10 Pucciniomycotina

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I. Introduction

More than **8,400 species of Pucciniomycotina** have been described (Table 10.1), or more than 8 % of all described Fungi (at 98,998 spp.) (Kirk et al. 2008). Pucciniomycotina is the sister to the Ustilaginomycotina and Agaricomycotina, forming the basal lineage of Basidiomycota. **All members of the subphylum** thus far studied **have simple septal pores** lacking dolipores (septal pore swellings) and septal pore caps, which, along with predominant cell wall sugars (mannose, Prillinger et al. 1993) and disclike spindle pole bodies (McLaughlin et al. 1995; Wells 1994), distinguishes them from most other Basidiomycota. Although some Ustilaginomycotina species appear to have simple septal pores (e.g., Lutzoni et al. 2004), these are reportedly associated with membranous plates that are continuous with the plasma membrane (Bauer et al. 2006). While the position of Pucciniomycotina and the monophyly of eight of the nine classes have been established, deeper level phylogenetic relationships within the subphylum have yet to be resolved (Fig. 10.1).

Fungi belonging to Pucciniomycotina are found in a diversity of habitats, including specialized niches that are historically undersampled for Fungi. Ecologically, most discovered species are plant associates, predominantly phytopathogens but also including asymptomatic members of the phylloplane and species that form mycorrhizal associations with orchids. Others are insect and fungal pathogens, and a few are presumably saprobic. Pucciniomycotina species have been recovered from soils, freshwater and marine habitats, and the Arctic and tropical environments. They are shown to **have an array of life cycles, ranging from simple teliosporic yeasts** (Fig. 10.2) **to the elaborate five-stage life cycles of the biotrophic rust fungi** (Fig. 10.3), often regarded as the most complex organisms in Kingdom Fungi (Lutzoni et al. 2004). The number of new species and new lineages of Pucciniomycotina continues to rise, and it is predicted that much diversity within this group remains to be discovered.

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Table 10.1 Pucciniomycotina: classes, orders, families, and number of species

Class	Order	Family	No. spp.
Agaricostilbomycetes R. Bauer et al.[a] 75 spp.	Agaricostilbales Oberw. & R. Bauer	Agaricostilbaceae Oberw. & R. Bauer	30
		Chionosphaeraceae Oberw. & Bandoni	34
		Kondoaceae R. Bauer et al.[a]	6
	Spiculogloeales R. Bauer et al.[a]	Spiculogloeaceae Denchev	5
Atractiellomycetes R. Bauer et al.[a] 44 spp.	Atractiellales Oberw. & Bandoni	Hoehnelomycetaceae Jülich	38
		Phleogenaceae Gäum.	1
		Saccoblastiaceae Jülich	2
	Incertae sedis		3
Classiculomycetes R. Bauer et al.[a] 2 spp.	Classiculales R. Bauer, Begerow, Oberw. & Marvanová	Classiculaceae R. Bauer, Begerow, Oberw. & Marvanová	2
Cryptomycocolacomycetes R. Bauer et al.[a] 2 spp.	Cryptomycocolacales Oberw. & R. Bauer	Cryptomycocolacaceae Oberw. & R. Bauer	2
Cystobasidiomycetes R. Bauer et al.[a] 43 spp.	Cystobasidiales R. Bauer et al.[a]	Cystobasidiaceae Gum.	11
	Erythrobasidiales R. Bauer et al.[a]	Erythrobasidiaceae Denchev	11
	Naohideales R. Bauer et al.[a]	Naohideaceae Denchev	1
	Incertae sedis		20
Microbotryomycetes R. Bauer et al.[a] 227 spp.	Heterogastridiales Oberw. & R. Bauer	Heterogastridiaceae Oberw. & R. Bauer	7
	Kriegeriales Toome & Aime	Kriegeriaceae Toome & Aime	9
	Leucosporidiales J.P. Samp. M. Weiss & R. Bauer	Camptobasidiaceae R.T. Moore	5
		Leucosporidiaceae Jülich	15
	Microbotryales R. Bauer & Oberw.	Microbotryaceae R.T. Moore	105
		Ustilentylomataceae R. Bauer & Oberw.	11
	Sporidiobolales Doweld	Sporidiobolaceae R.T. Moore	37
	Incertae sedis		39
Mixiomycetes R. Bauer et al.[a] 1 sp.	Mixiales R. Bauer et al.[a]	Mixiaceae C.L. Kramer	1
Pucciniomycetes R. Bauer et al.[a] 8016 spp.	Helicobasidiales R. Bauer et al.[a]	Helicobasidiaceae P.M. Kirk	17
	Pachnocybales Bauer et al.	Pachnocybaceae Oberw. & R. Bauer	1
	Platygloeales R.T. Moore	Eocronartiaceae Jülich	9
		Platygloeaceae Racib.	6
	Pucciniales Clem. & Shear	Chaconiaceae Cummins & Y. Hirats.	75
		Coleosporiaceae Dietel	313
		Melampsoraceae Dietel	90
		Mikronegeriaceae Cummins & Y. Hirats.	13
		Phakopsoraceae Cummins & Y. Hirats.	205
		Phragmidiaceae Corda	164
		Pileolariaceae Cummins & Y. Hirats.	34
		Pucciniaceae Chevall.	6,095
		Raveneliaceae Leppik	323
		Uncolaceae Buriticá	3
		Uropyxidaceae Cummins & Y. Hirats.	143
	Septobasidiales Couch ex Donk	*Incertae sedis*	340
		Septobasidiaceae Racib.	179
	Incertae sedis		6
Tritirachiomycetes Aime & Schell 6 spp.	Tritirachiales Aime & Schell	Tritirachiaceae Aime & Schell	6

Numbers are approximate estimates from Kirk et al. (2008), Kurtzman et al. (2011), and newly published papers cited in text

[a] R. Bauer, Begerow, J. P. Samp., M. Weiss & Oberw.

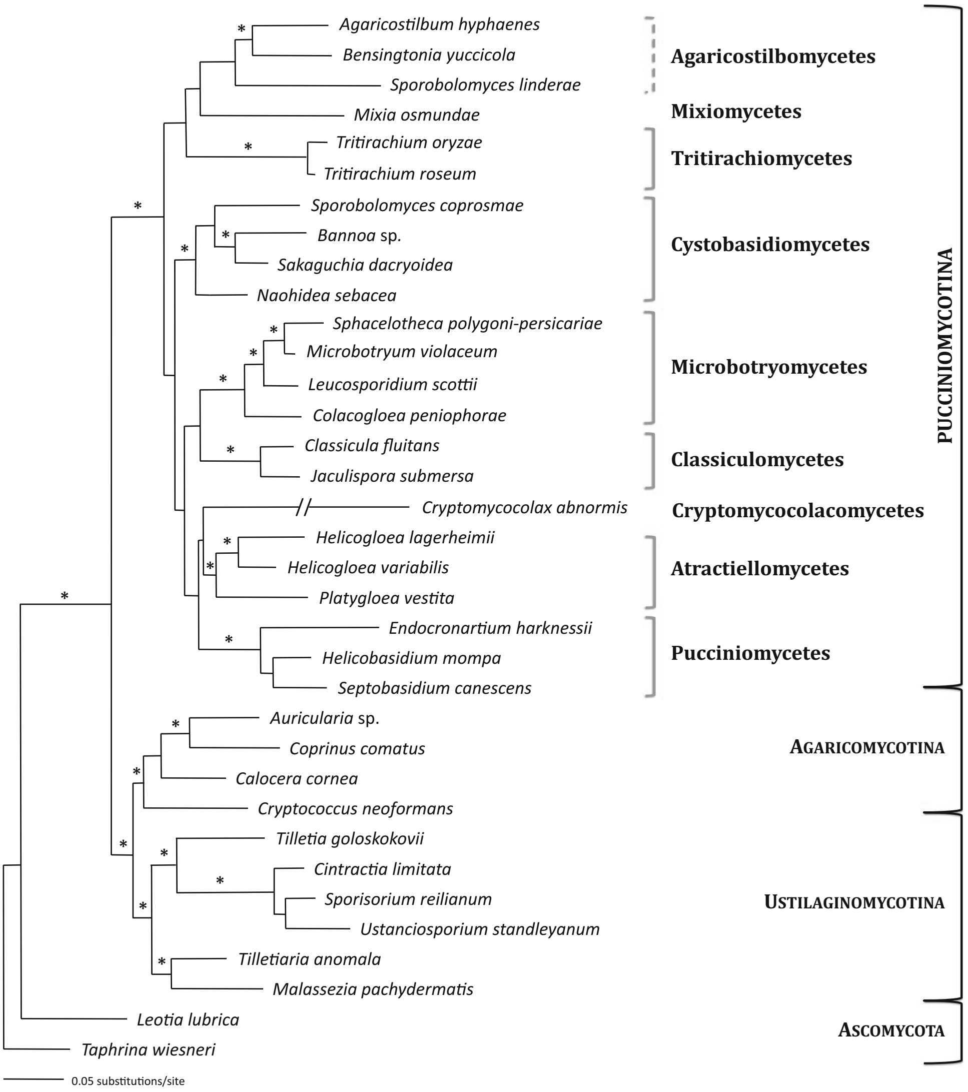


Fig. 10.1 Phylogenetic resolution of Pucciniomycotina classes. Tree based on maximum likelihood analyses of combined nuclear ribosomal small and large subunits and translation elongation factor 1-alpha DNA sequences. Ascomycota sequences included as outgroups; representative Agaricomycotina and Ustilaginomycotina sequences included to show monophyly of Pucciniomycotina. Asterisk (*) denotes nodes that have received strong (>80 %) support in the analyses of Aime et al. (2006), Padamsee et al. (2012), and Schell et al. (2011). Backbone resolution remains poor within Pucciniomycotina. Figure adapted from Schell et al. (2011)

II. Systematics of Pucciniomycotina

Most early treatments of basidiomycetes recognized one main division in the group, between those species that formed holobasidia (homobasidiomycetes) and those with phragmobasidia (heterobasidiomycetes). However, analyses of 5S ribosomal RNA sequences by Walker and Doolittle (Walker and Doolittle 1982) divided Basidiomycota into two groups, not by any traditional characters but by whether they possessed simple pores or dolipores.

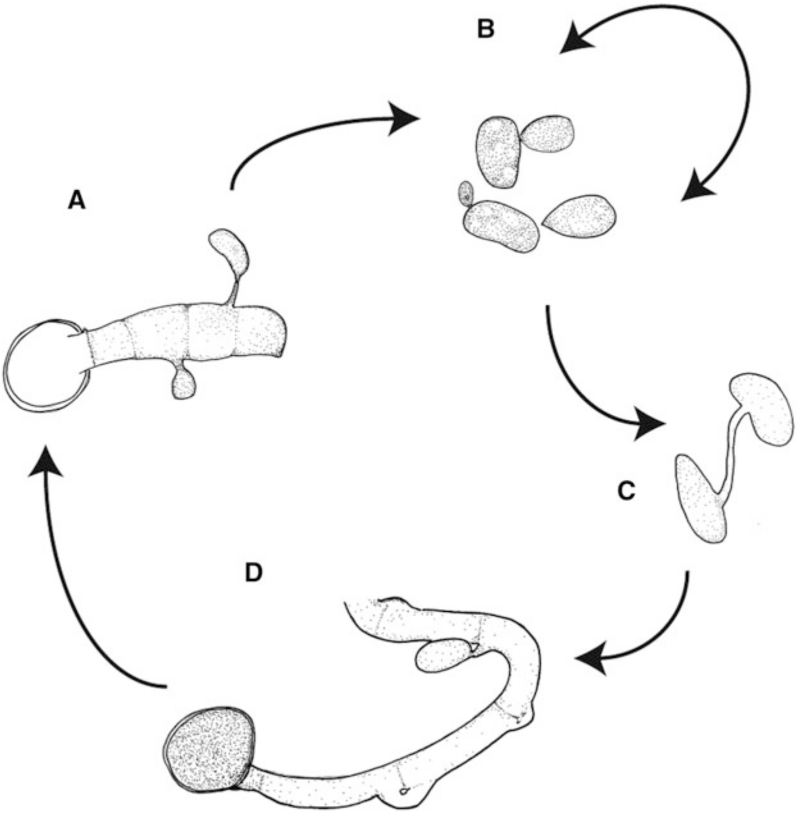


Fig. 10.2 Life cycle of *Rhodosporidium toruloides* (Sporidiobolales). A. A transversely septate basidium arises from a teliospore and gives rise to spores. B. The spores bud and persist as yeasts. C. Yeast cells of the proper mating types fuse via a thin hyphal connection to form a dikaryon. D. The dikaryon forms hyphae that will eventually give rise to teliospores. Figure from Aime et al. (2006), courtesy of D. Henk and reprinted with permission of *Mycologia*. copyright The Mycological Society of America

Gottschalk and Blanz (Gottschalk and Blanz 1985) expanded that work by sampling a large diversity of mostly basidiomycetous yeasts and taking into account the **5S RNA secondary structure** in addition to sequence, again **showing a deep division of Basidiomycota into two groups.** Those with type A secondary structure included members of the smut group *pro parte* (p.p.) (including the anther smut *Microbotryum*) and members of the heterobasidiomycetes that had simple septal pores, including members of Auriculariales p.p. and Atractiellales p.p. (Gottschalk and Blanz 1985). Species with type B secondary structure were found in most of the smut groups excepting the anther smuts, in heterobasidiomycetes with dolipore septa, and in mushroom-forming fungi (Gottschalk and Blanz 1985). The ascomycete *Taphrina deformans* was found to have a 5S secondary structure of type A, while the rust fungi, represented by four species in their analyses, were reported to have type B secondary structure (Gottschalk and Blanz 1984, 1985). Cladistic analyses by these authors of the representative 5S RNA sequences provided evidence for a basal lineage of Basidiomycota that included many yeast-forming fungi, phragmobasidiate fungi, and smutlike fungi that could be distinguished from their convergent cohorts by the absence of dolipore septa. **The group with type A secondary structure was initially referred to as the *simple***

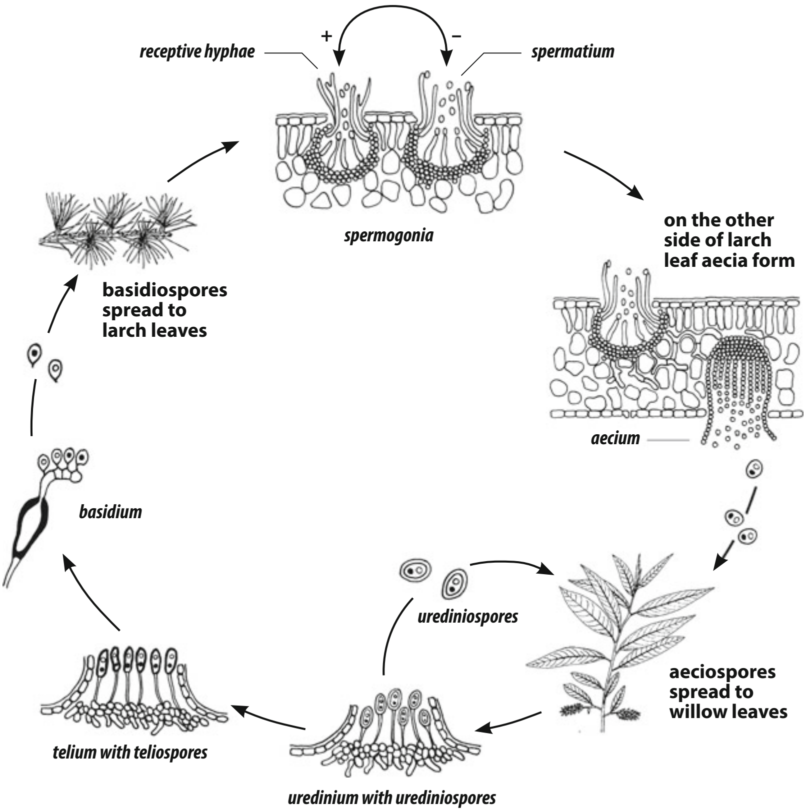


Fig. 10.3 Life cycle of a heteroecious macrocyclic rust fungus, *Melampsora larici-epitea*. The cycle begins with the germination of haploid basidiospores on new leaves of the alternate or aecial host (e.g., larch), where they form spermogonia. Spermogonia are haploid, producing receptive hyphae and specialized spores called spermatia. Fertilization occurs by the fusing of spermatia or hyphae of two opposite mating types. Dikaryotic hyphae form aecial sori containing long chains of aeciospores. Aeciospores function as wind-disseminated propagules that serve to colonize the primary or telial host (e.g., willow). Germinating aeciospores produce dikaryotic uredinia with urediniospores. The uredinial stage is the cyclic asexual stage, capable of continuously reinfecting the primary host under favorable conditions. In general, only when the host starts to prepare for dormancy is the fifth, or telial, stage triggered. Teliospores form within telia that are produced from the same mycelium that previously produced urediniospores. Karyogamy occurs in the teliospores, which often have thick cell walls and an endogenous dormancy period, serving as the overwintering stage. In the spring, teliospores act as probasidia and germinate into basidia. Meiosis occurs within basidia of the auricularioid phragmobasidium type, producing four haploid basidiospores that are forcibly discharged to a new aecial host, completing the life cycle. Figure from Toome (2010)

septate basidiomycete lineage (e.g., Nishida et al. 1995) **or Atractiellales *sensu lato*** (s.l.) (Hawksworth et al. 1995).

Subsequent analyses of small subunit ribosomal DNA (rDNA) sequence (18S rDNA) data revealed the existence of three, rather than two, major lineages of Basidiomycota (Swann and Taylor 1993, 1995). With the exception of the rust fungi, those with a type B secondary structure belonged to two lineages, Ustilaginomycetes (true smut fungi, now Ustilaginomycotina) and Hymenomycetes (mushroom-forming fungi and their relatives with dolipore septa, now Agaricomycotina). **The lineage containing the simple septate basidiomycetes with type A secondary structure and the rust fungi were united in Urediniomycetes (now Pucciniomycotina)** (Swann and Taylor 1995).

However, resolution of the relationship between these three lineages of Basidiomycota has been problematic with conventional molecular systematics. Many studies, most relying on rDNA sequence data, have recovered a topology that places **Pucciniomycotina as sister to the other two subphyla**, although these have been weakly supported or unsupported (e.g., Bauer et al. 2006; Lutzoni et al. 2004), whereas alternate topologies, such as Ustilaginomycotina as sister to the other two subphyla, have also been recovered (Medina et al. 2011). In the higher-level classification for Fungi proposed by the Assembling the Fungal Tree of Life project, this node remained unresolved (Hibbett et al. 2007). However, recent analyses, based on 71 protein-coding genes, have resolved the basal position of Pucciniomycotina within Basidiomycota (Padamsee et al. 2012). **This topology is supported by studies of basidiomycete cell wall carbohydrates, which in Pucciniomycotina**, in contrast to Agaricomycotina and Ustilaginomycotina, **are predominantly of mannose and lack xylose** (Prillinger et al. 1993) and by the septal pore and spindle pole body data discussed subsequently.

Molecular phylogenetic analyses fully support Pucciniomycotina as monophyletic and the monophyly of most of the classes therein (e.g., Aime et al. 2006; Lutzoni et al. 2004; Schell et al. 2011). However, backbone nodes within Pucciniomycotina have not been resolved despite intensive sampling efforts that included nearly the entire known generic diversity (excluding that of the rust fungi) in the subphylum (Aime et al. 2006); current research is now focused on increased locus sampling. Phylogenetic relationships within the subphylum as currently understood are presented in Fig. 10.1. The systematics of the lineages will be discussed in the classification section.

III. Diversity

A. Ecological Diversity

Pucciniomycotina species play diverse ecological roles, although these are incompletely known or can only be inferred for a number of species and lineages (Table 10.2). **Plant associations dominate and phytopathogens have arisen in several classes** (e.g., Pucciniomycetes, Microbotryomycetes, Mixiomycetes). **The rust fungi form both the largest natural group of plant pathogens** in Fungi and the most speciose order in Pucciniomycotina (Table 10.1), comprising 95 % of the subphylum and ca. 8 % of all described Fungi (Kirk et al. 2008). Asymptomatic and presumably **saprobic phylloplane yeasts** can be found in Microbotryomycetes, Cystobasidiomycetes, and Agaricostilbomycetes on hosts ranging from lichens to *Sphagnum* mosses to vascular plants (e.g., Inácio et al. 2010; Kachalkin et al. 2008; Sláviková et al. 2009). The discovery that **some members of Atractiellomycetes form mycorrhizae with neotropical orchids** (Kottke et al. 2010) makes this **the basalmost lineage of mycorrhizal associates in Basidiomycota** since these symbioses were previously known only from Agaricomycotina.

Mycoparasitism is observed or inferred from culture characters (such as self-parasitization), specialized subcellular characters (such as presence of colacosomes), or mycophilic associations. Many **mycoparasitic species** have been described from isolations made from fungal fruiting bodies or co-isolated with ascomycetous molds (e.g., Bauer et al. 2003; Beguin 2010; Kirschner et al. 2001), and they **are found to belong to several different classes**. Septobasidiales contains the only entomopathogens, comprising species that are symbiotic with scale insect colonies (Couch 1938), although the true nature of the association may be more commensal than truly parasitic (Henk and Vilgalys 2007).

Freshwater and marine yeasts can be found primarily in Cystobasidiomycetes and some Microbotryomycetes (Fell 1966; Sampaio 2004), but they also include the enigmatic fungus *Reniforma strues*, which was isolated from biofilms in a wastewater treatment plant (Pore and Sorenson 1990) and is placed *incertae sedis* within Pucciniomycotina by rDNA sequences (Aime et al. 2006). Classiculomycetes and *Cyrenella elegans* (Cystobasidiomycetes) are **aquatic hyphomycetes** that share convergent characters with other primarily ascomycetous aquatic fungi (Bauer et al. 2003; Gochenaur 1981).

Table 10.2 Pucciniomycotina: Synopsis of key ecological and morphological characters by class

		Asexual reproduction		Sexual reproduction		Subcellular characters			
Class	Ecological diversity	Yeast state	Conidia	Fruiting body	Basidia	Clamps	Septal pore associations	Spindle pole body	Other features
Agaricostilbomycetes	Mycoparasites, saprobes	+	+ (blasto-)	Various—stilboid, pustulate or none	Phragmo-, holo-	+/−	Microbodies	Multilayered disc	Tremelloid haustoria
Atractiellomycetes	Saprobes, orchid mycorrhiza	−	+	Stilboid, resupinate	Phragmo-	+	Atractosomes, microbodies	Multilayered disc	Microscala/symplechosomes
Classiculomycetes	Aquatic, mycoparasites	−	+ (triradiate)	−	Phragmo- w/subapically swollen sterigmata	+	Microbodies	n/a	Binucleate tremelloid haustoria
Cryptomycocolacomycetes	Mycoparasites	− (basidiospores may form yeast-like buds)	+	−	Holo- (w/unique development)	+	Microbodies, pore plugs	Layered disc	Colacosomes/lenticular bodies
Cystobasidiomycetes	Mycoparasites, saprobes	+	− (+in *Cyrenella*)	−	Holo-, phragmo-	+	Cystosome pore plug	n/a	Tremelloid haustoria
Microbotryomycetes	Phyto- or mycoparasites, saprobes (aquatic)	+	−/+	Various—pycnidioid, sori	Phragmo-	+	Pulley-wheel-shaped pore plug, microbodies (*Colacosiphon*)	Subgloboid with flat internalized layer	Colacosomes/lenticular bodies
Mixiomycetes	Phytoparasite	+	?	−	Unknown	−	n/a	n/a	n/a
Pucciniomycetes	Obligate phyto-, entomo- or mycoparasites (saprobe)	− (+in Septobasidiales)	+	Various—stilboid, resupinate, clavarioid, sori	Phragmo-, holo-	−	Pulley-wheel-shaped pore plug	Multilayered disc	Microscala/symplechosomes
Tritirachiomycetes	Saprobes, human pathogens, mycoparasites	−	+	−	Unknown	−	Pore plug	n/a	n/a

Because of the microscopic or cryptic nature of most of the fungi in Pucciniomycotina, their presence and ecological roles may have been overlooked in the past. For example, **sequences generated by environmental sampling** studies are providing data that **suggest the presence of unknown species of Pucciniomycotina in soil rhizospheres** (e.g., Porter et al. (2008), as uncultured basidiomycete; Stefani et al. (2010), as uncultured soil fungus), **anoxic deep-sea habitats** (e.g., Bas et al. (2007), as Urediniomycetes; Jebaraj et al. (2010), as unnamed Pucciniomycotina), **and Arctic ice** (D'Elia et al. 2009). In fact, extreme environments can harbor a diversity of psychrophilic (e.g., Libkind et al. 2005; Libkind et al. 2010; Turchetti et al. 2011), osmotolerant (e.g., Fell 1966), and toxicity-tolerant (e.g., Pohl et al. 2011) Pucciniomycotina yeasts, and such environments may prove to harbor additional untapped diversity.

B. Life Cycles

A striking feature of Pucciniomycotina is the **predominance of asexual stages within most lineages**. Some lineages, in fact, are known only from anamorphs, such as Tritirachiomycetes and, potentially, Mixiomycetes (Table 10.2). Perhaps another striking character of Pucciniomycotina is the number of unique developmental patterns and life cycles that apparently arose in what might be thought of as early experiments into basidiomycetization, culminating in the elaborate life cycles in Pucciniales wherein up to five different sporulating stages can be produced on two unrelated hosts (Fig. 10.3). Interestingly, the character of **heteroecism seems to have arisen only once in Fungi outside of Pucciniomycetes** in the unrelated chytrid genus *Coelomomyces* (Blastocladiales, Blastocladiomycetes) (Whisler et al. 1975; see James et al. 2014). The complexity of the rust life cycle is perhaps why complete life cycle data are missing for many of the species, including emerging pathogens of great agricultural significance such as *Phakopsora pachyrhizi*, *Puccinia psidii*, and *Hemileia vastatrix*. At the other extreme are simple teliosporic yeasts, such as found in Sporidiobolales (Fig. 10.2). Other life cycles will be discussed within the relevant sections to follow.

C. Morphological and Genomic Diversity

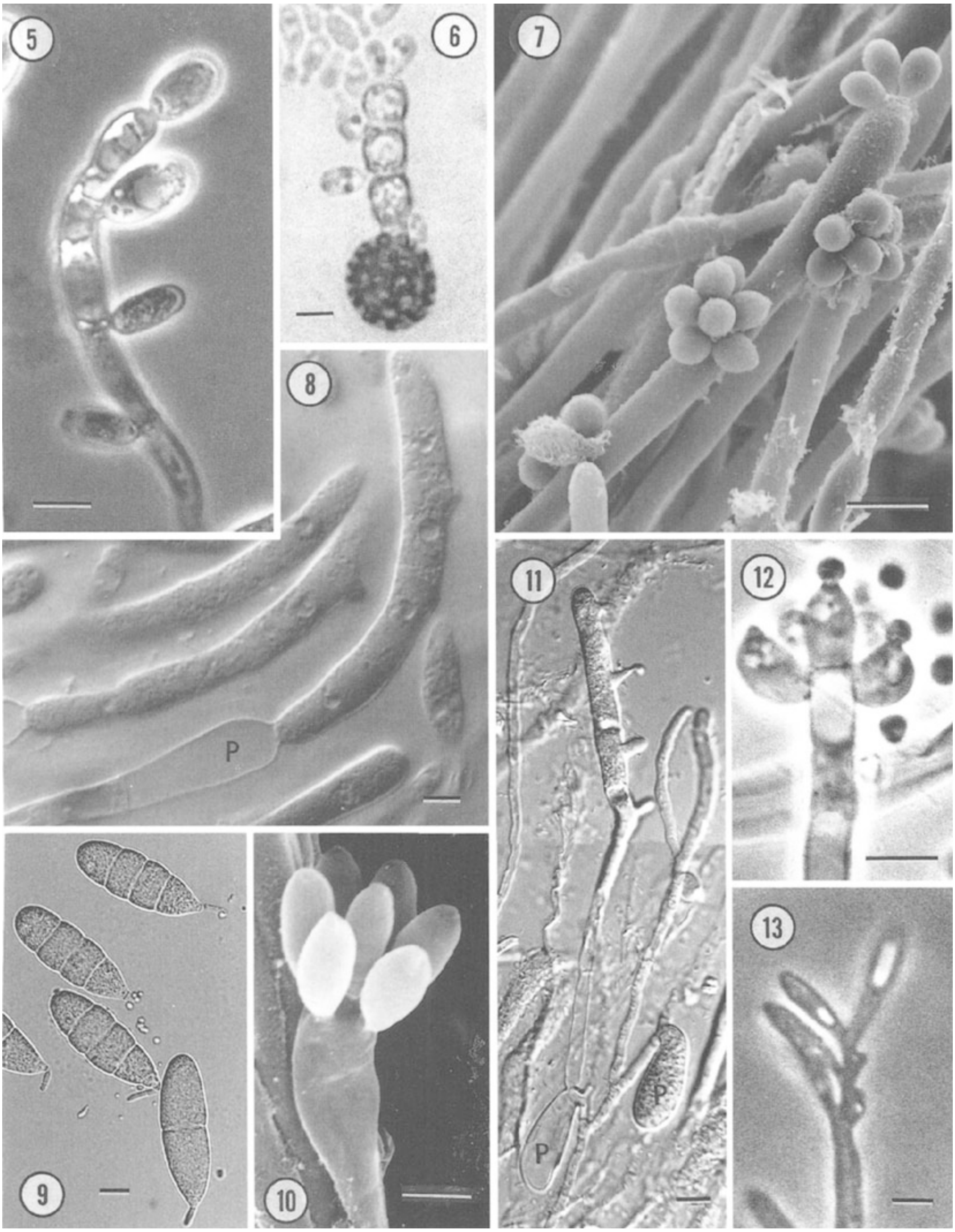
The morphological diversity in Pucciniomycotina is immense. Table 10.2 presents some salient morphological characters by class. **A diversity of sporulating forms** is exhibited in Pucciniomycotina species, **ranging from macrobasidiocarp formers to single-celled yeasts** (e.g., Fig. 10.4). To cite a few examples, when present, basidiocarps may be stipitate-capitate or stilboid, such as the fruiting bodies of *Agaricostilbum* species, resupinate, as is found in, for example, *Septobasidium* and *Helicobasidium* species, sporodochial, as in *Mycogloea* species, or, rarely, clavarioid, as in *Eocronartium muscicola*; others, such as Pucciniales and *Microbotryum* species, form spore-filled sori within their hosts.

As early basidiomycetes evolved, new mechanisms for spore formation and dispersal must have arisen, resulting in the amazing **variety of basidial morphologies** present in extant Pucciniomycotina (e.g., Figs. 10.5–11). In Cystobasidiomycetes alone basidia may be unicelled, phragmobasidia of the auricularioid type (i.e., transversely septate), elongate filamentous phragmobasidia, or two-celled with budding basidiospores, and they may germinate from probasidia, teliospores, or directly from terminal hyphal cells. Mechanisms for producing and dispersing mitospores are also diverse (e.g., Fig. 10.12). These may reproduce, for example, by budding, ballistosporic discharge from stalklike condiophores, or production of sessile conidia. Mitospores may be single-celled, multicelled and coiled (e.g., *Hobsonia* spp.), or resemble those of Ingoldian fungi with filamentous appendages adapted for water dispersal (e.g., *C. elegans*). The anamorphic yeast *Reniforma strues* has kidney-shaped cells that produce miniature reniform buds (Pore and Sorenson 1990). One unique spore developmental pattern is found

Fig. 10.4 Representatives of Pucciniomycotina. a. *Jola* cf. *javensis* (Platygloeales) fruiting on *Sematophyllum swartzii* (E. Frieders). b. *Septobasidium burtii* (Septobasidiales) fungal mat completely covering scale insects (D. Henk). c. *Eocronartium muscicola* (Platygloeales) fruiting on moss *Climacium dendroides* (E. Frieders). d. Yeast and filamentous cells of *Sporidiobolus pararoseus* (Sporidiobolales) (M.C. Aime). e. Cultures of two *Sporidiobolus* species in *S. pararoseus* clade (Sporidiobolales) (M.C. Aime). f. *Phragmidium* sp. (Pucciniales) on *Rosa rubiginosa* (M.C. Aime). Figure from Aime et al. (2006) and reprinted with permission of *Mycologia*. copyright The Mycological Society of America

within the monotypic *Mixia osmundae*, which produces hundreds of exogenous, enteroblastic spores at a time from a single saclike sporogenous cell (Nishida et al. 1995). Although the life cycle of this fungus remains to be fully described, recent genomic studies have suggested that the spores on these sporogenous cells are likely mitotic (Toome et al. 2014).

A uniting feature of Pucciniomycotina is the presence of simple septal pores that lack dolipores and septal pore caps (parenthesomes) that otherwise characterize most Basidiomycota (Celio et al. 2006). The presence of Woronin bodies in association with the septal pore is characteristic of Pezizomycotina in the Ascomycota. Although Woronin-like bodies



Figs. 10.5–10.13 Basidial and conidial morphology in Pucciniomycotina. **5–11.** Basidia. **5.** Gasteroid auricularioid basidium of *Atractiella* sp. with sessile basidiospores; differentiated probasidium absent (E. Swann, ECS CR27); *bar* 10 μm. **6.** Gasteroid basidium of *Microbotryum reticulatum* with teliospore, sessile basidiospores, and yeast stage (E. Swann, ECS 698); *bar* 5 μm. **7.** Gasteroid auricularioid basidium of *Agaricostilbum pulcherrimum* with multiple basidiospores on each compartment (F. Oberwinkler, F219); *bar* 5 μm. **8.** Ballistosporic auricularioid basidium of *Jola* cf. *javensis* with differentiated probasidium (*P*) (E. Frieders, EMF 004); *bar* 5 μm. **9.** Deciduous auricularioid metabasidia of *Kriegeria eriophori* prior to basidiospore production

have been reported in Agaricostilbomycetes and Cryptomycocolacomycetes (Kirschner et al. 2001; Oberwinkler and Bauer 1989, 1990), cytochemical data are needed to ascertain whether these are homologous with the similar structures in ascomycetes (Celio et al. 2006; Dhavale and Jedd 2007; Roberson et al. 2010). Additional **septal pore features may be diagnostic for some classes.** For instance, pores may be occluded by a pulley-wheel-shaped plug associated with a zone of organelle exclusion bounded by microbodies (e.g., Pucciniomycetes) (Fig. 10.14) or by a cystosome, a more or less cylindrical plug with a reticulate surface (e.g., Cystobasidiomycetes; Sampaio et al. 1999), or distinctive pore-associated microbodies may be present (e.g., Atractiellomycetes) (Fig. 10.15).

Spindle pole bodies (SPBs), organelles that organize microtubules during nuclear division, and nuclear division characters have been examined for many Pucciniomycotina (e.g., McLaughlin et al. 1995; Swann et al. 2001 and references therein). **All species** in Pucciniomycotina **have layered discoid** (although this may verge on globoid) **SPBs** (Figs. 10.16, 17). SPB morphology has not been studied in all classes, but it seems to be a diagnostic character for at least some (Celio et al. 2006) (Table 10.2). During nuclear division the SPB in many Pucciniomycotina is **more or less internalized within the nucleus**, but in the Pucciniomycetes and Atractiellomycetes it is inserted in a nuclear pore (Figs. 10.16, 17). In Pucciniomycetes, except for Pucciniales, and Atractiellomycetes the SPB is surrounded by an endoplasmic reticulum cap (Fig. 10.17), the loss of which seems to be apomorphic in Pucciniales (Fig. 10.16).

One subcellular character that seems to be synapomorphic for Atractiellomycetes is the presence of membrane complexes called **microscala or symplechosomes** (McLaughlin 1990; Oberwinkler and Bauer 1989). These **consist of stacked cisternae of endoplasmic reticulum that are regularly cross-linked by filaments** that may also connect them with mitochondria (Fig. 10.18). **Colacosomes** (sometimes referred to as lenticular bodies), subcellular organelles associated with mycoparasitism that **serve to connect the hyphal cell of the host with that of the parasite**, are found in many species (Bauer et al. 1997), especially in Cryptomycocolacomycetes and Microbotryomycetes.

Tremelloid haustoria, named for the type of haustoria formed by mycoparasitic Tremellales (Agaricomycotina), **can be found in many mycoparasitic** or presumed mycoparasitic Pucciniomycotina, although it is not known whether these structures are truly homologous with those formed in Tremellales. Nonetheless, in Classiculomycetes these haustorial cells are binucleate, rather than uninucleate as in all other studied species, and are thus diagnostic for this class (Bauer et al. 2003). The production of coenocytic hyphae in Mixiomycetes may be synapomorphic for that lineage and is otherwise rare in basidiomycetes. Another rare character in Fungi is branch origin, involving the breaking of the hyphal wall. However, this pattern occurs in both Pucciniomycetes and Atractiellomycetes (Fig. 10.19) and seems to be diagnostic for these classes (Swann et al. 2001).

Whole-genome data are lacking for most lineages of Pucciniomycotina. However, genome sizes for those known range from as small as 13 Mbp for *Mixia osmundae* to 415 Mbp for the rust fungus *Uromyces fabae*, one of the largest known in Fungi (Eilam et al. 1994; Grigoriev et al. 2012). Complete genome sequence data have been released for representatives of three classes, Pucciniomycetes, Microbotryomycetes and Mixiomycetes – *Puccinia graminis* f. sp. *tritici*, *P. triticina*, *P. striiformis*,

Figs. 10.5–10.13 (continued) (J.C. Doublés in Doublés and McLaughlin 1992); *bar* 10 µm. **10.** Gasteroid holobasidium of *Pachnocybe ferruginea* with apical basidiospores (Kleven and McLaughlin 1988); *bar* 2.5 µm. **11.** Maturing ballistosporic auricularioid basidium of *Helicogloea intermedia* with saccate lateral probasidium (*P*) and an adjacent probasidium prior to metabasidium formation (J.C. Doublés); *bar* 10 µm. **12, 13.** Conidia and conidiophores. **12.** Microconidia formation in *Atractiella* sp. (D.J. McLaughlin, DJM 969); *bar* 5 µm. **13.** Sympodial conidium formation in *Jola* cf. *javensis* (D.J. McLaughlin, DJM 739); *bar* 5 µm. **5, 6, 8, 9, 11–13.** Bright-field micrographs. **7, 10.** Scanning electron micrographs. Figures reproduced from Swann et al. (2001); collection or culture number in parentheses

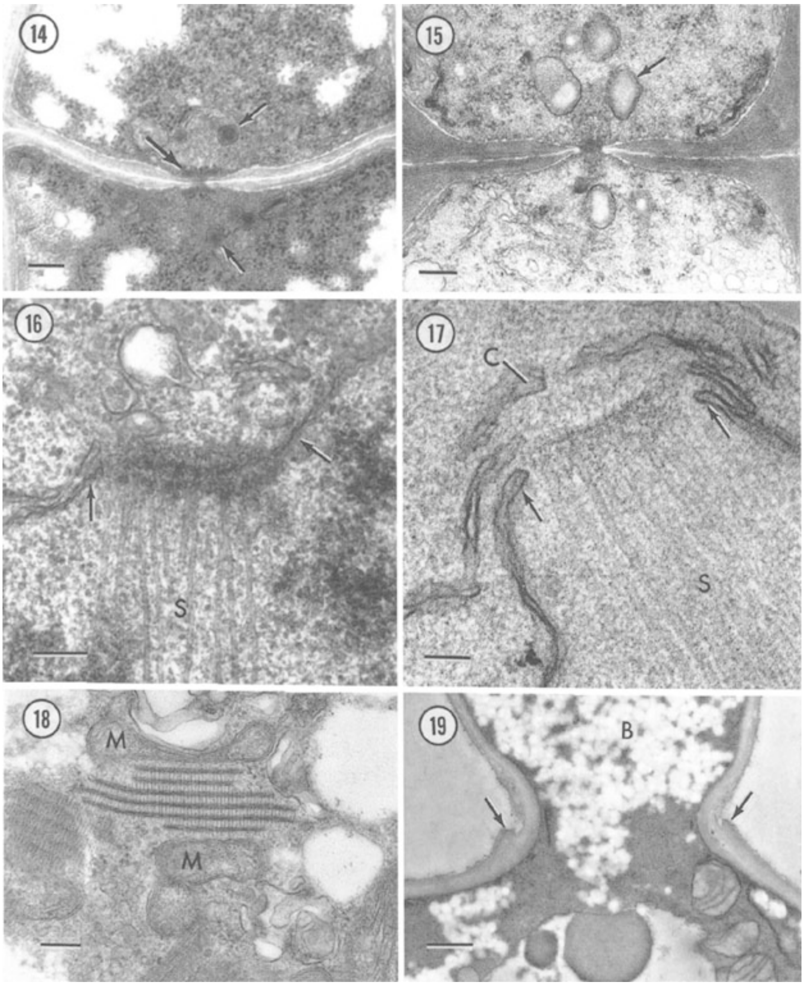


Fig. 10.14–10.19 Subcellular structure in Pucciniomycotina. Transmission electron micrographs. **14, 15.** Septal pore structure. **14.** Pulley-wheel-shaped plug (*large arrow*) in septal pore of *Eocronartium muscicola* and zone of ribosome exclusion surrounded by microbodies (*small arrows*) (D.J. McLaughlin, DJM 757-5); *bar* 0.2 μm. **15.** Septal pore of *Helicogloea* sp. with adjacent microbodies (*arrow*) (R.J. Bandoni, RJB 6478-5); *bar* 0.2 μm. **16, 17.** Spindle pole bodies (SPB). **16.** Early meiotic metaphase I SPB of *Puccinia malvacearum* inserted into a pore of the nuclear envelope (*arrows*). Spindle (*S*) (K.L. O'Donnell, in O'Donnell and McLaughlin 1981); *bar* 0.2 μm. **17.** Early mitotic metaphase SPB of *Helicobasidium purpureum* with endoplasmic reticulum cap (*C*). Nuclear envelope (*arrows*); spindle (*S*) (T.M. Bourett, CBS 324.47); *bar* 0.1 μm. **18.** Microscala in hypha of *Helicogloea variabilis* with rodlets cross-linking endoplasmic reticulum and mitochondria (*M*) (from McLaughlin 1990); *bar* 0.2 μm. **19.** Break (*arrows*) in outer hyphal wall during branch (*B*) initiation in *Jola* cf. *javensis* (D.J. McLaughlin, DJM 739 ps); *bar* 1 μm. Figures reproduced from Swann et al. (2001); collection or culture number provided in parentheses

Cronartium quercuum, and *Melampsora laricipopulina* (Pucciniales), *R. graminis*, *Sporobolomyces* sp. (as *S. roseus*) (Sporidiobolales), and *Microbotryum violaceum* (Microbotryales) and *Mixia osmundae* (Mixiales) [Grigoriev et al. (2012); *Microbotryum violaceum* Sequencing Project, Broad Institute of Harvard and MIT (http://www.broadinstitute.org/); *Puccinia* Group Sequencing Project, Broad Institute of Harvard and MIT (http://www.broadinstitute.org/]. Comparative genomics of these fungi has already impacted our understanding of the molecular bases of obligate biotrophy (Duplessis et al. 2011).

D. Species Discovery and Diversity

Approximately 8,416 species of Pucciniomycotina have been described to date (Table 10.1), the majority belonging to Pucciniales. **A number of higher-level Pucciniomycotina lineages are monotypic** (e.g., Mixiomycetes, Naohideales, Pachnocybaceae) or contain less than ten described species (Tritirachiomycetes, Classiculomycetes, Cryptomycocolacomycetes).

New species discovery continues at a high rate. A recent study of the moldlike genus *Tritirachium* reassigned these fungi to Pucciniomycotina, revealing several cryptic species in the genus (Schell et al. 2011). New species and genera have been recently described from habitats not traditionally associated with Pucciniomycotina, such as soil (e.g., Bauer et al. 2009; Yurkov et al. 2011), beetle galleries (e.g., Oberwinkler et al. 2006), and extreme or toxic environments (e.g., Libkind et al. 2010; Pohl et al. 2011). The phylloplane has continued to be a rich source of species discovery, especially of yeasts in Microbotryomycetes (e.g., Golubev and Scorzetti 2010; Toome et al. 2013; Valério et al. 2008).

Even within Pucciniales, whose members, due to their importance in agriculture, have been one of the better studied groups of Fungi, new species discovery continues as molecular systematic studies show that some morphologically circumscribed species are, in fact, composed of numerous, sometimes unrelated, cryptic species. For example, in one study, rust fungi morphologically assigned to *Melampsora epitea* in the Pacific Northwest of North America were found to belong to 14 different phylospecies, of which none seems to have been previously described (Bennett et al. 2011), and investigations of the previously monotypic genus *Dasyspora* revealed it to contain at least 11 species within Central and South America (Beenken et al. 2012).

IV. Classification

Pucciniomycotina contains **9 classes divided into 20 orders and 37 families** (Table 10.1). The systematics and composition of the three major lineages of Basidiomycota have been rapidly evolving over the last two decades, none more so than within Pucciniomycotina. **Before 2006 these fungi were known as class Urediniomycetes,** which comprised four lineages (Swann and Taylor 1995). The application of molecular systematics to fungal studies has driven the expansion of Pucciniomycotina to now include many lineages of fungi that had previously been placed within other groups. Plesiomorphic characters, such as that of a simple septal pore apparatus, led to the original assignment of fungi in classes Mixiomycetes and Tritirachiomycetes within Ascomycota (Nishida et al. 1995; Schell et al. 2011). Another potentially plesiomorphic character, that of phragmobasidia of the auricularioid type (Fig. 10.11), led to the original classification of most members of Platygloeales in Auriculariales (Agaricomycotina). Similarity in life cycles and morphology, now known to be the result of convergent evolution, led to the original classification of Microbotryomycetes within the smut fungi (Ustilaginomycotina).

Basidiomycetes with yeast states occur in all three subphyla. **Anamorphic yeasts** under previous versions of the International Code of Botanical Nomenclature **were treated separately from teleomorphic species and assigned to form genera principally based on carbon assimilation tests** (Kurtzman et al. 2011 and references therein). Numerous molecular phylogenetic studies have highlighted the artificiality of this system. For example, **species of *Sporobolomyces* occur across most of the yeast-forming Pucciniomycotina classes; species of *Rhodotorula* can be found in Ustilaginomycotina and Pucciniomycotina** (Sampaio 2004; Scorzetti et al. 2002). The type species for both *Rhodotorula* (*R. glutinus*) and *Sporobolomyces* (*S. salmonicolor*) are placed in Sporidiobolales with molecular data (Scorzetti et al. 2002). At the 2011 meeting of the International Botanical Congress changes were adopted that will discontinue the use of a dual nomenclature in Fungi (Hawksworth 2011). One challenge for the future will be to implement the changes now allowed under the new *Code* and integrate the various clades of

Sporobolomyces and *Rhodotorula* and other polyphyletic anamorphic yeast genera into a phylogenetic classification.

A. Agaricostilbomycetes

The type genus ***Agaricostilbum*** **was originally described as an anamorphic member of the Ascomycota** and later transferred to the Auriculariales (Agaricomycotina) (Wright 1970; Wright et al. 1981) before being allied in Pucciniomycotina. Agaricostilbomycetes as currently defined contains two orders, Agaricostilbales and Spiculogloeales (Bauer et al. 2006). The monophyly of both orders has been demonstrated using molecular data (e.g., Aime et al. 2006; Bauer et al. 2009), but strong support for a monophyletic Agaricostilbomycetes as currently circumscribed is lacking. Genera included in Agaricostilbales are ***Agaricostilbum*****,** ***Bensingtonia*** **(anamorphic),** ***Chionosphaera*****,** ***Cystobasidiopsis*****,** ***Kondoa*****,** ***Kurtzmanomyces*** **(anamorphic),** ***Mycogloea*** **p. p.,** ***Sterigmatomyces*** **(anamorphic), and** ***Stilbum*****;** *Mycogloea* p.p. and *Spiculogloea* are assigned to Spiculogloeales; anamorphic *Sporobolomyces* yeasts are found in both orders (Aime et al. 2006; Bauer et al. 2006 and references therein; Bauer et al. 2009; Kurtzman et al. 2011). *Mycogloea* s.l. is not monophyletic (Aime et al. 2006; Bauer et al. 2009), and sampling of the type species, *M. carnosa*, is needed to resolve the placement of this genus.

Together, the species of Agaricostilbomycetes possess a wide array of ecological and morphological variation. **Most species are believed to be either saprobic or mycoparasitic.** *Agaricostilbum* and *Stilbum* species are typically isolated from dead plant material (of palms in the case of *A. pulcherrimum*), and *Cystobasidiopsis* is known only from soil (Bauer et al. 2009). However, there is evidence for a mycoparasitic habit for many of the species, and many could be mycoparasitic rather than saprobic. For instance, the original description of *A. palmicola*, the type species of *Agaricostilbum*, notes that the fungus was almost always found in association with an ascomycetous *Anthostoma*-like fungus (Wright 1970). *Chionosphaera*, *Mycogloea*, and *Kondoa* species are found similarly in association with other fungi, and species of *Spiculogloea* are known mycoparasites. *Mycogloea* and *Spiculogloea* species also produce tremelloid haustorial cells such as are commonly found in other known mycoparasitic fungi, especially those in Tremellales (Agaricomycotina) (Bauer et al. 2006). Species of *Kurtzmanomyces* seem to be very rare and are known only from type cultures (Kurtzman et al. 2011), in contrast to *A. pulcherrimum*, which is pantropical in distribution. *Sterigmatomyces halophilus* is usually found in association with marine environments, and both species of *Sterigmatomyces* are osmotolerant (Fell 1966). The ecological niche of many species, however, remains unknown.

All species form a yeastlike stage, with the exception of *Cystobasidiopsis nirenbergiae* (Bauer et al. 2009), and, excepting *C. nirenbergiae*, those with known teleomorphs are dimorphic. With one exception (members of the genus *Chionosphaera*), teleomorphic species in Agaricostilbomycetes produce phragmobasidia; species of *Spiculogloea* and *Kondoa* are ballistosporic (Bauer et al. 2006), and *Kurtzmanomyces* and *Sterigmatomyces* species form ballistoconidia on a stalked conidiophore, a character otherwise not found in Pucciniomycotina (Kurtzman et al. 2011). Stilboid basidiocarps are formed in three genera (*Agaricostilbum*, *Stilbum*, and *Chionosphaera*), and minute pustulate fruiting bodies are formed by members of *Mycogloea* (Bandoni 1998). Basidia are formed directly from probasidia on hyphae in *Cystobasidiopsis* (Bauer et al. 2009).

The septal pore in *Agaricostilbum* species is associated with microbodies containing electron-dense material that has been suggested to resemble the Woronin bodies of Ascomycota (Oberwinkler and Bauer 1989). Additionally, **in studied members of the Agaricostilbaceae and Chionosphaeraceae an unusual pattern of mitosis has been documented wherein, in the yeast phage, the nucleus divides in the parent cell, rather than migrating into the bud prior**

to division (Frieders and McLaughlin 1996; McLaughlin et al. 2004; Swann et al. 2001).

B. Atractiellomycetes

This class contains a single order, Atractiellales, and **fewer than 50 species** in the genera ***Atractiella, Basidiopycnis, Helicogloea, Hobsonia* (anamorphic), *Infundibura* (anamorphic), *Leucogloea* (anamorphic), *Phleogena, Proceropycnis* (anamorphic), and *Saccoblastia*.** Atractiellales was originally erected to accommodate a number of genera and species formerly placed in Auriculariales (Agaricomycotina) and subsequently separated by the presence of simple septal pores and 5S RNA secondary structure (Gottschalk and Blanz 1985; Oberwinkler and Bandoni 1982). As in Agaricostilbomycetes, stilboid fruiting bodies are formed in *Atractiella* and *Phleogena* and basidia are phragmobasidia of the auricularioid type. However, yeast states are not known for these fungi, and anamorphic states are typically conidial. In *Hobsonia* species conidia are tightly coiled on short conidiophores, forming a minute sporodochium-like fruiting body on dead vegetation (Martin 1959).

Ultrastructurally, members possess **organelles termed microscala or symplechosomes that have no known function but seem to be synapomorphic for the class** (Bauer et al. 2006; McLaughlin 1990; Oberwinkler and Bauer 1989). Perhaps the most intriguing Pucciniomycotina discovery of recent years was that of the association of three unidentified species of Atractiellomycetes with tropical orchids, confirmed by transmission electron microscopy and molecular phylogenetics (Kottke et al. 2010). Prior to this discovery, all Atractiellomycetes were presumed saprobic, and the basalmost mycorrhizal formers known in Basidiomycota were to be found within Auriculariales. The sampling area of Kottke et al. (Kottke et al. 2010) was limited to a tropical montane rainforest in southern Ecuador; thus, it is unknown how widespread this association is. Nonetheless, the find remains significant for documenting the first known instance of a plant mutualistic association within Pucciniomycotina.

C. Classiculomycetes

This class contains a single order, Classiculales, for which **only two species are known, *Classicula fluitans* (anamorph *Naiadella fluitans*) and the hyphomycete *Jaculispora submersa*** (teleomorph unknown) (Hudson and Ingold 1960; Marvanová and Bandoni 1987). Morphological and sequence data clearly show that *C. fluitans* and *J. submersa* form a separate lineage in Pucciniomycotina (Aime et al. 2006; Bauer et al. 2006). Both species are **aquatic and are associated with leaf litter in freshwater habitats.** Plant host preferences have been tested for *J. submersa* and suggest an affinity for oak leaves (Prokhorov and Bodyagin 2007). Additionally, there is evidence that they may be mycoparasitic; *C. fluitans* has been observed to parasitize its own hyphae in culture, and both species form tremelloid haustorial cells such as are commonly found in other known mycoparasitic fungi (Bauer et al. 2003).

In both *C. fluitans* and *J. submersa* the septal pores are surrounded by microbodies that are arranged in a circular pattern, such as are also found in Pucciniales and a few other members of Pucciniomycotina (Bauer et al. 2003). The **combination of binucleate, tremelloid haustorial cells and pore-associated microbodies, however, is unique to Classiculomycetes.** Both species are hyphal with hyaline cells. Primary septa are formed in association with nuclear division and have clamp connections; adventitious septa may also be formed independently of nuclear division and are clampless. Asexual reproduction takes place via conidia that have two to three long fusiform subapical appendages resembling the conidia of other unrelated aquatic fungi (Marvanová and Bandoni 1987), including the cystobasidiomycete *C. elegans*. The sexual stage of *C. fluitans* has been observed to occur only on the surface of water. The basidia occur in clusters and have auricularioid septation and **subapically swollen sterigmata**, the last of which is unique in Pucciniomycotina. Basidiospores are small and fusiform, which is another convergent character found in other unrelated aquatic fungi (Bauer et al. 2003).

D. Cryptomycocolacomycetes

This is a small enigmatic class with **two known species, *Cryptomycocolax abnormis* (published as *C. abnorme*) and *Colacosiphon filiformis* (anamorphic)** (Kirschner et al. 2001; Oberwinkler and Bauer 1990). Both species are apparently **rare**, having been isolated only once each from a parasitized ascomycete (*C. abnormis*) and bark beetle galleries, where it was found parasitizing a co-isolated ascomycete (*C. filiformis*). Available DNA sequence data of the nuclear ribosomal large subunit indicate that these fungi form a separate class-level lineage within Pucciniomycotina (Bauer et al. 2006). Unfortunately, type or other material of either species could not be located for additional analyses, and thus phylogenetic resolution of this lineage will not be possible until additional isolates are discovered.

Within Pucciniomycotina, the **extremely elongate holobasidia** produced by *C. abnormis* **are unique**. *C. filiformis* is described as mitosporic with elongate conidiophores (Kirschner et al. 2001), although Bauer et al. (2006) indicate that this species also produces elongate basidia of the *Cryptomycocolax* type. Species form hyaline hyphae that are clamped in *Cryptomycocolax*; basidia are produced on the host surface and undergo a unique developmental pattern (Oberwinkler and Bauer 1990). Members of Cryptomycocolacomycetes possess mycoparasitic organelles termed colacosomes, a character that is shared only with some Microbotryomycetes. Microbodies interpreted as Woronin-like bodies have been reported in association with the septal pores of both species (Kirschner et al. 2001; Oberwinkler and Bauer 1990); septal-pore-associated microbodies and pore plugs are present on some, but not all, septa of *C. abnormis* (Oberwinkler and Bauer 1990).

E. Cystobasidiomycetes

This is a small class of **predominantly yeast-like fungi**. Genera include ***Bannoa*, *Cyrenella* (anamorphic), *Cystobasidium*, *Erythrobasidium*, *Naohidea*, *Occultifur*, and *Sakaguchia*, as well as** several anamorphic yeasts currently placed in *Rhodotorula* and *Sporobolomyces* (Aime et al. 2006; Kurtzman et al. 2011), most of which are, or presumably are, mycoparasitic. For instance, *C. elegans* was isolated from a mushroom that had been submerged in freshwater (Gochenaur 1981). Species of *Cystobasidium*, *Erythrobasidium*, *Naohidea*, and *Occultifur* have been isolated from ascomycete or basidiomycete fruiting bodies. The number of known species in this class has probably tripled in the last decade, primarily because of the discovery of new yeast species from extreme habitats (e.g., Libkind et al. 2010; Pohl et al. 2011). As is also true of some Microbotryomycetes, a number of species seem to be psychrophiles (e.g., Libkind et al. 2008). The majority of Cystobasidiomycetes genera (*Bannoa*, *Cyrenella*, *Erythrobasidium*, *Naohidea*, and *Sakaguchia*) are monotypic, and most of these are known from single cultures or a single geographic locale, making it likely that a tremendous amount of undiscovered diversity exists within the class.

The variety of sexual state morphologies in this group is unusual, although not all researchers have reached similar interpretations of the structures involved, especially for *Bannoa* and *Erythrobasidium*, for which the same reproductive cells have been described as basidial (e.g., Sugiyama and Suh 1993) or conidial (Bauer et al. 2006). However, Kurtzman et al. (2011) provide convincing evidence, including the illustration of conjugation tubes and basidiospore germination, that these are indeed teleomorphic species. *Bannoa* and *Erythrobasidium* species form holobasidia; *Naohidea*, *Cystobasidium*, and *Occultifur* members form phragmobasidia of the auricularioid type, which germinate from probasidia in the latter two but not in *Naohidea*; and in *Sakaguchia dacryoidea* two- to four-celled basidia germinate from teliospores produced on short hyphal stalks (Kurtzman et al. 2011; Oberwinkler 1990; Sugiyama and Suh 1993; Yamada et al. 1994).

The bipolar multiallelic mating system of *Bannoa hahajimensis* is unique within Pucciniomycotina (Kurtzman et al. 2011). *C. elegans* is also unique among yeast species in producing subclavate tetraradiate conidia, which are found in unrelated aquatic hyphomycetes, making an aquatic habit likely for this species (Kurtzman et al. 2011). These differ from the aquatic conidia produced in Classiculomycetes in shape and number of appendages. Mycoparasitic tremelloid haustorial cells are produced by members of Cystobasidiales (Bauer et al. 2006). Ultrastructurally, septal pores of Cystobasidiales are occluded by a cystosome.

F. Microbotryomycetes

Microbotryomycetes are known for containing the model genetic organism *Microbotryum violaceum* and several ubiquitous red yeasts including *Sporidiobolus pararoseus*. Three members of Microbotryomycetes, the yeasts *Sporobolomyces* sp. (as *S. roseus*) and *Rhodotorula graminis* and the anther smut *M. violaceum*, are the only Pucciniomycotina species outside of Pucciniales to be whole-genome sequenced to date [Grigoriev et al. (2012); *Microbotryum violaceum* Sequencing Project, Broad Institute of Harvard and MIT (http://www.broadinstitute.org/)]. With more than 200 described species, it is the **second largest class in Pucciniomycotina** (Kirk et al. 2008) (Table 10.1). Five orders and seven families have been described. Genera include ***Atractocolax, Aurantiosporium, Baueraago, Camptobasidium, Colacogloea, Curvibasidium, Fulvisporium, Heterogastridium, Kriegeria, Krieglsteinera, Leucosporidium* p.p., *Liroa, Mastigobasidium, Meredithblackwellia, Microbotryum, Rhodosporidium, Sphacelotheca, Sporidiobolus, Ustilentyloma, Zundeliomyces*, and *Zymoxenogloea* (anamorphic), and numerous anamorphic yeasts placed in *Glaciozyma, Leucosporidiella, Rhodotorula*, and *Sporobolomyces*, including the type species of *Rhodotorula* and *Sporobolomyces*** (Aime et al. 2006; Bauer et al. 2006; Toome et al. 2013; Turchetti et al. 2011). A large percentage of the described genera are monotypic (e.g., *Atractocolax, Camptobasidium, Fulvisporium, Heterogastridium, Krieglsteinera, Liroa, Mastigobasidium, Meredithblackwellia*, and *Zundeliomyces*), which may be an indication of an as yet undiscovered diversity.

Microbotryum species, often referred to as the **anther smuts**, were originally classified within Ustilaginomycotina, although numerous lines of evidence now show that the smut syndrome, including an anamorphic yeast phase, gasteroid basidia, pigmented teliospores, and parasitism of plant reproductive parts, has independently evolved at least twice within Basidiomycota. Most phylogenetic analyses recover Microbotryomycetes as a monophyletic class (e.g., Aime 2006; Bauer et al. 2006), yet the backbone within the class has not been adequately resolved, and nearly 20 % of the species now classified in Microbotryomycetes have not been confidently placed to order or family (Table 10.1).

Yeast stages of this group are increasingly recovered in environmental samplings of phylloplanes, soils, and extremely cold habitats with concomitant new species discovery (e.g., Golubev and Scorzetti 2010; Kachalkin et al. 2008; Libkind et al. 2005; Toome et al. 2013; Turchetti et al. 2011; Valério et al. 2008; Yurkov et al. 2011). The tractability of many of these organisms in the laboratory has led to the development of molecular biological and genomics tools for studying genetics and gene function in Microbotryomycetes that are lacking in other Pucciniomycotina (e.g., Coelho et al. 2011; Ianiri et al. 2011). The first studies to identify mating type loci in Pucciniomycotina were conducted with a member of Microbotryomycetes (Coelho et al. 2008; Giraud et al. 2008).

Most teleomorphic species are dimorphic with haploid yeast stages and phragmobasidiate teleomorphs, with the exception of *Curvibasidium* (Bauer et al. 2006). **Colacosomes, subcellular organelles associated with mycoparasitism**, of similar appearance to those in Cryptomycocolacomycetes, **are found in many species** (Bauer et al. 1997), but otherwise there is a tremendous diversity in morphology and ecology within this class, which is discussed in detail in Bauer et al. (2006) and Swann et al. (2001). There is a range of fruiting morphologies from the simple teliosporic yeasts, e.g., *Rhodosporidium* (Fig. 10.2), to the pycnidioid fruiting bodies of *Heterogastridium* species. Ecologically, many are plant associates, either as presumably saprobic yeasts on plant surfaces or as pathogens of leaves (e.g., *Kriegeria*) and plant anthers (e.g., *Microbotryum*). *Heterogastridium* species are mycoparasites, and the presence of colacosomes in most other genera in Heterogastridiales would suggest a similar habit for these. The yeast *Camptobasidium hydrophilum* is aquatic (Marvanová and Suberkropp 1990), and several Sporidiobolales members are cosmopolitan, having been recovered from many terrestrial and marine habitats (e.g., Sampaio 2004).

G. Mixiomycetes

***Mixia osmundae* is the only species** currently known in Mixiomycetes. It was first described as an ascomycete (*Taphrina osmundae*) and remained classified within Ascomycota for more than 80 years, primarily due to superficial similarities between the sporogenous cells of *Mixia* and the asci produced by some Ascomycota. However, molecular and closer morphological studies of the sporogenous cells in the 1990s provided multiple lines of evidence that *Mixia* belongs to Basidiomycota (Nishida et al. 1995). Later phylogenetic analyses of rDNA sequences support its placement in Basidiomycota and show clearly that it is a member of Pucciniomycotina (Aime et al. 2006; Bauer et al. 2006) (Fig. 10.1).

The fungus is an **intracellular parasite of ferns in the genus *Osmunda*,** in which it causes small yellow to brown leaf spots. *Mixia* is known from *Osmunda regalis* in Japan and Taiwan and *Osmunda cinnamomea* in the USA (Kramer 1958; Mix 1947; Nishida 1911; Sugiyama and Katumoto 2008), but it is rarely found, and many aspects of its biology are unknown.

When growing within a host, *Mixia* forms intercellular coenocytic hyphal cells, forming large saclike, nonseptate, sporogenous cells on the surface of the host epidermis. **The production of coenocytic hyphae is a rare condition in Basidiomycota, and the sporogenous cells produced by *Mixia* are unique in the phylum.** Spore production is very unusual in that the spores are formed on the surface of the sporogenous cell simultaneously, creating a powdery layer on fern leaves (Nishida et al. 1995). Genome sequencing revealed that these spores are haploid and likely produced via asexual reproduction (Toome et al. 2014). In culture, *M. osmundae* forms yeastlike cells that reproduce by budding. Septal pore ultrastructure has not yet been determined for this fungus, likely due to the limited formation of septa (Bauer et al. 2006).

H. Pucciniomycetes

Pucciniomycetes is a diverse class containing **the vast majority** (ca. 8000; Kirk et al. 2008) **of Pucciniomycotina species.** Before the availability of DNA sequence data, Pucciniomycetes were placed in various positions on the fungal tree of life. For instance, based on some of their structural characters (e.g., lack of clamp connections) and parasitic life style, Pucciniales and their relatives were often thought to represent an early diverging lineage of Basidiomycota. Phylogenetic studies based on rDNA have shown that rust fungi and their closest relatives in Pucciniomycetes are a derived group within the Pucciniomycotina (Aime et al. 2006). One earlier name for this lineage is Urediniomycetidae sensu Swann et al. (2001).

Almost all of the organisms in Pucciniomycetes are **parasites of plants, insects, or other fungi.** The class contains five orders (Table 10.1), **the most speciose** of which, at ca. 7,800 species in ca. 150 genera (Kirk et al. 2008), **is Pucciniales**, or rust fungi, named for the typically rusty coloration of their urediniospores. Rust fungi are parasites of vascular plants with highly complex life cycles requiring the production of up to five different spore stages on two different host plants (Cummins and Hiratsuka 2003) (Fig. 10.3). In Fungi true obligate biotrophs, i.e., organisms that completely depend on a living host to complete their life cycle, are rare, mainly comprising the powdery mildews (Erysiphales, Ascomycota) and the rust fungi. **Species of Pucciniales cause some of the most devastating plant diseases and therefore have been studied in greater detail than other Pucciniomycotina.** However, their obligately biotrophic nature renders them recalcitrant organisms for molecular studies. Thus, family and generic concepts are predominantly morphology-based, which has led to the recognition of several artificial taxa. Comprehensive phylogenetic treatments of the order include Aime (2006), Maier et al. (2003), and Wingfield et al. (2004). Descriptions of families and genera can be found in Cummins and Hiratsuka (2003).

The remaining approximately 200 species in the Pucciniomycetes are of little economic importance. The largest among these is **Septobasidiales [*Auriculoscypha*, *Coccidiodictyon*, *Johncouchia* (anamorphic), *Ordonia*, *Septobasidium*, and *Uredinella*]**, of which more than 150 species are known and which contains the only entomopathogenic species in Pucciniomycotina. Members of Septobasidiales **parasitize scale insects that feed on trees**, forming dense fungal mats that cover the insects on their hosts (Couch 1938). **The next two largest orders contain species parasitic on mosses and ferns (Platygloeales, ca. 20 species in *Eocronartium*, *Herpobasidium*, *Jola*, *Insolibasidium*, *Platygloea* s.s., *Platycarpa*, and *Ptechetelium*) or parasites that alternate between plant roots and rust fungi (Helicobasidiales, ca. 17 species of *Helicobasidium*, and its *Tuberculina* anamorph).** Some species in Helicobasidiales have been the focus of ecological studies to determine their potential as biocontrol agents against rust fungi, but very little is known about the other species in these orders. The fifth order, **Pachnocybales, contains a single species, *Pachnocybe ferruginea***, which seems to be a saprobe, having been repeatedly isolated from creosoted telephone poles, and therefore differs significantly from all other Pucciniomycetes by having a nonparasitic habit.

The **dikaryon is the dominant phase in Pucciniomycetes,** and only one of the orders, Septobasidiales, is known to have a yeast stage. However, production of asexual spores is often well developed, especially among rust fungi. Members of Pucciniomycetes lack clamp connections (Bauer et al. 2006). Basidia are of the auricularioid type, germinating from a probasidium that, in the rust fungi, is a thick-walled resting spore (i.e., teliospore). *P. ferruginea* is again the exception for Pucciniomycetes in that it produces holobasidia rather than phragmobasidia (Kropp and Corden 1986). Pucciniales are heteroecious, i.e., they alternate between two unrelated hosts during different stages of their life cycle. Members of Helicobasidiales also need to alternate between two hosts; the dikaryon parasitizes plant stems and roots, whereas the monokaryotic stage parasitizes rust fungi in the Pucciniales (Lutz et al. 2004).

The most important ultrastructural character of Pucciniomycetes is that of a **simple septal wall with a central pore that in many species has a pulley-wheel-shaped plug** (Swann et al. 2001), and the SPB is inserted into a pore of the nuclear envelope (Bauer et al. 2006). In Septobasidiales and Pachnocybales, the presence of microscala has also been reported (Swann et al. 2001).

I. Tritirachiomycetes

This class contains a single order, Tritirachiales, with **six currently known *Tritirachium* species.** Until recently the genus *Tritirachium* was placed in phylum Ascomycota, primarily due to similarities in conidiophore morphology with other mold species in subphylum Pezizomycotina. However, multigene analyses based on nuclear small and large subunits and translation elongation factor 1-alpha revealed that most species currently placed in *Tritirachium*, including the type species, belong to Pucciniomycotina (Schell et al. 2011).

All the members of Tritirachiomycetes are **anamorphic molds with no known teleomorphic stage**. Species have been isolated from dead plant roots, indoor environments, and insects (Beguin 2010; Jebaraj et al. 2010; Limber 1940; Schell et al. 2011). While the precise role of *Tritirachium* species in the environment is not known, there is strong evidence that *T. dependens* is a potentially obligate parasite of *Penicillium* and other ascomycetous species, on which it depends for certain micronutrients (Beguin 2010, as *T. egenum*). Two species, *T. oryzae* and *T. roseum*, can be causal agents of infections on human cornea and scalp (Moraes et al. 2010; Rodrigues and Laibson 1975). There is little information about the biology of *Tritirachium* species, and only those of potential medical importance have been studied in any detail. Although not originally identified as such, environmental sequences of what seem to be species of *Tritirachium* have been generated from soil clones from a rhizosphere in Canada in a study by Stefani et al. (2010) and from minimally oxygenated deep waters of the Arabian Sea reported by Jebaraj et al. (2010).

There is some overlapping of cultural and morphological characteristics between the species currently placed in *Tritirachium*; therefore, morphological observations alone may not be sufficient for diagnosing all members of this genus at the species level. At the genus level, *Tritirachium* species are hyphal in culture, producing conidiophores that branch in a characteristic zigzaglike pattern. Conidia are hyaline and single-celled. Septal pores are uniperforate with a small pore plug (Schell et al. 2011), but little else is currently known of the subcellular characters of these fungi.

V. Culturing

For the majority of Pucciniomycotina species **in Pucciniales, culturing on standard media is not possible because these are obligate plant pathogens**. Nevertheless, various methods have been developed to facilitate the multiplication of rust fungi, and uredinial spore states can be maintained on susceptible host plant tissue for a number of species. A few species of rust fungi have been successfully cultured from germinating basidiospores or hyphae from leaves; however, complex media are needed, and the growth rate of such cultures is extremely slow and limited (Kinloch and Dupper 1996; Moricca and Ragazzi 2001).

Most other known members of Pucciniomycotina are culturable and grow well on standard nutrient sources, both in liquid and on solid media. Those with forcible spore discharge can be isolated via the spore fall method by suspending the substrate (such as plant leaf) above nutrient media with antibiotics (e.g., Toome et al. 2013). This method works well for separating many mycoparasites from their fungal hosts (e.g., Langer and Oberwinkler 1998). Gasteroid species, yeasts, and anther smuts can be isolated via streak plating on antibiotic media (e.g., Kurtzman and Fell 2004). Some halotolerant species, such as *Sterigmatomyces* spp., can be isolated by exposing air to media with high sodium (up to 20 %) or glucose (up to 50 %) content (e.g., Fell 1966).

VI. Conclusion

Pucciniomycotina contains a diversity of fungi that are united in possessing simple septal pores that lack dolipores and septal pore caps. Most, but not all, produce phragmobasidia, and many have yeast states. Members now united in Pucciniomycotina were previously placed within Ascomycota and the other two subphyla (Ustilaginomycotina and Agaricomycotina) of Basidiomycota. More than 8 % of all described Fungi belong to Pucciniomycotina, whose members can be found in habitats ranging from deep oceans and Arctic ice to most terrestrial systems. Plant associations dominate, and the majority of described species are phytopathogens of vascular plants, ferns, and mosses, but other members are known as asymptomatic members of the phylloplane, entomopathogens and mycoparasites, or mycorrhizal symbionts of orchids. Life cycles range from simple teliosporic yeasts to the elaborate life cycles found in the biotrophic rust fungi. The description of new species of Pucciniomycotina has been steadily rising in the last 10 years, and it is predicted that much diversity within this group remains to be discovered.

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