

14 Agaricomycetes

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I. Introduction

Agaricomycetes is a clade of Basidiomycota that contains ca. 21,000 described species, which is one-fifth of all known Fungi (Kirk et al. 2008). However, new taxa are continually being described, and molecular ecologists routinely detect DNA sequences of Agaricomycetes that cannot be referred to known species, suggesting that the actual diversity of the group far exceeds the current catalog (Blackwell 2011; Hibbett et al. 2011). Many members of Agaricomycetes produce conspicuous fruiting bodies that are popular subjects for artists and amateur naturalists (Petersen 2012). In addition, most edible mushrooms are Agaricomycetes, including cultivated saprotrophs, such as *Agaricus bisporus* (champignon), *Pleurotus ostreatus* (oyster mushroom), and *Lentinula edodes* (shiitake), and wild-collected ectomycorrhizal (ECM) species, such as *Boletus edulis* (porcini), *Cantharellus cibarius* (chanterelle), and *Tricholoma matsutake* (matsutake). Psychoactive taxa, particularly species of *Psilocybe*, have

been used both as recreational drugs and religious sacraments (Heim and Wasson 1958). Other members of Agaricomycetes are toxic, with effects that range from gastrointestinal distress, caused by diverse taxa such as *Chlorophyllum molybdites*, to life-threatening amatoxin poisoning, caused by *Amanita phalloides*, *Galerina autumnalis*, and others (Benjamin 1995). The toxic compound phalloidin (from *A. phalloides*) binds to actin, making it useful as a component of fluorescent stains for visualizing the cytoskeleton.

Agaricomycetes are not common as human pathogens, although *Schizophyllum commune*, which normally occurs as a wood-decay fungus, is known to cause serious infections of lungs and other organs (Sigler et al. 1995). Several Agaricomycetes have been important as model systems in studies of fungal mating genetics and development (*S. commune*, *Coprinopsis cinerea*) (Ohm et al. 2010; Raper and Miles 1958; Stajich et al. 2010) and the biochemistry of wood decay (*Phanerochaete chrysosporium*, *Postia placenta*, and others) (Martinez et al. 2004, 2009). Finally, there is interest in uses of Agaricomycetes in industrial bioconversion processes and bioremediation (Ruiz-Dueñas and Martínez 2009).

Most of the taxa now classified in the Agaricomycetes were included in a chapter on Homobasidiomycetes in the previous edition of *The Mycota* (Hibbett and Thorn 2001). Eight informally named clades (e.g., euagarics clade, russuloid clade) were proposed, based almost entirely on analyses of ribosomal RNA (rRNA) gene sequences. A separate chapter treated Heterobasidiomycetes (Wells and Bandoni 2001), which included jelly fungi and others with mostly septate basidia (Weiß et al. 2004a). Today, Agaricomycetes is recognized as one of four major clades of Agaricomycotina, the others being the Dacrymycetes (see Oberwinkler 2014), Tremellomycetes (see Weiß et al. 2014), and Wallemiomycetes (Fig. 14.1) (Hibbett 2006; Padamsee et al. 2012). The 2007 AFTOL classification of Fungi (Hibbett et al. 2007) included 17 orders of Agaricomycetes, three of which contain species formerly classified as Heterobasidiomycetes, namely Auriculariales, Sebaciales, and Cantharellales pro

parte (i.e., Ceratobasidiaceae and Tulasnella-ceae). Since 2007, three new orders of Agaricomycetes have been proposed: Amylocorticiales, Jaapiales, and Lepidostromatales (Binder et al. 2010; Hodkinson et al. 2013). This chapter provides a phylogenetic overview of Agaricomycetes, emphasizing recent molecular studies that address the diversity and phylogenetic relationships of each order (of course, clades of Agaricomycetes classified as orders are simply mutually exclusive groups; they are not necessarily equivalent in age, number of species, or phenotypic diversity).

A. Higher-Level Relationships

All currently recognized orders of Agaricomycetes have been resolved as monophyletic in at least one analysis of rRNA genes, but support for some groups has been weak or absent, in part because of elevated rates of evolution in nuclear rRNA (nrRNA) genes in certain Cantharellales and other lineages (Binder and Hibbett 2002; Binder et al. 2005; Hibbett et al. 1997b; Moncalvo et al. 2006). Genes encoding proteins, such as subunits 1 and 2 of RNA polymerase II (*rpb1*, *rpb2*), mitochondrial ATPase subunit 6 (*atp6*), and translation elongation factor 1- α (*tef1*), started to be used in fungal molecular systematics in the late twentieth century (Kretzer and Bruns 1999; Liu et al. 1999; O'Donnell et al. 2001), and by 2006 a 6-gene, 200-species, kingdom-wide fungal phylogeny had been produced that included 37 species of Agaricomycetes (James et al. 2006). The first in-depth study of Agaricomycetes combining rRNA and protein-coding genes was that of Matheny et al. (2007), who analyzed a 6.6 kb data set of *rpb2*, *tef1*, and nrRNA genes in 146 species (119 species of Agaricomycetes). This was the first analysis to provide strong support for the monophyly of Polyporales (which had been weakly supported in rRNA analyses), and it suggested that the Sebaciales, Cantharellales, Auriculariales, and Phallomycetidae formed a paraphyletic assemblage, within which a clade containing the remaining Agaricomycetes is nested.

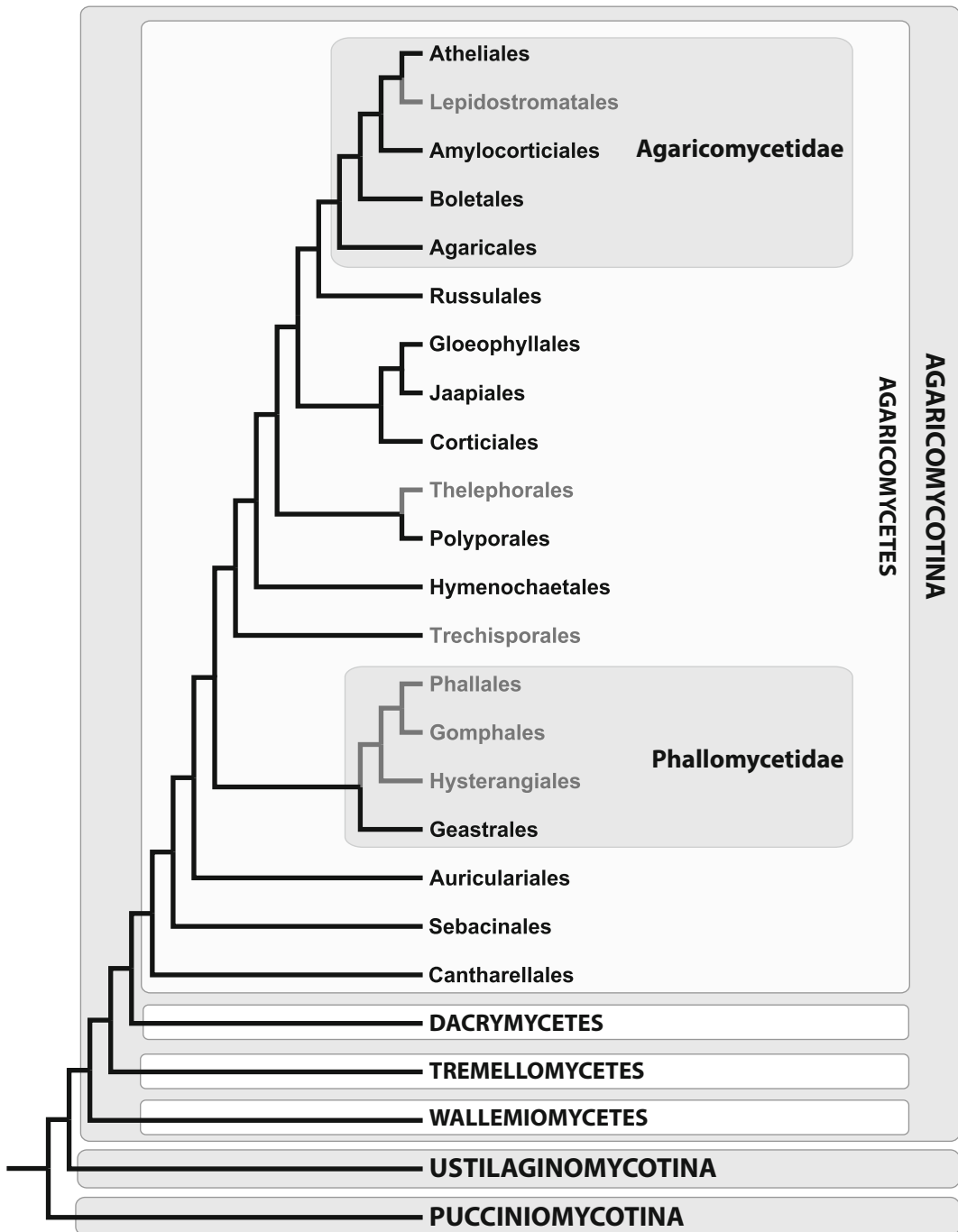


Fig. 14.1 Higher-level phylogenetic relationships of major groups of Agaricomycetes and other Basidiomycota. The major topology (black lines and text) is based on published Floudas et al. 2012; Padamsee et al. 2012) and unpublished (L. Nagy, D. Floudas, R. Riley, D. Hibbett et al., unpublished) phylogenomic analyses.

Names in *gray* represent groups that have not been included in phylogenomic analyses; placements of these taxa are based on studies combining rRNA genes with 2–3 protein-coding genes (Hodkinson et al. 2013; Hosaka et al. 2006; Matheny et al. 2007)

Genome-based analyses are providing enhanced resolution and support for the higher-level relationships of Agaricomycetes, although so far only a few broad-scale phylogenomic studies of Agaricomycetes and other Fungi have been published (Hibbett et al. 2013). As of this writing, the most inclusive published analysis contains representatives of 8 orders of Agaricomycetes (Floudas et al. 2012), but over 70 Agaricomycete genomes have been completed, many by the Joint Genome Institute of the US Department of Energy (Grigoriev et al. 2012). The phylogeny in Fig. 14.1 represents a consensus of published (Binder et al. 2013; Floudas et al. 2012; Padamsee et al. 2012) and unpublished (L. Nagy, D. Floudas, D. Hibbett, and R. Riley, unpublished) phylogenomic analyses that collectively draw on more than 40 whole-genome sequences from 15 orders of Agaricomycetes, as well as representatives of Dacrymycetes, Tremellomycetes, Wallemiomycetes, and other Fungi. Gomphales, Hysterangiales, Lepidostromatales, Phallales, Thelephorales, and Trechisporales have yet to be included in phylogenomic analyses; placements of these groups in Fig. 14.1 are based on studies combining rRNA genes with protein-coding genes (Hodkinson et al. 2013; Hosaka et al. 2006; Matheny et al. 2007).

Phylogenomic analyses have confirmed some aspects of the phylogeny of Agaricomycetes that had been resolved in earlier studies of rRNA and protein-coding genes, such as the monophyly of Agaricomycetidae (Agaricales, Boletales, Atheliales, Amylocorticiales, and Lepidostromatales) and its sister group relationship to Russulales. Novel results from phylogenomics include the placements of Jaapiales, Corticiales, and Gloeophyllales. In previous analyses combining rRNA and protein-coding genes, *Jaapia* was placed as the sister group to Agaricomycetidae, and the higher-level position of Gloeophyllales was unresolved (Binder et al. 2010; Garcia-Sandoval et al. 2011). Recent phylogenomic analyses indicate that Jaapiales, Gloeophyllales, and Corticiales form a strongly supported clade, but its higher-level position is ambiguous.

B. Taxonomic Characters and Ecological Diversity

Agaricomycete systematists have traditionally used morphological, biochemical, and ecological characters to formulate phylogenetic hypotheses and structure classifications, and a rich descriptive literature has evolved (Clémenceçon 2004; Donk 1964; Jülich 1981; Kühner 1984; Oberwinkler 1977; Petersen 1971a; Reijnders and Stalpers 1992; Singer 1986). Nonmolecular characters that have been emphasized include anatomical features (e.g., shapes and staining reactions of spores, basidia, and cystidia, hyphal systems of fruiting bodies, rhizomorph structures), macromorphology of fruiting bodies (including developmental characters), pigment chemistry, and cytological characters (e.g., nuclear behavior in basidiosporogenesis). Cultural characters, wood-decay modes (white rot vs. brown rot), and asexual reproductive forms have also been used to address relationships and provide tools for identification (Nakasone 1990a; Redhead and Ginns 1985; Stalpers 1978). The previous version of this chapter (Hibbett and Thorn 2001) contained a review of nonmolecular characters and ecological modes across major groups of Agaricomycetes, which is not repeated here. Part II of the present chapter summarizes the major morphological and ecological features within each order of Agaricomycetes, as informed by recent phylogenetic studies. The following sections discuss septal pore ultrastructure (Fig. 14.2), the evolution of fruiting body forms (Figs. 14.3, 14.4, 14.5, 14.6, 14.7, 14.8, and 14.9), and the phylogenetic distribution of major ecological modes (Table 14.1a, b) across the major groups of Agaricomycetes.

1. Septal Pore Ultrastructure

Septal pore ultrastructure provided clues to the higher-level relationships of Agaricomycetes long before the advent of molecular characters. The union of Dacrymycetes and Agaricomycetes is supported by their shared possession of dolipores that are surrounded at each side by a more or less dome-shaped modified ER (endoplasmic reticulum) cisterna, the so-called

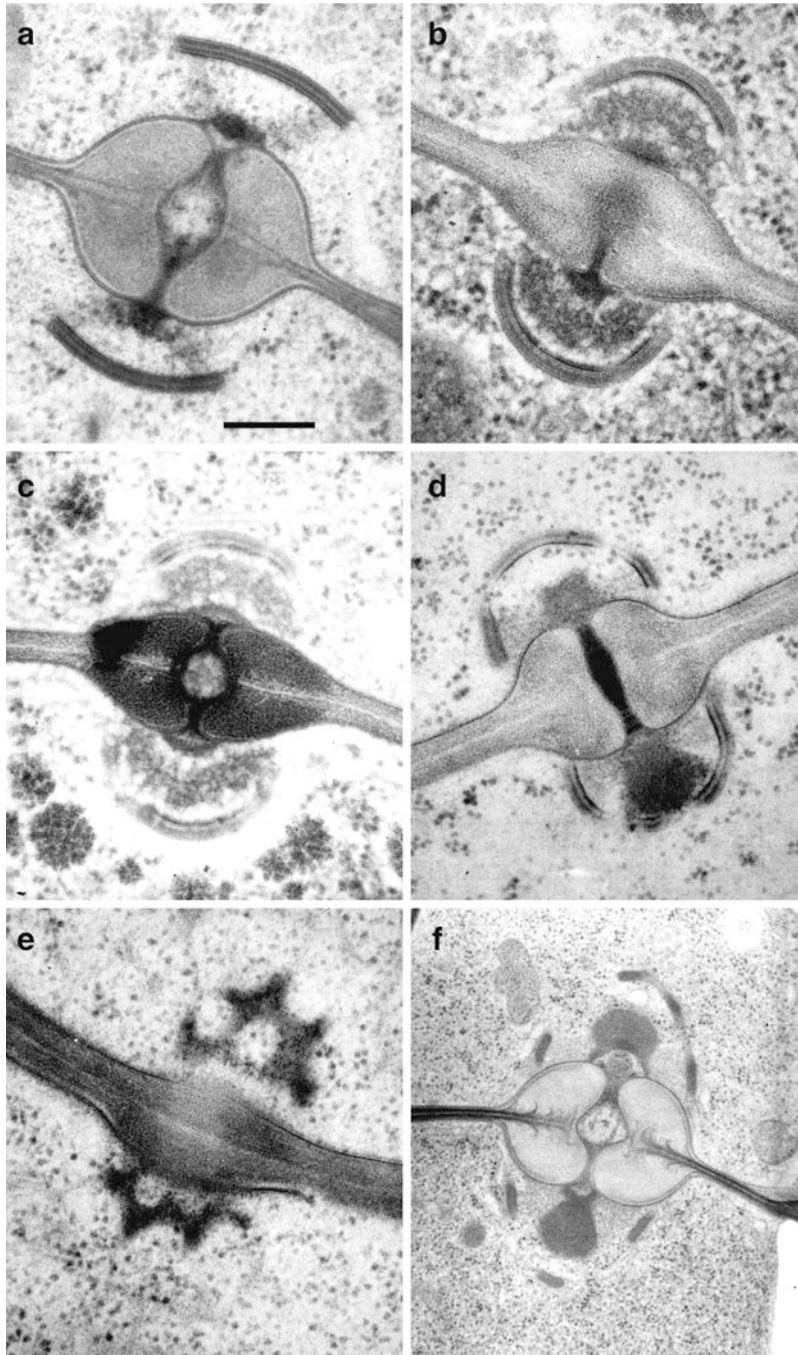


Fig. 14.2 Dolipores of Agaricomycetes in transverse (a–d, f) or tangential sections (e) through the septal pore caps (SPCs). Material was prepared by freeze substitution. *Bar* = 0.2 μ m in (a)–(e), and 0.5 μ m in (f). (a) *Tulasnella* sp.

(b, c) *Sphaerobolus* sp. Note the imperforate SPCs in (b) and the perforate SPCs in (c). (d, e) *Schizophyllum commune*. The regularly arranged perforations are especially visible in (e). (f) *Ceratobasidium* sp.



Fig. 14.3 Sebacinales (a, b), Auriculariales (c, d), and Cantharellales (e, f). (a) *Sebacina epigaea*. (b) *Craterocolla cerasi*. (c) *Pseudohydnum gelatinosum*. (d) *Exidia*

truncata. (e) *Craterellus tubaeformis*. (f) *Clavulina cristata*. Photos by Michael Wood (a, e, f; <http://www.mykoweb.com>) and Jaroslav Maly (b–d)

septal pore cap (SPC), also termed the parthesome. In contrast, the SPCs of Tremellomycetes and Wallemiomycetes are composed of saccules or fingerlike projections arising from the endoplasmic reticulum (SPCs are also occasionally absent in both groups) (Wells and Bandoni 2001; Padamsee et al. 2012). The intracisternal space of the SPCs of Agaricomycetes is sandwiched by a fine electron-opaque layer so that the SPCs altogether appear nine-lamellate in optimal sections (the double-sectioned cisternal membrane with three layers each and the intracisternal lumen with three layers). Variation in the perforation of SPCs within Agaricomycetes was summarized by van Driel et al. (2009, and references therein). The following account completes and corrects

this synopsis with new observations (by R. Bauer) using serial sections. Accordingly, within the Dacrymycetes/Agaricomycetes union, four types of SPC are evident.

Imperforate to uni-perforate SPCs (Fig. 14.2a). Probably depending on the section, no or only one median perforation of ca. 100 nm appears in one section of the series. This type is typical for Dacrymycetes and within Agaricomycetes for Sebacinales, Auriculariales, Trechisporales, the *Botryobasidium* and *Tulasnella* clades within Cantharellales, and the Hymenochaetaeae, *Hyphodontia*, *Coltricia*, *Kneiffiella*, and *Trichaptum* clades within Hymenochaetales [for the taxa and clades see Hibbett (2006) and van Driel et al. (2009)].



Fig. 14.4 Phallomycetidae, including Phallales (a), Geastrales (b), Hysterangiales (c), and Gomphales (d, e). (a) *Clathrus ruber*. (b) *Geastrum saccatum*.

(c) *Hysterangium coriaceum*. (d) *Turbinellus floccosus*. (e) *Kavinia himantioides*. Photos by Michael Wood (a–d; <http://www.mykoweb.com>) and Otto Miettinen (e)

Unstable perforate SPCs (Fig. 14.2b, c). In all members of the Phallomycetidae studied, such as *Aseroe* sp., *Clathrus archeri*, *Geastrum* spp., *Gomphus clavatus*, *Phallus impudicus*, *Ramaria* spp., and *Sphaerobolus* sp., there are predominantly imperforate SPCs, but in each species, often in the same sections, there are also dolipores with perforate SPCs. Usually, the intracisternal layering of the imperforate SPCs appears somehow incomplete. These observations suggest that the perforation formation in the Phallomycetidae begins later in comparison to that in the other accordant groups. Accordingly, the SPCs in this group may represent a unique type.

Regularly perforate SPCs with openings of roughly 100 nm (Fig. 14.2d, e). Usually, the openings are more or less hexagonally arranged. This type is realized in the Agaricomycetidae and related groups (i.e., Russulales, Corticiales, Gloeophyllales, Polyporales, and Thelephorales), the *Rickenella* and *Peniophora* clades within the Hymenochaetales, and the core cantharelloid group within Cantharellales [for the taxa and clades see Hibbett (2006) and van Driel et al. (2009)].

Irregularly perforate SPCs with a few large openings of several hundred nanometers (Fig. 14.2f). This type characterizes the Ceratobasidiales clade within the Cantharellales.



Fig. 14.5 Hymenochaetales (a–e) and Trechisporales (f–h). (a) *Hymenochaete* sp. (b) *Coltricia perennis*; (c) *Alloclavia purpurea*. (d) *Rickenella fibula*. (e) *Xylodon* (= *Hyphodontia*) *crustosus*. (f) *Trechispora stevensonii*, with pustulate anamorphic regions. (g) *Trechispora hymenocystis*. (h) *Scytinopogon angulisporus*. Photos by Otto Miettinen (a, b, e–g), Ellen Larsson (c), Lasse Kosonen (d), and Nourou Yourou (h)

2. Fruiting Bodies

The **morphological diversity** of fruiting bodies in Agaricomycetes is unparalleled in any other clade of Fungi. Agaricomycete fruiting bodies include complex, developmentally integrated forms, such as stinkhorns (e.g., *Clathrus*

ruber, Phallales) and veiled agarics (e.g., *Lepiota lilacina*, Agaricales), as well as relatively simple corticioid forms (e.g., *Trechispora stevensonii*, Trechisporales). Agaricomycete fruiting bodies range over several orders of magnitude in size, from tiny cyphelloid forms, such as *Henningsomyces candidus* or

ruber, Phallales) and veiled agarics (e.g., *Lepiota lilacina*, Agaricales), as well as relatively simple corticioid forms (e.g., *Trechispora stevensonii*, Trechisporales). Agaricomycete fruiting bodies range over several orders of magnitude in size, from tiny cyphelloid forms, such as *Henningsomyces candidus* or



Fig. 14.6 Polyporales. (a) *Panus* sp. (b) *Perenniporia ochroleuca*. (c) *Phlebia femsjoeensis*. (d) *Mycoacia aurea*. (e) *Polyporus* sp. (f) *Podoscypha* sp. Photos by Otto Miettinen (a, b, d–f) and O. Manninen (c)

the minute red algal parasite *Mycaureola dil-seae* (Agaricales), which are often less than 1 mm in diameter (Binder et al. 2006; Bodensteiner et al. 2004), to giant polypores, like *Bridgeoporus nobilissimus* and *Phellinus ellipsoideus* (Hymenochaetales), which can be more than 1 m in diameter (Burdall et al. 1996; Dai and Cui 2011; Redberg et al. 2003). They may be ephemeral, with deliquescent forms such as

Coprinopsis cinerea (Agaricales) appearing and disappearing over a few hours, or perennial, with woody “conks” like *Fomes fomentarius* (Polyporales) persisting for years.

The phylogenetic distribution of fruiting body forms and hymenophore configurations across orders of Agaricomycetes was reviewed by Hibbett (2007). All of the major morphotypes (e.g., pileate-stipitate, coralloid, polyporoid,



Fig. 14.7 Gloeophyllales (a, b) and Thelephorales (c, d). (a) *Neolentinus ponderosus*. (b) *Veluticeps fimbriata*. (c) *Hydnellum aurantiacum*. (d) *Polyozellus multiplex*. Photos by Michael Wood (<http://www.mykoweb.com>)



Fig. 14.8 Russulales. (a) *Lactarius subcircellatus*. (b) *Laurilia sulcata*. (c) *Artomyces pyxidatus*. (d, e). *Macowanites vinaceodorus*. Photos by Ellen Larsson (a–c) and M. Jeppson (d, e)

corticoid, and gasteroid forms) have evolved repeatedly. Several orders are composed exclusively (or almost exclusively) of resupinate forms (Amylocorticiales, Atheliales, Corticiales, Jaapiales, Trechisporales, and Lepidostromatales), and this is the only morphotype that is known in all orders of Agaricomycetes (except Geastrales, Hysterangiales, and Phallales). Analyses of character evolution using likelihood

and parsimony methods suggest that corticioid forms may represent the plesiomorphic condition in Agaricomycetes, with many independent origins of pileate-erect fruiting bodies, as well as reversals to resupinate forms (Hibbett 2004; Hibbett and Binder 2002). These analyses should be interpreted with caution because they are based on limited taxon samples and simplistic models of



Fig. 14.9 Agaricomycetidae, including Agaricales (a, c), Amylocorticales (b), Atheliales (d), and Boletales (e, f). (a) *Lepiota lilacea*. (b) *Anomoporia bombycina*. (c) *Lycoperdon perlatum*. (d) *Athelia salicum*. (e) *Boletus lupi-*

nus. (f) *Serpula lacrymans*. Photos by Guillermo Muñoz (a, c, e), Yu-Cheng Dai [b, reprinted from Binder et al. (2010), with permission of the Mycological Society of America], Paul Diederich (d), and Doris Haas (f)

character evolution (Hibbett 2007). Nonetheless, it is plausible that the ancestor of the Agaricomycetes may have been a corticioid fungus. Alternatively, the paraphyletic arrangement of Tremellomycetes and Dacrymycetes within Agaricomycotina could indicate that the ancestor was a jelly fungus.

3. Ecological Roles

Agaricomycetes function as **saprotrophs**, **pathogens**, and **mutualists**. The group contains the major concentration of ECM taxa, as well as white-rot and brown-rot decayers of massive woody substrates. The distribution of major ecological roles across the orders of

Table 14.1a Nutritional modes in Agaricomycete orders, with exemplar genera (Saprotrophs^a)

	White rot	Brown rot	Other/uncertain ^b
Agaricales	<i>Pleurotus</i>	<i>Fistulina</i>	<i>Coprinopsis</i>
Boletales		<i>Serpula</i>	
Amylocorticiales	<i>Plicaturopsis</i>	<i>Anomoporia</i>	
Atheliales	<i>Athelopsis</i>		<i>Athelopsis</i>
Lepidostromatales			
Polyporales	<i>Phanerochaete</i>	<i>Postia</i>	
Russulales	<i>Stereum</i>		
Thelephorales	<i>Lenzites</i>		
Gloeophyllales		<i>Gloeophyllum</i>	<i>Boreostereum</i>
Jaapiales			<i>Jaapia</i>
Corticiales	<i>Punctularia</i>		
Hymenochaetales	<i>Trichaptum</i>	<i>Bridgeoporus?</i>	<i>Tubulicrinis</i>
Trechisporales	<i>Sistotremastrum</i>		<i>Porpomyces</i>
Hysterangiales			<i>Phallophaster</i>
Gomphales	<i>Lentaria</i>		<i>Kavinia</i>
Phallales	<i>Phallus</i>		
Geastrales	<i>Sphaerobolus</i>		<i>Sclerogaster</i>
Auriculariales	<i>Auricularia</i>		
Sebacinales			<i>Craterocolla</i>
Cantharellales	<i>Sistotrema</i>		<i>Botryobasidium</i>

^aBold = genome sequence of at least one species completed; ? indicates uncertainty. Bacteriophages, algal and cyanobacterial parasites, and animal pathogens are not included. For references, see this text and Hibbett and Thorn (2001). Some endophyte observations by R. Gazis and R. Martin (unpublished)

^bThis broad category includes saprotrophs on soil, litter, dung, and keratinic substrates, as well as wood decayers of uncertain rot type or that do not correspond to classical white or brown rot definitions

Agaricomycetes is presented in Table 14.1a, b. Saprotrophic taxa occur in all orders of Agaricomycetes, and ECM taxa occur in at least 13 orders. As many as 37 independent ECM lineages have been estimated to occur in Agaricomycetes (Tedersoo et al. 2010; Rinaldi et al. 2008). It has been proposed that the ancestor of Agaricomycetes might have been ECM, based on the occurrence of ECM taxa in Sebacinales (Weiß et al. 2004b), but molecular clock analyses (see below) suggest that the group is much older than potential ECM hosts, including Pinaceae (Floudas et al. 2012; Hibbett and Matheny 2009). Phylogenomic analyses suggest that the common ancestor of Agaricomycetes possessed multiple ligninolytic class II fungal peroxidases (PODs) and other plant cell wall (PCW)-decaying enzymes, implying that it was capable of producing a white rot (in which both the lignin and cellulose components of PCWs are degraded) (Floudas et al. 2012; Ruiz-Duenas et al. 2013). Wood decayers with multiple PODs and enzymes capable of attacking crys-

talline cellulose occur in diverse lineages of Agaricomycetes, and these may have retained the plesiomorphic white-rot mode of saprotrophy. Multiple origins of brown rot (in which lignin is not appreciably removed) in Polyporales, Boletales, and Gloeophyllales and the evolution of the ECM condition in *Laccaria bicolor* (Agaricales) seem to be associated with repeated losses of PODs and other PCW-degrading enzymes. Ongoing genomic comparisons are showing that some saprotrophic Agaricomycetes do not conform to the typical models of either white rot or brown rot, including wood decayers, such as *Schizophyllum commune* and *Fistulina hepatica*, and soil, litter, and dung fungi, such as *Agaricus bisporus* and *Coprinopsis cinerea* (Morin et al. 2012; Ohm et al. 2010; Stajich et al. 2010). Similarly, increased sampling of ECM genomes is revealing considerable diversity in genes encoding PCW-degrading enzymes among independently evolved symbiotic lineages (F. Martin and colleagues, unpublished).

Table 14.1b Nutritional modes in Agaricomycete orders, with exemplar genera (Biotrophs)

	ECM	Orchid	Endophyte	Mycoparasite	Insect symbionts	Lichenized	Lichenicolous	Bryophilous	Plant pathogens	Nematode-trappers
Agaricales	Laccaria	Armillaria	Coprinellus	Asterophora	Termitomyces	Dictyonema		Tephrocye	Armillaria	Pleurotus
Boletales	Paxillus			Pseudoboletus			Leucogyrophana			
Amylocorticiales	Podoserpula?								Athelia rolfsii	
Atheliales	Ploderma		Athelia		Fibulorhizoctonia		Atheliaaarachnoidea		Athelia	
Lepidostromatales						Lepidostroma				
Polyporales		Microporus	Phlebia	Lenzites?	Cerrena				Heterobasidium	
Russulales	Russula		Peniophora		Entomocorticium					
Thelephorales	Tomentella									
Gloeophyllales										
Jaapiales										
Corticiales										
Hymenochaetales	Coltricia	Phellinus	Rigidoporus			Marchandiomyces	Marchandiomyces	Rickenella	Fomitiporia	Peniophorella
Trechisporales	Trechispora?					Resinicum?			“Trechispora alnicola”	
Hysterangiales	Hysterangium									
Gomphales	Ramaria									
Phallales	Protuberata?									
Geastrales	Geastrum?									
Auriculariales			Elmerina							
Sebacinales	Sebacina		Piriformospora							
Cantharellales	Cantharellus	Tulasnella	Sistotrema			Multiclavula	Burgella		Rhizoctonia	

Environmental studies are expanding our concepts of the ecological roles and diversity of Agaricomycetes (Hibbett et al. 2011). ECM and soil communities have been studied intensively for many years (Horton and Bruns 2001; Peay et al. 2008), but molecular environmental surveys are demonstrating the occurrence of diverse Agaricomycetes in other, often surprising, habitats. For example, a small number of freshwater, marine, and mangrove-inhabiting Agaricomycetes are known from cultures and fruiting bodies (Binder et al. 2006; Hibbett and Binder 2001; Frank et al. 2010; Jones and Fell 2012; Yamaguchi et al. 2008), but recent studies using molecular approaches have detected Agaricomycetes in marine planktonic communities (Gao et al. 2010) and in corals, which seem to harbor species of Agaricales, Auriculariales, Boletales, Corticiales, Hymenochaetales, Polyporales, and Russulales (Amend et al. 2012). The functional biology of these marine taxa, known only from DNA sequences, remains obscure. Numerous species of Agaricomycetes have also been discovered as endophytes (Oses et al. 2008; Rungiindamai et al. 2008; Thomas et al. 2008; Weiß et al. 2011). For example, culture-based studies of the foliar and sapwood endophytes of the rubber tree *Hevea brasiliensis* have detected many species of Polyporales (almost all white rot taxa), as well as Agaricales, Atheliales, Auriculariales, Cantharellales, Hymenochaetales, and Russulales (R. Gazis and R. Martin, unpublished). Most of the sapwood endophytes are closely related to known wood-decay species, suggesting that the endophytes may exist as latent saprotrophs. Other ecological associations of Agaricomycetes that have received significant attention recently include lichenized and lichenicolous forms (DePriest et al. 2005; Diederich et al. 2011; Diederich and Lawrey 2007; Lawrey et al. 2007) and insect symbionts (Aanen et al. 2002; Mueller et al. 2005; Nobre et al. 2011; Slippers et al. 2003). The latter group includes *Fibulorhizoctonia* (Atheliales), which produces sclerotia that mimic the eggs of its termite symbionts (Matsuura 2006; Matsuura et al. 2009).

C. Fossils and Molecular Clock Dating

Molecular clock studies have yielded diverse age estimates for Fungi, with the origin of the Basidiomycota inferred to be anywhere from 450 million years ago (mya) to over 1 billion years ago (Berbee and Taylor 2010; Blair 2009; Douzery et al. 2004; Gueidan et al. 2011; Hedges et al. 2004; Taylor and Berbee 2006). A genome-based molecular clock analysis (Floudas et al. 2012) estimated the age of the Agaricomycetes at ca. 290 million years (with a 95 % highest posterior density interval of 222–372 million years). Other molecular clock studies using rRNA genes, alone or in combination with selected protein-coding genes, have focused on groups within Agaricomycetes, such as Boletales (Skrede et al. 2011; Wilson et al. 2012), Agaricales (Matheny et al. 2009; Ryberg and Matheny 2012), and brown-rot lineages (Garcia-Sandoval et al. 2011). Taxon sampling in these analyses has been very divergent, and their results have often been inconsistent. For example, an analysis focused on Inocybaceae (Agaricales) (Matheny et al. 2009) suggested that the group arose 143 (99–191) mya, while another study that focused on Boletales but included diverse Agaricales (Skrede et al. 2011) suggested that the common ancestor of Inocybaceae and Crepidotaceae existed ca. 45 (30–60) mya.

New genome sequences are providing a wealth of data for molecular clock analyses in Agaricomycetes, but the paucity of reliably identified fossils continues to be a limiting factor. Basidiomycetous hyphae with clamp connections are known from the Pennsylvanian (ca. 330 mya) (Dennis 1970, 1976; Krings et al. 2011; see Taylor et al., Chap. 10, Vol. VII, Part B), but the earliest fossils that are clearly Agaricomycetes do not occur until the Cretaceous. The oldest, *Quatsinoporites cranhamii*, is a fragment of a poroid hymenophore from the lower Cretaceous (130–125 mya) that has simple (nonclamped) septate hyphae and hymenial elements that resemble setae, suggesting that it may be a member of Hymenochaetales (Smith et al. 2004). Two gilled mushrooms that are

probably Agaricales are known from somewhat younger deposits, including *Archaeomarasmius leggetti*, from New Jersey amber (ca. 90–94 mya) (Hibbett et al. 1995, 1997a), and *Palaeoagaricites antiquus*, from Burmese amber (ca. 100 mya) (Poinar and Buckley 2007). Another fossil from Burmese amber, *Palaeoclavaria burmites* (Poinar and Brown 2003), was originally interpreted as a clavarioid member of the so-called Aphyllophorales (this name refers to a polyphyletic taxon and is no longer in use), but there are insufficient characters visible to determine its taxonomic placement. Eocene fossils of Agaricomycetes include ectomycorrhizae associated with pine roots that were interpreted as Suillaceae (Boletales) (LePage et al. 1997) and *Appianoporites vancouverensis*, a poroid fruiting body fragment similar to *Q. cranhamii* (Smith et al. 2004). Dominican amber from the Miocene–Oligocene (ca. 15–30 mya) has yielded several well-preserved mushrooms that resemble extant Agaricales (Hibbett et al. 1997a, 2003; Poinar and Singer 1990).

Of the fossils listed previously, several have been repeatedly used as calibration points in molecular clock analyses, including *Q. cranhamii*, *A. leggetti*, and the putative suilloid ectomycorrhiza (Floudas et al. 2012; Gueidan et al. 2011; Skrede et al. 2011). Additional fossils will surely be discovered, but it seems unlikely that they will ever provide numerous rigorously identified calibration points for the major clades of Agaricomycetes. Other sources of evidence that have the potential to address ages of diverse lineages of Agaricomycetes include vicariant events and fossils of obligate symbionts, such as ECM hosts (Hibbett 2001; Hibbett and Matheny 2009; Matheny et al. 2009; Wilson et al. 2012) and the arthropods associated with taxa such as *Termitomyces*, *Amylostereum*, and attine ant cultivars (Mikheyev et al. 2010; Nobre et al. 2011; Slippers et al. 2003).

II. Phylogenetic Diversity

A. Cantharellales

Overview: Cantharellales is a small order, comprising about 260 described and currently

recognized species (Kirk et al. 2008), and is represented on all continents. Effused, skinlike fruiting bodies characterize roughly half of the species, e.g., in *Sistotrema*, *Botryobasidium*, and *Tulasnella*, some of which are extremely delicate and inconspicuous. Stipitate-hydroid and stipitate-veined fruiting bodies occur in the edible genera *Hydnum* and *Cantharellus*, respectively, while coralloid fruiting structures are found in *Clavulina* and *Multiclavula* (Fig. 14.3e, f). The hymenophore is mostly smooth but sometimes hydroid or poroid, while truly gilled structures are lacking.

With the possible exception of the genus *Tulasnella* (Rogers 1932), species in Cantharellales have a unique type of basidia called stichic, characterized by a longitudinal orientation of the spindle during meiosis, in contrast to the chiasitic type with transversely oriented spindle present in all other Agaricomycetes. While the presence of four-spored basidia constitutes an almost universal condition within Agaricomycetes, it is not so in Cantharellales. Basidia with two sterigmata are found in, for example, *Clavulina* and *Membranomyces*, and six or eight sterigmata predominate in *Botryobasidium* and *Sistotrema*. Many species in *Cantharellus* have predominantly five-sterigmate basidia. The explanation for this variation in sterigma number is not known, but a connection to the unique mode of meiosis is perhaps not unlikely.

Species in Cantharellales also show variation in septal pore morphology. *Botryobasidium* and *Tulasnella* are examples of genera with imperforate parenthesomes, while species in *Cantharellus* and *Sistotrema* and at least some species in *Ceratobasidium* have perforate parenthesomes (van Driel et al. 2009).

Ecological diversity: most resupinate species in Cantharellales seem to be saprotrophs. However, most species in *Botryobasidium* and *Tulasnella* and the majority of species in *Sistotrema* are capable of growing on common malt agar, a likely indication of the presence of cellulolytic enzymes. On the other hand, no species in Cantharellales occur as primary decayers, and they do not develop an extensive mycelium within logs. Forthcoming genomes of *Botryobasidium botryosum*, *Sistotrema brinkmannii*, *Tulasnella calospora*, and others

should provide clues to ecological capabilities within the order.

Symbiotic relationships are widespread within the order and occur in all families accepted here. ECM lineages include *Cantharellus*/*Craterellus*, *Clavulina*/*Membranomyces*, *Hydnum*/*Sistotrema* sensu stricto, *Ceratobasidium*/*Thanatephorus*, and *Tulasnella* (Teder-soo et al. 2010 and references therein). Another type of symbiosis is present in the lichenized *Multiclavula* species that always grow associated with unicellular green algae (Lawrey et al. 2007).

A parasitic lifestyle occurs in *Ceratobasidium*, where a common anamorph stage known as *Rhizoctonia solani* is a widespread and troublesome crop pest, seemingly capable of infecting a wide range of hosts (Mosquera-Espinosa et al. 2013; Parmeter 1970; Sneh et al. 1996; Veldre et al. 2013). The anamorph genera *Burgoa* and *Minimedusa*, both related to *Sistotrema*, are reported as lichen parasites (Diederich and Lawrey 2007).

Systematics: the first comprehensive, multiple-gene phylogeny of Cantharellales was presented by Moncalvo et al. (2006). Veldre et al. (2013) is the most recent phylogeny with coverage of the whole order. These studies support a division of Cantharellales into four families, which may be defined by septal pore structure and secondary spore production.

Ceratobasidiaceae (eight genera) includes species with thin, resupinate fruiting bodies developing on various kinds of fine woody debris and other plant remains, but also on living plants. Hyphae are broad and without clamps. With the exception of the type species of *Ceratobasidium*, all species studied so far have perforate parentheses (van Driel et al. 2009; Weiß and Oberwinkler 2001). Basidia are short, with 2–4 long sterigmata. Basidiospores are capable of forming secondary spores through the development of a functional sterigma from the primary spore. The formation of a secondary spore has been interpreted as a second chance to send propagules into the air. This ability is common also in Tulasnellaceae, Auriculariales, and Sebaciales but not known from other orders in Agaricomycotina. A recent molecular study of Ceratobasidiaceae suggests that only two or, perhaps, three genera should be recognized. *Ceratobasidium* is reduced to the type species, and most other species are referred to *Rhizoctonia* (Oberwinkler et al. 2013a).

Tulasnellaceae (three genera) is characterized by a unique basidium morphology. The young basidium is globose to club-shaped and develops four globose sterigma initials that at maturity become onion-shaped before developing spores, which are forcibly discharged. The unusual sterigmata have been interpreted as monosporic epibasidia. All species can form secondary spores in the same way as described for Ceratobasidiaceae. Hyphal septa have imperforate parentheses. Members of the family form thin resupinate basidiomata or develop a loose mycelium within fruiting bodies of other resupinate fungi, apparently without any interaction. Species seem to be saprotrophs or mutualists capable of forming orchid mycorrhizae (Cruz et al. 2011; Preussing et al. 2010) or ectomycorrhizae (Bidartondo et al. 2003). The nuclear ribosomal genes of large parts of the genus *Tulasnella* are inexplicably deviant from those of other fungi and often require tailored polymerase chain reaction primers for amplification (Taylor and McCormick 2008).

Botryobasidiaceae includes, as far as is known, a single genus, *Botryobasidium*. It is characterized by basidia that in most cases produce six or eight spores. A few species have spiny spores and four sterigmata. They were earlier referred to *Botryohypochnus*, but molecular data place all species examined firmly within *Botryobasidium* (Binder et al. 2005). Secondary spore formation has not been observed in the family, and septal pore parentheses are nonperforate. The basidiomata are very delicate, and hyphae are wide with a characteristic cruciate branching on subcicular hyphae. Many species have an anamorph stage referred to the form genus *Haplotrichum*. They usually develop as separate, often brownish colonies sometimes integrated, however, with the teleomorph. Saprotrophy has been the assumed nutritional strategy, but a recent study detected orchid symbionts that, on the basis of DNA sequences, belong to *Botryobasidium* (Yukawa et al. 2009). There is no comprehensive molecular phylogeny for the family.

Hydnaceae (syn. Cantharellaceae, Clavulinaceae, Sistotremataceae; nine genera) is the largest family in Cantharellales in terms of the number of constituent genera and the most diverse in terms of described species. As in many other cases, genera dominated by corticioid species seem to represent the ancestral condition, and lineages with erect fruiting bodies seem to have evolved from such species (Moncalvo et al. 2006). The corticioid species belong to *Sistotrema* and *Membranomyces*. *Sistotrema* is a polyphyletic and ecologically diverse genus. The type species forms a stipitate fruiting body with a weakly hydroid hymenophore and is closely related to *Hydnum*. Other species related to the type have resupinate basidiomata with a poroid or hydroid hymenophore. They all seem to form ectomycorrhiza and share this strategy with the stipitate-hydroid genus *Hydnum* (Nilsson et al. 2006). *Membranomyces* largely shares the micromorphological characteristics, ECM habit, and phylogenetic placement

with the coralloid genus *Clavulina*. *Cantharellus* and *Craterellus* seem to make up a monophyletic group, and together they form a third lineage within Hydnaceae with ECM capacity. Fruiting bodies within this lineage are of the cantharelloid type, viz. more or less funnel-shaped and with a smooth, veined, or coarsely semigilled hymenophore. Secondary spore production is not known within this family, and the species examined have septa with perforate parentheses. Recent molecular studies in South America and Africa have unearthed a considerable number of new species and lineages in the family (Buyck et al. 2013a, b; Henkel et al. 2011; Tibuhwa et al. 2012; Uehling et al. 2012a, b). However, a comprehensive phylogeny for the family is still lacking. Several species in Hydnaceae (*Cantharellus cibarius*, *Craterellus tubaeformis*, and *Hydnum repandum*) are highly prized as culinary mushrooms, yet attempts to keep these fungi in culture and to grow mushrooms from those cultures have largely proved unsuccessful. As with *Tulasnella*, the nuclear ribosomal genes of the genus *Cantharellus* are very deviant from those of other fungi (Moncalvo et al. 2006).

B. Sebacinales

Overview: Sebacinales (Weiß et al. 2004b), one of the basal clades in Agaricomycetes, presently includes 8 genera with ca. 30 described species (Kirk et al. 2008). In contrast to these figures from the taxonomic literature, recent molecular phylogenetic studies have revealed a huge amount of cryptic species in this group (e.g., Riess et al. 2013; Selosse et al. 2007; Weiß et al. 2011) and also suggest that generic concepts will have to be revised in the future to yield monophyletic taxa. Morphological key features of Sebacinales include the ability of basidiospores to form ballistoconidia (secondary spores), dolipores with continuous parentheses, longitudinally septate basidia, septa without clamp connections, and often thickened hyphal walls in substrate hyphae (Weiß et al. 2004b; Wells and Bandoni 2001; Wells and Oberwinkler 1982); unique apomorphies are not known for this group. There is a remarkable range of basidiome shapes in Sebacinales, from taxa that completely lack macroscopically visible basidiomes (*Serendipita*) to forms with corticioid (*Sebacina*) (Fig. 14.3a), pustulate-confluent (*Efibulobasidium*), cushion-shaped (*Craterocolla*) (Fig. 14.3b), coralloid (*Tremello-dendron*), or even stereoid (*Tremellostereum*)

to infundibuliform (*Tremelloscypha*) appearance. Sebacinalean basidiomes most often have a gelatinous consistency. Known anamorphs in the Sebacinales comprise the species of *Piriformospora*, pycnidial conidiomata in *Craterocolla cerasi*, and coremioid stages of species of *Efibulobasidium* (Kirschner and Oberwinkler 2009; Wells and Bandoni 2001). Sebacinales species have a worldwide distribution and are even known from Antarctica (Newsham and Bridge 2010). A comprehensive review of this group was recently published by Oberwinkler et al. (2013b).

Ecological diversity: over the past decade, Sebacinales has received much attention because of the exceptionally wide spectrum and the ubiquity of mutualistic associations with plant roots in which members of this group are involved. Sebacinalean mycobionts have been detected in ectomycorrhizae (Glen et al. 2002; Tedersoo and Smith 2013; Urban et al. 2003) and orchid mycorrhizae (Selosse et al. 2002; Warcup 1988), as well as in ericoid (Allen et al. 2003; Selosse et al. 2007), arbutoid (Hynson et al. 2013), and cavendishoid (Setaro et al. 2006) mycorrhizae, and even in jungermannian mycothalli (associations with liverworts) (Kottke et al. 2003). No other fungal group is known to have a broader spectrum of mycorrhizal types. In addition, members of Sebacinales have recently been shown to occur abundantly as endophytes in plant roots (Selosse et al. 2009; Weiß et al. 2011). A few Sebacinales strains have been studied in vitro for their impact on host plants in endophytic associations. Most of these studies used the anamorphic strain *Piriformospora indica* and reported significant increases in growth and yield and improved resistance of the plant hosts to abiotic and biotic stress (Qiang et al. 2012), rendering the members of Sebacinales promising bioagents for organic plant production. The genome sequence of *Piriformospora indica* (Zuccaro et al. 2011) facilitates functional studies. Because of the richness of their mutualistic associations with land plants, Sebacinales is a model group for studying the evolution of plant–fungal interactions.

Though there is an increasing body of evidence on the importance of Sebacinales as mutu-

alistic mycobionts of plant roots in terrestrial ecosystems, some species seem to have a saprotrophic lifestyle (*Craterocola*, *Efibulobasidium*). Since *P. indica* and members of the morphospecies *Serendipita vermifera* grow axenically in standard media, it can be assumed that many, if not all, species of Sebaciniales Group B (see below) have saprotrophic abilities.

Systematics: the monophyly of the Sebaciniales has been demonstrated in molecular phylogenetic analyses (Weiß and Oberwinkler 2001; Weiß et al. 2004b). All comprehensive analyses of phylogenetic relationships within Sebaciniales have been based on nuclear-encoded rRNA genes, including the internal transcribed spacers (ITS) and partial large subunit (nuc-18S) regions. Most of the sequences analyzed have come from environmental sources; multilocus data derived from fruiting bodies or cultures are needed to solidify the systematics of Sebaciniales. The available molecular phylogenetic analyses indicate that Sebaciniales is divided into two monophyletic subgroups, informally known as Group A and Group B.

Group A: Species forming macroscopically visible basidiomes have only been reported from Group A. The types of interactions with plant roots are not uniformly distributed over Groups A and B; most of the reported taxa known to be involved in ectomycorrhizae belong to Group A, whereas sebacinean mycobionts of ericoid mycorrhizae have only been reported from Group B.

Group B: The vast majority of Group B taxa are known only from environmental sequences. *S. vermifera* is the only known teleomorph in this group, yet it has been shown that this morphospecies is in fact a broad complex of cryptic species (Weiß et al. 2004b), all of which may lack macroscopic basidiomes, that produce exceptionally long vermiform basidiospores and are very poor in distinctive microscopic characters. It is possible that all teleomorphic species in Sebaciniales Group B belong to this morphospecies and that the anamorphic genus *Piriformospora*, with two currently described species, evolved within this group from a *S. vermifera*-like ancestor that lost the ability to reproduce sexually.

C. Auriculariales

Overview: Auriculariales in its current concept includes ca. 30 genera with ca. 200 described species (Kirk et al. 2008; Weiß et al. 2004a). It comprises wood-decaying fungi with a broad

spectrum of basidiome shapes, including effused (*Exidiopsis*, *Basidioidendron*), effuso-reflex (*Eichleriella*), odontoid (*Stypella*), hydroid (*Pseudohydnum*) (Fig. 14.3c), and infundibuliform (*Tremiscus*) basidiomes. Basidiomes of some species even have a poroid or daedaleoid habit (*Elmerina* [including *Aporpium* and *Protodaedalea*], *Protomerulius*) (Zhou and Dai 2013). All known species cause a white rot, some are regularly found on buried wood (*Tremiscus helvelloides*). Key characters of the Auriculariales include dolipores with continuous parenthesomes and the ability of basidiospores to form ballistoconidia (secondary basidiospores). With the exception of *Hyaloria pilacre*, all species are ballistosporic.

Most of the known species in the Auriculariales have longitudinally septate basidia, but there are also species with transversely (*Auricularia*) or obliquely septate (*Patouillardina*) and even nonseptate (*Oliveonia*) or apically partially septate (*Tremellodendropsis*) basidia. In some genera (e.g., *Myxarium*, *Protodontia*, *Pseudohydnum*, *Pseudomerulius*, *Stypella*, *Tremiscus*), basidia have a plasma-devoid “stalk” (*myxarioid*, *sphaeropedunculate* basidia), which probably represents a taxonomically relevant character (Weiß and Oberwinkler 2001; Wells and Bandoni 2001). An explanation of this peculiar morphology was given by Bandoni (1984), who interpreted the basidial compartments themselves as intrabasidial meiotic products (endospores) that in germination break the outer basidial wall and develop a single conidium, the “basidiospore” in common terminology. In the myxarioid members of the Auriculariales the endospores do not fill the complete basidium but leave the characteristic stalk.

Many investigated species show clamps with characteristic retrorse projections (so-called spurred clamps) (Bandoni and Wells 1992). Another characteristic microscopic feature reported from many species of Auriculariales is the ability of basidiospores to produce mostly crescent-shaped microconidia on short sterigmatalike projections (Ingold 1982a, b). Little is known about other anamorphs in Auriculariales. From recent reports about sporodochial, synnematosus, bulbiferous, and possibly also pycnidial examples in this group

(Kirschner 2010; Kirschner and Chen 2004; Kirschner et al. 2010, 2012) we can extrapolate that there might be a rich diversity of forms still to be detected. Their ecological function in nature is still unknown.

Most species of Auriculariales are so-called jelly fungi. As in Tremellomycetes, Dacrymycetes, and Sebaciales, the basidiomes of most members of Auriculariales have a gelatinous consistency and are able to experience drought conditions in a state of cryptobiosis, where the water content of the basidiomes is drastically reduced and the basidiomes revive and continue growing and sporulating when soaked again (Wells 1994). The *Auricularia auricula-judae* complex includes the broadly distributed wood-ear (mu-err) fungus, which occurs on dead wood and is one of the most important edible mushroom species of the world, particularly in Asia (Chang and Wasser 2012). The group contains other edible mushrooms, for example, *Tremiscus helvelloides*; however, these are only sporadically collected in the field and not produced on an industrial scale.

Systematics: the monophyly of a core Auriculariales (excluding *Ceratosebacina* and *Exidiopsis gloeophora*) has been suggested by the molecular phylogenetic analysis of Weiß and Oberwinkler (2001), who included the broadest sampling of species of this group to date. Some prior analyses using only rRNA genes focused on Agaricomycetes (Binder et al. 2005; Hibbett and Binder 2002) resolved the Auriculariales as a paraphyletic grade, but support for these topologies has never been strong, and other analyses show the group to be monophyletic. Multigene or phylogenomic analyses are still lacking for this group. Given that many taxa of Auriculariales have not yet been sequenced and the monophyly of the group is still tentative, an infraordinal classification is not yet available. Elements of a future classification may include a family, Auriculariaceae, comprising *Auricularia*, *Eichleriella*, *Elmerina* [including *Aporpium* and *Protodaedalea*], *Exidia*, *Exidiopsis*, and *Heterochaete*; a clade comprising *Myxarium* (including *Hyaloria* with gasteroid sporulation) and the sporodochial anamorph *Helicomyxa everhartioides*; a clade including *Heterochaetella*, *Protodontia picei-*

cola, *Protomerulius*, and possibly *Tremellodendropsis*; and a clade comprising *Basidiendendron*, *Bourdotia*, *Ductifera*, and the cyphelloid bulbilliferous anamorph *Ovipoculum* (Weiß and Oberwinkler 2001; Zhou and Dai 2013).

D. Phallomycetidae

The group informally labeled the gomphoid-phalloid clade (Hibbett and Thorn 2001) has been classified as the subclass Phallomycetidae, with four orders: Geastrales, Phallales, Gomphales, and Hysterangiales (Hosaka et al. 2006) (Fig. 14.4).

1. Geastrales

Overview: this group is represented by earth-stars (*Geastrum*) (Fig. 14.4b), cannonball fungi (*Sphaerobolus*), and false truffles (*Radiigera*, *Sclerogaster*, and *Schenella*). Taxa with nonsequestrate fruit bodies possess an exoperidium that opens in a stellate manner as it matures, exposing the endoperidium with one (*Geastrum*) or multiple stomata (*Myriostoma*) (Sunhede 1989). Most taxa, except *Sclerogaster* and *Sphaerobolus*, have a brownish to blackish gleba, which becomes powdery at maturity. Basidiospores of most taxa, including *Sclerogaster*, are globose with a warty to spiny ornamentation. The fruiting body structure of *Sphaerobolus* is unique for Geastrales in having a single peridiole instead of a powdery gleba. The mechanism of forcible ejection of peridioles was described in detail by Ingold (1972).

Ecological diversity: the ecological characters of this group have rarely been investigated. Many species of the order grow on soil but without obvious ECM plants nearby. In addition, some species of *Geastrum*, *Sclerogaster*, and *Sphaerobolus* often fruit on rotten wood or wood chips (Hosaka and Castellano 2008), and *Sphaerobolus* fruits abundantly on artificial media (Geml et al. 2005). Several species of *Geastrum* favor semiarid to arid environments, for example, well-drained sandy soils of coasts and deserts (Kasuya et al. 2011). Such evidence suggests that most, if not all, species in the

order are saprotrophic, as suggested by several authors (Kreisel 1969; Sunhede 1989). Most trufflelike fungi are believed to form ectomycorrhizae; *Sclerogaster* is an exception. One species of *Geastrum*, *G. fimbriatum*, has been described as forming ectomycorrhizae with *Fagus* (Agerer and Beenken 1998), but their observation indicated the absence of a Hartig net. The ecological roles of Geastrales species warrant further investigation.

Systematics: most taxa in Geastrales have been treated in the order Lycoperdales, along with puffballs (*Lycoperdon*) (Fischer 1900; Miller and Miller 1988; Zeller 1949), but early molecular studies (Hibbett et al. 1997a) demonstrated that *Geastrum* and *Lycoperdon*, both of which possess a powdery gleba at maturity, are only distantly related. Kreisel (1969) first segregated Geastrales from Lycoperdales but did not provide a Latin diagnosis. In addition, Kreisel (1969) included only two genera, *Geastrum* and *Myriostoma*, in the order. Hosaka et al. (2006) formally described Geastrales with a broader concept, including several previously unrecognized taxa in the order.

Geastrales, which as a whole is moderately supported as monophyletic, is divided into four families—Geastraceae, Sclerogastraceae, Schenellaceae, and Sphaerobolaceae—that are all strongly supported as clades (Hosaka and Castellano 2008; Hosaka et al. 2006). Geastraceae, Sclerogastraceae, and Schenellaceae form a clade, with an ambiguous relationship among families (Hosaka and Castellano 2008). Within Geastraceae, *Myriostoma*, the only taxon possessing multiple stomata, represents the earliest branch, suggesting that the evolutionary trend is reduction from multiple stomata to a single stoma. The early-diverging taxa within the order, Sphaerobolaceae and Schenellaceae, form basidiospores in peridioles, and this may be the ancestral character state.

A total of 7 genera and 64 species are currently recorded in the order (Kirk et al. 2008), but a number of undescribed species have been discovered for *Geastrum* and *Sclerogaster* (Hosaka and Castellano 2008; Kasuya et al. 2012). Furthermore, Kasuya et al. (2012) demonstrated that *Geastrum triplex*, which was recorded from all continents except

Antarctica, should be separated into multiple species. Therefore, a significantly higher number of species may be recognized in the future.

2. Phallales

Overview: this order is famous for its stinkhorns (Phallaceae) and lattice stinkhorns (Clathraceae) (Fig. 14.4a), but recent molecular phylogenetic studies have shown that a number of sequestrate taxa are also included. Most taxa in the Phallales have fruiting bodies with a gelatinous layer and a gelatinous to mucilaginous gleba. Fruiting bodies of epigeous stinkhorns are often brightly colored (white and yellow to bright red) and composed of a pseudoparenchymatous receptacle with multiple arms (Fig. 14.4a). The fruiting bodies of most sequestrate taxa contain thick gelatinous layers, and their gleba remains gelatinous to mucilaginous. However, *Gastrosporium* and *Calvarula* have a powdery gleba at maturity (Domínguez de Toledo and Castellano 1997). Spores of most taxa are small, ellipsoid, smooth, and without ornamentation, but a few taxa, such as *Kjeldsenia* and *Gastrosporium*, have warty spore surfaces (Colgan et al. 1995; Domínguez de Toledo and Castellano 1997).

Ecological diversity: most taxa are thought to be saprotrophic due to their lignicolous habit, but at least one species (*Protuberia canescens*) has been reported to be ECM (Malajczuk 1988). This report, however, is suspect because *P. canescens* has recently been confirmed as an immature form of *Ileodictyon* (May et al. 2010). It is likely that all members of the order are saprotrophic, but further investigation is necessary.

Phallales represents one of the prime examples of interactions of Fungi with arthropods (Nouhra and Domínguez de Toledo 1994). The fruiting bodies of epigeous stinkhorns possess a gleba that becomes slimy and malodorous at maturity. The odor of a mature gleba attracts a variety of mycophagous arthropods, especially flies, that disperse the basidiospores (Tuno 1998). Unlike spores of many sequestrate fungi, those of Phallales (including sequestrate

taxa) are rarely documented from mammal feces. It is possible that spore dispersal of Phallales is entirely dependent on arthropods.

Systematics: Phallales was described by Fischer (1900) with two families, Phallaceae and Clathraceae. A third family, Claustulaceae, was added to the order (Cunningham 1931; Jülich 1981; Zeller 1949), and this concept has been accepted for a long time. Miller and Miller (1988) further expanded the ordinal concept by including Protophallaceae in the order, but they also included Hysterangiaceae (now in Hysterangiales). Currently the order contains six families (Phallaceae, Clathraceae, Lysuraceae, Protophallaceae, Claustulaceae, and Trappeaceae), and the monophyly of the order and each family is strongly supported by multigene phylogenetic analyses (Hosaka et al. 2006).

The basal grades of the order are composed of Protophallaceae, Claustulaceae, and Trappeaceae, all of which exhibit an exclusively sequestrate habit, indicating that stinkhornlike fruit bodies are derived morphologies in Phallales (Hosaka et al. 2006). Among phylogenies of Agaricomycetes, Phallales represents the sole example of an unambiguous transition from sequestrate to nonsequestrate forms.

A total of 29 genera and ca. 100 species are currently recorded in the order (Kirk et al. 2008), but some genera, such as *Protuber* and *Trappea*, are polyphyletic, with species in both Phallales and Hysterangiales (Hosaka et al. 2006), and require further taxonomic revision. Some new genera and species have been described recently (Cabral et al. 2012; Desjardin and Perry 2009). Because the center of diversity of this order probably lies in the tropics (Miller and Miller 1988) and many such areas have not been extensively investigated, the number of taxa in this group will be significantly higher in the future.

3. Gomphales

Overview: the fungi in Gomphales (Jülich 1981; from the Greek *pluglike*) have long been recognized as a distinct, highly variable clade of Agaricomycetes (Bruns et al. 1998; Hibbett and Thorn 2001; Hosaka et al. 2006; Pine

et al. 1999). They are characterized by a wide range of fruiting body morphologies, from stalked ramarioid/clavarioid (e.g., *Ramaria*, *Phaeoclavulina*, and *Lentariaceae*) to club (Clavariadelphaceae), gilled (*Gloeocantharellus*), cantharelloid-gomphoid (*Gomphus*, *Phaeoclavulina*, and *Turbinellus*) (Fig. 14.4d), tooth (*Beenakia*), resupinate-odontoid (*Kavinia*) (Fig. 14.4e), all the way to sequestrate fungi (Gauteriaceae) (Giachini et al. 2010; Hosaka et al. 2006; Humpert et al. 2001).

Ecological diversity: members of Gomphales show heterogeneity in their ecological characters. Most species in Beenakiaceae, Lentariaceae, Kaviniaceae, *Gloeocantharellus*, and *Phaeoclavulina* and some species of *Ramaria* (e.g., *R. moelleriana*, *R. stricta*, and *R. circinans*) grow and fruit on woody debris, a trait that has led to their general categorization as saprotrophs. The other taxa of the order are generally considered ECM, and while the nutritional status of many species of Gomphales is still unknown, the formation of ectomycorrhizae by *Turbinellus*, *Gomphus*, and some *Ramaria* species has been confirmed (Agerer 1996a, b, c, d; Agerer and Iosifidou 2004; Agerer et al. 1998; Castellano 1988; Griffiths et al. 1991; Masui 1926, 1927; Miller and Miller 1988; Nouhra et al. 2005; Rinaldi et al. 2008).

Systematics: the taxonomy and systematics of the Gomphales has traditionally relied on morphological characters now known to be subject to parallel evolution and phenotypic plasticity (Moncalvo et al. 2000). As a family, Gomphaceae has traditionally been classified within the Aphylophorales, along with distantly related taxa such as Cantharellaceae, Ganodermataceae, and Polyporaceae (Donk 1964). The phylogenetic relationships of members of the order Gomphales, including its monophyly, have been estimated using molecular data (Giachini et al. 2010; Hosaka et al. 2006; Humpert et al. 2001), which revealed that gomphoid fungi are closely related to taxa in Geastrales, Hysterangiales, and Phallales in the subclass Phallomycetidae (Colgan et al. 1997; Giachini et al. 2010; Hibbett et al. 1997a; Hosaka et al. 2006; Humpert et al. 2001; Pine et al. 1999). Currently, the order encompasses six well-supported families, namely

Beenakiaceae (*Beenakia*, *Kavinia* and *Ramari-cium*), Clavariadelphaceae (*Clavariadelphus*), Gautieriaceae (*Gautieria*), Gomphaceae (*Gloeocantharellus*, *Gomphus*, *Phaeoclavulina*, and *Turbinellus*), Lentariaceae (*Lentaria*), and Ramariaceae (*Ramaria*), distributed within 18 genera and ca. 336 species (Kirk et al. 2008).

Despite their macromorphological variation, the members of the order share a number of microscopic and macrochemical characters, including cyanophilic spore ornamentation, chiasitic basidia, similar hyphal construction, and positive hymenial reaction to ferric sulfate (Donk 1961, 1964; Eriksson 1954; Humpert et al. 2001; Petersen 1971b; Villegas et al. 1999, 2005). In the studies of Hosaka et al. (2006), both Bayesian and parsimony analyses showed strong support for the monophyly of the Phallomycetidae. Even though no definitive synapomorphies have been identified for this gomphoid-phalloid clade, some potential synapomorphic characters, including rhizomorph morphology (presence of ampullate hyphae and acanthohypha), pistillarin content, and structures of septal pore cap, have been proposed (Agerer and Iosifidou 2004; Hibbett and Thorn 2001). In addition, some members of the gomphoid-phalloid clade, such as *Gautieria*, *Hysterangium*, *Ramaria*, and *Geastrum*, are known to produce thick hyphal mats in soil (Agerer and Iosifidou 2004; Nouhra et al. 2005; Sunhede 1989). Although most of these characters are not exclusive to the gomphoid-phalloid fungi, the yellowish filled acanthocystidia and associated “exuded drops of pigments” have been reported only from the gomphoid-phalloid fungi [e.g., *Geastrum*, *Gomphus*, *Phallogaster*, and *Ramaria* (Agerer and Iosifidou 2004)].

4. Hysterangiales

Overview: this group has long been considered a sequestrate (trufflelike) relative of stinkhorns (Phallales). The ordinal status was accepted by some authors (Hosaka et al. 2006; Jülich 1981; Zeller 1939), but others have included the group in the order Phallales (Kirk et al. 2008; Miller and Miller 1988). The order contains

exclusively sequestrate taxa with hypogeous fruit bodies (e.g., *Hysterangium*, *Mesophellia*, *Austrogautieria*) (Fig. 14.4c), but taxa of epigeous habit (e.g., *Gallaceae*, *Phallogaster*) are also known, and they often expose a gleba at maturity (Castellano and Beever 1994). Most taxa are characterized as having gelatinous to cartilaginous glebae of greenish to brownish tint, except Mesophelliaceae, which has a powdery gleba at maturity.

Ecological diversity: most taxa form ectomycorrhizae with various host trees, including Pinaceae and Fagaceae in the Northern Hemisphere and Myrtaceae (mostly *Eucalyptus* and *Leptospermum*) and Nothofagaceae in the Southern Hemisphere. In addition, some recent studies have extended the range of hosts to Caesalpiniaceae, Phyllanthaceae, and Dipterocarpaceae (Castellano et al. 2000; Henkel et al. 2012). Phallogastraceae is the only family in the order with a saprotrophic habit. Some species of *Hysterangium* form dense perennial hyphal mats, which change the soil chemistry and microorganism biomass (Griffiths et al. 1994). Fruiting bodies of Hysterangiaceae and Mesophelliaceae are consumed by small mammals and marsupials, and they often make up a significant portion of the animals’ diet (Claridge 2002; Lehmkuhl et al. 2004).

Systematics: this order was proposed by Zeller (1939), whose treatment was followed by those of Locquin (1974) and Jülich (1981). However, a Latin diagnosis was not provided until Hosaka et al. (2006) formally described the order. The order is strongly supported as being monophyletic by multigene phylogenetic studies (Hosaka et al. 2006, 2008), but its relationships to other orders in Phallomycetidae are not well supported.

Hysterangiales is divided into four families, Hysterangiaceae, Mesophelliaceae, Gallaceaceae, and Phallogastraceae, all of which are strongly supported as being monophyletic (Hosaka et al. 2006, 2008). Hysterangiaceae and Mesophelliaceae form a clade, to which Gallaceaceae is the sister family (Hosaka et al. 2006). Phallogastraceae, the only saprotrophic member of the order, represents the earliest branch, which is separated from the remaining Hysterangiales (Hosaka et al. 2008), suggesting

that the ECM habit was gained only once within the order.

Fifteen genera and ca. 110 species are currently recorded in the order (Kirk et al. 2008), but a number of new species have recently been discovered, mainly from the Southern Hemisphere (Henkel et al. 2011; Hosaka et al. 2008). It has been demonstrated that many genera in this order are polyphyletic. For example, *Hysterangium* spp. are placed in both Hysterangiaceae and Mesophelliaceae (Hosaka et al. 2008). Kirk et al. (2008) included Trappeaceae as the fourth family of the order, but because the genus *Trappea* is also polyphyletic and the type species, *Trappea darkeri*, belongs to Phallales (Hosaka et al. 2006), Trappeaceae should not be included in Hysterangiales.

The biogeography of the order was extensively studied by Hosaka et al. (2008), who demonstrated that the ECM lineages (Hysterangiaceae, Mesophelliaceae, and Gallaceaceae) originated in the Southern Hemisphere (presumably east Gondwana), with a few range expansions to the Northern Hemisphere. Although some area relationships can be explained by vicariance, many sister-group relationships, such as those of taxa from Australia and New Zealand separated by short branches, can only be explained by long-distance dispersal, suggesting that truffle-like fungi are capable of crossing ocean barriers.

E. Trechisporales

Overview: Trechisporales K. H. Larss. (2007) is a relatively small order with ca. 100 species and 8–13 genera. It was described only recently (Hibbett et al. 2007), after DNA studies confirmed it as a distinct clade (Binder et al. 2005; Larsson 2004; Matheny et al. 2007). The majority of species in the order belong to the genus *Trechispora* (including *Cristelloporia*, *Scytinopogon*), a highly diverse genus of mostly corticioid fungi. The other genera contain only corticioid fungi, with the exception of the monotypic polypore genus *Porpomyces*. A number of species in the order have an anamorphic stage: *Aegerita tortuosa* for *Subulicystidium* and *Osteomorpha* for *Trechispora*. Considering that almost all species

in the order form inconspicuous fruiting bodies that rarely get collected and identified, the known species number is likely a fraction of the true diversity.

Fruiting body morphology ranges from clavarioid (*Scytinopogon*), stipitate hydroid (*Trechispora thelephora*), and resupinate polyporeoid (*Porpomyces*, *Trechispora*) to corticioid (Fig. 14.5f–h). Most species either have small spines (aculei) covering their hymenophore or are completely smooth. Fruiting-body-associated rhizomorphs are common, and all species have light-colored fruiting bodies that produce hyaline spores. Some dimitic species are found in *Cristelloporia*, *Fibrodontia*, and *Trechispora*, but most species are monomitic and bear clamps on all septa. Spore morphology is very variable, from very long and narrow spores of *Subulicystidium* to tiny ellipsoid spores of *Porpomyces* and spinose spores in most species of *Trechispora*. Conspicuous subulate cystidia are found in *Subulicystidium* and *Tubulicium*. Calcium oxalate crystals are common on subicular hyphae of *Trechispora* and have been shown to be species-specific in form (Larsson 1994).

Ecological diversity: most species in the genus appear to be white-rot wood-inhabiting (e.g., *Sistotremastrum*) or soil-inhabiting (e.g., *Porpomyces*, *Trechispora*) saprotrophs. *Trechispora* species are difficult to grow with standard culturing techniques for wood-decay fungi, whereas *Sistotremastrum* spp. pose no difficulties. Dunham et al. (2007) reported root-associated mycelial mats formed by *Trechispora*, indicating a possible mycorrhizal association, but further work is needed to confirm this inference. One species (misidentified as *T. alnicola*) has been reported as a grass parasite (Wilkinson 1987).

Systematics: Larsson (2007b) divides the order into two families: Hydnodontaceae Jülich 1982 (=Subulicystidiaceae Jülich 1982) with *Fibrodontia*, *Luellia*, *Porpomyces*, *Subulicystidium*, *Trechispora* (including *Cristelloporia*, *Hydnodon*), *Tubulicium*, and possibly *Subulicium*; and *Sistotremastrum* in its own, yet formally unnamed, family. Telleria et al. (2013) produced a phylogeny of the order and confirmed that *Brevicellicium* is also part of the Hydnodontaceae. Larsson et al. (2011)

and Birkebak et al. (2013) found that the clavarioid genus *Scytinopogon* was nested within *Trechispora*.

Only a few DNA-based species-level papers on Trechisporales have been published: Albee-Scott and Kropp (2010) on *Trechispora*, Telleria et al. (2012) on *Sistotremastrum*, and Telleria et al. (2013) on *Brevicellicium*. Other genera that may belong to the order include the corticioid *Brevicellopsis*, *Dextrinocystis*, and *Dextrinodontia*. A major open question in the systematics of the order is whether *Trechispora* should be divided or kept together so that it includes *Cristelloporia*, *Echinotrema*, *Hydnodon*, and *Scytinopogon*, as most authors currently do.

F. Hymenochaetales

Overview: Hymenochaetales Oberw. 1977 is one of the larger orders of basidiomycetes, with over 900 species and ca. 75 currently recognized genera. The order is dominated by wood-inhabiting polypores and bracket fungi (e.g., *Phellinus*, *Trichaptum*), as well as stereoid and corticioid fungi with a smooth or hydroid hymenophore (e.g., *Hyphodontia*, *Resinicium*). A few coralloid fungi (*Alloclavaria*, *Clavaria-chaete*) and moss-associated agarics (e.g., *Rickenella*) are found in the order (Fig. 14.5a–e). The largest known fruiting body belongs to *Phellinus ellipsoideus* (Dai and Cui 2011).

Most Hymenochaetales species that have been studied have dolipore septa with continuous (imperforate) parenthesomes, in contrast to most other polypores, agarics, and corticioid fungi (van Driel et al. 2009). *Peniophorella praetermissa*, a corticioid fungus, is the only species in the order reported with perforate parenthesomes, but much of the diversity in the order remains unstudied in this respect.

Economically important pathogens of trees include *Rigidoporus microporus* in rubber and other tropical tree plantations (Farid et al. 2009) and *Phellinus sulphurascens* on temperate conifers (Lim et al. 2005). The fruiting bodies of *Inonotus sanghuan*, many *Phellinus* spp., and cankers of *I. obliquus* are used in herbal medicine and are reported to have anti-

cancer properties (Dai et al. 2010; Ju et al. 2010; Wu et al. 2012).

Ecological diversity: the order exhibits a wide variety of different ecological strategies. Most species of Hymenochaetales are white-rot fungi. They are everywhere a major, and often the dominant, part of the wood-rot communities (e.g., species of *Hyphodontia*, *Phellinus*, *Trichaptum*). Two polypore genera (*Coltricia* and *Coltriciella*) form ectomycorrhizae (Tedersoo et al. 2007), and a number of species in other genera are parasites or pathogens of woody plants (e.g., many species of *Inonotus*, *Phellinus* s.l., and *Oxyporus*). Several species of *Peniophorella* have specialized organs for catching invertebrates, apparently an adaptation to a nitrogen-deprived environment (Tzean and Liou 1993). A peculiar ecological group of mostly agarics are moss-associated. Whether the association is parasitic or mutualistic is not clear (Larsson et al. 2006; Redhead 1981).

Systematics: Hymenochaetales as a clade is well supported, but its internal structure is largely unresolved. Larsson et al. (2006) provided the only broad phylogenetic overview of the order. They defined six clades using nuclear rRNA sequences. Some of those clades were not corroborated in other studies using nrDNA, and the branching order of the groups varies from one analysis to another (Ghobad-Nejhad and Dai 2010; Larsson 2007b; Miettinen and Larsson 2010). The genome of *Fomitiporia mediterranea* has been published (Floudas et al. 2012), and two additional genomes (*Rickenella mellea*, *Trichaptum abietinum*) were produced in the US Department of Energy Joint Genome Institute in 2013.

Hymenochaetaceae: this family contains 60 % of described Hymenochaetales species, mostly polypores, a number of stereoid fungi, and a few hydroid fungi. All species in this family are characterized by brown pigments that turn black in KOH (xanthochroic reaction). Hyphae are simple-septate and parenthesomes imperforate in all species studied so far. Many species have characteristic brown cystidia, setae, in the hymenium (which explains the name of the type genus, *Hymenochaete*). Due to morphological similarities, this order has long been recognized in the literature in a way that corresponds to the

current concept: *Phellinus* s.l. (dimitic polypores), *Inonotus* s.l. (monomitic polypores), *Hymenochaete* s.l. (corticoid and hydroid), and *Asterodon* (hydroid). All species are wood inhabiting, and many species are parasites of living trees and bushes. A strange exception is *Phylloporia parasitica*, which reportedly grows on living leaves (Wagner and Ryvarden 2002). Whether the ECM *Coltricia* and *Coltriciella*, traditionally assigned to Hymenochaetaceae, belong here is unclear (see below). Recent regional morphology-based treatments of Hymenochaetaceae include Nuñez and Ryvarden (2000) for East Asia, Ryvarden (2004) for the Neotropics, and Dai (2010) for China. The basis for DNA-based assessments of generic concepts in the group comes from studies of Wagner and Fischer (2001, 2002a, b). Later family-level studies have been few and based on one or two ribosomal genes only (Jeong et al. 2005; Larsson et al. 2006; Parmasto et al. 2013). Many of the newly defined genera have received attention in more focused phylogeny papers: *Inonotus* (Tian et al. 2013), *Phellinus* s.s. (Cui and Decock 2012; Decock et al. 2006; Fischer and Binder 2004; Tomšovský et al. 2010b), *Phellinopsis* (Zhou and Qin 2013), *Phellopilus* (Keller and Hohn 1997), *Porodaedalea* (Brazee and Lindner 2013; Tomšovský et al. 2009), and *Phylloporia* (Valenzuela et al. 2010; Wagner and Ryvarden 2002; Zhou and Dai 2012). The genus *Fomitiporia* in particular has been the subject of many studies (Amalfi and Decock 2013; Amalfi et al. 2010, 2012; Decock et al. 2005, 2007; Fischer 2002; Fischer et al. 2005; Vlasák and Kout 2010). The corticioid genus *Hymenochaete* has turned out to be polyphyletic, and part of the species belongs to a new genus, *Pseudochaete* (He and Dai 2012; He and Li 2013; Parmasto et al. 2013; Wagner and Fischer 2002a). The genus now also includes poroid *Cyclomyces* spp. and hydroid *Hydnochaete* spp. The position of the *Hymenochaete*-like coralloid genus *Clavariachaete* has not been studied, but morphologically it is a typical member of the Hymenochaetaceae (Parmasto 2010).

Schizoporaceae: this species-rich clade contains the bulk of corticioid *Hyphodontia*, now classified in the genus *Xylodon*, one of the largest genera of wood-rotting fungi (Hjortstam and Ryvarden 2007, 2009). Most poroid *Hyphodontia* or *Schizopora* belong here, and micromorphologically the clade is relatively homogeneous. Larsson et al. (2006) included the genus *Coltricia* here and called it the *Coltricia* clade. Here we consider the position of *Coltricia* unresolved. No phylogenetic overview of *Hyphodontia* s.l. or this clade exists. Paulus et al. (2000) studied species phylogeny in *Schizopora*.

Tubulicrinaceae: initially called the *Hyphodontia* clade, Larsson (2007b) used the family name Tubulicrinaceae for this clade. It contains inconspicuous wood-rotting corticioid fungi with a variable micromorphology. The largest genus is *Tubulicrinis*.

Kneiffiella clade: *Kneiffiella* is another segregate genus of *Hyphodontia* sensu lato with many hydroid species. Most species in the clade have characteristic tubular tramal cystidia.

Oxyporus clade: this small clade contains the polypore genus *Oxyporus* and poroid-hydroid *Botryodontia* (Sell et al. 2013). The extent of the genus *Oxyporus* and delimitation against *Rigidoporus* is unclear.

Rickenella clade: this is the most diverse in terms of morphology and ecological strategies of all the Hymenochaetales clades and includes moss-associated agarics (e.g., *Rickenella*), stereoid (*Cotylidia*), clavarioid (*Alloclavaria*), poroid (*Sidera*), and many wood-rotting corticioid (*Peniophorella*, *Resinicium*) species. Larsson (2007b) and Miettinen and Larsson (2010) found this clade to be paraphyletic, and clearly multigene data sets are needed to resolve the structure in this part of the fungal tree. It may be basal to the order, but again the current DNA data do not permit strong statements in this regard. A handful of studies have been conducted at the genus level in this group: Moncalvo et al. (2002) and Redhead et al. (2002) dealt with agarics, Dentinger and McLaughlin (2006) with *Alloclavaria*, Sjökvist et al. (2012) with *Cotylidia* and *Musciniupta*, Larsson (2007b) with *Peniophorella* and other *Hyphoderma* s. l., Miettinen and Larsson (2010) with *Sidera*, and Nakasone (2007, 2012) with *Resinicium* and *Tsugacorticium*. Hallenberg et al. (2007) studied the *Peniophorella praetermissa* species complex.

Lineages of uncertain position: *Coltricia* and *Coltriciella* are the only ECM genera in the order. Larsson et al. (2006) included them in the same clade (named *Coltricia* clade) with parts of *Hyphodontia* (the Schizoporaceae here). The nrDNA of *Coltricia* is highly divergent from that of other Hymenochaetales and occupies a long branch in nrDNA-based analysis, jumping around in phylogenies. Considering the long branch and divergent ecology and morphology, the position of *Coltricia* and *Coltriciella* within the order is in need of further study. Tedersoo et al. (2007) provide the only DNA-based study of the group. The wood-rotting polypore and corticioid genera *Trichaptum*, *Basidiaradulum*, *Cyanotrampa*, *Fibricium*, and *Porodontia* belong in the vicinity of Hymenochaetaceae, but not within it. These genera seem to be somewhat closely related; they do not seem to form a monophyletic group (Binder et al. 2005; Ghobad-Nejhad and Dai 2010; Larsson et al. 2006; Miettinen and Larsson 2010). The polypore genus *Bridgeoporus* is a segregate of *Oxyporus* and has been shown to belong to Hymenochaetales (Redberg et al. 2003). It does not seem to be very closely related to *Oxyporus*, and its position in the order is open.

G. Polyporales

Overview: Polyporales (Gäumann 1926) includes approximately 1,800 described species (Kirk et al. 2008), making it one of the larger orders of Agaricomycetes. However, new spe-

cies are continually being described, even in relatively well-studied areas such as western Europe (Bernicchia et al. 2010; Spirin et al. 2012; Vampola and Vlasak 2012), and the number of species known only from environmental sampling and studies of endophytic communities has increased dramatically in recent years (Fröhlich-Nowoisky et al. 2009, 2012; Hallenberg et al. 2008). Polyporales contains conspicuous bracket fungi, including perennial “conks” (e.g., *Ganoderma applanatum*, *Fomes fomentarius*), as well as more cryptic effused (resupinate) forms, which often fruit on the undersides of logs (Fig. 14.6b–d). Other species have pileate-stipitate fruiting bodies or multiple flabelliform lobes (e.g., *Sparassis*, *Hydnopolyporus*) (Fig. 14.6a, e, f). The hymenophore is frequently poroid (e.g., *Polyporus*) but can also be hydroid (*Steccherinum*), lamellate (*Trametes* [*Lenzites*] *betulina*), merulioid (*Phlebia*), or smooth (*Phanerochaete*). No gasteroid taxa are known, but *Lentinus tigrinus* has a naturally occurring secotioid form in addition to the typical agaricoid form (Hibbett et al. 1994). A few species produce underground sclerotia (e.g., *Lignosus*, *Polyporus*, *Wolfiporia*). The order has varied hyphal anatomy, including monomitic forms (with only generative hyphae, e.g., *Ceriporia*), as well as dimitic and trimitic forms (with thick-walled skeletal or binding hyphae) (Gilbertson and Ryvarden 1986). No morphological synapomorphy characterizes the Polyporales, and the most common morphological types described previously also occur in other orders of Agaricomycetes.

Ecological diversity: along with members of Hymenochaetales and Russulales, members of this order dominate wood-decay communities in terrestrial ecosystems. A few species act as plant pathogens, causing timber damage (e.g., species of *Ganoderma*, *Fomitopsis*, and *Wolfiporia*), and others are major decay agents of structural timber (e.g., *Antrodia*). Wood decayers in Polyporales can be divided into two major groups: white-rot species, which are able to decay both lignin and cellulosic compounds, and brown-rot species, which remove cellulose and hemicellulose without significant lignin degradation (Worrall et al. 1997). *P. chrysosporium* and *P. placenta*, which

are the model systems for white-rot and brown-rot biochemistry (respectively), are both in the Polyporales (Martinez et al. 2004, 2009). No mycorrhizal taxa are known in the order. Many members of Polyporales are commonly isolated as part of the endophytic communities in woody tissues and roots, and though several ecological roles have been proposed for these fungi, from latent saprotrophs to protective agents, their true function remains largely unknown (Porrás-Alfaro et al. 2011).

Systematics: approximately 150 genera and 40 legitimate family names are available for use in Polyporales (Larsson 2007b; Ryvarden 1991), but there is no broadly accepted consensus infraordinal classification. Recent monographs on Polyporales include those of Nuñez and Ryvarden (2000) on East Asian polypores, Ryvarden (2004) on neotropical polypores (Ganodermataceae), Niemelä (2005) and Bernicchia (2005) on European polypores, and Bernicchia et al. (2010) on European corticioid fungi.

The monophyly of Polyporales was not well supported in analyses of rRNA gene sequences (Binder et al. 2005; Larsson 2007b). However, analyses adding single-copy protein-coding genes (García-Sandoval et al. 2011; Justo and Hibbett 2011; Matheny et al. 2007; Miettinen et al. 2012; Sjökvist et al. 2012) and genome-based phylogenetic analyses (Binder et al. 2013; Floudas et al. 2012) have strongly supported the monophyly of the order. The sister group of Polyporales is not known with confidence; in the studies just mentioned, Corticiales, Gloeophyllales, Russulales, and Thelephorales usually seem to be closely related to Polyporales, but relationships between these orders remain in need of further study.

The studies of Binder et al. (2005, 2013) provide broad overviews of the major lineages of Polyporales based on taxon-rich sampling of rRNA genes in combination with *rpb1*, *rpb2*, and *tef1* sequences, as well as gene-dense phylogenomic analyses. Four major groups have been informally labeled as the *Antrodia*, core polyporoid, phlebioid, and “residual” clades, the latter being more a mixed bag of taxa that did not fit in the other clades. Larsson (2007b) and Miettinen et al. (2012) sought to apply

existing family names to parts of the clades recognized in phylogenetic analyses.

Residual polyporoid clade: the monophyly of this clade remains uncertain. All taxa in this group produce a white rot, which is probably plesiomorphic for the Polyporales (Floudas et al. 2012), but morphologically they are very diverse and include poroid (*Rigidoporus*), agaricoid (*Panus*), corticioid (*Hyphoderma*), resupinate-hydroid (*Steccherinum*), and stipitate-steroid forms (*Podoscypha*). Representative taxa that have been the subject of recent phylogenetic studies include *Anetrodiella* (Miettinen et al. 2012), *Cerrera* (Lee and Lim 2009), *Hyphoderma* (Larsson 2007a), *Hypochnicium* (Telleria et al. 2010), *Pseudolagarobasidium* (Hallenberg et al. 2008), *Podoscypha* (Sjkvist et al. 2012), and *Steccherinum* (Miettinen et al. 2012). The group exemplifies the numerous transitions in hymenophore types and microscopic characters (e.g., cystidia and hyphal types) that have occurred repeatedly during the evolution of the Polyporales (Miettinen et al. 2012).

Phlebioid clade: largely dominated by corticioid forms, much of the taxonomy of this diverse group revolves around two large, highly polyphyletic genera, *Phlebia* and *Phanerochaete*, and their limits and relations with respect to several smaller genera. A number of polypore genera are also found in the clade (e.g., *Bjerkandera*, *Ceriporia* and *Irpex*). Taxa that have been the subject of phylogenetic studies include *Ceriporia* (Jia et al. 2013), *Ceriporiopsis* (Tomšovský et al. 2010a), *Phanerochaete* (De Koker et al. 2003; Greslebin 2004; Wu et al. 2010), and *Trametopsis* (Tomšovský 2008). *Leptoporus*, a close relative of *Ceriporia*, is often considered a brown-rot fungus (Gilbertson and Ryvarden 1986) and would be the only brown rotter in this lineage of white-rot taxa (Lindner and Banik 2008).

Antrodia clade: this lineage includes exclusively species that produce a brown-rot type of decay. The majority of all known brown-rot fungi belong to this clade. Pileate and resupinate polypores are predominant, along with a few corticioid taxa (e.g., *Dacryobolus*, possibly *Crustoderma*). Several genera have received attention in phylogenetic studies, including *Antrodia* sensu lato (Bernicchia et al. 2010; Rajchenberg et al. 2011; Spirin et al. 2013; Yu et al. 2010), *Daedalea* (Lindner et al. 2011), *Fomitopsis* (Kim et al. 2007), *Laetiporus* (Lindner and Banik 2008), *Postia* sensu lato (Pildain and Rajchenberg 2013), and *Sparassis* (Dai et al. 2006; Wang et al. 2004). A general overview of the clade is given by Ortiz-Santana et al. (2013), who showed that generic delimitation remains highly problematic, with most of the traditionally recognized genera being poly- or paraphyletic.

Core polyporoid clade: this group roughly corresponds to the families Polyporaceae and Ganodermataceae in the sense of Ryvarden (1991) and includes mostly polypores with a trimitic hyphal system. Some corticioid (*Epithele*, *Lopharia*) and agaricoid

taxa (*Lentinus*) are also nested in the clade. This is the best sampled lineage of Polyporales, both in terms of taxa and genes, and the only one with a well-supported internal structure. Three major lineages were recognized by Justo and Hibbett (2011), termed the *Dentocorticium*, trametoid, and *Polyporus* clades. Representative genera with recent phylogenetic studies include *Lentinus* (Grand et al. 2010), *Megasporoporia* (Li and Cui 2013), *Melanoderma* (Cui et al. 2011), *Perenniporia* s. lato (Decock and Ryvarden 2003; Robledo et al. 2009; Zhao et al. 2013), *Polyporus* s. lato (Krger 2008, 2010; Krger and Gargas 2004; Sotome et al. 2008, 2013), and *Trametes* (Justo and Hibbett 2011; Tomšovský 2008; Welti et al. 2012).

Lineages of uncertain position: three relatively small lineages of white-rot polypores seem to be closely related to the *Antrodia* or core polyporoid clades, but they apparently do not belong to either group (Binder et al. 2013; Miettinen and Rajchenberg 2011). These lineages include the genus *Grifola*, the *Tyromyces* clade (*Piloporia*, *Skeletocutis*, *Tyromyces*), and the *Cinereomyces*/*Gelatoporia* clade (*Cinereomyces*, *Gelatoporia*, *Obba*, *Sebipora*). Resolving the position of these lineages and the phylogenetic structure of the residual polyporoid clade are two major issues for the higher-level taxonomy of Polyporales. Improving the internal resolution in the phlebioid, antrodia, and core polyporoid clades is necessary to move forward in the family-level and generic taxonomy of these groups.

H. Thelephorales

Overview: Thelephorales is a strongly supported clade that currently includes ca. 18 genera and 269 described species (Kirk et al. 2008). The group is morphologically diverse and contains corticioid (*Tomentella*), cantharelloid (*Polyozellus multiplex*), clavarioid (*Thelephora*), and pileate forms (*Hydnellum*) (Fig. 14.7c, d). Hymenophores of pileate taxa may be poroid (*Boletopsis*), toothed (*Hydnellum*, *Sarcodon*), smooth to wrinkled or tuberculate (*Thelephora*), or lamellate (*Lenzites*). It was once suggested that the pileate-stipitate agaric *Horakia* (= *Verrucospora*) was related to Thelephoraceae based on spore morphology (Oberwinkler 1975), but molecular data place it in Agaricales (Matheny et al. 2006), as had been suggested by Singer (1986). Basidiospores are mostly dark, ornamented, and with a distinctive angular outline but may also be subglobose and spinose (*Bankera* and *Phellodon*). Thelephoric acid (a terphenyl quinone, similar to atrotomentin) is found in *Bankera*,

Boletopsis, *Hydnellum*, *Phellodon*, *Polyozellus*, *Pseudotomentella*, *Sarcodon*, and *Thelephora*. This compound also occurs in Boletales and other orders but nonetheless seems to be a distinguishing feature of the group (Bresinsky and Rennschmid 1971).

Ecological diversity: most members of Thelephorales are ECM and are often dominant components of mycorrhizal communities (Bruns et al. 1998; Tedersoo et al. 2010). However, *Lenzites* produces fruiting bodies on wood of junipers and is reported to produce a white rot (Zhou and Kõljalg 2013). *Amaurodon* is also reported to grow on wood of living trees (U. Kõljalg, unpublished) and is presumably nonmycorrhizal. *Amaurodon* has been placed as the sister group to the remaining Thelephorales, but *Lenzites* is nested within the group, closely related to *Tomentellopsis*, suggesting that there have been multiple transitions between nutritional modes (Larsson 2007b; Zhou and Kõljalg 2013).

Systematics: the current classification of Thelephorales (Kirk et al. 2008) includes two families, Thelephoraceae and Bankeraceae. Donk (1964, p. 247) thought that the similarity of the Bankeraceae to certain Thelephoraceae was “an example of extreme convergence,” but other authors suggested that the two families were closely related (Jülich 1981; Stalpers 1993), and this has been repeatedly supported by molecular data (Binder et al. 2005; Bruns et al. 1998; Larsson 2004, 2007b; Zhou and Kõljalg 2013). The analysis of Zhou and Kõljalg (2013) resolved two nonsister clades corresponding to Bankeraceae (one including *Bankera* and *Phellodon* and another containing *Hydnellum*, *Sarcodon*, and *Boletopsis*) and a paraphyletic assemblage of taxa corresponding to Thelephoraceae. However, internal support for many deep nodes was weak. An in-depth multi-gene phylogenetic analysis is needed to assess the classification of the order.

I. Corticiales

Overview: Corticiales K.H. Larsson is a small order established to accommodate basidiomycetes recognized in recent molecular phyloge-

netic studies and included previously in the Vuilleminiales (Boidin et al. 1998), the *Dendrocorticium* clade (Binder and Hibbett 2002), and the corticioid clade (Binder et al. 2005; Larsson et al. 2004). It has been represented by a single family, Corticiaeae Herter, made up of ca. 29 genera and 136 species (Kirk et al. 2008), but the molecular phylogenetic study of Ghobad-Nejhad et al. (2010) recognized three families and several new genera (discussed subsequently). The order is made up of mostly resupinate species that produce smooth hymenophores, a monomitic hyphal system with or without clamps, and smooth basidiospores, often with pink walls. Many species produce pink or red basidiomata with a cataphymenium in which young basidia do not form a palisade but are formed deep within a layer of hyphidia and then elongate to reach the hymenial surface, and some have dendrohyphidia; however, there is no morphological synapomorphy that characterizes the entire order.

Some species are known only from asexual stages. One genus of these is the anamorph-typified *Marchandiomyces*, which was commonly included as a core genus in recent molecular studies. The genus was originally established for asexual lichen parasites (Diederich 1990; Etayo and Diederich 1996), but sexual forms are also now known for the group. These include *Marchandiobasidium aurantiacum* as the teleomorph of *Marchandiomyces aurantiacus* (Diederich et al. 2003) and *Marchandiopsis quercina*, a species previously assigned to *Laeticorticium* or *Vuilleminia* that was found to be nested among asexual *Marchandiomyces* species by Ghobad-Nejhad et al. (2010). The clade containing *Marchandiomyces* also includes described plant pathogens in the teleomorph-typified genera *Laetisaria* and *Limonomyces*, indicating that sexual–asexual relationships among these species will require more study. The type species of the order, *Corticium roseum*, may form a bulbil-like anamorph known as *Hyphelia rosea*; these bulbils are similar to those of *Laetisaria* and *Marchandiomyces* (Eriksson and Ryvarden 1976).

Ecological diversity: fungi in Corticiales exhibit a remarkable range of ecologies, including saprotrophs, plant pathogens, lichen

pathogens, and lichenized species (Lawrey et al. 2008). The basal position of saprotrophic species in Vuilleminiaceae and Punctulariaceae would indicate that this is the ancestral condition for the order, but the most derived clade, Corticiaceae, contains a complex mixture of ecological forms, which suggests an unusual tendency for ecological transitions (Ghobad-Nejhad et al. 2010; Lawrey et al. 2008). Ecology can sometimes be used to characterize genera, but most clades in this order have mixtures of nutritional modes. Entirely saprotrophic genera include *Corticium*, *Giulia*, and *Galzinia*, but *Erythrimum*, which is mostly saprotrophic, also includes the plant pathogen *Erythrimum salmonicolor*.

Most species of *Limonomyces*, *Laetisaria*, and *Waitea* are plant pathogens or endophytes but are able to persist in the field as saprotrophs (Andjic et al. 2005; Burdsall 1979; Burdsall et al. 1980; Stalpers and Loerakker 1982). However, *Laetisaria* also includes the lichen parasite *L. lichenicola* (Diederich et al. 2011). *Marchandiomyces*, originally described for lichen parasites (Diederich 1990; Etayo and Diederich 1996), is now known to include saprotrophic and foliicolous species (Diederich and Lawrey 2007; Lawrey et al. 2007, 2008). There is also one lichen-forming species, *Marchandiomphalina foliacea* (Lawrey et al. 2008; Palice et al. 2005), which seems to be most closely related to the lichen parasite *Marchandiobasidium aurantiacum* and the saprotrophic *Erythrimum laetum*. Lichen mutualisms have evolved independently in Basidiomycota at least five times (Diederich and Lawrey 2007; Diederich et al. 2003, 2011; Ertz et al. 2008; Fischer et al. 2007; Hodkinson et al. 2012; Lawrey et al. 2007, 2008, 2009; Nelsen et al. 2007; Redhead et al. 2002). *Marchandiomphalina foliacea* is the only described lichen species in Corticiales. It forms a foliose thallus structure and asexual goniocysts resembling soredia, but no sexual stages are known (Jørgensen 1989).

Systematics: the monophyly of Corticiales is strongly supported by molecular phylogenies, mostly based on rRNA gene sequences (Binder et al. 2005; Boidin et al. 1998; DePriest et al. 2005; Diederich et al. 2011; Ghobad-Nejhad et al. 2010; Hibbett et al. 2007; Langer

2002; Larsson 2007b; Larsson et al. 2004; Lawrey et al. 2008). The sister group of Corticiales seems, on the basis of many of these studies, to be the order Gloeophyllales. One species of Corticiales, *Punctularia strigoso-zonata*, has been subject to whole-genome sequencing; phylogenomic analyses suggest that it is in a clade that also includes Gloeophyllales and Jaapiales (Fig. 14.1). A recent attempt to produce an infraordinal classification of Corticiales is based on a molecular phylogeny using nuc-lsu rRNA sequences (Ghobad-Nejhad et al. 2010). This analysis resolved three groups that were recognized at the family level using the existing names, Vuilleminiaceae, Punctulariaceae, and Corticiaceae. Until more sequences become available and more specimens sequenced, this represents the best current hypothesis for a family classification of the order.

Vuilleminiaceae Maire ex Lotsy: this clade contains saprotrophic species that develop dendrohyphidia and produce clamps and generally allantoid spores and gelatinous fruiting bodies. It includes the genera *Vuilleminia* and *Cytidia* and a new genus, *Australovuilleminia* (for *Vuilleminia coccinea*). Based on their molecular phylogeny and incompatibility crossing tests, Ghobad-Nejhad et al. (2010) found that the so-called core *Vuilleminia* species (*V. macrospora*, *V. pseudocystidia*, *V. alni*, *V. comedens*, *V. megalospora*) form a monophyletic group. These species are all decorating, produce a gelatinous fruiting body, and exhibit a unique 13 bp insertion in the ITS2. Other described *Vuilleminia* species (*V. cystidiata* and *V. macrospora*) were recovered in the *Vuilleminia* clade but outside of the core *Vuilleminia* clade. Other species were recovered outside of the *Vuilleminia* clade and reassigned to new genera, including *V. (Punctulariopsis) obdusces* and *V. (Punctulariopsis) subglobispora*, which were recovered in the *Punctularia* clade, and *Vuilleminia (Marchandiopsis) quercina*, which was recovered in the *Corticium* clade.

Punctulariaceae Donk: the family introduced by Donk (1964) was intended to separate *Punctularia* species from other corticioid fungi in the Aphyllophorales, but few classifications recognized it, placing most corticioid species in the Corticiaceae. In the nuc-lsu rRNA phylogeny of Ghobad-Nejhad et al. (2010), this is a clade of saprotrophic species that produces clamps and ellipsoid spores and includes the genera *Punctularia* and *Dendrocorticium* and a new genus, *Punctulariopsis* (for *Vuilleminia subglobispora* and *Vuilleminia obdusces*). These species cause a vigorous white rot compared to species in *Corticium*.

Corticiaceae Herter: this family, originally conserved against Vuilleminiaceae (Pouzar 1985) to represent a much broader circumscription than has emerged in recent molecular-based classifications, is now viewed by Ghobad-Nejhad et al. (2010) as a well-supported clade containing species with and without clamps, including the type species of *Corticium*, and a variety of sexual and asexual genera with diverse nutritional modes (*Erythricium*, *Galzinia*, *Giulia*, *Laetisaria*, *Limonomycetes*, *Marchandiobasidium*, *Marchandiophyalina*, *Marchandiomyces*, *Marchandiopsis*, and *Waitea*). As mentioned by these authors, Corticiaceae is by far the most diverse family in Corticiales, both morphologically and ecologically. It also contains several polyphyletic genera in need of revision. The single most problematic clade, containing *Marchandiomyces*, *Marchandiopsis*, *Limonomycetes*, and *Laetisaria*, is also the most interesting ecologically. Improving the internal resolution in this clade will not only resolve the generic taxonomy of these groups but also help to clarify some of the most interesting ecological transitions in Agaricomycetes.

J. Jaapiales

Overview: Jaapiales Manfr. Binder, K.H. Larss. & Hibbett (Binder et al. 2010) is the smallest order of Agaricomycetes, with a single genus of just two species, *Jaapia argillacea* and *J. ochroleuca*. Fruiting bodies of both species are resupinate, at first patchy, then thinly effused and monomitic, with thin-walled hyphae and frequent clamp connections. Basidiospores are narrowly fusoid (boletinoid) and cyanophilous.

Ecological diversity: both species of *Jaapia* fruit on wet, rotting wood on the margins of lakes and streams and are collected infrequently (Eriksson and Ryvarden 1976). Only *J. argillacea* is known in culture, and it is unreactive in tests for laccase, peroxidases, or tyrosinase (Stalpers 1978). Thus, *Jaapia* species might be brown-rot saprotrophs or ECM, but the biology of this group is unknown. BLAST searches using the sequences of *J. argillacea* or *J. ochroleuca* yield very few matches among environmental sequences, a rarity in the Agaricomycetes. At present, the only sequence matches are to a few ITS sequences of uncultured fungi from permafrost. It is likely that woody substrates in aquatic habitats have

been undersampled for sequences of Basidiomycota, as well as for their fruiting bodies.

Systematics: the genus *Jaapia* Bres. was referred to the Coniophoraceae (Boletales) (Eriksson and Ryvarden 1976; Nannfeldt and Eriksson 1953) but later recognized as distinct from Boletales in rDNA analyses of Binder et al. (2005) and Larsson (2007a). The latter study, based on analyses of sequences of 5.8S and nuclear rRNA, confirmed that *J. ochroleuca* is a member of the same lineage as the type species, *J. argillacea*. A 6-gene phylogeny placed *J. argillacea* as a sister group to Agaricomycetidae (Atheliales, Boletales, Amylocorticiales, and Agaricales) (Binder et al. 2010), but phylogenomic analyses place Jaapiales in a well-supported clade with Corticiales and Gloeophyllales (Fig. 14.1).

K. Gloeophyllales

Overview: Gloeophyllales Thorn is an odd taxon with no morphological or ecological characters that unite the 6 genera and perhaps 40 species (Hibbett et al. 2007; Kirk et al. 2008). The type genus, *Gloeophyllum*, is a bracket fungus with resupinate, effused-reflexed, or pileate fruiting bodies and poroid, daedaleoid, or lamellate hymenophores (Gilbertson and Ryvarden 1986). *Boreostereum*, *Chaetodermella*, and *Veluticeps* (including *Columnocystis*) are corticioid to stereoid, with resupinate to effused-reflexed fruiting bodies having a smooth or rugose-wrinkled hymenophore (Chamuris 1988; Eriksson and Ryvarden 1973; Nakasone 1990b) (Fig. 14.7b). *Neolentinus* and *Heliocybe* produce agaricoid fruiting bodies with a central or eccentric stipe, a convex to upturned pileus, and adnexed to decurrent lamellae (Redhead and Ginns 1985) (Fig. 14.7a). Most taxa are dimitic, but some are monomitic, and others trimitic. Simple clamp connections are constant (most taxa), rare (some *Veluticeps* in culture), or absent (*Boreostereum*). The context is pallid in *Heliocybe* and *Neolentinus* but brown in most other taxa and browning in KOH (turning green with KOH in *Boreostereum*) (Hibbett et al. 2007).

Sexuality ranges from homothallic (*Boreostereum*, several *Veluticeps*) to heterothallic and bipolar (*Gloeophyllum*, *Heliocybe*, *Neolentinus*) or tetrapolar (*V. berkeleyi*) (Ginns and Lefebvre 1993).

Ecological diversity: members of Gloeophyllales are wood-decay fungi mostly causing a brown rot of conifers, occasionally angiosperms, and frequently in wood in service. *Neolentinus lepideus* is known as the “train-wrecker” for its propensity to decay wooden railway trestles in bygone days (Redhead and Ginns 1985), and species of *Gloeophyllum* commonly decay outdoor wooden structures such as decks, playground equipment, and picnic tables, and sometimes wooden joists and timbers in homes (Gilbertson and Ryvarden 1986). *Chaetodermella* and *Veluticeps* cause brown rots of conifers, *Heliocybe* on angiosperms, often in quite dry situations such as fence posts or rails and exposed, decorticated logs. However, *Boreostereum*, which seems to be a sister group to the remainder of the order in a 6-gene phylogenetic analysis (Garcia-Sandoval et al. 2011), is associated with white rot of fire-charred coniferous or angiosperm wood, although spot tests for laccases, peroxidases, and tyrosinase in culture have been equivocal (Chamuris 1988; Nakasone 1990a).

Systematics: the core of Gloeophyllales was recognized by Kim and Jung (2000) as Chaetodermataceae, and the link between *Gloeophyllum*, *Heliocybe*, and *Neolentinus* was made by Thorn et al. (2000). Studies by Binder et al. (2005) strongly supported early suggestions (Hibbett and Donoghue 1995; Hibbett et al. 1997b) that *Gloeophyllum* was set apart from the true polypores and formed the basis for describing the Gloeophyllales (Hibbett et al. 2007). The polypore *Donkioporia*, which causes a white rot of conifer wood in service, was included in the order when it was first described (Hibbett et al. 2007) on the basis of its clustering in the *Gloeophyllum* clade in analyses of nuc-18S rRNA sequence data by Kim and Jung (2000, 2001), but it can now be excluded as a member of the core polyporoid clade (Garcia-Sandoval et al. 2011). In addition to the six genera known to belong to the order on the basis of molecular studies, *Campylo-*

myces and *Pileodon*, which are segregates of *Veluticeps* (Nakasone 1990b), and *Mycothele* have been referred here, but no sequence data are available. *Mycobonia*, from which *Mycothele* was segregated, has also been suggested as belonging in Gloeophyllales, but analyses of rRNA gene sequences place it in the core polyporoid clade of Polyporales (Krüger and Gargas 2004).

Garcia-Sandoval et al. (2011) presented a 6-gene phylogenetic analysis of 18 species representing the 6 genera accepted in Gloeophyllales. Their results suggest that *Gloeophyllum* consists of at least two clades, one containing the type species, *G. sepium*, as well as *G. striatum*, *G. subferrugineum*, and *G. trabeum* (all species known from wood in service), and the other containing the type species of *Osmoporus*, *O. odoratus*, as well as *Osmoporus protractus* (both on exposed conifer wood in boreal-subarctic environments) (Garcia-Sandoval et al. 2011). *Gloeophyllum mexicanum* and *Gloeophyllum carbonarium* were basal to *Osmoporus*, and each might represent segregate genera upon further study. In addition, the type species of *Veluticeps* (*V. berkeleyi*), *Columnocystis* (*C. abietina*), and *Chaetodermella* (*C. luna*) formed a weakly supported clade for which the oldest generic name is *Veluticeps*. A sequence of *V. fimbriata* was placed on a long branch that split the genus *Neolentinus*, but other analyses placed it together with the remaining species of *Veluticeps*, and *Heliocybe* was recovered as sister to *Neolentinus*, leaving the possibility of its synonymy with *Neolentinus* undecided (Garcia-Sandoval et al. 2011). Thus, for the moment we advocate recognition of *Boreostereum*, *Gloeophyllum*, *Heliocybe*, *Neolentinus*, *Osmoporus*, and *Veluticeps* in Gloeophyllales.

L. Russulales

Overview: Russulales currently includes more than 1,700 described species (Kirk et al. 2008). This high number corresponds to an equally astonishing diversity of fruiting body morphologies (Fig. 14.8) and life strategies. From a phylogenetic perspective, the dominant life form is

the skinlike, effused, and resupinate basidioma, often developing out of sight at the underside of decaying wood on the ground (Larsson and Larsson 2003). Examples include *Asterostroma*, *Gloeocystidiellum*, and *Boidinia*. From ancestors with such inconspicuous basidiomata, elaborate fruiting structures have developed, for example, coralloid in *Lachnocladium*, *Hericium*, and *Arctomyces* (Fig. 14.8c); reflexed and bracketlike as in *Echinodontium*, *Stereum*, *Laurilia* (Fig. 14.8b), and (some species of) *Lentinellus*; pileate-stipitate mushrooms as in *Russula*, *Lactarius* (Fig. 14.8a), and *Albatrellus*; or sequestrate as in *Macowanites* (Fig. 14.8d, e) and *Leucophleps*. The hymenophore is most often smooth (e.g., *Peniophora*, *Stereum*) or hydroid (e.g., *Auriscalpium*, *Hericium*), while a poroid hymenophore configuration is comparatively rare (e.g., *Albatrellus*, *Heterobasidion*, *Wrightoporia*). A lamellate hymenophore is known from Auriscalpiaceae (*Lentinellus*) and Russulaceae only. Many species have basidiospores with an amyloid reaction of the spore wall, and for most of them the amyloidity is combined with an ornamented outline of the wall.

There is no obvious morphological synapomorphy for Russulales, but the presence of gloeoplerous hyphae or gloecystidia with contents rich in sesquiterpenes has not been demonstrated in any other basidiomycete order (Larsson and Larsson 2003). In a few cases such structures seem to have been secondarily lost (e.g., in *Byssoporia*) or transformed into homologous structures such as the lactiferous hyphae in *Stereum*. The term *gloeocystidium* refers to enclosed, bladderlike structures in fruiting bodies (Cléménçon 2004). Structures termed *gloeocystidia* have been reported in many orders, but the specific type present in Russulales is associated with unique vesicles with tubular invaginations, which may constitute a synapomorphy for the order (McLaughlin et al. 2008). In Russulales the gloeoplerous hyphae and gloecystidia have been suggested to serve as a chemical defense system against mycophagy (Sterner et al. 1985).

Ecological diversity: the dominant nutritional strategy in Russulales is saprotrophic decay of organic matter, primarily wood. In Russulales only white rot has been documen-

ted. It can be highly intense, for example, by species in *Stereum* and *Scytinostroma*, and sometimes characteristic like the white pocket rot produced by *Conferticium* and *Xylobolus* spp. (Otjen and Blanchette 1984). Some species are capable of infecting living trees and perform decay in roots or heartwood. *Heterobasidion annosum* is considered the most severe forest pathogen in conifer forests in the Northern Hemisphere, causing economic losses of \$1 billion annually in the USA alone (Woodward et al. 1998). Other species with a potentially pathogenic behavior in managed forests are *Echinodontium tinctorium*, *Hericium erinaceus*, *Scytinostroma galactinum*, and *Stereum sanguinolentum*.

Another threat to forestry is caused by wood wasps from the family Siricidae living in symbiosis with members of *Amylostereum* (Slippers et al. 2003). The wasp female transfers conidia of the fungus when she places eggs inside the wood of stressed trees using her needlelike ovipositor organ. Larvae then feed on the fungus while mining through fungus-infested wood. Infection by *Amylostereum areolatum* and its vector, *Sirex noctilio*, normally does not cause much damage within its native range in Europe and Asia. However, when the wasp was accidentally introduced into the Southern Hemisphere and in North America, infections in both exotic pine plantations and native American pine stands have become severe (Nielsen et al. 2009; Slippers et al. 2001).

ECM associations have developed independently within two Russulales lineages, in Russulaceae and in Albatrellaceae. Molecular phylogenies suggest that in Russulaceae the evolution proceeded from a saprotrophic to a mycorrhizal nutritional strategy and coincides with the development of erect fruiting bodies from effused ancestors (Larsson and Larsson 2003). Another trend confined to the same families is gasteromycetization (Albee-Scott 2007), which involves the evolution of closed fruiting bodies adapted for a dryer climate and animal dispersal. It is likely that change in lifestyle has driven the development of erect and closed fruiting structures since both are better adapted for a soil-oriented life than the effused structure typical for wood decayers.

Systematics: the potential presence of a russuloid lineage with the wide circumscription accepted here was first discussed by Donk (1971). Oberwinkler (1977) elaborated on Donk's ideas and used Russulales as an example of a higher-order group that contained multiple fruiting body morphologies. Molecular data have confirmed that Russulales sensu Oberwinkler is a monophyletic group (Bruns et al. 1998; Hibbett et al. 1997b, 2000; Larsson 2007b; Larsson et al. 2004; Binder et al. 2005). The most comprehensive phylogenies for Russulales have been published by Larsson and Larsson (2003) and Miller et al. (2006). Larsson and Larsson (2003) identified ten well-supported lineages that can be understood as representing families; the main lineages are briefly discussed in what follows. For many genera relationships are still not resolved.

Stereaceae (14 genera) is dominated by corticioid forms with a smooth hymenophore and smooth basidiospores. Most species fruit in exposed places like living or recently dead trunks and branches and have morphological adaptations for resisting drought. Examples include *Stereum*, *Aleurodiscus* sensu lato, *Aleurocystidiellum*, and *Xylobolus*. Only *Aleurodiscus* has been the subject of a detailed phylogenetic study (Wu et al. 2001).

Peniophoraceae (16 genera) includes mainly corticioid species with a smooth hymenophore and smooth spores, not always with an amyloid reaction of the spore wall. Some genera are characterized by branched, dextrinoid skeletal hyphae (e.g., *Scytinostroma*, *Vararia*). These genera are often referred to a separate family Lachnocladiaceae, but molecular data do not support its recognition. Also in this family, many species grow rather exposed and decay dead but still attached branches (*Peniophora*, *Scytinostroma*). Closely related to *Peniophora* is *Entomocorticium*, known as symbionts of bark beetles of the genus *Dendroctonus* that cause great damage to pine forests (Harrington 2005). Morphological studies of single genera are available, but a comprehensive phylogeny for the family is lacking.

Russulaceae (six genera) is the most species-rich family due to the high diversity seen in the mushroom genera *Lactarius* and *Russula*. Recent phylogenetic studies have shown that *Russula* is monophyletic, but *Lactarius* in a traditional sense is not (Buyck et al. 2008). The latter group is now divided into *Lactarius*, *Lactifluus*, and *Multifurca*. The many genera with sequestrate species recognized earlier (e.g., *Arcangeliiella*, *Macowanites*) are now considered examples of adaptations to a dry habitat and animal dispersal that

has repeatedly taken place within *Lactarius* and *Russula*, respectively (Lebel and Tonkin 2007; Miller et al. 2001; Nuytinck et al. 2004). Basal lineages are composed of saprotrophic taxa with corticioid fruiting bodies (*Boidinia*, *Gloeopeniophorella*) (Larsson and Larsson 2003). All species in Russulaceae have ornamented spores.

Albatrellaceae (six genera) is the second family where a mycorrhizal life strategy predominates. Species are stipitate-poroid (*Albatrellus*, *Polyporoletus*), effused-poroid (*Byssoporia*), or sequestrate (e.g., *Mycoscleris*). Smith et al. (2013) present a phylogeny for the family.

Hericiaceae (three genera) species have coralloid or effused basidiocarps that are mostly strongly hydroid. *Hericium erinaceus* (lion's mane, monkey's head) has been much used in Chinese folk medicine, and modern studies have demonstrated the presence of many medically active substances in this and related species (Lindequist et al. 2005; Mizuno 1999). A phylogeny for the genus is presented by Hallenberg et al. (2013).

Auriscalpiaceae (four genera) includes lamellate (*Lentinellus*), stipitate-hydroid (*Auriscalpium*), and effused-hydroid basidiocarps (*Dentipratulum*, *Gloioodon*).

Bondarzewiaceae (four genera) is a small family of hard and robust wood-decaying species with either a poroid (*Bondarzewia*, *Heterobasidium*) or a hydroid hymenophore (*Echinodontium*).

***Incertae sedis*:** the clavarioid genus *Artomyces* is sometimes included in Auriscalpiaceae, but that arrangement is not unambiguously supported by molecular data. *Amylostereum* could be placed in Bondarzewiaceae but also recognized as a separate family (Binder et al. 2005).

M. Agaricomycetidae

Agaricomycetidae contains two large and well-known orders, Agaricales and Boletales, as well as three small groups containing mostly corticioid forms, Atheliales, Amylocorticiales, and Lepidostromatales. Russulales seems to be the sister group of Agaricomycetidae. The clade containing Agaricomycetidae and Russulales largely corresponds to Agaricales sensu Singer (1986), which included four suborders, Agaricineae, Boletineae, Russulineae, and Polyporineae. The latter included agaricoid forms in *Lentinus* and other genera that are now known to be distributed among Polyporales, Gloeophyllales, and Agaricales.

1. Atheliales and Lepidostromatales

Overview: Atheliales Jülich in a broad sense includes 22 genera with 110 described species (Kirk et al. 2008). However, several genera of Atheliales are polyphyletic (e.g., some *Athelia*, *Athelopsis*, and *Leptosporomyces* species) with species in Agaricales, Amylocorticiales, Cantharellales, and Polyporales (Binder et al. 2005, 2010; Ertz et al. 2008; Larsson 2007b; Larsson et al. 2004; Matheny et al. 2006; Oberwinkler 2012). Many athelioid species produce loosely connected resupinate fruiting bodies lacking conspicuous morphological differentiation on various substrates, including branches, wooden debris, and mosses (Fig. 14.9d) (Larsson et al. 2004). *Stereopsis vitellina* forming stipitate-stereoid basidiocarps was recently separated from Cantharellales and placed in Atheliales (Sjökqvist et al. 2012). The lichenized Lepidostromataceae was originally placed in a sister-group relationship to Atheliales and included three species that produce clavarioid basidiocarps similar to *Multiclavula* spp. in Cantharellales (Ertz et al. 2008).

Ecological diversity: Atheliales is not a species-rich group, but it is pervasive in terrestrial ecosystems. Some *Athelia* species parasitize cyanobacteria, green algae, and lichens (Oberwinkler 1970; Yurchenko and Golubkov 2003), and it has been suggested that the lifestyle of the lichen-forming Lepidostromataceae can be considered a similar form of interaction (Oberwinkler 2012). Other *Athelia*, *Athelopsis*, and *Tretomyces* spp. produce white rot on various trees, debris, leaf litter, grasses, and ferns (Eriksson and Ryvarden 1973; Kotiranta and Saarenoksa 2005; Kotiranta et al. 2011). Brown rot is absent in Atheliales (Binder et al. 2010). The *Athelia* anamorph *Fibulorhizoctonia* forms symbioses with termites by producing sclerotia that mimic termite eggs (Matsuura et al. 2000). *Amphinema*, *Byssocorticium*, *Piloderma*, and *Tylospora* spp. are ECM with Pinaceae and Fagaceae and are often dominant in ECM fungal communities (Erland and Taylor 1999; Lilleskov et al. 2004).

Systematics: Atheliales currently includes Atheliaceae as a single family. Lepidostromataceae had been formally left in Agaricomyceti-

dae *incertae sedis* based on mixed support values from rDNA analyses (Ertz et al. 2008). In a recent multigene study this family was recognized as the order Lepidostromatales, including the genera *Lepidostroma*, *Sulzbacheromyces*, and *Ertzia* (Hodkinson et al. 2013). A taxonomic revision of Atheliaceae on the generic level is needed because new taxa are being described (Kotiranta et al. 2011) and previously unknown lineages are being added to the family (Sjökqvist et al. 2012).

2. Amylocorticiales

Overview: Amylocorticiales K.H. Larss., Manfr. Binder & Hibbett is a recently described order (Binder et al. 2010) that includes roughly 70 species. Taxonomic concepts at the generic level are still in flux (Binder et al. 2005, 2010; Buyck et al. 2012; Gorjón et al. 2011; Larsson 2007b; Niemelä et al. 2007; Zmitrovich and Spirin 2002). Species of the nine genera accepted in Amylocorticiales usually form corticioid and resupinate fruiting bodies and produce smooth, merulioid, or sometimes poroid hymenophores (*Amylocorticium*, *Amylocorticium*, *Anomoloma*, *Anomoporia*, *Ceraceomyces*, *Serpulomyces*) (Fig. 14.9b). Others have evolved more elaborate fruiting bodies, including multistoried pileate-stipitate structures (*Podoserpula pusio*, the pagoda fungus), pendant fan-shaped fruiting bodies with wrinkled gill-like hymenophores (*Plicaturopsis crispa*), or hydroid hymenophores (*Irpicodon pendulus*). Anatomical characters in Amylocorticiales are also diverse. The basidiospores are either thin- or thick-walled, smooth, ellipsoid, cylindrical, or allantoid, and most react positively (amyloid) to Melzer's reagent. All hyphal systems are monomitic (i.e., consist of generative hyphae only) and nodose septate; however, this character combination is not synapomorphic for Amylocorticiales and occurs in other groups (e.g., Polyporales). Cystidia are rare in Amylocorticiales.

Ecological diversity: species placed in Amylocorticiales are predominantly saprotrophic or, rarely, biotrophic. The modes of wood decay include brown rot (e.g., *Amylocorticium*, *Anomoporia*, *Podoserpula*) and white

rot (e.g., *Anomoloma*, *Irpicodon*, *Plicaturopsis*). *Hypochniciellum molle* (*Leucogyrophana molle*) is of economic importance as a causal agent of brown rot in timber (Mattsson et al. 2010; Niemelä et al. 2007). The decay strategy of *Serpulomyces* has not been studied in detail. ECM forms are seemingly absent in Amylocorticiales, but it has been suggested that *Anomoloma flavissimum* and *Podoserpula pusio* may represent transitions to ECM symbioses (Bougher and Syme 1998; Niemelä et al. 2007). “*Athelia*” *rolfsii* (anamorph *Sclerotium rolfsii*) is a serious soilborne pathogen, also known as Southern blight, that infects more than 500 plant species, including peanut, potato, and tomato (Punja 1985).

Systematics: Amylocorticiaceae Jülich is the single family in Amylocorticiales to date, and a major taxonomic revision on the generic level is needed. *Amyloathelia crassiuscula*, *Amyloxenasma allantosporum*, *Anomoporia kamtschatica*, *Athelia rolfsii*, *Athelopsis lacerata*, *Leptosporomyces septentrionalis*, and *Hypochniciellum molle* are distinct lineages in Amylocorticiales, but they do not represent the generic types.

3. Boletales

Overview: Boletales E.-J. Gilbert is one of the larger orders of fleshy Agaricomycetes, including 17 families, 88 genera, and roughly 1,400 species (Binder and Hibbett 2006; Kirk et al. 2008). The typical fruiting body of a bolete is pileate-stipitate with a tubular (e.g., *Boletus*, *Suillus*) (Fig. 14.9e) or sometimes gilled hymenophore (*Paxillus*, *Phylloporus*). Gasteroid forms (*Scleroderma*, *Rhizopogon*, *Astraeus*) have evolved several times independently from this morphology (Binder and Bresinsky 2002; Binder and Hibbett 2006; Bruns et al. 1989; Thiers 1984; Wilson et al. 2011). Roughly 77 % of the described species produce pileate-stipitate fruiting bodies (Binder et al. 2010). In addition, there are resupinate forms with smooth or warty (*Coniophora*, *Serpula*) (Fig. 14.9f), merulioid (*Leucogyrophana*), and toothed (*Gyrodontium*) hymenophores, and it has been suggested that pileate-stipitate fungi

with gilled hymenophores, such as *Tapinella* or *Hygrophoropsis*, have evolved at least five times from resupinate ancestors (Binder et al. 2005, 2010). *Bondarcevomyces taxi* is the only species developing polyporelike basidiocarps (Larsson 2007b), but no coralloid or clavarioid forms are known in the order. The fruiting bodies of Boletales are specifically attacked by the ascomycete anamorph genus *Sepedonium* (teleomorph *Hypomyces*), suggesting some degree of coevolution between parasites and hosts (Douhan and Rizzo 2003; Sahr et al. 1999).

The morphological characters of Boletales have been studied intensively (Agerer 1999; Arpin and Kühner 1977; Both 1993; Corner 1972; Horak 2004, 2011; Moser 1983; Pegler and Young 1981; Singer 1986; Smith and Thiers 1971; Watling 1970), but there is no synapomorphic trait for the order as a whole. Boletales species produce unique pigments and colorless compounds during secondary metabolism, and the terphenyl quinone atromentin plays an essential role as building block for the synthesis of derivatives, including pulvinic acids (e.g., variegatic acid and xerocomic acid), cyclopentenones, grevillins, and other substances (Besl and Bresinsky 1977, 1997; Besl et al. 1986; Bresinsky 1974; Bresinsky and Orendi 1970; Gill and Steglich 1987). An atromentin pathway has evolved independently in Thelephorales, but it produces only simple terphenyl quinones, not the structurally more complex pigments (Besl and Bresinsky 1997).

Ecological diversity: members of Boletales have a worldwide distribution in forest ecosystems, with biodiversity hot spots in Southeast Asia and North America (Corner 1972; Singer 1965; Smith and Thiers 1971). The major nutritional modes of Boletales include brown-rot saprotrophy, ECM symbioses, and mycoparasitism; biotrophic plant pathogens and white-rot fungi are not known (Binder and Hibbett 2006). It has been suggested that brown rot is the ancestral lifestyle of Boletales, having a single evolutionary origin in the early branching lineages (Binder and Hibbett 2006). Based on the unique capability of brown-rot-producing Boletales to selectively depolymerize microcrystalline cellulose, which weakens the strength of wood, this form of wood decay has

also been called Coniophoraceae-type rot (Kämmerer et al. 1985; Nilsson and Ginns 1979) to separate it from other brown-rot types. Most brown-rot-causing species contribute to carbon sequestration in conifer forests (*Tapinella*, *Pseudomerulius*), but a few have specialized on human-built timber environments. The so-called cellar fungus *Coniophora puteana* and especially the so-called dry rot fungus *Serpula lacrymans* cause significant damage in wooden building structures (Schmidt and Kebernik 1989; Schmidt et al. 2002), and the ecological diversification and structure of geographical lineages of these aggressive decayers have been studied in detail (Eastwood et al. 2011; Kausarud et al. 2007a, b; Skrede et al. 2011; Watkinson and Eastwood 2012). Serpulaceae is also a prime example of transitions from brown-rot to ectomycorrhiza associated with major morphological changes. *Austropaxillus* species (pileate-stipitate fruiting bodies with gilled hymenophores) and *Gymnopaxillus* species (gasteroid) are derived from within *Serpula* and form ectomycorrhizae with *Eucalyptus* and *Nothofagus* (Bresinsky et al. 1999; Jarosch 2001; Skrede et al. 2011).

Approximately 90 % of species in Boletales are involved in ECM symbioses, particularly with Betulaceae, Caesalpiniaceae, Dipterocarpaceae, Fagaceae, Myrtaceae, Nothofagaceae, Pinaceae, and Salicaceae, or in arbutoid mycorrhiza with Ericaceae (Newman and Reddell 1987; Rinaldi et al. 2008; Tedersoo et al. 2010). *Boletus* and *Leccinum* spp. show an increased tendency to associate with specific hosts; for example, *Leccinum scabrum* forms ectomycorrhizae with *Betula* (Singer 1967). *Suillus*, *Gomphidius*, *Chroogomphus*, and *Rhizopogon* spp. in the suborder Suillineae are almost exclusively associated with Pinaceae, which is probably the oldest clade of ECM partners for Boletales (Hibbett and Matheny 2009). Most ECM species are placed among the Boletaceae (roughly 400 plus species), which include highly prized edibles such as *Boletus edulis* (porcini).

Mycoparasites in Boletales represent transitions from the ECM lifestyle (Binder and Hibbett 2006) and have evolved at least twice independently. *Gomphidius* and *Chroogomphus* spp. are capable of parasitizing the established

ectomycorrhizae of the closely related *Suillus* and *Rhizopogon* by penetrating their rhizomorphs (Agerer 1990, 1999; Miller 1964; Olsson et al. 2000), thereby circumventing competition for host plants (Binder and Hibbett 2006). *Pseudoboletus parasiticus* in Boletaceae produces its fruiting bodies on *Scleroderma citrinum* (a gasteroid bolete) while eroding the gleba of the host (Binder and Hibbett 2006). Other putative mycoparasites from the basal lineages of Boletaceae include the sister taxa *Buchwaldoboletus* and *Chalciporus* (Nuhn et al. 2013).

Systematics: Boletales includes five suborders that have been described based on disparate characteristics and methods: Boletineae, Suillineae, Sclerodermatineae, Tapinellineae, and Coniophorineae (Binder and Hibbett 2006). Boletineae was first introduced by Gilbert (1931) using fruiting body morphology and spore shape as distinctive characteristics. This suborder included all species with tubular hymenophores at that time and a few species with gilled hymenophores. Suillineae was separated later from Boletineae based on unique pigments occurring in this group (Besl and Bresinsky 1997). In addition, numerous resupinate and paxilloid taxa producing a brown rot were known to be closely related to Boletales based on their pigments (Besl et al. 1986), but they remained *incertae sedis*. The morphology of belowground rhizomorphs helped to formally place these taxa in Tapinellineae and Coniophorineae (Agerer 1999), which was supported by early major studies using DNA sequences (Bruns et al. 1998; Kretzer and Bruns 1999). Sclerodermatineae was described based on nuc-lsu rRNA sequences (Binder and Bresinsky 2002) integrating the gasteroid Sclerodermatales into Boletales.

Resupinate taxa are still a source of taxonomic uncertainty in Tapinellineae and Coniophorineae, particularly concerning the polyphyletic genus *Leucogyrophana* (Binder et al. 2010; Jarosch and Besl 2001). Coniophorineae, including three clades of *Leucogyrophana*, has been resolved as a monophyletic group, but without significant statistical support (Binder et al. 2010). Together, Boletineae, Sclerodermatineae, and Suillineae form the largest clade, including the overwhelming

majority of ECM taxa (except *Austropaxillus* and *Gymnopaxillus*) and mycoparasites. *Hydnomerulius pinastri* (formerly *Leucogyrophana*), a single species that is not placed in any of the suborders, is sister to the remaining Boletineae members (Jarosch and Besl 2001). Current research is focused on the ecology of Sclerodermatineae (Wilson et al. 2007, 2012) and the taxonomic structure of Boletineae, especially the Boletaceae. Monographic work has led to a better definition of *Boletus* and its being restricted to the *B. edulis* group (Dentinger et al. 2010; Nuhn et al. 2013), the revision of gilled boletes in *Phylloporus* (Neves et al. 2012), and *Xerocomus*, which has been split into several new genera (Šutara 2008). Since 2007, 14 new genera have been described in Boletaceae (Desjardin et al. 2008, 2009; Halling et al. 2007, 2012a, b; Hosen et al. 2013; Lebel et al. 2012; Li et al. 2011; Orihara et al. 2010; Šutara 2008; Trappe et al. 2013; Zeng et al. 2012).

4. Agaricales

Overview: Agaricales (Underwood 1899) includes over 13,000 described species (Kirk et al. 2008), making it the largest order of Agaricomycetes. Despite being one of the most conspicuous and comparatively better studied groups of fungi, an immense amount of the actual diversity remains undescribed, hiding under commonly used names that molecular data have revealed to be clusters of morphologically cryptic species (e.g., *Amanita muscaria*) (Geml et al. 2006) and part of hyperdiverse lineages with over 2,000 estimated species such as *Cortinarius* (e.g., Harrower et al. 2011).

Agaricales is dominated by pileate-stipitate forms with lamellate hymenophores (e.g., *Amanita*, *Agaricus*, *Coprinus* s.l., *Entoloma*, *Lepiota*, *Tricholoma*) (Fig. 14.9a), but there is wide variation on this basic fruit-body morphology regarding characters such as the size of the basidiocarp, the presence of veils (universal and partial), gill attachment, and spore-print color (white, brown, purple-brown, black, pink). Microscopically, there is also a great diversity of characters, including spore size, shape, ornamentation, and chemical reactions;

the arrangement of the covering layers of the fruit body (pileipellis, stipitipellis) and the hymenophoral trama; and the presence of specialized structures (cystidia, setae) (Clémenceçon 2004; Reijnders and Stalpers 1992; Singer 1986). All these characters have played a central role in defining the approximately 400 genera and 30 families in the order, but much of the taxonomy of the order is currently in flux as data from molecular phylogenies become incorporated. A promising pool of micromorphological features that may be useful as future systematic markers in Agaricales is the complex of characters related to conidiogenesis in anamorphic stages (Walther et al. 2005). Since monosporic cultures obtained from basidiospores are usually needed to study these characters, this complex of features has clearly been understudied.

The second major morphological component of Agaricales are the secotioid and gasteroid forms, including false truffles, puffballs, and bird-nest fungi, that have evolved repeatedly in different lineages within the order (e.g., *Lycoperdon*) (Fig. 14.9c). Additional morphologies that can be found in the order include resupinate (e.g., *Cylindrobasidium*), coralloid (e.g., *Clavaria*), cyphelloid (e.g., *Henningsomyces*), pileate with poroid (e.g., *Favolaschia*), or tubular hymenophores (e.g., *Fistulina*). There is no morphological synapomorphy that unites the Agaricales, and the typical pileate-stipitate gilled mushroom morphology that dominates the order also occurs in other orders of Agaricomycetes.

Ecological diversity: two ecological roles characterize the majority of Agaricales species: saprotrophy and ECM symbiosis. Saprotrophs can be broadly subdivided into soil/litter/dung fungi (e.g., *Agaricus*, *Coprinopsis*, *Gymnopus*) and wood decayers (e.g., *Pholiota*, *Pleurotus*), but the exact roles and capabilities of members of both ecological guilds remain largely unknown, although the emerging field of fungal genomics is bringing new insights into these aspects (e.g., Morin et al. 2012). There have been at least ten independent and asynchronous origins of the ECM symbiosis in Agaricales, involving associations with a great variety of vascular plants (Matheny et al. 2006; Ryberg and Matheny 2012; Tedersoo et al. 2012). There

are many additional ecological roles in Agaricales, including plant pathogens (e.g., *Moniliophthora/Crinipellis*) (Meinhardt et al. 2008), mycoparasites (e.g., *Squamanita*) (Matheny and Griffith 2010), basidiolichens (e.g., *Lichenomphalia* and *Dictyonema*) (Dal-Forno et al. 2013; Lawrey et al. 2009), attine ant cultivars (*Leucoagaricus/Leucocoprinus* clade) (Mueller et al. 2005), or termite cultivars (*Termitomyces*) (Aanen et al. 2002). The ecology of many Agaricales species remains poorly understood, and new insights from molecular and isotopic data are challenging long-standing views even in relatively well-studied groups. For example, the so-called waxcaps (*Hygrocybe* sensu lato) have historically been considered saprotrophs but now are thought to be involved in some kind of biotrophic association (Lodge et al. 2013; Seitzman et al. 2011).

Systematics: three landmark papers published in recent years have redefined the taxonomic organization of Agaricales species and their closest relatives: (1) Moncalvo et al. (2002) presented the first broad phylogeny of the order, based on nuc-18S rRNA, which resolved 117 clades and outlined conflicts with traditional morphologically defined groups; (2) Matheny et al. (2006) presented the first major multilocus overview of the order, including the protein-coding genes *rpb1*, *rpb2*, and *tef1-alpha*, and defined six major infraordinal clades: agaricoid, tricholomatoid, marasmioid, hygrophoroid, pluteoid, and plicaturopsidoid clades, although support for some of these groupings was weak; (3) Binder et al. (2010) built on the data set of Matheny et al. (2006) and formally recognized the plicaturopsidoid clade as the order Amylocorticiales.

Recent monographs on Agaricales include the titles of the *Fungi Europaei* series on *Agaricus* (Parra-Sánchez 2008), *Amanita* (Neville and Poumarat 2004), *Conocybe-Pholiotina* (Hausknecht 2009), and the family Strophariaceae (Noordeloos 2011). Outside Europe monographic work at the continental scale is rare, a situation that may change with large-scale cataloging efforts that include the use of molecular data, such as the North American Mycoflora project (Bruns 2012). Modern global mono-

graphs are lacking for all major genera of Agaricales.

Agaricoid clade: this clade is well supported in the study of Matheny et al. (2006) and is dominated by gilled pileate-stipitate forms with pigmented spores (brown, purple-brown, black). Exceptions to this general pattern include (1) white-spored taxa in Agaricaceae (*Lepiota* and allied genera), Cystodermataceae, and Hydnangiaceae (e.g., *Laccaria*); (2) secotoid and gasteroid taxa that have repeatedly evolved in different lineages (e.g., Agaricaceae, *Cortinarius*); and (3) cyphelloid forms in the genera *Pellidiscus* and *Phaeosolenia* (Bodensteiner et al. 2004). At least six ECM lineages are included in this clade: *Cortinarius*, *Descolea* (and allied sequestrate taxa), Inocybaceae, *Laccaria* (and allied sequestrate taxa), *Phaeocollybia*, and some groups of Hymenogastreae (*Alnicola*, *Hebeloma*). Most other members of the agaricoid clade are saprotrophs associated with the litter layer and similar substrates (e.g., *Agaricus*, *Coprinopsis*) or wood decayers (e.g., *Hypholoma*). Taxa with recent phylogenetic studies include Agaricaceae (Vellinga 2004; Vellinga et al. 2011), Bolbitiaceae (Tóth et al. 2013), Cortinariaceae (Frøslev et al. 2005; Garnica et al. 2005; Peintner et al. 2004), Crepidotaceae (Aime et al. 2005), Cystodermataceae (Saar et al. 2009), Gymnopileae (Guzmán-Dávalos et al. 2003), Hebelomataceae (Boyle et al. 2006; Moreau et al. 2006), Inocybaceae (Matheny 2005; Ryberg et al. 2010), Nidulariaceae (Zhao et al. 2007), Psathyrellaceae (Nagy et al. 2012), Strophariaceae (Ramírez-Cruz et al. 2013), Tubariaeae (Gulden et al. 2005), and several secotoid/gasteroid taxa usually nested within agaricoid relatives (Larsson and Jeppson 2008; Lebel and Syme 2012).

Tricholomatoid clade: pileate-stipitate gilled mushrooms with white or pink spores dominate this lineage, which includes four traditionally recognized families: Entolomataceae, Lyophyllaceae, Mycenaceae, and a restricted version of Tricholomataceae. A fifth lineage includes the ECM *Catathelasma* and the saprotrophic *Callistosporium*. Additional ECM origins have also occurred in *Entoloma*, *Lyophyllum*, and Tricholomataceae. The clade also includes soil/litter saprotrophs (e.g., *Clitocybe*), mycoparasites (e.g., *Asterophora*), wood decayers associated with white rot (e.g., *Mycena*) or brown rot (e.g., *Ossicaulis*), and termite cultivars (*Termitomyces*). Entolomataceae remains one of the most distinct groups in Agaricales because of the pinkish spores that are warted, ridged, or angular. Co-David et al. (2009) recognize two broadly defined genera in the family (*Entoloma* and *Clitopilus*), while other authors prefer to recognize several narrowly defined genera (Baroni and Matheny 2011; Largent et al. 2011). The Lyophyllaceae has also been reviewed using molecular phylogenies (Hofstetter et al. 2002). The taxonomy of many traditionally recognized genera (e.g., *Tricholoma*, *Clitocybe*, *Lepista*, *Mycena*) is still in flux.

Marasmioid clade: this lineage is dominated by white-spored saprotrophic species associated with

wood or leaf-litter substrates (e.g., *Lentinula*, *Marasmius*, *Xerula*), but important plant pathogens also belong here (e.g., *Armillaria*, *Moniliophthora*). Schizophyllaceae (*Fistulina*, *Schizophyllum*) and Lachnaceae, dominated by cyphelloid forms, were recovered as part of the marasmoid clade by Matheny et al. (2006) but as independent lineages in Binder et al. (2010). Resupinate genera (e.g., *Chondrostereum*) also occur in the marasmoid clade. Representative taxa with recent phylogenetic studies include a general overview of marasmoid/gymnopoid fungi (Wilson and Desjardin 2005), *Omphalotus* (Kirchmair et al. 2004), *Rhodocollybia* (Mata et al. 2004), *Marasmius*, and *Crinipellis* (Kerekes and Desjardin 2009; Wannathes et al. 2009), and genera in the *Xerula/Oudemansiella* complex (Petersen and Hughes 2010).

Hygrophoroid clade: in the analyses of Matheny et al. (2006) this clade includes an expanded version of Hygrophoraceae as traditionally defined plus the club and coralloid fungi in the families Pterulaceae and Typhulaceae. However, these two families were later resolved as a separate lineage in Agaricales (Binder et al. 2010). The family Hygrophoraceae was recently extensively studied and redefined by Lodge et al. (2013) and now includes 18 genera, including the ECM *Hygrophorus*, several segregates from *Hygrocybe* sensu lato, and a diverse clade of basidiolichens such as *Dictyonema* s. l. (Dal-Forno et al. 2013). All members of the family are now assumed to be involved in some kind of biotrophic relation, but its exact nature remains obscure in most cases (Seitzman et al. 2011).

Pluteoid clade: this clade received weak support in Matheny et al. (2006), and its limits and composition require further study. The grouping of the Pluteaceae and *Melanoleuca* is well supported in most phylogenies (Justo et al. 2011; Matheny et al. 2006). The aquatic gasteromycete *Limnoperdon* is also part of this core pluteoid group in some analyses (Matheny et al. 2006). Amanitaceae, Pleurotaceae, and the genus *Macrocyttidia* are, in some topologies, recovered as closely related to the core pluteoid genera but not always with statistical support or in a consistent position. Important taxonomic revisions include articles on the Pluteaceae (Justo et al. 2011), *Melanoleuca* (Sánchez-García et al. 2013; Vizzini et al. 2012), Pleurotaceae (Thorn et al. 2000), and sequestrate forms in *Amanita* (Justo et al. 2009). The iconic genus *Amanita* has received considerable attention in relation to biogeography (Geml et al. 2006), invasive species (Pringle et al. 2009), and transitions from saprotrophic to ECM nutrition (Wolfe et al. 2012).

III. Conclusions

The previous edition of *The Mycota* included a preliminary phylogenetic outline of Homobasi-

diomycetes, with eight informally named clades, that was based on 25 published and unpublished analyses (Hibbett and Thorn 2001). The present chapter cites nearly 300 phylogenetic studies, many combining rRNA and protein-coding genes, and a handful of phylogenomic analyses. Twenty strongly supported, mutually exclusive clades of Agaricomycetes are recognized as orders. Numerous studies, most of which are not cited here, have addressed species- and genus-level relationships within these groups. Nevertheless, the classification of Agaricomycetes is far from complete. There are weakly supported nodes throughout the phylogeny, and the catalog of described species is thought to be a tiny fraction of the actual diversity in the group (Blackwell 2011).

An overarching challenge of fungal systematics is to capture and integrate the massive volumes of data flowing from taxonomy, phylogenetics, genomics, and molecular ecology. Unfortunately, some common practices make it difficult to combine the products of different areas of research. For example, curated sequence databases are important for the identification of environmental sequences (Köljalg et al. 2013), so it is unfortunate that many recent species descriptions have been published without sequences (Hibbett et al. 2011). It is also unfortunate that only about 17 % of published phylogenies, including those from fungal studies, are available in electronic form (not graphics files, but treefiles, in Newick or other formats), which limits efforts to assemble maximally inclusive phylogenies and combine them with taxonomic hierarchies (Collins et al. 2013; Drew et al. 2013). To approach a comprehensive phylogenetic classification of Agaricomycetes and other Fungi, it will be necessary to increase the pace of taxon discovery, encourage researchers to generate and deposit sequences, alignments, trees, and associated metadata (Hyde et al. 2013), and create new bioinformatics tools to synthesize the prodigious output of the fungal systematics community.

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