
2 Pezizomycotina: Pezizomycetes, Orbiliomycetes

DONALD H. PFISTER¹

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I. Introduction

Members of two classes, Orbiliomycetes and Pezizomycetes, of Pezizomycotina are consistently shown in molecular phylogenetic studies to diverge at the base of the Pezizomycotina phylogeny (Gernandt et al. 2001; Hansen and Pfister 2006; Spatafora et al. 2006). Kumar et al. (2012) give ultrastructural data on the septal structure, ascus wall construction, and nuclear division that suggest the Orbiliomycetes represent the earliest diverging lineage of the Pezizomycotina. The relationship of these two classes and the family diversity within the Pezizomycetes are shown in Fig. 2.1. These two groups show very few shared characteristics other than the formation, for the most part, of well-developed apothecial ascomata in which asci are generally arranged in a hymenium with paraphyses. Orbiliomycetes was recognized as a class only recently (Baral 2003). There is a single order, Orbiliales, and a single family, Orbiliaceae, with perhaps 300 species currently arranged in three teleomorphic

¹Farlow Herbarium and Library of Cryptogamic Botany, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, 02138, USA; e-mail: dpfister@oeb.harvard.edu

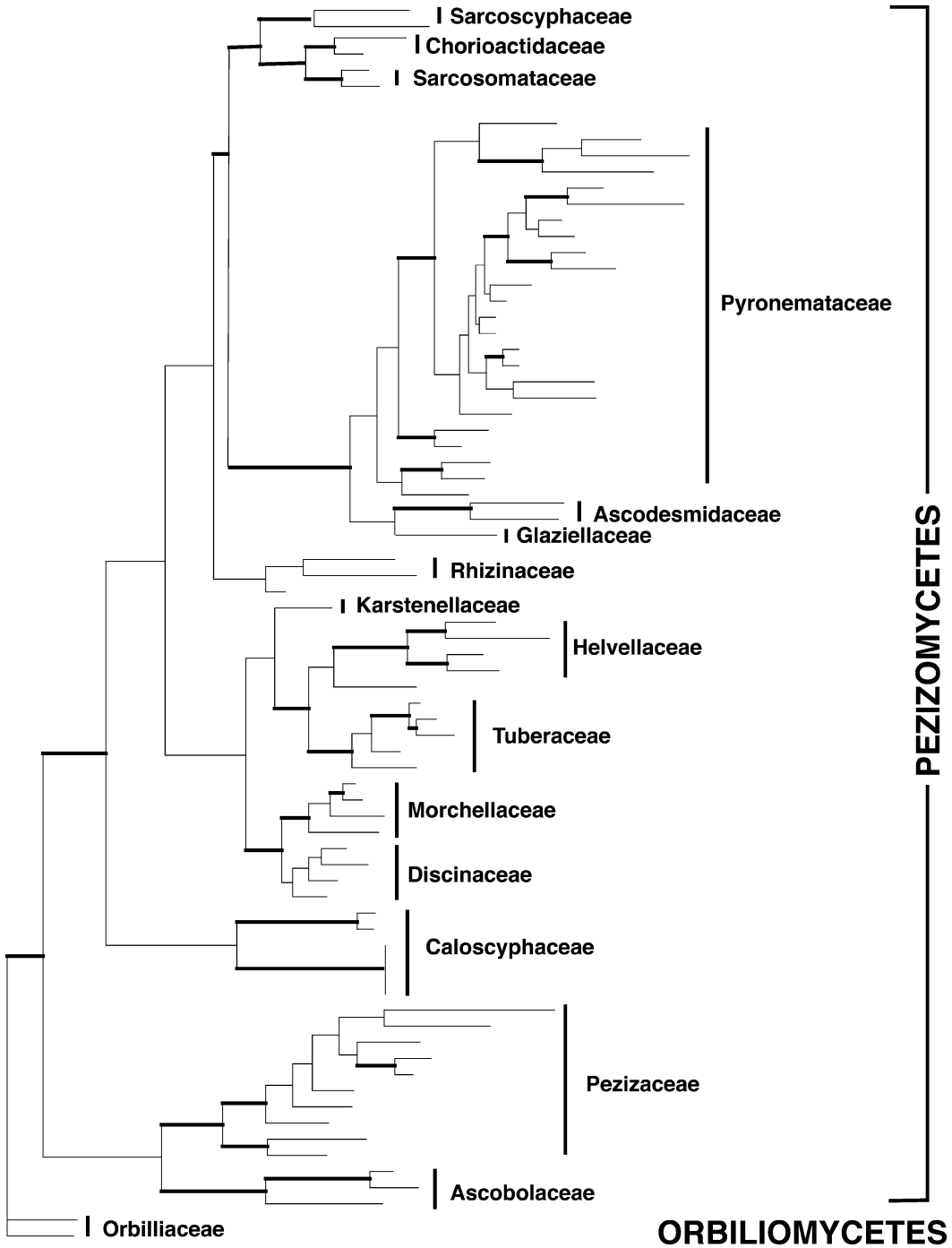


Fig. 2.1 A diagrammatic representation of the relationships of the Pezizomycetes and Orbiliomycetes, including the families of the Pezizomycetes, based on Hansen et al. (2013) and Pfister et al. (2013). Branches that

received maximum parsimony, posterior probability, and maximum-likelihood support $\geq 75\%$, 95% , and 75% , respectively, are in *bold*

genera. An early diverging position of the class has been confirmed by morphological studies and molecular phylogenetic analyses (Kumar et al. 2012; Spatafora 2006; Wang et al. 2006). Previously, the Orbiliaceae was placed among the Helotiales as a family based on Nannfeldt's (1932) classic work on the nonlichenized inoperculate discomycetes. The Pezizomycetes have long been recognized to include a single order, the Pezizales, and include 16 families and approximately 1,200 species. The group, in whole or in part, has been the subject of recent surveys (Hansen and Pfister 2006; Harrington et al. 1999; Perry et al. 2007; Pfister et al. 2008).

In regard to morphological characteristics and ecology, the two classes also are distinct. The Orbiliomycetes are saprobic and in some cases supplement their nutrition through the capture and consumption of small invertebrates. Their spores are small, nonseptate (save for a single example), uninucleate, and contain a membrane-bound structure, the spore body (Baral 1994; Benny et al. 1978; Kumar et al. 2012). Spores are discharged actively. Asci are small and generally lack a well-developed apical apparatus. Anamorphic states are frequently formed, and their number has increased steadily in the literature in recent years. Species are found on dung, on wet wood on the forest floor, in water-soaked areas where they are somewhat ephemeral, or on dead wood hanging in trees where, because of their drought resistance, they are persistent (Baral 2011). No species are plant parasitic.

The Pezizomycetes are saprobic, plant parasitic, or associated with plants as ectotrophic mycorrhizae (Hansen and Pfister 2006; Teder-soo et al. 2006; Wei et al. 2010). The ascomata are always to some degree ephemeral. Spores are large, generally more than 10 μm and may reach a length of 60 μm , and single-celled. Spores generally are actively discharged through a well-developed opening created by the rupture of the ascus wall forming an operculum that is either terminal or eccentric in position. The truffle-like habit has developed independently in several lineages across the class (Læssøe and Hansen 2007). These hypogeous taxa generally do not have active spore release.

In this chapter, the two classes are treated independently in separate sections.

II. Orbiliomycetes: An Overview

The family Orbiliaceae was proposed by Nannfeldt (1932) and was restricted to those fungi with small so-called inoperculate asci, minute ascospores, and a waxy texture. The asci and paraphyses are often agglutinated. Nannfeldt illustrated several species showing details of the thin-walled globose to angular cells of the excipulum. A monograph on the genus *Orbilia* by Svrcek (1954) included 16 species that were distinguished based on ascospore size and shape, the color of the ascomata, and the form of the paraphyses. The groundbreaking work of Hans-Otto Baral and his collaborator, Guy Marson, has led to a refinement of the family and recognition of many more species. Kirk et al. (2008) proposed 288 species, but the extent of the diversity to be described is in flux. A monograph has been in preparation by Baral for many years. Modern methods employ morphological and histochemical characters previously not used and incorporate ecological characters as well. Of particular note is the reliance on fresh, living material (Baral 1992). There has been a burst of activity focusing on the description of teleomorphic taxa and associated anamorphs (e.g., Kohlmeyer et al. 1998; Liu et al. 2005a, b, 2006; Mo et al. 2005; Pfister 1994; Pfister and Lifting 1995; Qiao et al. 2011; Qin et al. 2010; Su et al. 2011; Tanabe et al. 1999; Webster et al. 1998; Wu et al. 2007; Yang and Liu 2005; Yu et al. 2007a, b, c, 2011; Zhang et al. 2007), and in this work there has been an intense interest in the diversity and functional morphology of the anamorphic states. This is particularly the case regarding those that capture nematodes, i.e., species referred to *Arthrotrix* and allied form genera.

III. Occurrence and Distribution

Members of the Orbiliomycetes are found around the world in boreal to tropical habitats. Furthermore, several species complexes, such

as *O. luteorubella* and *O. xanthostigma*, that represent morphologically very similar collections seem to be found broadly distributed around the world and across latitudes. There are two major ecological groups—those that occur in moist habitats such as on dung, old polypores, and moist wood on the forest floor or near streams and species that are drought tolerant. These drought-tolerant species are found on dead twigs and small woody branches in the canopy of living trees. Often species of both ecological types are found in association with unicellular green algae, but there is no evidence that the fungi are lichenized.

A. Species Trapping Nematodes and Other Invertebrates

Since the classic work of Drechsler (1937a) on the nematode-trapping hyphomycetes, these fungi have attracted many researchers to this fascinating system. The work of Barron (1977, 1981) further set the stage for ecological and descriptive work on these fungi. Pfister (1994, 1997) and Pfister and Liftik (1995) documented the life history connection between these nematode-trapping hyphomycetes and teleomorphic members of the Orbiliomycetes. The several anamorphic form genera involved are discussed in what follows.

Trapping of nematodes and other invertebrates is accomplished by the formation of constricting rings, hyphal networks, or sticky knobs. These trapping structures are often, but not exclusively, initiated in the presence of prey. When nematodes become ensnared in the trap, the fungus then grows and penetrates the body of its prey and proliferates within it. Conidia are formed in the presence or absence of nematodes and are generally dispersed across the medium, that is, they are not concentrated around trapped nematodes (Barron 1977). Earlier classification schemes for these fungi relied primarily on conidial morphology, particularly spore shape and septation. Phylogenetic studies have indicated that the form of the trapping devices gives important information for classification (Hagedorn and Scholler 1999; Rubner 1996; Scholler et al. 1999). In

addition to trapping nematodes, some hyphomycetes in the orbiliaceous lineage trap other small invertebrates such as collembolans and rhizopods (e.g., Barron 1981; Drechsler 1936, 1937b). Even though these fungi may occur on wood or cellulose-rich substrates, there is evidence that few of the nematode-trapping fungi are able to break down cellulose (Park et al. 2002).

B. Saprobic Species

Until the work of Baral (2011) and Marson, most studies of diversity within the Orbiliomycetes were focused on those species on moist substrates. The discovery that these fungi are highly diverse in the dry habitats of hanging branches in living trees has greatly expanded the number of species that have been described through intense collecting in such habitats. Although these species are treated here as saprobic, there is little clear evidence of their mode of nutrition. Drechsler (1938) discussed at length hyphomycetes that are parasitic on oospores of Oomycota; these also seem now to be clearly referable to the Orbiliaceae. These fungi were “considered from a morphological viewpoint... [to] fit acceptably in the predacious series” (Drechsler 1938). Whether they fall in the main clade of nematode trapping Orbiliaceae or outside it remains to be studied, but that a variety of life styles and biotic modes are found within the family is unquestionable. It is important to note as well that no plant parasitic species have been discovered so far in this lineage.

IV. Morphological Features

A. Ascomata

Apothecial ascomata range in size from 0.5 to 5 mm and are saucer-shaped to pulvinate. Macroscopically they have been described as appearing waxy at sight or to touch. This is a reference at least in part to their shiny, translucent appearance. The sterile tissues of the ascomata are composed of an outer layer, or

ectal excipulum, of globose or angular cells that in some species give rise to superficial hairs. These cells may contain one or more cytoplasmic bodies that may take on several different shapes but disappear when material is mounted in KOH. Cells in the outer excipulum may be encrusted with granules or produce glassy projections or the cells may be embedded in an amorphous matrix. The inner layers of the ascomata are of interwoven hyphae or compressed angular cells (Nannfeldt 1932).

B. Asci

The asci of members of this class are small cylindrical to broad cylindrical with or without croziers; in some cases they have elongate, forked bases. Asci contain eight to many ascospores per ascus. Asci are inamyloid. The apex ranges from hemispherical conical to truncate. Walls are thin, composed of two layers in transmission electron microscopy (Benny et al. 1978; Kumar et al. 2012). The apex is generally little developed. Benny et al. (1978) reported no pores; Kumar et al. (2012) found an electron-light zone at the apex. In some taxa, an opening develops on the shoulder of the truncate asci (Zhang et al. 2007), and this was confirmed by Kumar et al. (2012). In some species, the apical walls may be thickened to form a cap (Kohlmeyer et al. 1998), as in *Orbilia* subgenus *Hemiorbilia*, in which the apex of the ascus is thickened (Baral 2011). In all cases, asci appear to dehisce by irregular tearing. Kumar et al. (2012) found similarities between the asci of the *Orbilia* species they studied and members of the Taphrinomycotina. Asci and paraphyses may be embedded in a gelatinous matrix that causes them to stick together and not fan out when crushed for microscopic observation. This is particularly the case in members of the genus *Hyalorbilia*.

C. Ascospores

The initial striking feature of the ascospores is their small size. They range in size from 3 to 8 μm . Observation of them is difficult in some situations and requires oil immersion and

enhanced magnification. Spores are globose, ellipsoidal, ovoid, reniform, acicular, or filiform and mostly smooth, although spore wall ornamentations are known, for example, in *O. xanthostigma*. Ascospores of the Orbiliomycetes contain an inclusion, the spore body. This membrane-bound body was suggested to derive from the plasma membrane by Baral (2003), but Kumar et al. (2012) and Benny et al. (1978) showed that the spore body is derived from mitochondria. The spore body is attached to the cell membrane and is surrounded by a rough endoplasmic reticulum (Benny et al. 1978). The contents are electron dense (Benny et al. 1978). Under a light microscope it is seen in unstained living spores as a refractive body. Its appearance can be enhanced by application of aqueous brilliant cresyl blue or other vital stains. It disappears in dead spores and can be destroyed by application of KOH. The spore body is a synapomorphy for the class and can take on many different forms, from globose to tear-shaped to elongate. Its shape and orientation is consistent within the ascospores of a particular species. The shape and position of the spore body is considered a critical taxonomic character. Generally spores have a single spore body, but an example of a spore with two spore bodies is known (Wu et al. 2007). As mentioned previously, its contents are electron dense; it does not appear to be composed of lipids but may be proteinaceous (Kumar et al. 2012). No function has been attributed to the spore body, but Benny et al. (1978) offered three possible functions: for flotation and balance in a liquid environment before and during germination, storage of waste products, and storage of materials for use during germination. None of these functions has been documented, and ultimately the function of the spore body may have to do with special metabolic activities within the spore.

D. Paraphyses

Paraphyses are sparingly septate, broad, sometimes with a prominent capitate terminal cell. They may be encrusted or contain refractive materials. In some species, the paraphyses and

asci are closely adherent and are difficult to separate.

E. Septal Structures

Ascus, ascogenous, and nonascogenous hyphae have simple septa, with septal pores plugged by unelaborated electron-dense, nonmembranous occlusions. Globose Woronin bodies were located on both sides of the septum (Kumar et al. 2012).

F. Nuclear Division

Division is characterized by the retention of an intact nuclear envelope and a two-layered disk-shaped spindle pole body (Kumar et al. 2012).

G. Anamorphic States

Many members of the Orbiliomycetes have been shown to produce mitospores in culture; they are hyphomycetous or synnematosus. All conidia are formed by holoblastic wall extension. A variety of named form genera have been applied to these conidial states. Anamorphs can provide some useful information on the biology and ecology of these fungi. Those that have been demonstrated to trap nematodes and other invertebrates fall into the following genera: *Arthrotrix* (Li et al. 2005; Mo et al. 2005; Pfister 1994, 1997; Pfister and Liftik 1995; Qiao et al. 2011), *Drechlerella* (Li et al. 2005), *Dwayaangam* (Barron 1991), *Gamsylella*, known only in its anamorphic state (Scholler et al. 1999), *Lecophagus* (Tanabe et al. 1999), and *Monacrosporium* (Li et al. 2005; Pfister 1997). There remains debate about the application of some of these names. For general overviews the interested reader may consult Hagedorn and Scholler (1999), Liou and Tzean (1997), and Scholler et al. (1999). Through a multigene analysis Yang et al. (2007) postulated that two lineages evolved trapping mechanisms, with one lineage giving rise to constricting rings

and the other adhesive traps, but, importantly, these fungi form a single clade. Yang et al. (2007) proposed a scheme for the evolution of trapping structures.

Other form genera are those that produce staurosporous or helicosporous conidia or are associated with aquatic habitats. These include *Angulospora* (Pfister 1997; Webster 1992; Webster and Descals 1979), *Dicranidion* (reports summarized by Pfister 1997), *Dwayaangam* (Kohlmeyer et al. 1998), *Helicoon* (Pfister 1997), *Trinacrium* (Matsushima 1995), and *Tridentaria*. Others are found on a variety of plant materials in terrestrial habitats, and these include *Brachyphoris* (Chen et al. 2007a, c), *Dactylellina* (Li et al. 2005; Qin et al. 2010), *Dactylella* (Chen et al. 2007a, b, c; Pfister 1997; Qin et al. 2010), and *Pseudotriporiconidium* (Yu et al. 2011).

Staurosporous conidia and those reported from other aquatic anamorphs are detected in stem flow, through-fall, and treeholes (Gönczöl and Révay 2003, 2004, 2006; Révay and Gönczöl 2011). Among these are conidia referred to form genera of anamorphs associated with species of Orbiliomycetes. These include species of *Angulospora*, *Dactylaria*, *Dicranidion*, *Dwayaangam*, *Trinacrium*, and *Tridentaria*. Of these Gönczöl and Révay (2004) found that *Trinacrium* in particular was prevalent and that *Dwayaangam* and *Trinacrium* species were particularly diverse and geographically widespread (Gönczöl and Révay 2006). Such observations suggest that canopies are important habitats for these fungi. We expect that these are likely *Orbilium* anamorphs that are associated with the drought-tolerant, canopy-inhabiting Orbiliomycetes, which are fungi on dead branches in many woody plants. Gönczöl and Révay (2006) say, regarding their findings of aquatic hyphomycetes in these terrestrial habitats, that “this reinforces our belief that an ecological group of hyphomycetes distinct from those in lotic habitats exists and functions in canopies.” By extension, we might assume that branches and twigs inhabited by Orbiliomycetes are a major part of this canopy ecosystem.

V. Reproduction

Although many of the Orbiliomycetes have been grown in culture, few reports have been published on apothecial production in the lab. Spontaneous production of ascomata has been noted (Drechsler 1937a; Rubner 1994). Zachariah (1983) was able to induce ascomatal primorida. Breeding systems have not been studied in part because of the unpredictability of producing ascomata in culture.

VI. History of Classification and Current Hypotheses

The family Orbiliaceae was created in 1932 in Nannfeldt's (1932) classic treatment of the inoperculate discomycetes. Recognizing the special features of this group, he removed the genera *Orbilina* and *Hyalina* from the core group of inoperculate discomycetes. Primary treatments of the family were those by Svrcek (1954) and Spooner (1987). Nannfeldt's circumscription of the family was used with few changes until the 1990s. The placement of the family outside the Leotiomycetes lineage initially began to be questioned by Pfister (1997), and subsequent work has confirmed the placement as an early diverging lineage within the Pezizomycotina (Gernandt et al. 2001; Spatafora et al. 2006). The position of the Orbiliomycetes as an early diverging lineage in the filamentous Ascomycota along with the Pezizomycetes was one of the major surprises in the era of molecular phylogenetic studies.

Within the Orbiliomycetes there is a single order, and only three teleomorphic genera are recognized. Other genera may well be proposed as more of these fungi come to be known through wider collection of them and collections come under deeper scrutiny. The described genera are *Orbilina*, the largest and most diverse genus with two subgenera and nine sections in Baral's treatment (2011), *Hyalorbilia* with six to eight species (Baral and Marson 2000), and *Pseudorbilia*, with a single species (Zhang et al. 2007). These genera are distinguished based on characteristics of the

ascus, the ectal excipulum, spore bodies, the presence or absence of gelatinous material in the hymenium, and pigmentation [see Zhang et al. (2007) for a summary of the genera].

VII. Growth in Culture

One of the most remarkable features of the Orbiliomycetes is the ease with which most of the species can be cultivated on standard media. Spores deposited on the surface of agar media germinate readily, with the exception of the species of *Hyalorbilia* for which there are only a few reports of successful cultivation. Spores germinate quickly, and growth is often luxuriant on substrates containing glucose. Sporulation is common under room conditions.

VIII. Pezizomycetes: An Overview

The Pezizomycetes comprise a single order, Pezizales, with 16 families currently recognized. The full diversity of the order has not yet been completely recognized in the classification, and no doubt other lineages will of necessity be named. Ascomata are both epigeous and hypogeous. The epigeous types are apothecial, cleistothecial, or highly reduced, being composed of only a few asci in clusters on vegetative hyphae with little or no excipular tissue. In epigeous lineages, spores are generally forcibly discharged with the asci rupturing by the formation of an operculum. Hypogeous members occur in most families containing mycorrhizal members. To date, more than 15 independent origins of trufflelike members are known within a majority of the families (Læssøe and Hansen 2007).

IX. Occurrence and Distribution

Pezizomycetes can be found around the world, but representatives are unevenly distributed. Members of certain families, such as the Pezizaceae, Morchellaceae, Helvellaceae,

Rhizinaceae, and many of the Pyronemataceae, show a particularly high diversity in temperate regions. Others are more abundant in tropical areas, as exemplified by the Sarcosomataceae and Sarcoscyphaceae. Recent studies have made clear that, although collecting in this group is robust in many areas of the Northern Hemisphere, the Southern Hemisphere is poorly documented. Nutritionally, Pezizomycetes are saprobic or mutualistic (Tedersoo et al. 2006) or are parasitic on bryophytes and vascular plants (Hansen and Pfister 2006). Many of the species collected on soil occur in disturbed areas or in soil that has a high pH and low content of organic matter. Petersen (1985) provides a review of the edaphic factors involved in growth and reproduction.

A. Parasitic Species

The plant parasitic species are scattered in various lineages. *Rhizina undulata* is a serious root parasite of conifers (Ginns 1968). *Pithya* species may cause dieback on conifers. *Caloscypha fulgens* is implicated as a seed pathogen of conifers (Paden et al. 1978; Salt 1974). *Urnula craterium* has been implicated as the causal agent of strumella canker in oak (Davidson 1950). *Phymatothrichopsis ominivora* is a root pathogen of cotton and other dicotyledonous plants and is known only in its anamorphic state (Uppalapati et al. 2010). A clade in the Pyronemataceae, including *Octospora* and *Lamprospora*, is parasitic on bryophytes (Hansen and Pfister 2006). Apothecia occur on the thalli or surrounding soil if they are rhizoidal parasites (Döbbler 1979).

B. Mycorrhizal Species

With the advent of molecular approaches to studying mycorrhizal root tips a number of examples of mycorrhizal Pezizomycetes have been documented, and it is now known that mycorrhizal lineages are found throughout the class (Tedersoo et al. 2006). Morphologically, the mycorrhizae have a mantle that is often thin, have a well-developed Hartig net, and

generally do not form rhizomorphs (Tedersoo et al. 2006; Wei et al. 2010). Mycorrhizal species seem to predominate in areas that experience xeric conditions (Smith et al. 2006). Mycorrhizal lineages are often also those that contain truffle or truffle-like taxa. There are no truffle-like species in the families Sarcoscyphaceae and Sarcosomataceae, and likewise there are no known mycorrhizal species.

C. Saprobic Species

Pezizomycetes occur on organic material of various types—decaying wood, dung, leaf litter, and twigs. The diversity of Pezizales on dung is well documented, with many studies and keys available (Bell 1983; Doveri 2004; Richardson and Watling 1997). Some clades are nearly exclusively found on dung, most notably species of Ascobolaceae (Brummelen 1967). Dung-inhabiting species are found in several clades of the Pyronemataceae and Pezizaceae (Hansen and Pfister 2006; Hansen et al. 2001; Perry et al. 2007). In most cases, little is known of the biology of saprobic species. Sarcoscyphaceae, Sarcosomataceae, and Chorioactidaceae are found exclusively on wood, leaves, and plant debris.

X. Morphological Features

A. Ascomata

Apothecia are the basic type of ascomata. These range in size from several millimeters to several centimeters and 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 are little more than small fascicules of asci such as in *Ascodesmis*. Further reductions include highly reduced forms found in *Eleutherascus* and *Monascella* (Guarro and Arx 1986; Stchigel et al. 2001). Here the asci are formed in clusters on unspecialized hyphae. Ascomata are often highly pigmented, particularly the hymenium. Carotenoid pigments have been characterized (Arpin 1969).

Variations are found in typical apothecial ascomata. On the one hand, there are highly reduced types that are merely asci scattered on hyphae as mentioned previously, but small cleistothecial ascomata have also been found in a few cases (Hansen et al. 2005b). In the case of *Orbicula parietina*, active discharge is lost and spores are presented in a powdery mass. *Heydenia* species form stalked cleistothecial fruit bodies closely related to *O. parietina* (Lechtman and Cl  men  on 2011). The ascomata of *Heydenia*, which was recently placed in the Pyronemataceae (Lechtman and Cl  men  on 2011), deserve special comment. *H. alpina* is a small fungus that occurs on plant debris and mosses. It is stipitate with a dark stipe that at the top expands to hold a pale mass of hyaline spores and radiating hyphae. No asci are present, but molecular evidence confirms that this species belongs in the Pyronemataceae as a close neighbor of *Orbicula*, another fungus that produces dry powdery masses of spores at maturity. The two genera share a cleistothecial fruit body and asci that seem to disintegrate early in the development of the ascomata but diverge on important morphological features (Lechtman and Cl  men  on 2011). These genera, often placed outside of the Pezizales, have been demonstrated through molecular systematic studies to be members of the order.

Truffleoid fruit bodies are found in several lineages. Following the terminology of Weber et al. (1997), these are stereothechia, exothechia, or ptychothechia, depending on the arrangement of the asci and the presence or absence of well-developed hymenial layers. Truffle-type ascomata are derived from apothecial forms. L  ss  e and Hansen (2007) summarize much of the literature on these taxa.

Some highly reduced forms are found among bryophyte parasites. The fruit bodies are partly closed and have only a few asci. They give the appearance of perithecia.

B. Asci

Brummelen (1978, 1994) summarized the structural characters of the ascus in the Pezizomycetes. The apical apparatus, when present, is

in the form of an operculum, and its position, the reaction of the wall layers in various staining agents in light microscopy, and the ultrastructure of the ascus wall are all important characters. Amyloid asci are found in Pezizaceae and Ascobolaceae (Hansen et al. 2001), but this character has been lost several times, most notably in the hypogeous members of the Pezizaceae. Amyloid asci are not found outside these families.

The layering of the wall as seen in transmission electron microscopy helps delimit groups, particularly the taxa with thick lateral walls in the Sarcoscyphaceae and Sarcosomataceae. The asci of these fungi were termed suboperculate by Le Gal (1946a, b, 1953). Subsequently, Eclblad (1968) and Samuelson (1975) discounted the term.

Not all members of the class have opercula. Hypogeous (L  ss  e and Hansen 2007) and some cleistothecial taxa (Hansen et al. 2005a, b) have lost the operculum and spores remain either within asci until eaten and the fruit body is broken down, or the asci disintegrate and a powdery mass is formed.

C. Ascospores

No member of the Pezizomycetes has septate spores at maturity. Septa may form in germinating spores, but only when a germ tube has already been established. The spores may take on a variety of shapes from globose to naviculate, with smooth or ornamented surfaces. Generally, the ornamentations are derived from secondary wall material, although a few examples are known of spore ornamentation without a contribution of secondary walls. The spore walls are multilayered and may be thin or thick (Merkus 1976). The number of nuclei per spore varies from one, two, or four to many, and such variation has been shown to have some taxonomic value (Berthet 1964; Korf 1972, 1973).

D. Paraphyses

The pigmentation of the hymenium is attributed to the pigments found in the paraphyses.

Yellow, red, and orange carotenoid pigments are distinctive features of some of these fungi. These pigments are dissolved in oil droplets in the paraphyses. A variety of carotenoid pigments are known to occur in these fungi, as summarized by Arpin (1969). Paraphyses are generally septate and may be either uninucleate or multinucleate, this latter character being used in the classification (Berthet 1964; Pfister et al. 2008). In some cases, paraphyses are interspersed with hyaline or darkly pigmented, often thick-walled elements or setae. Examples of such setae are found in members of the Rhiziniaceae, Sarcosomataceae, Chorioactidaceae, and Sarcoscyphaceae.

E. Septal Structures

Ultrastructural characters of septal pore plugs and Woronin bodies correlate to some degree with families and lineages in the order. Kimbrough (1994) summarizes much of the information. Septal pores in vegetative hyphae generally have lamellae embedded in a matrix. These septa generally have associated Woronin bodies. The Woronin bodies take on several forms—globular, hexagonal, or cylindrical, sometimes 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. These septa are occluded by dome-shaped, pyramidal, or dumbbell-shaped structures. These plugging structures show electron-dense bands, lamellae, and raylike extensions.

F. Anamorphic States

Anamorphic states have been reported across many families. Conidia are blastic in development and are generally hyphomycetous. Table 2.1 provides a summary of the known anamorphs. In many of these anamorphs, the germination of conidia has not been observed, suggesting that they may rather act as spermatia. The investigations by Healy et al. (2013) identify anamorphic spore mats in several clades in the Pezizaceae and Tuberales.

Attempts to germinate mitospores from these mats have failed, and the function of these spores remains unknown. Several anamorphic states have been discovered through molecular phylogenetic studies to belong within the Pezizomycetes, but they have no known teleomorphs. Most notable among these is *Phymatotrichopsis omnivora*, the cotton root pathogen. This falls within the Rhiziniaceae based on molecular studies, but despite intensive study of this important pathogen, no evidence of a teleomorph has been discovered. Another example is *Cephalophora*, a dung-inhabiting fungus and one that has been implicated in causing keratitis (Hoog 2000).

XI. Reproduction

Extensive studies have been carried out on several members of the class. *Ascobolus* was early incorporated as a genetic tool. *Pyronema* has also been extensively studied. Early cytological studies on members of the Pyronemataceae were used to explore mitotic events in asci.

XII. History of Classification and Current Hypotheses

The current classification has its origins in the work of Boudier (1885, 1907), who was the first to use the presence of an operculum to define this group. Hypogeous, truffloid members previously treated in the order Tuberales have now been placed in the Pezizales based on morphology, cytology (Trappe 1975), and molecular sequence analyses (Læssøe and Hansen 2007). Wide-ranging phylogenetic work within the order led to the recognition of three primary lineages (Landvik et al. 1997). Subsequent work has expanded this framework and has suggested groupings of families that in part reflect those previously based on morphological, cytological, and pigment data and are noted in earlier work (Korf 1972, 1973; Rifai 1968). The most recent comprehensive overview of the class is that of Hansen and Pfister (2006). Currently, 15 families are recognized (Fig. 2.1),

Table 2.1 Summary of known anamorphs of Pezizomycetes

Family	Anamorphic form genus	Teleomorphic genus	References
Asכולolaceae	<i>Rhizostilbella</i>	<i>Asכולobolus</i>	Seifert (1985)
	<i>Papulospora</i>	<i>Asכולobolus</i>	Brummelen (1967)
	An oidial state	<i>Asכולobolus</i>	Brummelen (1967)
Caloscyphaceae	<i>Geniculodendron</i>	<i>Caloscypha</i>	Paden et al. (1978)
	<i>Kumanasamuhia geaster</i>	<i>Chorioactis geaster</i>	Nagao et al. (2009)
Chorioactidaceae	<i>Verticilladium</i>	<i>Desmazierella acicola</i>	Paden (1972)
	<i>Costantinella</i>	<i>Morchella</i>	Paden (1972)
	<i>Glichroderna</i>	Pezizaceae	Norman and Egger (1999), Hansen et al. (2001), Healy et al. (2013)
Pezizaceae	<i>Chromelosporium</i>	<i>Peziza</i> , <i>Plicaria</i> , <i>Mucitumbo</i>	Hennebert (1973), Paden (1972), Warcup and Talbot (1989), Healy et al. (2013)
	<i>Oedocephalum</i> , including highly reduced forms	<i>Peziza</i> , <i>Pachyella</i> , <i>Iodophanus</i> , <i>Cleistothophanus</i>	Hennebert (1973), Hennebert and Bellemère (1979), Paden (1972), Bezerra and Kimbrough (1976)
Pyronemataceae	<i>Actinosporella megalispora</i>	<i>Miladina lechithina</i>	Descals et al. (1998)
	<i>Alciphila vulgaris</i>	<i>Byssonectria</i>	Harmaja (2002a, b)
	<i>Ascorhizoctonia</i>	<i>Tricharina</i>	Yang and Korf (1985), Barrera and Romero (2001)
	<i>Cephaliphora</i>	None known	Tanabe et al. (1999)
	<i>Complexipes</i>	<i>Wilcoxina</i>	Yang and Korf (1985)
	<i>Dichobotrys</i>	<i>Trichophaea</i>	Hennebert (1973)
	<i>Micronematobotrys</i>	None known	Sun and Guo (2010)
Rhiziniaceae	“ <i>Nodulosporium</i> ”-like	<i>Geopyxis majalis</i>	Paden (1972)
	<i>Phymatotrichopsis</i>	None known	Uppalapati et al. (2010)
Sarcosomataceae	<i>Conoplea</i>	<i>Urnula craterium</i> , <i>Plectania</i> , <i>Sarcosoma latahensis</i>	Hughes (1958), Paden (1972)
	<i>Mollardiomyces</i>	<i>Phillipsia</i> , <i>Sarcoscypha</i> , <i>Nanoscypha</i>	Paden (1984), Pfister (1973b)
Tuberaceae	Unnamed sympodulosporous type	<i>Tuber</i>	Urban et al. (2004), Healy et al. (2013)

though the relationship among those families in many instances is not well resolved. Although this group is reasonably well known, future sampling will certainly change our understanding of the relationships and of these lineages. A particular focus is on the large and heterogeneous family Pyronemataceae, in which several lineages are recognizable based on both sequence analyses and expanded knowledge of nutritional modes, morphology, and anamorphic states.

General overviews of the families can be found in Cannon and Kirk (2007). The following augmented descriptions include available structural and cytological information that has been used in refining the classification.

A. Families of the Pezizomycetes

1. Ascobolaceae

Only epigeous members are known, and these occur primarily on dung, but a few species are found on plant material; *Ascobolus carbonarius* is found on burned material (Brummelen 1967). All species are saprobic and ascomata have multiple cell layers. Developmental patterns have been characterized by Brummelen (1967). Cleistothecial developmental types are found. Asci blue diffusely along the walls in iodine solutions. Ascospores are uninucleate (Berthet 1964); in *Ascobolus* and *Saccobolus* the spore walls are ornamented with purple brown pigments that become fissured at maturity (Brummelen 1967). The placement here of *Thecotheus* species, with their hyaline ascospores, has been suggested on morphological grounds and has been confirmed in molecular phylogenetic studies (Landvik et al. 1997). Septa associated with the ascogenous system are dome-shaped (Kimbrough 1994; Kimbrough and Curry 1985). Three genera are generally recognized.

2. Ascodesmidiaceae

Ascomata are much reduced in most genera; for example, in *Eleutherascus* species the asci are scattered on hyphae. In *Ascodesmis*, several asci

are formed on a much-reduced excipulum (Brummelen 1981). These species are saprobic on dung and often are isolated from soil. Asci are inamyloid and are saccate or pyriform. Ascospores are brownish and have reticulate spore ornamentations. Septa in ascogenous cells and the ascus bases are dome-shaped with arrays of radiating tubular elements and a striate structure associated with the septal pore rim in vegetative cells (Brummelen 1989; Kimbrough 1994). Four genera are placed in the family (Hansen et al. 2005b). A recent study by Hansen et al. (2013) places this family within the larger and highly diverse sister group to the Pyronemataceae *sensu stricto*.

3. Caloscyphaceae

The brightly colored cupulate ascomata stain blue green when bruised. No hypogeous members are known. *Caloscypha fulgens* is a parasite of conifer seeds and seedlings. The ascomata have a well-developed inner layer of interwoven hyphae and an outer layer of globose or angular cells. Ascospores are globose, and their walls are smooth (Harmaja 2002a). The genus *Caloscypha* was previously placed in the Pyronemataceae, in part because of its carotenoid pigments and because of the globose spores (Arpin 1969; Korf 1972, 1973). For details on septal construction see Kimbrough and Curry (1986b). Recently a second genus was added to the family, *Kallistoskypha*, with a single species, *K. incarnata*, which is associated with *Eucalyptus* found around the Mediterranean region (Pfister et al. 2013).

4. Chorioactidaceae

The ascomata are cupulate or deep urnulate and dark on the outer surface; the hymenium is beige, brownish, or orange. No hypogeous members are known in this family, and all the species are considered to be saprobic. The ascomata have a well-developed inner layer and an outer layer of globose or angular cells that give rise to thick, brown hairs encrusted with granular material. The asci are inamyloid and thick-walled with a terminal operculum. Ascospore

ornamentation is in the form of warts or ribs. Four genera have been included (Pfister et al. 2008).

5. Discinaceae

The ascomata of this family are discoid or gyromitroid. Both epigeous and hypogeous members are known. Many species in the family are mycorrhizal (Tedersoo et al. 2006, 2010). The ascomata are characteristically constructed with an inner layer of interwoven hyphae and an outer layer of elongate cells oriented perpendicularly to the outer surface. Asci are inamyloid, and ascospores are tetranucleate (Berthet 1964), smooth, or elaborately ornamented with warts, often with apiculae. Woronin bodies are elongate and often surround the septal pore. The septa at the base of asci are accompanied by an electron-opaque, hemispherical structure that becomes cone- to dumbbell-shaped with V-shaped striations; an electron-translucent torus separates the pore plug from the septal pore border (Kimbrough 1991, 1994). The septal ultrastructure is similar to that of the Helvellaceae. Generally, five or six genera are recognized.

6. Glaziellaceae

The ascomata in this family are large and hollow with a basal opening. The unispore, clavate to globose asci are embedded in the rindlike wall. Ascus walls break down, but the spores remain embedded in this peridiumlike wall. The single species, *Glaziella aurantiaca*, is presumed to be mycorrhizal. See Gibson et al. (1986) for ultrastructural details that initially supported the placement of *Glaziella* in the Ascomycota.

7. Helvellaceae

Ascomata are sessile cupulate or stipitate cupulate, saddle-shaped, or columnar (Abbott and Currah 1997; Dissing 1966). Both epigeous and hypogeous species are found in the family (Hansen and Pfister 2006; Kimbrough et al. 1996). Many or most are mycorrhizal (Tedersoo

et al. 2006). The ascomata are characteristically constructed with an inner layer of interwoven hyphae and an outer layer of elongate cells oriented perpendicularly to the outer surface. Asci are inamyloid. Ascospores are tetranucleate (Berthet 1964), smooth, or ornamented with irregular warts, and Woronin bodies are elongate, hexagonal, or globose (Kimbrough 1994). Septa at the base of the asci are electron-opaque. There are hemispherical structures that become cone- to dumbbell-shaped with V-shaped striations; in vegetative cells, an electron-translucent torus separates the pore plug from the septal pore border. Vegetative cells possess globular or slightly angled Woronin bodies (Kimbrough 1994; Kimbrough and Gibson 1989; Kimbrough et al. 1996).

8. Karstenellaceae

In this family, the ascomata are little more than a very thin, resupinate crust situated on leaf litter and wood surfaces. Asci are scattered on this mycelial mat. Nothing is known of its mode of nutrition. Asci are inamyloid and operculate. Ascospores are binucleate or multiguttulate (Hansen et al. 2008; Harmaja 1969). No ultrastructural details are known for the vegetative septal construction or for the septa of the asci. Molecular data place it in an unresolved position near Helvellaceae and Tuberaceae. There is a single genus with a single species recognized, *Karstenella vernalis*.

9. Morchellaceae

The morels are characterized by stipitate apothecia, with an interrupted hymenial layer giving a honeycomb appearance, or by cupulate forms such as *Disciotus*. Hypogeous members include *Leucoangium* (Li 1997) and *Kalapuya* (Trappe et al. 2010). Species are saprobic and have been implicated in mycorrhizal relationships (Buscot 1994; Dahlstrom et al. 2000). Asci are inamyloid. Ascospores are multinucleate (Berthet 1964) and lack both prominent wall ornamentation and internal oil droplets. Traditional classifications of the species accept six to eight species, but phylogenetic studies indicate

the presence of many species (Du et al. 2012; Kuo et al. 2012; Taskin et al. 2010) that seem restricted to specific continents (O'Donnell et al. 2011). Some of these species are morphologically distinct; others are cryptic (O'Donnell et al. 1997, 2011). The septal construction is similar to that found in the Helvellaceae. At the base of the asci, dome-shaped structures with V-shaped striations are found at the septal pore. Lamellate structures are found within septal pores of most vegetative cells. Elongate Woronin bodies have been found along with hexagonal ones (Kimbrough 1994). Five or six genera are recognized.

10. Pezizaceae

Both epigeous and hypogeous taxa are found; there are multiple origins of the hypogeous taxa within several clades (Hansen et al. 2001, 2002, 2005a; Healy et al. 2009). Saprobiic members include those on dung, wood, and other plant debris. Mycorrhizal taxa are found in several lineages. Some taxa are found exclusively on burned areas. The ascomatal structure varies, but multiple layers composed of large, thin-walled globose cells are often present. Asci generally become blue in iodine solutions. This bluing can take several forms. The reaction may be diffuse along the entire wall or concentrated in the upper portion of the ascus but most intensely at the tip, or in the upper portion with a more intense ring surrounding the opercular region (Hansen et al. 2001). The bluing reaction has been lost in several taxa, including some that are hypogeous. Ascospores are uninucleate (Berthet 1964), with or without secondary wall ornamentations (Hansen et al. 2001, 2002). Oil droplets may or may not be present in the ascospores. Septa in vegetative cells are lamellate with large globose Woronin bodies. At the ascus bases, septa are occluded by convex or biconvex bands that become covered with electron-opaque amorphous material or by an additional secondary wall (Curry and Kimbrough 1983; Kimbrough 1994; Kimbrough et al. 1991). Approximately 30 genera are currently recognized in the family, but it is well established that the genus *Peziza* is nonmono-

phyletic and will need to be broken down into several additional genera (Hansen et al. 2001, 2005a, b).

11. Pyronemataceae

Pyronemataceae is the largest of the families of the class and the most diverse ecologically and morphologically. As recognized here, the family includes Aleuriaceae, Humariaceae, Otideaceae, and Geneaceae. These fungi are saprobic, mycorrhizal vascular plants or parasitic on bryophytes. Epigeous members are cupulate, often possessing hairs on the outer surface. Hypogeous members are scattered in the family. The ascomata show considerable variation in construction and development. Asci are inamyloid, and ascospores vary in shape and ornamentation from smooth to variously ornamented (Perry et al. 2007). Several different septal types are present; at least four types of septa plugging have been associated with asci (Kimbrough 1994). These are the aleurioid type, which have a granular, opaque matrix that borders both the ascal and ascogenous hyphal sides of pores; later this becomes fan-shaped with a lamellate electron-translucent torus adjacent to the pore rim. The otideoid type, is characterized by double translucent bands in a granular, opaque pore matrix. Later the pore plug is differentiated into two zones, an inner dense zone and an outer less opaque zone. The pulvinuloid type, is similar to the Helvellaceae at maturity with V-shaped striations, but these are fewer and less prominent than in Helvellaceae. The scutellinioid type has a large hemispherical septal pore plug that becomes zonate; the inner zone adjacent to the pore lumen is electron-opaque, and an outer, thicker zone is composed of less dense material. In general, in this family, vegetative cells have a lamellate structure in the septal pores. Woronin bodies are small and largely globular, but often hexagonal.

The pyronema type has asci and ascogenous hyphae that are similar to those of the Ascobolaceae but with a different electron density core and small, radiating tubular bands similar to those of *Ascodesmis* (Kimbrough 1994; Kimbrough and Curry 1986a, b).

The family includes approximately 80 genera. It is perhaps highly heterogeneous and one that will see future division and refinement. The family was recently studied by Hansen et al. (2013), and this work provides the most accurate overview of the family.

12. Rhizinaceae

The ascomata in members of this family are flat, recurved, or pulvinate. *Rhizina undulata* is a pathogen of conifer roots. Also included here is *Psilopezia*, whose species are found on water-soaked wood and which is presumed to be a saprobe (Pfister 1973a). The construction of the ascomata follows a pattern of interwoven hyphae forming the medulla, with more densely interwoven hyphae contributing to the cortical layer. These fungi are characterized by indeterminate marginal growth. The asci are inamyloid, and ascospores are smooth or ornamented with warts and apiculae. The spores are presumed to be tetranucleate. Studies are needed on the septal structure. The family encompasses the two genera mentioned earlier as well as *Phymatotrichopsis omnivora*, which is known only as an anamorph.

13. Sarcoscyphaceae

Ascomata are generally cupulate, bright colored, stipitate, or sessile. No hypogeous members are known; all are considered saprobic. The ascomata have a well-developed inner layer and an outer layer of globose or angular cells or of tightly interwoven hyphoid cells oriented parallel to the outer surface. Cells on the outer surface sometimes give rise to single or fasciculate hairs. Ascospores are smooth or ornamented with ridges and ribs. In vegetative cells, lamellate structures are poorly differentiated or missing. Septa in vegetative cells are imperforate, plugged by an electron-opaque, fan-shaped matrix surrounded by a number of globose electron-dense Woronin bodies. The Woronin bodies are globose or occasionally hexagonal and electron-opaque. At maturity obscure V-shaped striations may be found (Benny and Samuelson 1980; Kimbrough 1994;

Li and Kimbrough 1995b). Twelve genera are commonly recognized within this family. Romero et al. (2012) review the classification within the family.

14. Sarcosomataceae

In this family, ascomata are cupulate or urnulate, tough and leathery of moderate to large size, and black or dark brown on the outside, often with a paler hymenium. No hypogeous members are known. Most species are presumed to be saprobic on plant debris, but in the case of *Urnula*, the species is said to be parasitic. The ascomata have a well-developed inner layer, with gelatinous material, and an outer layer of globose or angular cells that give rise to dark hyphoid hairs. Asci are inamyloid and thick-walled with a terminal operculum. The ultrastructure of the asci and ascospores have been studied by Bellemère et al. (1990). The ascospores are smooth or with wrinkled or folded walls or with low warts. In addition, they are multinucleate. Septal structures are composed of an electron-dense matrix and globose Woronin bodies that are often accompanied by short or long, cylindrical, hexagonal Woronin bodies. Septa at the ascus bases are composed of a dumbbell-shaped matrix with V-shaped bands. The septal structure was studied by Li and Kimbrough (1995b). Five or six genera are commonly accepted.

15. Tuberaceae

Until recently, all members of this family were considered to be hypogeous. The recent placement of *Nothojafnea thaxteri* among these fungi is notable as the first epigeous member of the family (Bonito et al. 2013). The truffles of commerce (*Tuber melanosporum* and *T. magnatum*) belong here. Ascomata are highly convoluted and folded, often with chambers or pockets of asci. The large, primarily Northern Hemisphere genus *Tuber* has been investigated by Bonito et al. (2010). All members are mycorrhizal on a range of plant families (Tedersoo et al. 2006). The asci are inamyloid, globose, or pyriform with one to

eight spores per ascus. The ascospores, in addition to being often multinucleate, are often elaborately ornamented with reticula, ridges, and warts. Septal structure was studied by Li and Kimbrough (1995b), who determined that there was some heterogeneity among those species examined. In that study, the researchers found long, cylindrical Woronin bodies in some of the species, similar to those of the Morchellaceae, Discinaceae, and Helvellaceae, and rectangular ones in another, similar to those of the Pyronemataceae. Septa associated with ascogenous hyphae and ascus bases also differed among the sampled taxa. O'Donnell et al. (1997) included a series of genera in addition to *Tuber*. Seven genera are commonly recognized. Bonito et al. (2013) estimate a late Jurassic origin of the genus *Tuber* and discuss the Southern Hemisphere diversity.

XIII. Growth in Culture

The ascospores of saprobic species germinate, and often an anamorphic state is produced. Fungi in mycorrhizal lineages do not easily germinate, and few examples are known of their anamorphic states. In some cases, field collections of anamorphs have proven to be pezizalean, and there are many examples of environmental samples linked with Pezizomycetes (Healy et al. 2013).

XIV. Conclusion

The Orbiliomycetes and Pezizomycetes are early divergent lineages within the filamentous Ascomycota. The two classes are remarkably different in their ecology and in the structure of their asci. So far as is known, there are no mycorrhizal taxa in the Orbiliomycetes, whereas the mycorrhizal life style is found in most families of the Pezizomycetes. Although anamorphs are known in the Pezizomycetes, their diversity is low; in the Orbiliomycetes, on the other hand, there is a wide range of conidial morphologies. Within the Pezizomycetes there are no known examples of predatory

behavior, whereas some members of the Orbiliomycetes trap and consume invertebrates. Recent studies have placed many hypogeous Pezizomycetes within families. These studies highlight the evolutionary patterns within the class in which suites of changes, including loss of active spore discharge mechanisms and extended ascomata developmental times, take place in distantly related clades. Most hypogeous Pezizomycetes are found within clades with other mycorrhizal members. The diversity in both Orbiliomycetes and the Pezizomycetes has proven to be greater than previously anticipated, and much researches remains to be done regarding the biogeography and evolutionary histories of the group.

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