Chorioactidaceae: Chorioactis geaster, D. Chorioactidaceae: Desmazierella acicola; E. Discinaceae: Gyromitra brunnea; F. Geomoriaceae: Geomorium furciae; G. Glaziellaceae: Glaziella aurantiaca; H. Helvellaceae: Helvella stevensii; I. Morchellaceae: Morchella americana; J. Otideaceae: Otidea concinna; K. Pezizaceae: Hydnobolites sp. nov.; L. Pezizaceae: Peziza varia; M. Pyronemataceae: Humaria hemisphaerica; N. Pyronemataceae: Scutellinia pennsylvanica; O. Pulvinulaceae: Pulvinula convexella; P. Sarcoscyphaceae: Microstoma floccosum; Q. Sarcosomataceae: Galiella rufa; R. Tarzettaceae: Tarzetta sp.; S. Tuberaceae: Tuber mexiusanum; T. Wynneaceae: Wynnea americana. Photo credits: A, E, H-S, R. Healy; B, Arthur Grupe; C, D.H. Pfister; D, Roy Kristiansen, F., Matthew, E., Smith, G., Alan Franck, T., Mark Elliot.

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dikaryotic. These dikaryotic cells may proliferate by the production of croziers. Croziers are hook-like structures formed at the base of the ascus. They are formed by an outgrowth of the ascus before karyogamy and allow for the formation of a new dikaryotic cell. This aids in the proliferation of the dikaryotic system and gives rise to additional asci. Although considered a characteristic of the filamentous Ascomycota, not all Ascomycota produce croziers. Along with asci, the hymenium generally has paraphyses. These are located between the asci and arise from the sterile tissues surrounding the developing ascogenous hyphae.

#### The Ascus

Brummelen (1994,1978) summarized the structural characters of the ascus in the Pezizomycetes. Important characters are the apical apparatus, the operculum in most taxa, its position, the reaction of the ascus wall layers in various staining agents as seen in light microscopy and the ultrastructure of the ascus walls. Asci that stain blue in iodine-containing reagents (said to be amyloid) are found in Pezizaceae and Ascobolaceae (Hansen *et al.*, 2001) but this character has been lost several times in members of the Pezizaceae, most notably in some of the hypogeous species. Amyloid asci are not found outside these families. The bluing material is a long-chain polysaccharide. The function of this polysaccharide is unknown but it seems to be located on the outer surface of the wall and is sometimes seen in the gelatin matrix of the hymenium (Samuelson, 1978).

The layering of the wall as seen in TEM helps delimit groups, particularly the taxa with thick lateral walls in the Chorioactidaceae, Sarcoscyphaceae and Sarcosomataceae. The asci of these fungi were termed "suboperculate" by Le Gal (1953, 1946) because of their thick, sometimes eccentrically placed operculum. Later Eckblad (1968) and Samuelson (1975) discounted the term finding that the opercula were variously placed and wall construction conformed with that of other Pezizomycetes. In these groups the operculum is often eccentrically positioned at the ascus tip.

Asci are typically cylindrical in shape, and there are usually eight ascospores per ascus. Ascus shape can vary and spore number is often reduced in some truffle-like species, and spores may be more numerous in certain coprophilous species. In most epigeous members ascospores are actively discharged from the ascus by the build-up of osmotic pressure within the ascus. This causes a rupture at thinner areas at the apex of the ascus which creates the operculum. The releasing pressure causes the wall to give way and for the operculum to fold back allowing the ascospores and the cytoplasm of the ascus to be expelled. In some cases the asci deliquesce or are mechanically broken down and dry powdery masses of spores are produced, as in *Orbicula*. In these cases the spores are passively liberated and spread by air currents. Not all members of the Pezizomycetes have opercula or forcible discharge of ascospores. Hypogeous taxa (Læssøe and Hansen, 2007) and some cleistothecial forms (Hansen *et al.*, 2005) have lost the operculum and spores remain either within asci until the fruitbody is eaten or broken down, or the asci disintegrate and a powdery mass is formed. Most hypogeous species produce odors that attract animals and the fruiting bodies are eaten. Ascospore liberation and dispersal for these truffle-like fungi occurs through the process of digestion and excretion.

#### Ascospores

No member of the Pezizomycetes has septate ascospores. Septa may develop as spores germinate but only at the time a germ tube has been established. The spores may take on a variety of shapes from globose to naviculate. Spore surfaces may be smooth or with various types of surface ornamentations. Generally the ornamentations are derived from deposition of secondary wall material although a few examples of spore ornamentation without a contribution of secondary walls are known. The spore walls are multilayered and the thickness of each wall is highly variable (Merkus, 1976). Most ascospores are hyaline but purple, brown or yellowish ascospores are known. The number of nuclei per spore varies from 1, 2, 4 to many and such variation has been shown to have some taxonomic value (Berthet, 1964; Korf, 1972, 1973). Ascospores also may contain an oil guttule, which is seen under the light microscope as a refractive body within the spore. The number of guttules can also vary; some spores have one guttule, some have two guttules and in some species there are many small guttules in each spore. In some taxa there are no oil droplets. Spore guttulation may provide an important taxonomic character in identification at the genus and species level. It is important to understand that guttulation may be altered when specimens are dried, under such conditions oil droplets may fuse into a single large inclusion.

#### **Paraphyses**

Hymenium color is attributed to pigments found in the paraphyses. Yellow, red and orange carotenoid pigments are distinctive features of some of these fungi. These pigments are often present in lipid inclusions in the paraphyses. There are a variety of carotenoid pigments known to occur in these fungi as summarized by Arpin (1968). Other pigments are present either within the cytoplasm of the cells of the paraphyses or encrusted on the cell surface. The chemical composition of these other pigments is largely unknown; they give the hymenium brown, purple or black coloration. Paraphyses are generally septate. The individual cells in the paraphyses may be either uninucleate or multinucleate and this can be useful for classification (Berthet, 1964; Pfister *et al.*, 2008). In some species paraphyses are interspersed with hyaline or darkly pigmented, often thick-walled, elements or setae. Examples of such setae are found in members of the Rhizinaceae, Sarcosomataceae, Chorioactidaceae, and Sarcoscyphaceae. Paraphyses may be simple (unbranched) or they may branch either at the base or along their length. They may also anastomose (fuse) with a cell of a neighboring paraphysis. The apical cell may be the same width as subtending cells or it may be swollen, curved or bent. In some hypogeous species (e.g., *Genea* spp.), paraphyses that have elongated substantially beyond ascus length may interweave to form an epithecium over the asci.

### **Septal Structures**

Ultrastructural characters of septal pore plugs and Woronin bodies correlate to some degree with families and lineages in the class. Kimbrough (1994) summarizes much of the information. Septal pores in vegetative hyphae generally have a lamella embedded in a matrix. Woronin bodies are generally associated with septa. The Woronin bodies take on several morphologies – globular, hexagonal or cylindrical, ranging from globose to considerably elongate. The form of the Woronin bodies is an important taxonomic and phylogenetic character. The septa at the base of the asci also provide important characters. The simplest septal pore structure is the uni- or biconvex band found in the Pezizaceae. Other families exhibit asci with basal septa that are occluded by dome-shaped, pyramidal, or dumbbell-shaped structures. These plugging structures show electron dense bands, or lamellate structures that in some species produce ray-like extensions. In general, Woronin bodies are not found in the asci of Pezizales (but see *Leucangium* in Li, 1997).

#### **Anamorphic States**

Anamorphic states have been reported across many families, though they are not known in Glaziellaceae, Helvellaceae, Karstenellaceae, Otideaceae, or Pseudombrophilaceae. Fig. 2 provides some examples of the conidia and modes of conidial formation of members of the class. Conidia are holoblastic (spores are blown out from, and produced with both inner and outer wall of the conidiogenous cell) in development and are hyphomycetous (occurring in cushions or mats). In cases where the mitotic spores germinate to produce hyphae they are considered true conidia (e.g., Paden, 1967; Sánchez *et al.*, 2014). In many cases, however,



**Fig. 2** Schematic representations of some conidial states of Pezizomycetes. A. *Adelphella babingtonii* (Pezizaceae), redrawn from Harrington and Pfister (2001); B. Chromelosporium-like state (Pezizaceae) found in *Peziza* species, redrawn from Seifert *et al.* (2011) C. Reduced Ostracoderma-like state (Pezizaceae), redrawn from Berthet (1964); D. Conidial state of *Hydnocystis transitoria* (Tarzettaceae), Kumar *et al.* (2017); E. Conoplea-like state of a *Plectania* species (Sarcosomataceae), redrawn from Ellis (1971); F. Conidial state of Chorioactis geaster, redrawn from Peterson *et al.* (2004); G. *Verticicladium*-like state of *Desmazierella acicula* (Chorioactidaceae), redrawn from Ellis (1971); H. *Tuber* species (Tuberaceae), redrawn from unpublished images, R.A. Healy; I. *Ostracoderma* state of *Peziza varia* (Pezizaceae), redrawn from unpublished images, R.A. Healy; J. *Complexipes* species (Pyronemataceae) clamydospore, redrawn from Yang and Korf (1985); K. *Geniculodendron* state of *Caloscypha fulgens* (Caloscyphaceae), redrawn from Paden (1978); L. *Dichobotrys*-like state of *Trichophaea abundans* (Pyronemataceae), redrawn from Carmichael *et al.* (1980), M. *Dichobotrys*-like state of *Pyropyxis rubra* (Pyronemataceae), redrawn from Egger (1984); N. *Mollardiomyes* state of *Nanoscypha tetraspora* (Sarcoscyphaceae) redrawn from Pfister (1973).

germination of mitotic spores has not been observed and this suggests that mitotic spores may act as spermatia and are thus involved in the establishment of the dikaryon. Although sexual reproduction with spermatia in saprobic Pezizomycetes has long been documented, (e.g., Bistis and Raper, 1963; Harper, 1900) it is unverified in Pezizomycetes of other nutritional modes. However, sexual outcrossing is known in *Tuber* (Murat and Martin, 2008) and suggests a possible role of mitospores in plasmogamy. The investigations by Healy *et al.* (2013) identified spore mats in several clades in the Pezizoeae and Tuberaceae that are composed of masses of mitospores. Several anamorphic states with no known teleomorphs within the Pezizomycetes have been discovered through molecular phylogenetic studies. Most notable among these is *Phymatotrichopsis omnivora*, the cotton root pathogen. This falls within the Rhizinaceae based on molecular studies but despite intensive study of this important pathogen, no evidence of a teleomorph has been discovered (Duggar, 1916; Marek *et al.*, 2009; Uppalapati *et al.*, 2010). Another example is *Cephaliophora*, a soil and dung inhabiting fungus, and one that has been implicated in causing keratitis (Goos, 1964; Hoog *et al.*, 2000).

#### Genomes, Microbiomes, and Model Organisms

A few Pezizomycetes have been used as model organisms. These include species in the genera *Ascobolus* where classic genetic information has been collected (Decaris *et al.*, 1974) and *Pyronema confluens*, which has been used in research on ascocarp development as well as in studies of light detection and circadian rhythms (Traeger *et al.*, 2013; Traeger and Nowrousian, 2015; Nowrousian and Kück, 2006). Comparative fungal genomics has paved the way to a broader and deeper understanding of fungal evolution, phylogenetic structure, sexual reproduction, pathogenicity and epidemiology of plant pathogens, symbiosis and other fungal biology topics (e.g., Gow, 2005; Grigoriev *et al.*, 2014; Howlett *et al.*, 2015). Despite the systematic position of the Pezizomycetes as an early derived lineage of the Pezizomycotina, along with the Orbiliomycetes, there has been relatively limited whole genome sequencing within the class. There are currently 36 complete genomes of Pezizomycetes, out of 775 genomes known for the entire subphylum Pezizomycotina (Shen *et al.*, 2020). Much of the work has focused on edible members of economic importance, such as the morels, desert truffles and "true" truffles of the Morchellaceae, Pezizaceae, and Tuberaceae (Martin *et al.*, 2010; Murat and Martin, 2008, Murat *et al.*, 2010), and revealed the heterothallic nature of this species as well as predicting some of the genes involved in mating (Martin *et al.*, 2010, 2013).

Complete genomes of Pezizomycetes include the following: Ascobolus immersus, Ascodesmis nigricans, Caloscypha fulgens, Choiromyces venosus, Geopyxis carbonaria, Gyromitra esculenta, Kalaharituber pfeilii, Leucangium carthusianum, Morchella (9 species), Peziza echinospora, Plectania melastoma, Pyronema confluens, Rhizina undulata, Sarcoscypha coccinea, Sphaerosporella brunnea, Terfezia boudieri, Terfezia claveryi, Tirmania nivea, Tricharina praecox, Trichophaea hybrida, Tuber (6 species), Verpa conica, and Wilcoxina mikolae.

The average genome size in the subphylum Pezizomycotina, the filamentous Ascomycota, is around 42 Mb, which is larger than in the other two subphyla of the Ascomycota. The Pezizomycotina have a high number of genes that seem to be derived from prokaryotes whereas this is less common in Saccharomycotina (Shen *et al.*, 2020). The genome sizes of Pezizomycetes can be up to 192 Mb in size, with the genomes of *Tuberaceae* species being significantly larger and more complex than those in other families of Pezizomycetes. For example, genomes of *Morchella importuna* (48 Mb) and *Terfezia boudieri* (63 Mb) are much smaller compared to *Tuber magnatum* (192 Mb). The larger genomes in Tuberaceae species are due to the acquisition of an unusually high number of transposable elements (Murat *et al.*, 2018). Tuberaceae also has a significantly accelerated evolution of its gene repertoire compared to other ascomycetous species, possibly reflecting an increased rate of genomic evolution underlying traits specific to either symbiosis and/or hypogeous ascomatal formation. The higher rate of evolution has been hypothesized to result from the genome rearrangements caused by repositioning of transposable elements (Martin *et al.*, 2010).

Shen *et al.* (2020) used genomes in reconstruction of an Ascomycota phylogeny. This phylogeny attempted to clarify the relationship of the Pezizomycetes and the Orbiliomycetes in relationship to their position as basal taxa in the Pezizomycotina. Debate had centered on which of these classes were the most basal with several multigene phylogenies showing one or the other to have the most basal position. Shen *et al.* (2020) suggest that the Orbiliomycetes and Pezizomycetes together form a clade that is the sister group to the remainder of the Pezizomycetes.

The microbiome of yeasts, bacteria and fungi that characterize the Pezizomycetes has been an active area of study in recent years. A comparative study of bacterial microbiomes within fruiting bodies and mycelia of four genera of truffles revealed that although there are multiple bacterial genera in the microbiome, one *Bradyrhizobium* genotype was dominant in all analyzed *Tuber* species, regardless of geographic location, but not present to the same degree in the other truffles analyzed (Benucci and Bonito, 2016). Bradyrhizobiaceae bacteria have been implicated in the release of sulfur containing compounds from *Tuber borchii* microbiomes. It is though that a mixture of volatiles produced through interactions among the fungi and bacteria in the microbiome may characterize the odor perceived by humans (Splivallo *et al.*, 2015). These odors help to attract the animals that disperse the spores of truffles, and thus the bacterial-fungal relationship may be symbiotic. Similar studies of other species of epigeous and hypogeous Pezizomycetes may help to understand the extent of such interactions between these fungi and their microbiomes.

## **Classification and Phylogenetic Studies**

The class Pezizomycetes has undergone significant reorganization in recent years due to results from molecular phylogenetic studies. These studies have provided new insights into relationships and have facilitated the evaluation of both morphological and



**Fig. 3** Current phylogenetic framework for 22 families of Pezizales. Phylogeny based on maximum likelihood analysis of combined DNA loci (SSU, ITS, LSU, TEF, RPB2). Symbols depict known ascomatal form (epigeous and apothecial or hypogeous and truffle-like) and colors indicate ecological roles in each family. "Mixed" refers to a mixture of trophic modes within a family. Sizes of triangles are approximately proportional to numbers of known species in each family. Graphic of phylogenetic framework modified from Ekanayaka *et al.* with additional families approximately placed as determined by Kraisitudomsook *et al.* and Pfister *et al.* Modified from Ekanayaka, A.H., Hyde, K.D., Jones, E.B.G., Zhao, Q., 2018. Taxonomy and phylogeny of operculate discomycetes: Pezizomycetes. Fungal Divers. 90, 161–243. doi:10.1007/s13225-018-0402-z. Kraisitudomsook, N., Healy, R.A., Pfister, D.H., *et al.*, 2019. Resurrecting the genus Geomorium: Systematic study of fungi in the genera Underwoodia and Gymnohydnotrya (Pezizales) with the description of three new South American species. Persoonia 44, 98–112. doi:10.3767/ persoonia.2020.44.04. Pfister, D.H., Quijada, L., LoBuglio, K.F., 2020. Geodina (Pezizomycetes: Wynneaceae) has a single widespread species in tropical America. Fungal Syst. Evol. 5, 131–138. doi:10.3114/fuse.2020.05.08.

ecological characters. For example, the hypogeous species of Pezizomycetes were almost all previously treated in the order Tuberales due to their convergent morphological forms. However, recent studies have now placed these hypogeous taxa in at least ten different Pezizomycete families. All of these families with hypogeous members have at least some ectomycorrhizal species and indeed nearly all of the hypogeous Pezizomycetes are ectomycorrhizal, with exceptions in Glaziellaceae, Pezizaceae and Tarzettaceae. **Fig. 3** shows relationships among the Pezizomycetes as we currently recognize them and also indicates growth habit and trophic status.

The 22 families we currently recognize in the class are summarized below. Apothecial morphology varies greatly, particularly in the larger families; Fig. 1 provides an overview of the patterns of apothecial forms found in this class. Table 1 is a guide to some critical characters of the families.

#### Families

- (1) Ascobolaceae These generally small apothecial fungi have amyloid asci (asci that give a blue reaction in iodine solutions). This character is shared with the Pezizaceae listed below. This reaction is diffuse in the Ascobolaceae and is often detected in the gelatinous material in the hymenium. The members of the family are distributed worldwide and are mostly found on dung. A few species are found on soil or burned debris. In *Ascobolus* and *Saccobolus* the spores become purple or brownish at maturity. The genus *Thecotheus*, that occurs on dung but also other substrates, has unpigmented ascospores. Sclerotia are not known in this family. Names used for the anamorphs in *Ascobolus* referred to the form genera *Oidia, Papulaspora,* and *Rhizostilbella*. Genera included: *Ascobolus, Cleistoiodophanus, Saccobolus,* and *Thecotheus.*
- (2) Ascodesmidiaceae These fungi occur on dung but also on soil and debris. The morphology in the family ranges from a single ascus occurring along hyphae to simple fascicles of a few asci to apothecia with a hymenium and well-developed apothecial tissues. This family is currently placed as the sister group to Pulvinulaceae but there is low statistical support for this placement. Sclerotia are not known in this family. The family Coprotaceae was recently described recognizing a clade previously detected by Hansen *et al.* (2013). The genera included in this family are *Coprotus* and *Boubouvia*. Other genera

Family	Ascus J+	Ascus J —	Ascus +/- thick- walled	Asci indehiscent	Asci opening via an operculum	asci produced in naked fascicles or directly on hyphae	Saprobic	Plant parasitic including mosses	Mycorrhizal	Mycoparasitic	Ascomata epigeous	Ascomata hypogeous	ascomata minute cleistothecial or perithecial	ascomata stipitate	ascomata sessile or substipitate	Ascospores uninucleate	Ascospores multi- nucleate	2-4- nucleate	Ascospores hyaline	ascospores pigmented
Ascobolaceae	Х				Х		Х				Х		Х		Х	Х			Х	Х
Ascodesmidaceae		Х		Х	Х	Х	Х				Х				Х	Х			Х	Х
Caloscyphaceae		Х			Х		Х	Х			Х				Х	Х			Х	
Chorioactidaceae		Х	Х		Х		Х				Х				Х		Х		Х	
Discinaceae		Х		Х	Х		Х		Х		Х	Х		Х	Х			Х	Х	
Glaziellaceae		Х	Х	Х			Χ?		?			Х			Х	?	?	?	Х	
Geomoriaceae		Х		Х	Х				Х		Х	Х		Х	Х	?	?	?	Х	
Helvellaceae		Х		Х	Х				Х		Х	Х		Х	Х			Х	Х	
Karstenellaceae		Х			Х		?	?	?		Х				Х			Х	Х	
Morchellaceae		Х		Х	Х		Х		Х		Х	Х		Х	Х		Х		Х	
Otidiaceae		Х		Х	Х	Х	Х		Х		Х	Х	Х	Х	Х	Х			Х	
Pezizaceae	Х	Х		Х	Х		Х		Х		Х	Х		Х	Х	Х			Х	Х
Pseudombrophilaceae		Х		Х	Х	Х	Х				Х		Х		Х	Х			Х	
Pulvinulaceae		Х			Х		Х		Х		Х				Х	Х			Х	
Pyronemataceae		Х		Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х	Х			Х	
Rhizinaceae		Х			Х		Х	Х			Х				Х	?	?	?	Х	
Sarcosyphaceae		Х	Х		Х		Х	Х			Х			Х	Х		Х		Х	
Sarcomataceae		Х	Х		Х		Х				Х			Х	Х		Х		Х	
Strobiloscyphaceae		Х	Х		Х		Х				Х				Х	?	?		Х	
Tarzettaceae		Х		Х	Х		Х		Х		Х	Х			Х	Х			Х	
Tuberaceae		Х		Х	Х		Х		Х		Х	Х			Х	Х		Х	Х	Х
Wynneaceae		Х	Х		Х					Х	Х			Х			X?		Х	

 Table 1
 A guide to salient features of members of the families of the Pezizomycetes. This table is intended to offer guidance for the morphological placement of species within the framework of current families. Note that characters may appear in several columns

remaining in the Ascodesmidaceae may also belong here such as *Dictyocoprotus* and *Pseudobobouvia*. Two genera have no known teleomorphs: *Cephaliophora* and *Pulchromyces* (Hennebert, 1973; Tanabe *et al.*, 1999; Thaxter, 1903).

Genera included: Ascocalathium (?), Ascodesmis, Bobouvia, Cephaliophora, Coprotus, Dictyocoprotus, Eleutherascus, Lasiobolus, Ochotrichobolus, Pseudoboubovia, Pseudocoprotus, Pulchromyces (?) and Trichobolus.

- (3) Caloscyphaceae Two apothecial genera are placed in this family: *Caloscypha* and *Kallistoskypha*. *Caloscypha fulgens* is the only species currently recognized in the genus. It is yellow-orange and often colors blue green when handled. *Kallistoskypha* is also a monotypic genus, with *K*, *incarnata* as the sole member. Ekanayaka *et al.* (2018) placed it as the only genus in a separate family, Kallistoskyphaceae. However, this placement was based on only two genes in a five-gene analysis, resulting in its placement on a long branch. A study by Pfister *et al.* (2013) placed this species in the Caloscyphaceae with strong statistical support. More robust molecular data may better resolve the relationships between *Kallistoskypha* and other Pezizomycetes. The ascomata of *K. incarnata* are cupulate, pinkish and the ascospores are globose and smooth. The species has been collected on soil in the Mediterranean region. Because of its association with *Eucalypus* Pfister *et al.* (2013) suggested that it may represent an introduction of an australasian fungus to the Mediterranean region. *Caloscypha fulgens* is found on soil in north temperate regions. Sclerotia are not known in this family. The conidial state of *C. fulgens*, known as *Geniculodendron pyriforme*, has been implicated as a seed pathogen of conifers (Salt, 1974). Genera included: *Caloscypha, Kallistoskypha*.
- (4) Chorioactidaceae Members of this family are characterized by thick-walled asci with sometimes eccentrically-placed opercula. The apothecia are clothed with brown hairs that are generally encrusted with pigmented granules. The ascospores are ornamented with either pits or ridges. There is a tendency for the asci to mature simultaneously within a single apothecium. Sclerotia are not known in this family. The form genus *Kumanasamuha* was applied to the anamorphs in *Chorioactis* and *Trichaleurina* (Carbone *et al.*, 2013; Nagao *et al.*, 2009), and a *Verticicladium*-like conidial state was described for *Desmazierella acicula* (Gremmen, 1949).

Genera included: Chorioactis, Desmazierella, Neuronal, Psueodosarcosoma, Trichaleurina, and Wolfina.

(5) Discinaceae – There are both epigeous and hypogeous taxa in the family (Læssøe and Hansen, 2007). The hypogeous *Hydnotrya* is ectomycorrhizal; other taxa are saprobic associated with wood, soil with organic matter, or woody debris. The epigeous members are generally large and either stipitate or sessile. Some are distinctive members of the spring funga. Conidial states have been described by Carris *et al.* (2015) and Healy *et al.* (2013) and are similar to the *Costantinella* type observed in the Morchellaceae.

Genera included: Discina, Gyromitra, and Hydnotrya.

(6) Geomoriaceae – The single genus in this family includes both epigeous and hypogeous species. Ascomata are either modified columnar apothecia or exothecia, and vary widely in size from 1 to 40 mm high. Young ascomata are typically white or pale tan but often change to brown, purple, or black as the hymenium matures. The outer excipulum and stipe are only present in the epigeous taxa. Paraphyses may slightly or greatly exceed the asci in length. The asci lack opercula. They are ectomycorrhizal, found in forests or at forest edges, and known only from the Southern Hemisphere. Conidial states and sclerotia are unknown in this genus.

Genus included: Geomorium.

- (7) Glaziellaceae Large hollow ascomata of this fungus are generally formed under or on the surface of soil and debris on the forest floor in tropical localities. The family has a single genus and *G. aurantiaca* is the recognized species (Gibson *et al.*, 1986; Hansen and Pfister, 2006). Other species described as *Glaziella* have since been determined to belong to an unrelated lineage (Thaxter, 1922). Prior to electron microscopy and phylogenetic studies, *G. aurantiaca* was variously placed among the Endogonaceae (Mucoromycota) and other lineages of the Ascomycota. There has been limited molecular sampling of collections of *G. aurantiaca*, which appears to be restricted to the new world. Other species have been assigned to the genus from Asia but these are molecularly unverified. Transmission electron microscopy revealed single-spored asci that deliquesce with maturity (Gibson *et al.*, 1986), and molecular methods placed it in the Pezizomycetes (Landvik and Eriksson, 1994). The trophic status is not known; there is no convincing evidence that it forms ectomycorrhizae. The single-spored globose asci are scattered in the rind-like flesh of the ascomata. Conidial states are unknown in this genus. Genus included: *Glaziella*
- (8) Helvellaceae Ascomata are hypogeous or epigeous, they are ectomycorrhizal. Epigeous members are cupulate, ear-shaped, saddle-shape or sparassoid with or without a stipe. They are generally without carotenoid pigments. The asci are thin walled and the ascospores are smooth or irregularly ornamented. Generally there is a single large guttule and there are four nuclei per spore. *Balsamia* and *Barssia*, hypogeous genera, produce stereothecia or ptychothecia. Genera included: *Balsamia, Barssia, Helvella, Midotis, Pindara, Underwoodia*.
- (9) Karstenellaceae The only species in the genus, *Karstenella vernalis*, produces thin apothecia on a resupinate mycelial mat that grows directly on soil (Hansen *et al.*, 2008) or woodland litter (Harmaja, 1969). It is presumed to be saprobic (Ekanayaka *et al.*, 2018) but the ecology of this species is not well-known. Ascospores are bi- or multiguttulate. The species has been collected in widely disjunct geographical regions of Finland and New Mexico, USA (Hansen *et al.*, 2008). There have been no reports of sclerotia or conidial states in this species. Genus included: *Karstenella*.
- (10) Morchellaceae The morels are choice edible fungi and the family also has hypogeous members. The family includes the genus *Morchella* that is characterized by large stalked ascomata that have a convoluted and ridged fertile region. *Verpa* is

similarly constructed but with a continuous hymenial layer whereas *Disciotis* is cupulate, sessile and folded or convoluted. *Morchella, Disciotis* and *Verpa* are epigeous but there are several hypogeous genera in the family. These produce exothecial, ptychothecial or stereothecial ascomata. One, hypogeous species, *Fischerula subcaulis*, has a residual to well-formed stalk In the past some studies suggested that the species in this group are ectomycorrhizal but at least some species of *Morchella* grow without any ectomycorrhizal host plants nearby and they can be grown in culture. Tedersoo and Smith (2013) suggested that *Fischerula, Imaia, Kalapuya* and *Leucangium* are ectomycorrhizal based on morphological studies of ECM roots and based on the isotopic signatures of fruiting bodies but more evidence is needed to test this hypothesis. Sclerotia are formed by at least some *Morchella* species (Ower, 1982; Volk and Leonard, 1989). *Morchella* species have anamorphic states that were previously placed in the form genus *Costantinella*, and *Disciotis* has a similar anamorph (Carris *et al.*, 2015). An anamorph was also reported for *Fischerula* (Healy *et al.*, 2013).

Genera included: Disciotis, Fischerula, Imaia, Kalapuya, Leucangium, Morchella, Verpa.

(11) Otideaceae – The family was formerly used by some authors in a broad sense to include many of the Pyronemataceae. In the restricted sense, this family includes the ectomycorrhizal genus *Otidea* and a few others. At least one hypogeous *Otidea* species is known. Ascomata are apothecial in most species, ptychothecial in *O. subterranea*, or cleistothecial in *Warcupia*. In *Monascella* the asci are produced on hyphae in small clusters. The genus *Acervus* is apothecial but in early development the ascomata are closed. Species of *Otidea* form ectomycorrhizal associations whereas the other species are presumed saprotrophic. There are no sclerotia or anamorphs reported for this family.

Genera included: Acervus, Arpinia (?), Ascosparassis, Monascella, Otidea, Warcupia, and Wenyingia.

(12)Pezizaceae - Members are ectomycorrhizal or saprobic. Some species occur after fire. They range in size from small to large and generally are fragile due to the large cells that often compose the excipulum. Hypogeous species may be ptychothecial, stereothecial, or exothecial. Most members of the family have iodine positive asci (amyloid) but this character is lost in most of the hypogeous taxa and absent in some of the early derived lineages. This family and the Ascobolaceae are the only families with the iodine positive reaction of the asci. The extent, location and strength of the iodine reaction is diagnostic at the clade level. In some species there is a strong wall reaction with or without an apical ring. In other species the reaction is diffuse and often appears to be in the gel surrounding the asci. These differences in reactions in iodine have been discussed by VanVooren (2020), who also established or reinstated several genera to recognize groups within the heterogeneous genus Peziza. There are several species-rich hypogeous lineages that are derived within ectomycorrhizal clades (with exceptions noted in previous sections). The desert truffles belong to this family (Kovács and Trappe, 2014). Among the desert truffles, Terfezia and Tirmania, are economically important, and in some cases, medically important in the Middle East (Hamza et al., 2016; Shavit, 2014; Shavit and Shavit, 2014). Sclerotia are produced by species of Cheilymenia (Smith et al., 2015) and Mattirolomyces (Kovács et al., 2007). Anamorphic states described in this lineage were historically placed under the names Chromelosporium, Glischroderma, Oedocephalum, Ostracoderma, and Rhinotrichum (Hennebert, 1973; Norman and Egger, 1999; Paden, 1972), and a different anamorphic state was reported for Hydnobolites (Healy et al., 2013). Some of the ectomycorrhizal taxa are only known from their anamorphic states.

Genera included: Adelphella, Ahmadea, Amylascus. Antrelloides, Aquapeziza, Babosia, Boudiera, Calongea, Carbomyces, Cazia, Chromelosporiopsis, Cleistoiodophanus, Daleomyces, Delastria, Elaiopezia, Elderia, Eremiomyces, Geoscypha, Hansenopezia, Hapsidomyces, Hydnobolites, Hydnoplicata, Hydnotryopsis, Iodophanus, Iodowynnea, Ionopezia, Kalaharituber, Legaliana, Lepidotia, Luteoamylascus, Malvipezia, Marcelleina, Mattirolomyces, Mycoclelandia, Pachyella, Pachyphlodes, Paragalactinia, Peziza, Phaeopezia, Phylloscypha, Planamyces, Plicaria, Plicariella, Purpureodiscus, Rhodopeziza, Ruhlandiella, Sarcopeziza, Sarcosphaera, Sphaerosoma, Sphaerozone, Stouffera, Temperantia, Terfezia, Tirmania, Ulurua.

(13) Pseudombrophilaceae – Included here are several taxa that are saprobic on dung or decaying plant material. Several of the included taxa, such as *Heydenia* species, *Lasiobolidium orbicularis* and *Orbicula* species, produce cleistothecioid ascomata whereas *Pseudombrophila* species produce apothecia. Sclerotia are formed by some species of *Pseudombrophila* (Pfister, 1984). Anamorphs are not known in this family.

Genera included: Heydenia, Orbicula, Pseudombrophila, Lasiobolidium sensu lato

(14) Pulvinulaceae – These fungi produce small, pulvinate apothecia on soil. Many are orange or yellow due to carotenoid pigments. Some species in this group produce paraphyses that are clavate to circinate, which is an important diagnostic feature. Species of *Pulvinula* are ectomycorrhizal whereas taxa in the other genera are saprobic. Anamorphs and sclerotia are not known in this family.

Genera included: Lazuardia, Pseudoboubovia, Pulvinula

(15) Pyronemataceae – Despite a good deal of recent phylogenetic work this family remains difficult to characterize. Some species are saprobic on plant material and dung, others are ectomycorrhizal, and some are endophytic or endolichenic. Several species fruit prolifically in response to fire. Species of several genera are parasitic on bryophytes. Pigmentation ranges from those that are brightly colored with carotenoids to drably colored species lacking these pigments. Although some ascomata are smooth, many members have hairs at the base or hairs or setae that emanate from the excipulum. The family also has some hypogeous and perithecioid species. Sclerotia are produced by some species of *Cheilymenia* (Smith *et al.* 2015) and *Pyronema* (Moore, 1962). Anamorphs have been reported for some lineages, under the form genera names *Actinospora, Ascorhizoctonia* (recently separated from *Tricharina* as a holomorphic genus by Van Vooren *et al.* (2017)), *Complexipes, Dichobotrys* and *Micronematobotrys* (Egger, 1984; Hennebert, 1973; Sun and Guo, 2010; Yang and Korf, 1985). An anamorph was recently described for *Octospora* (Sochorová *et al.*, 2019). One form genus, *Sphaerosporium*, has no known teleomorph (Song *et al.*, 2019).

Genera included: Aleuria, Aleurina, Anthracobia, Ascorhizoctonia, Aurantiolachnea, Barlaea, Boudierella, Byssonectria, Chaetotheirsia, Chalazion, Cheilymenia, Cleistothelebolus, Cupulina, Eoaleurina, Filicupula, Galeoscypha, Genabea, Genea, Geopora, Gilkeya, Hiemsia, Hoffmannoscypha, Humaria, Hypotarzetta, Jafnea, Lamprospora, Lasiobolidium sensu stricto, Lasiocupulina, Lathraeodiscus, Leucoscypha, Lotinia, Luciotrichus (?), Melastiza, Miladina, Moravecia, Mycogalopsis, Myrmecocystis, Neottiella, Octospora, Octosporella, Octosporopsis, Oviascoma, Parascutellinia, Paratricharina, Paratrichophaea, Parawilcoxina, Perilachnea, Petchiomyces, Picoa, Pseudaleuria, Pseudo-tricharina, Pyronema, Pyropyxis, Ramsbottomia, Rhizoblepharia, Rhodoscypha, Rhodotarzetta, Scutellinia, Sepultaria, Spaerosporium, Sphaerosporella, Spooneromyces, Terracavicola, Tricharina, Tricharinopsis, Trichophaea, Trichophaeopsis, Wilcoxina

- (16) Rhizinaceae Three genera are placed in this family. Species of *Rhizina* and *Psilopezia* are known only as teleomorphs; they occur on wood and woody roots. *Rhizina*, which occurs on burned areas, has been implicated as causing a root rot. *Psilopezia* species grow on wet, water-soaked wood. Spores are large and in *Rhizina* ascospores are smooth and have a pronounced apiculus. Ascomata in these two genera expand through indeterminate marginal growth. The third genus in this family, *Phymatotrichopsis omnivora*, is a serious pathogen of cotton and other dicots (Marek *et al.*, 2009; Uppalapati *et al.*, 2010). Sclerotia are formed by *P. omnivorum*, and this taxon is only known from its anamorphic state (Marek *et al.* 2009). Genera included: *Phymatotrichopsis, Psilopezia, Rhizina*
- (17) Sarcoscyphaceae These include some of the most charismatic members of the class with their sometimes large apothecia that can be bright red to pink and are sometimes fringed with hairs. Some have a prominent stalk. Asci are thick-walled and the operculum is generally eccentrically placed. The bright colors originate in the paraphyses of the hymenia and the spores tend to be laterally asymmetrical. Spores may be smooth or in some species ornamented with ridges and folds. The ornamentation is cyanophobic (they do not take up cotton blue stain). Some species are found in temperate regions but many others are tropical or subtropical. They are assumed to be saprobes or weak plant parasites. The form genus *Molliardiomyces* has been applied to conidial states in species of *Nanoscypha*, *Pithya*, *Phillipsia* and *Sarcoscypha* (Paden, 1984; Pfister, 1973), and an anamorph has also been described for *Cookeina* species (Boedijn, 1929, 1932).

Genera included: Cookeina (including Boedijnopeziza), Kompsoscypha, Microstoma, Nanoscypha, Phillipsia (including Aurophora), Pithya, Pseudopithyella, Rickiella, Sarcoscypha, Thindia

(18) Sarcosomataceae – These fungi are black or darkly pigmented. Like the Sarcoscyphaceae the ascus walls tend to be thick and the operculum is eccentrically placed. The outer layers of the excipulum tend to be encrusted with dark pigments. Spores are thick-walled with or without folds and ornamentation. Often hymenial hairs or setae are present. Species are considered to be saprobic or weakly parasitic on plants. Anamorph states include *Conoplea* and possibly *Strumella* for *Urnula* and *Plectania* (Paden, 1972). At least one species of *Sarcosoma* also produces an anamorph (Paden, 1972).

Genera included: Donadinia, Galiella, Korfiella, Plectania, Pseudoplectania, Sarcosoma, Selenaspora, Urnula.

(19) Strobiloscyphaceae – A single genus, *Strobiloscypha*, with two species makes up the family. The species are small, have brown apothecia with olive-toned hymenia, and are presumed to be saprobic, occurring on the dead branches and cones of Cupressaceae (Perić *et al.*, 2013). Even with molecular data, the relationship between Strobiloscyphaceae and other Pezi-zomycetes is unsettled. Previous placement was speculative, and there is no strong support for its relationships in the most recent treatment (Ekanayaka *et al.*, 2018). A *Verticicladium*-like conidial state was described for one species in this family (Perić *et al.*, 2013).

Genus included: Strobiloscypha

- (20) Tarzettaceae This family contains both epigeous and hypogeous members. Kumar et al. (2017) treated the hypogeous members. Wang et al. (2016) treated the genus Geopyxis. Tarzetta is ectomycorrhizal but the nutritional strategies of the other genera are non-mycorrhizal and not well understood. At least some species of Geopyxis can act as root biotrophs but there is no strong evidence for ectomycorrhizal formation (Vrålstad et al., 1998). Anamorphs are known for three of the five genera and are similar within the family. The form genera Dicyma, Hansfordia and Nodulisporium have been misapplied to some of these conidial states (Conway, 1975; Egger, 1984; Hennebert, 1973; Paden, 1972; Vrålstad et al., 1998). Genera included: Densocarpa, Geopyxis, Paurocotylis, Tarzetta
- (21) Tuberaceae Most species are hypogeous with the exception of two in the Southern Hemisphere genus Nothojafnea, which form apothecial ascomata. All other known taxa form ptychothecial or stereothecial ascomata. All known species are ectomycorrhizal and most are considered early successional. The highly prized "true truffles" in the genus *Tuber* belong to this family. Sclerotia are not reported in this family. Conidial states that are similar in morphology have been described for some species in the/maculatum and/puberulum lineages of *Tuber* (Grupe et al., 2018; Healy et al., 2013; Urban et al., 2004). Genera included: *Choiromyces, Dingleya, Labyrinthomyces, Loculotuber, Nothojafnea, Reddellomyces, Tuber*
- (22) Wynneaceae Recently separated from the Sarcoscyphaceae based on molecular and ecological data (Pfister *et al.*, 2020). The elaborate fruitbodies of *Wynnea* species arise from a mass of tissues that include hyphae and rhizomorphs of *Armillaria* species. It is suggested that *Wynnea* species may parasitize fungi from the genus *Armillaria* and produce large sclerotia-like bodies built-up of hyphae from both *Amillaria* and *Wynnea* (Xu *et al.*, 2019). The biotrophic status of *Geodina* is unknown but the unusual report of this as occurring on soil suggests that, like *Wynnea* species, it may be associated with another fungus. Anamorphs are not known in this family.

Genera included: Wynnea, Geodina.

Genera of uncertain position include: Aparaphysaria, Ascocalathium, Microeurotium.

### Acknowledgments

We are grateful to Matthew E. Smith for his insightful reading, comments and improvements to the manuscript. Images of ascomata were provided by Matthew Smith (*Geomorium*), Mark Elliot (*Wynnea*), Roy Kristiansen (*Desmazierella*), Arthur Grupe (*Caloscypha*) and Alan Franck (*Glaziella*). Many individuals have contributed through world-wide collecting efforts.

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