
12 Tremellomycetes and Related Groups

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I. Introduction

Tremellomycetes is a fungal group full of contrasts. It includes jelly fungi with conspicuous macroscopic basidiomes, such as some species of *Tremella*, as well as macroscopically invisible inhabitants of other fungal fruiting bodies and a plethora of species known so far only as asexual yeasts. Tremellomycetes may be beneficial to humans, as exemplified by the production of edible *Tremella* fruiting bodies whose production increased in China alone from 100 MT in 1998 to more than 250,000 MT in 2007 (Chang and Wasser 2012), or extremely harmful, such as the systemic human pathogen *Cryptococcus neoformans*. The systematics and taxonomy of many species now contained in Tremellomycetes have significantly changed during the past three decades and are about to change again as a result of changes in the taxonomic treatment of anamorph forms in the International Code of Nomenclature for algae, fungi, and plants (McNeill et al. 2012). An integrated systematic view of the Tremellomycetes has been hampered by the fact that the anamorphic taxa, i.e., yeasts, and the basidiome-forming dimorphic taxa have traditionally been studied by different scientific communities. Recently, the group has been discussed in more integrative treatments (e.g., Boekhout et al. 2011; Millanes et al. 2011; Sampaio 2004).

Since the last edition of *The Mycota*, key systematic concepts in the Basidiomycota have changed conspicuously. While the tremellomycetous groups were then treated in a separate *Heterobasidiomycetes* chapter (Wells and

Dedicated to the memory of Robert Joseph Bandoni (1926–2009)

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Bandoni 2001), Heterobasidiomycetes is no longer considered a monophyletic group (Weiß et al. 2004); for the present edition its members are discussed in this chapter, in Agaricomycetes (*Tulasnella*, *Ceratobasidium* and relatives, Auriculariales, Sebaciales; see Hibbett et al. 2014), and in Dacrymycetes (see Oberwinkler 2014).

In this overview we provide an introduction to the taxonomy, morphology, ecology, and phylogenetic relationships of the Tremellomycetes, including a phylogenetic tree that covers the vast majority of species of this group for which molecular data [nuclear rDNA coding for the D1/D2 regions of the large ribosomal subunit (LSU)] are available, using type or ex-type sequences wherever possible. It illustrates both the phylogenetic resolution presently available in the Tremellomycetes and the degree to which current taxonomy matches the phylogenetic relationships in this group. Considering the impressive progress in genome sequencing and phylogenomics we anticipate that at least the higher-level relationships will be much better resolved in the near future.

A. Historical Concepts

The genus *Tremella* was validly described by Persoon (1794). Some years later (Fries 1821) the genus was the basis for the family Tremellaceae (as Tremellini, including also *Dacrymyces*), and for the order Tremellales (as Tremellinae)—one of the six orders that Fries described in his Hymenomycetes—which roughly corresponds to what today are called jelly fungi. Since the acceptance of basidial morphology as a key character in the systematics of the basidiomycetes (Brefeld 1888; Patouillard 1887; Tulasne 1853), Tremellaceae/Tremellales have often been used as the taxon containing all hymenomycetes with longitudinally septate basidia—as opposed to the Auriculariaceae/Auriculariales, which according to these concepts included taxa with transversely septate basidia [see Bandoni (1984) for a systematic treatment of the taxonomic history].

B. Modern View

This concept was challenged by Bandoni (1984), who redefined Tremellales and Auriculariales based on ultrastructural characters, the nature of the haploid states, and trophic strategies, rather than on basidial morphology. This alternative concept has been largely confirmed by molecular data (e.g., Swann and Taylor 1995; Weiß and Oberwinkler 2001) and is currently widely accepted (Hibbett et al. 2007).

Particular taxonomic problems in the Tremellomycetes to be solved in the future include the obvious nonmonophyly of established morphogenera, such as *Tremella*, and the question of how to best treat originally anamorphic genera, such as *Bullera* and *Cryptococcus*, in a modern nomenclature that no longer gives priority to generic names based on teleomorphs (Hawksworth 2011; McNeill et al. 2012). Since it is too early to solve these questions in this text, here we still adopt some widely used names that are likely to change in the near future.

II. Morphology and Anatomy

A. Basidiocarps

Basidiocarps (Fig. 12.1) are known from species of Tremellales, Holtermanniales, and Filobasidiales (*Syzygospora*). In species of Tremellales, basidiocarps are mostly of a **gelatinous consistency**. Many species can undergo prolonged phases of exsiccation, reviving when rehydrated, with renewed growth and production of conidia or basidiospores (Wells and Bandoni 2001). They are thus well adapted to habitats on dead wood, on which the more exposed species, for example, *Tremella*, are often found. Basidiocarp forms vary from **pustulate**, for example, *Tremella* spp., *Tetragoniomyces*, or *Sirobasidium*, to **cushion-shaped, lobose-cerebriform**, for example, *Tremella mesenterica* (Fig. 12.1a, b), to foliose, for example, *Tremella foliacea* (Fig. 12.1g) and *Tremella fuciformis* (Fig. 12.1h). Often they originate from a host fungus that they obviously parasitize (see below). Mature basidiocarps may even show a



Fig. 12.1 (a–e) *Tremella mesenterica*. (a) Young basidiocarps on *Peniophora laeta* growing on *Carpinus betulus*, bar=2 mm. (b) Mature basidiocarp, bar=5 mm. (c) Part of hymenium with basidia, bar=10 μ m. (d) Yeast budding, bar=10 μ m. (e) Basidiospore with secondary spore, bar=5 μ m. (f) *Tremella encephala* showing whitish core with hyphal mixture of host *Stereum sanguinolentum* and mycoparasite, bar=1 cm. (g) *Tremella foliacea*, bar=2 cm. (h) *Tremella*

fuciformis, bar=3 cm. (i) *Tremella aurantia*, bar=3 cm. (j) *Sirobasidium magnum*, bar 3 cm. (k–m) *Syzygospora pallida*. (k) Pustular basidiocarps emerging from host *Phanerochaete cremea*, bar=2 mm. (l) Basidium and conidiophores, bar=10 μ m. (m) Budding yeasts, bar=10 μ m. (n, o) *Tetragoniomyces uliginosus*. (n) Basidiocarps in culture, bar=1 mm. (o) Germinating basidium, bar=10 μ m

central core composed of hyphae of host and mycoparasite, as in *Tremella encephala* (Fig. 12.1f). Basidiocarps in the Holtermanniales are tough-gelatinous, with a clavarioid appearance.

Numerous teleomorphic species in the Tremellomycetes apparently lack basidiocarps. Such species grow **intrahymenially** in their fungal hosts, either without causing any macroscopic symptoms, such as *Tremella giraffa*, *Tremella obscura*, and *Tremella penetrans*, or inducing galls on their hosts, for example, lichenicolous species of *Tremella* or *Biatoropsis usnearum*. Sexual stages in some species of Tremellales, for example, *Bulleribasidium* (Fig. 12.2e), *Filobasidiella* (Fig. 12.3a), *Kwoniella*, and *Rhynchogastrema* (Fig. 12.2f), as well as all known sexual stages in Cystofilobasidiales, are known only from pure cultures.

B. Micromorphology

Most species in the Tremellomycetes grow as yeasts in their haploid stages (Figs. 12.2 and 12.3). Such yeast stages may proliferate by budding, but they may also produce **ballistoconidia** that are morphologically and functionally similar to basidiospores. Yeast cells are generally globose to ellipsoid but may also be elongate, as in *Carcinomyces*. Diploid stages are generally filamentous, with clamped hyphae.

There is conspicuous variation in basidial morphology, which has been one of the most important characters used in traditional morphogeneric concepts. The **basidia** of the species of *Tremella* are usually longitudinally septate (so-called tremelloid basidia), with the basidial compartments protruding into elongated tubes, designated as *epibasidia* by some authors (Wells and Bandoni 2001), that pervade the often gelatinous matrix of their own or the host basidiome and, finally, apically bear a sterigma, from which the mostly globular basidiospores are actively discharged into the air (Fig. 12.4). There are, however, numerous variations.

First, **tremelloid basidia** are only known in the Tremellales and in *Holtermannia*. In some other species of Tremellales the basidial compartments may be arranged in a more linear

order, with **transverse or oblique basidial septa**, as in *Auriculibuller*, *Bulleromyces*, and *Papiliotrema* (Fig. 12.2b). Development of the basidial compartments is often strongly desynchronized (Wells and Bandoni 2001), and basidial compartments may detach in some species, for example in *Sirobasidium* (Fig. 12.2h), before giving rise to a ballistospore (Bandoni 1984). Basidial septation may also be lacking, resulting in **holobasidia**, as in *Carcinomyces* (Fig. 12.3d) and *Filobasidiella* (Fig. 12.3a) (Tremellales); *Filobasidium* (Fig. 12.3b) and *Syzygospora* (Fig. 12.3e, f) (Filobasidiales); *Cystofilobasidium* (Fig. 12.3c); and *Xanthophyllomyces* (Cystofilobasidiales). In some species a **partial apical septation** in holobasidia has been reported, for example in *Rhynchogastrema* (Fig. 12.2f) and *Syzygospora* (Metzler et al. 1989; Oberwinkler and Lowy 1981). Obviously, a transition from phragmobasidia to holobasidia has occurred independently several times in the Tremellomycetes (Millanes et al. 2011).

Second, there are also exceptions concerning the development and arrangement of basidia. While basidia usually appear singly or in clusters proliferating from subbasidial clamps, for example in basidiomes of *Tremella*, **basidial chains** can be observed in species of *Sirobasidium* (Fig. 12.2h) and, to a lesser degree, in *Sirotrema*. In these species, basidia proliferate basipetally, starting from an apical basidium. In Cystofilobasidiales basidia arise from **teliospores** (Fig. 12.3c).

Third, Tremellomycete species differ concerning the release and functioning of **basidiospores**. In most teleomorphic species basidiospores are actively discharged from sterigmata. In *Sirobasidium*, on the other hand, basidia give rise to passively released fusoid basidiospores (Fig. 12.2h) [alternatively designated as epibasidia (Wells and Bandoni 2001)] that may proliferate by budding or by the formation of secondary spores (Bandoni 1984). Some other species in the Tremellomycetes, such as the phragmobasidiate species of *Kwoniella* and the holobasidiate species of *Carcinomyces*, produce sessile basidiospores.

A feasible concept uniting the heterogeneity in basidial morphology observed in the Tremellomycetes has been proposed by Bandoni

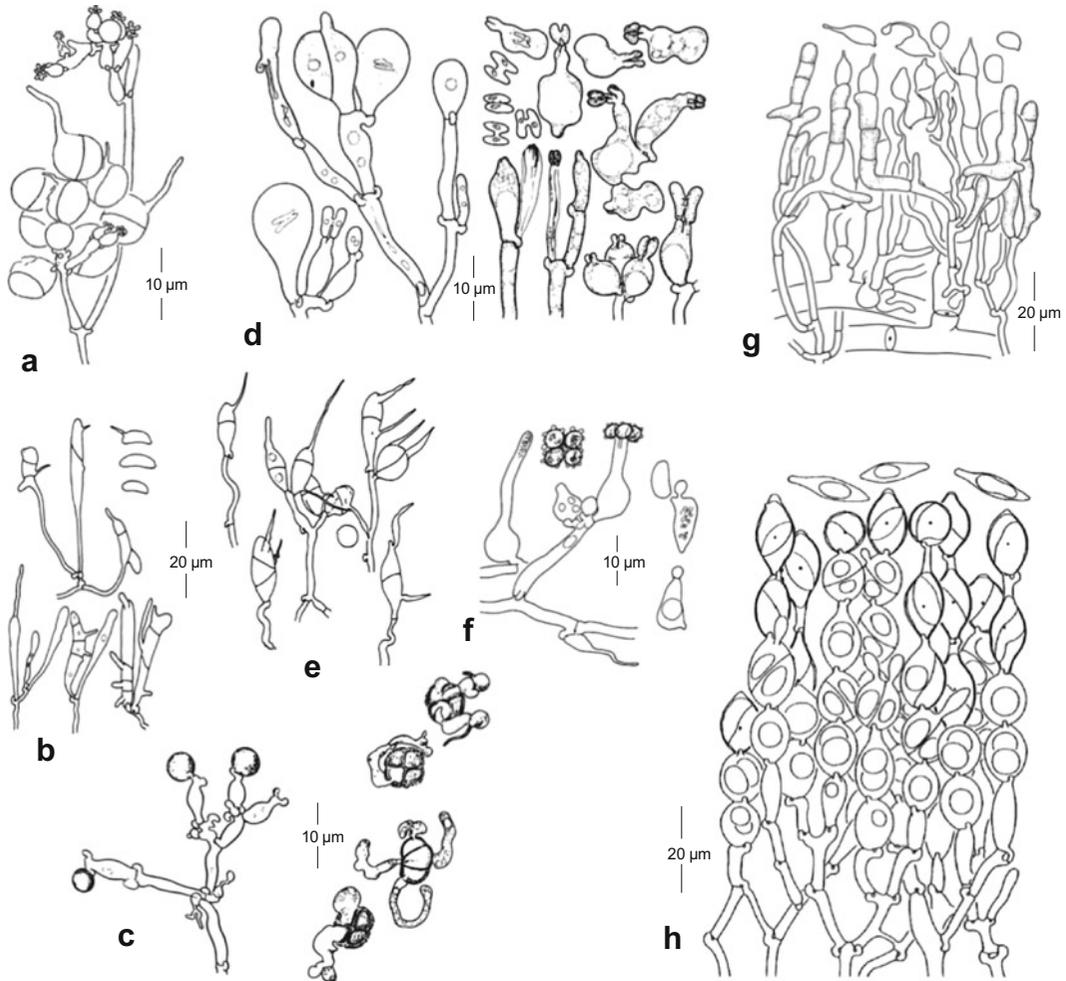


Fig. 12.2 Basidial characters in Tremellomycetes. (a) *Cuniculitrema polymorpha* (Kirschner et al. 2001). (b) *Papiliotrema bandonii* (Sampaio et al. 2001). (c) *Tetragoniomyces uliginosus* (Oberwinkler and Bandoni 1981). (d) *Trimorphomyces papilionaceus* (Oberwinkler

and Bandoni 1983). (e) *Bulleribasidium oberjochense* (Sampaio et al. 2001). (f) *Rhynchogastrema coronata* (Metzler et al. 1989). (g) *Phragmoxenidium mycophilum* (Oberwinkler et al. 1990). (h) *Sirobasidium magnum* (Chen 1998)

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(1984), who suggested that the basidial “compartments” themselves may actually be meiotic products (**endospores**) that in most species form a germtube (the so-called epibasidium) to produce a secondary spore (basidiospore in common terminology). Longitudinal, transverse, or oblique septation of the basidium then may simply result from a varying arrangement of the primary spores (endospores) within the basidium.

Teliospores, i.e., one-celled conidia that give rise to basidia after a resting period, are only known from species of Cystofilobasidiales.

These structures provide an eloquent example of convergent evolution as they are present in various distantly related groups of basidiomycetes, such as the rust and the smut fungi.

Many presumably mycoparasitic species of Tremellomycetes feature a characteristic tremelloid haustorial type in their filamentous stages (e.g., Chen 1998; Oberwinkler and Bandoni 1981; Zugmaier et al. 1994) (Fig. 12.2c, f, g). **Tremelloid haustoria** arise from clamp connections and consist of single cells that are globular or short clavate at the base and extend into one or more narrow filaments (Fig. 12.4).

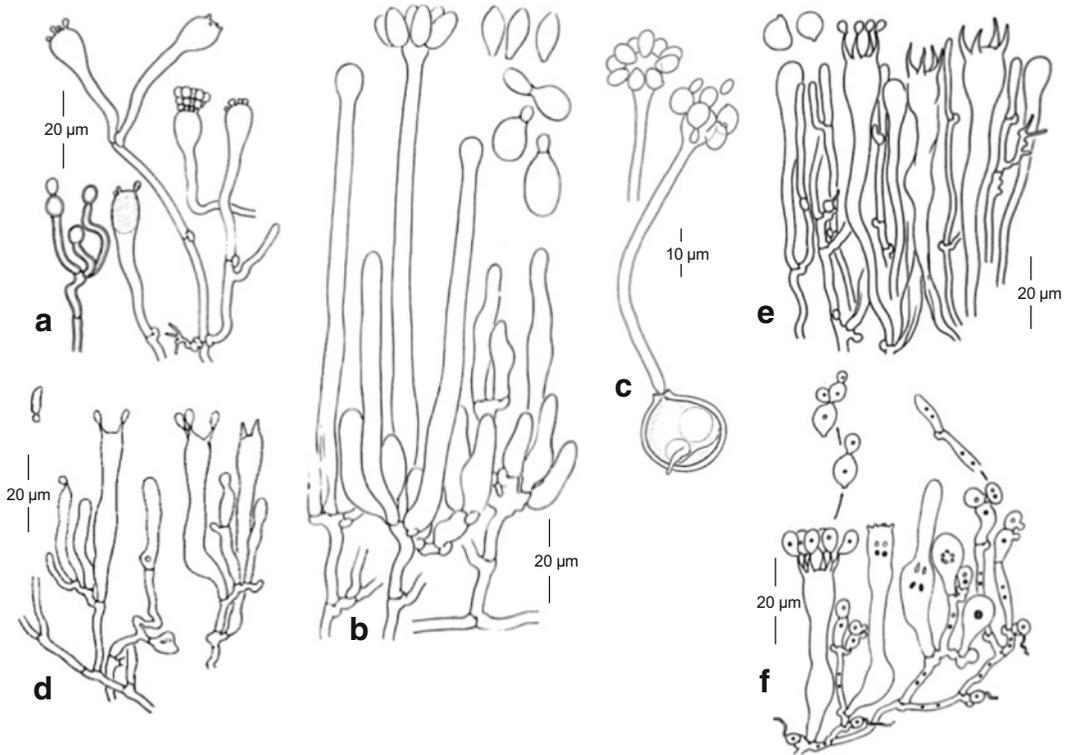


Fig. 12.3 Basial characters in Tremellomycetes. (a) *Filobasidiella neoformans* (Oberwinkler et al. 1983). (b) *Filobasidium floriforme* (Oberwinkler et al. 1983). (c) *Cystofilobasidium capitatum* (Oberwinkler et al. 1983). (d) *Carcinomyces effibulatus* (Oberwinkler and Bandoni 1982). (e) *Syzygospora alba* (Oberwinkler and Lowy 1981). (f) *Syzygospora pallida* (Oberwinkler et al. 1984)

In an established mycoparasitic interaction the apex of the filaments is in contact with a host hypha (see subsequent discussion for ultra-structural details).

Several types of conidia have been observed in the Tremellomycetes. Globular **blastoconidia** are occasionally found in Tremellales fruiting bodies [e.g., in *T. mesenterica* (Fig. 12.4), where ample production of blastoconidia creates the characteristic orange color of the fruiting bodies], before or synchronously with the production of basidia and basidiospores. Production of blastoconidia on elongated stalks is known from species of *Fellomyces* and *Cuniculitrema*. **Arthroconidia** are typical of most *Trichosporonales* species but can also be found in other species, for example, in *Guehomyces* and *Tausonia* (Cystofilobasidiales). Many species in the Tremellomycetes also form **ballistoconidia**.

The formation or absence of ballistoconidia was used in earlier classifications to separate the

genera *Cryptococcus*, *Bullera*, *Fellomyces*, and *Kockovaella*. Meanwhile, molecular phylogenetic studies have shown that this character is not useful for circumscribing monophyletic genera (Boekhout et al. 2011). Consequently, genera such as *Derxomyces*, *Dioszegia*, and *Hannaella* have been proposed for monophyletic groups that contain both species with or without the formation of ballistoconidia. However, the footprints of the old classification marker “presence/absence of ballistoconida” are still visible in the current tree of the Tremellomycetes (Fig. 12.7).

Zygoconidia, i.e., dikaryotic H-shaped conidia, are known from several distantly related taxa, such as *Carcinomyces*, *Papiliotrema*, and *Trimorphomyces* (Fig. 12.2d) (Tremellales), as well as from *Syzygospora* (Filobasidiales) (e.g., Oberwinkler and Bandoni 1983; Oberwinkler and Lowy 1981; Sampaio et al. 2002).

Finally, four-spined **asteroconidia** have been observed in some lichenicolous species

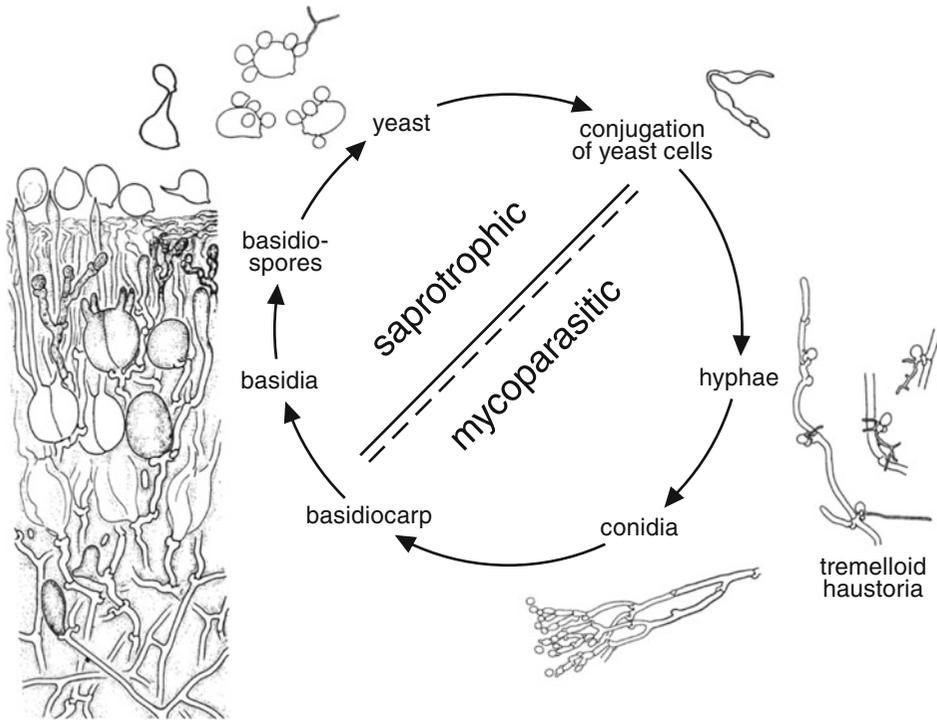


Fig. 12.4 Life cycle of *Tremella mesenterica*

of *Tremella* (Diederich 1996; Millanes et al. 2011).

C. Ultrastructure

Septal pores in the Tremellomycetes are **doli-pores** that, except for members of Cystofilobasidiales (Oberwinkler et al. 1983; Wells 1994; R. Bauer, unpublished), are surrounded at both sides by **sacculate caps** arranged in hemispherical outlines (Fig. 12.5) (Berbee and Wells 1988). In three-dimensional configurations these saccules represent fingerlike extensions of the endoplasmic reticulum surrounding the pore on either side (as is visible in one saccule illustrated in Fig. 12.5b), in which the intracisternal surface of the membrane is accompanied by an additional electron-opaque nonmembranous layer (Fig. 12.5b). In cross or oblique sections, these fingerlike extensions are mapped as saccules with abseptal openings (Fig. 12.5b, c). Saccular parenthesomal elements may, how-

ever, be missing in some pores of a studied specimen (R. Bauer, unpublished; Padamsee et al. 2012), which may help to explain some inconsistencies documented in the literature.

Spindle pole bodies of the studied species in Tremellales are biglobular during prophase (Berbee and Wells 1988), a character state that supports the inclusion of the Tremellomycetes in Agaricomycotina.

The cellular interaction between species of the Tremellomycetes and their presumed host fungi occurs via the formation of **tremelloid haustoria** (Figs. 12.2c, f, g and 12.4; see previous discussion). The haustorial filaments are capable of fusing with host cells via pores of roughly 15 nm in diameter, where plasma membranes of both fungi are continuous with each other (Fig. 12.6). This yields a direct cytoplasmic contact; however, the size of these **fusion channels prevents** an exchange of organelles, including ribosomes, between the interacting organisms (Bauer and Oberwinkler 1990a; Oberwinkler et al. 1984; Zugmaier et al. 1994). While in

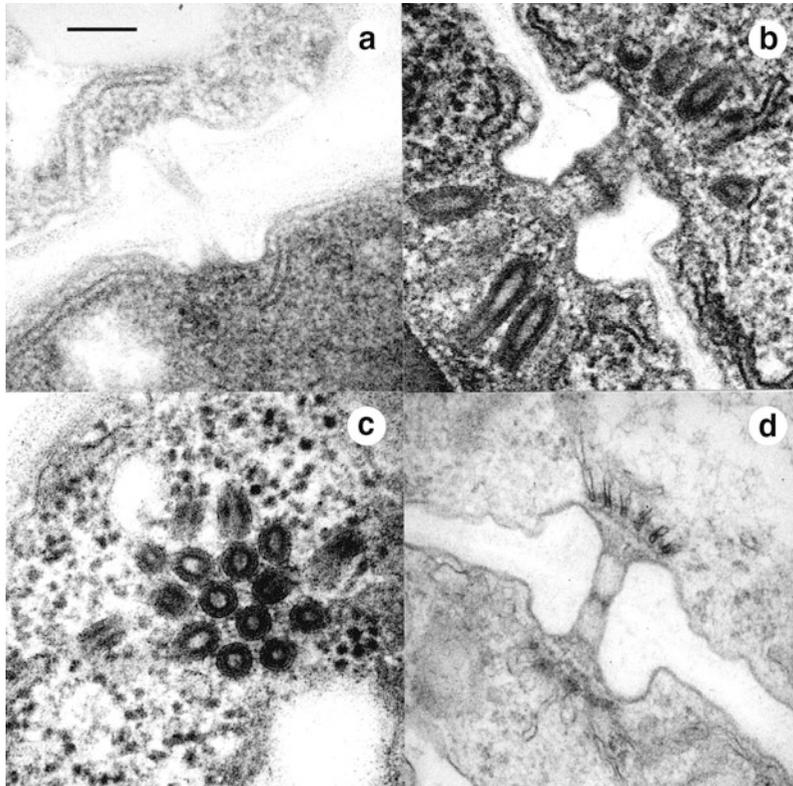


Fig. 12.5 Septal pore architecture in Tremellomycetes. *Bar*=0.1 μm in (a–c), 0.2 μm in (d). (a) Dolipore of *Cystofilobasidium ferigula* without specialized multilamellate caps, representative of Cystofilobasidiales. Note that pore is surrounded at each side by a more or less dome-shaped ER cisterna. (b–d) Dolipores surrounded at each side by many multilamellate cupulate cap ele-

ments, representative for Tremellomycetes [except for Cystofilobasidiales; see (a)] and *Wallemia*. (b, c) *Tremella* sp. Cupulate cap elements are sectioned longitudinally in (b), transversally in (c). Continuity between ER and saccules is visible for one of upper saccules in (b). (d) *Wallemia sebi*

most studied species of the Tremellomycetes a haustorial filament forms only one fusion channel (Fig. 12.6a, b), in *Syzygospora pallida* a single haustorial filament may form several protrusions into the host cytoplasm, resulting in numerous fusion channels per filament (Fig. 12.6c, d) (Bauer 2004; Bauer and Oberwinkler 1990b; Oberwinkler et al. 1984).

III. Life Cycles

A. Dimorphism

Dimorphism, i.e., differing morphological organization of different life stages, is a

characteristic trait in most species of the Tremellomycetes for which a teleomorph is known. A typical life cycle of a *Tremella* species is illustrated in Fig. 12.4. In these species, basidiospores germinate by budding to establish a **haploid yeast stage**. Since this stage can easily be maintained in pure culture in standard media, it is assumed that the yeast stage is saprotrophic. AU2

Conjugation of compatible yeast cells initiates a dikaryotic hyphal stage, which is considered mycoparasitic in many species based on two lines of evidence. First, axenic cultivation of this stage has seldom been reported (Zugmaier and Oberwinkler 1995; Zugmaier et al. 1994). Second, tremelloid haustoria attached

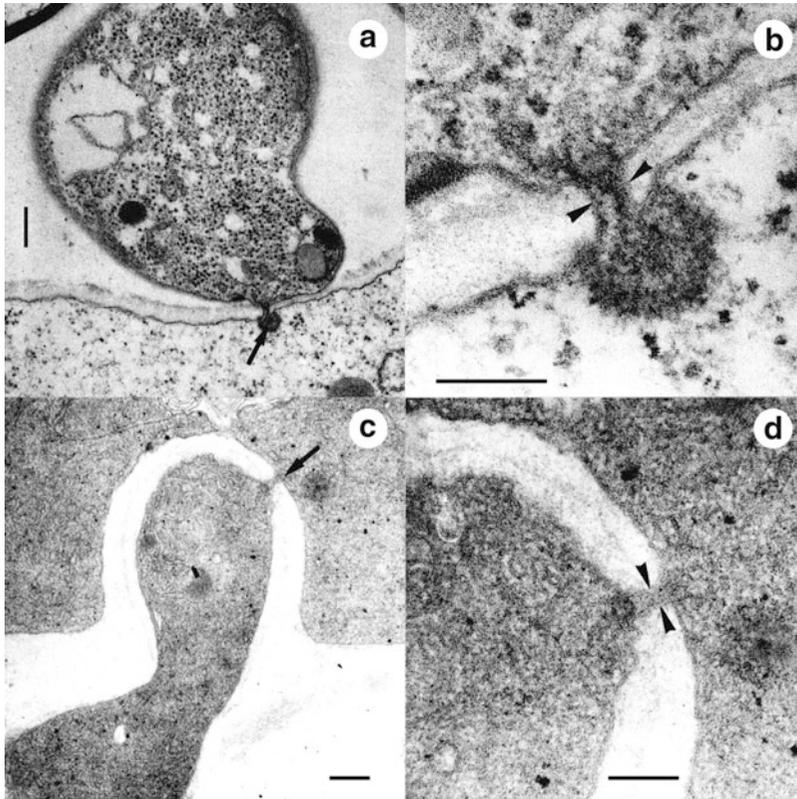


Fig. 12.6 Mycoparasitic interaction stages of some Tremellomycetes. Bars=0.2 μm in (a, c) and 0.1 μm in (b, d). (a, b) Haustorial filament of *Tetragoniomyces uliginosus* (upper cell) attached to cell of *Rhizoctonia* sp. (a) Note medianly sectioned micropore (arrow) connecting haustorial apex with host cell. (b) Detail from (a) Note that pore membrane (arrowheads) is continuous

with plasma membranes of both cells. (c, d) Haustorial filament of *Syzygospora pallida* penetrating a cell of *Phanerochaete cremea*. (c) One of several micropores connecting haustorial filament with host cell is medianly sectioned (arrow). (d) Detail from (c). Note that pore membrane (arrowheads) is continuous with plasma membranes of both cells

to hyphae of other fungal species are often observed microscopically (see previous discussion). **Dikaryotic hyphae** may constitute a fruiting body that ultimately produces basidia and basidiospores or conidiogenous hyphae, giving rise to conidia. In species lacking a fruiting body, dikaryotic hyphae grow inside a host fruiting body and finally sporulate at its surface.

Holtermanniella mycelialis has been reported to be dimorphic and haploid (Golubev and Golubev 2003). In this species, after some days of cultivation, yeast colonies build clamped hyphae with tremelloid haustoria and release blastoconidia. Basidia have not been observed in this species, which may represent an anamorph of a *Holtermannia* species, where

a teleomorph is possibly induced in the presence of a particular fungal host.

B. Deviance from Dimorphism

The designation of a species of the Tremellomycetes (typically a yeast) as monomorphic should always be considered as being preliminary. There are instances where a filamentous stage is obtained by mating compatible strains long after the first description of the yeast stage, for example, in *Bullera/Bulleromyces*, *Cryptococcus/Filobasidiella*, and *Cryptococcus/Kwooniella*. More recently, genomic methods have been used to predict and ultimately demonstrate sexuality in fungi that were previously

considered asexual (Metin et al. 2010; O’Gorman et al. 2009). Consequently, many other inconspicuous teleomorphs may still await detection and description (Metin et al. 2010).

Some species lack a yeast stage. In *Tetragoniomyces uliginosus* (Fig. 12.2c) basidia do not produce external basidiospores. Instead, the thick-walled basidia themselves detach, and compatible basidial compartments either mate directly or produce germination tubes that mate (Oberwinkler and Bandoni 1981), inducing the next hyphal generation. Yeast stages are also unknown for many species of Trichosporonales and in *Filobasidiella depauperata*.

Trimorphomyces papilionaceus (Tremellales) is the only known species of the Tremellomycetes that has a dikaryotic yeast stage in addition to the usual haploid yeast stage, which arises from budding basidiospores. Here, the dikaryotic yeast cells initiate from dikaryotic zygoconidia borne on two-tipped conidiogenous cells located in either conidiomata or fruiting bodies in which the conidiogenous cells occur together with basidia (Fig. 12.2d). In the presence of a suitable fungal host, zygoconidia alternatively germinate with hyphae that form clamps and tremelloid haustoria.

The life cycle of *Iterosonilia perplexans* comprises clamped dikaryotic hyphae, short unclamped monokaryotic hyphae, monokaryotic yeast cells, chlamydosporelike resting cells, and ballistoconidia (Boekhout 2011; F. Oberwinkler, unpublished).

IV. Ecology

A. Mycoparasitism

That a mycoparasitic lifestyle is a distinctive feature of the teleomorphic stages for many, if not all, members of the Tremellomycetes has been deduced from obvious host specificity, from morphological evidence, such as the presence of hyphae of putative host fungi growing inside fruiting bodies of Tremellomycetes, or from the presence of tremelloid haustoria, which may attach to host hyphae and establish minute cytoplasm-to-cytoplasm contacts (see

previous discussion; Bandoni 1984; Bauer and Oberwinkler 1990a; Zugmaier et al. 1994). However, a flux of carbon compounds or other nutrients from a fungal host species to a tremellomycete has not yet been demonstrated. Apparently, the mycoparasitic potential is initiated with the transition from the monokaryotic to the dikaryotic life stage. Molecular mechanisms, such as host recognition, are still unknown.

That hyphal stages of some phylogenetically close species of the Tremellomycetes are associated with fungi that are closely related inter se (Fig. 12.7: 22) may be taken as an additional piece of evidence in favor of a mycoparasitic lifestyle. Here, strongly dependent tremellomycetous mycoparasites may have coevolved together with their fungal hosts.

While for the majority of Tremellomycetes species studied to date the axenic cultivation of the dikaryotic stage has not been achieved [but see Zugmaier and Oberwinkler (1995)], a successful induction of the teleomorph by mating compatible yeast cells has been reported for some species for which only the haploid stage, i.e., the yeast in most cases, was known previously. These include *Filobasidiella neoformans*, *Bulleromyces* and *Kwoniella* (Tremellales), and *Cystofilobasidium* (Cystofilobasidiales).

B. Tremellomycetous Yeasts

Apparently, all of the known yeast stages in the Tremellomycetes can be cultured axenically in standard media. Tremellomycetous yeasts are ubiquitous elements of terrestrial and aquatic ecosystems and have been reported from Antarctic soils as well as from hydrothermal oceanic vents. They have been isolated from sources as diverse as the surface of land plants, including flowers and tree bark, from freshwater and seawater samples, from clinical specimens, and from animals or their excrements [see Kurtzman et al. (2011)]. Some species seem to occupy rather diverse niches, for example, *Cryptococcus curvatus* has been reported mainly from medical sources and from food products but was also shown to be the dominant microbial eukaryote in sediments of a

Tremellomycetes and Related Groups

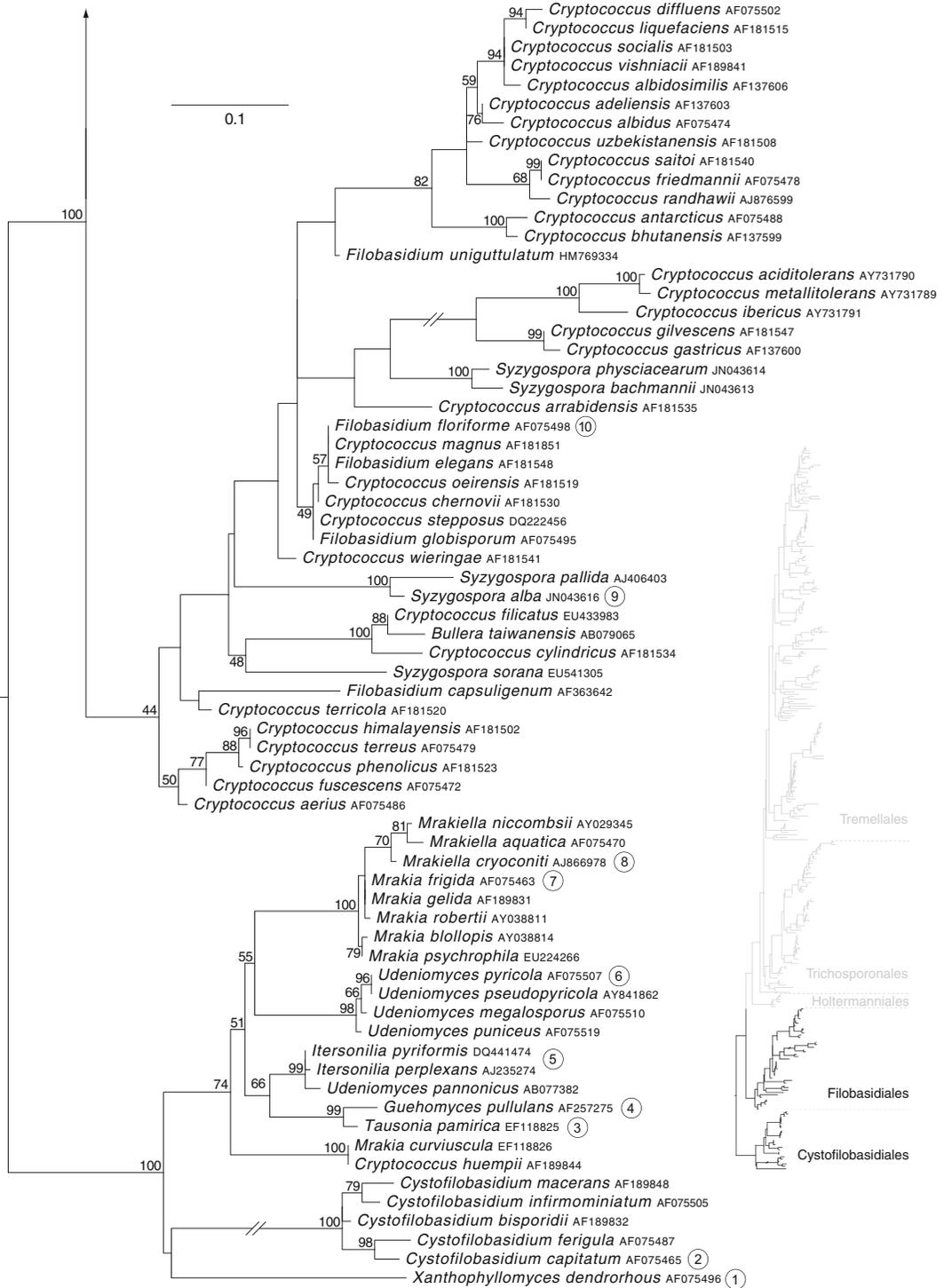


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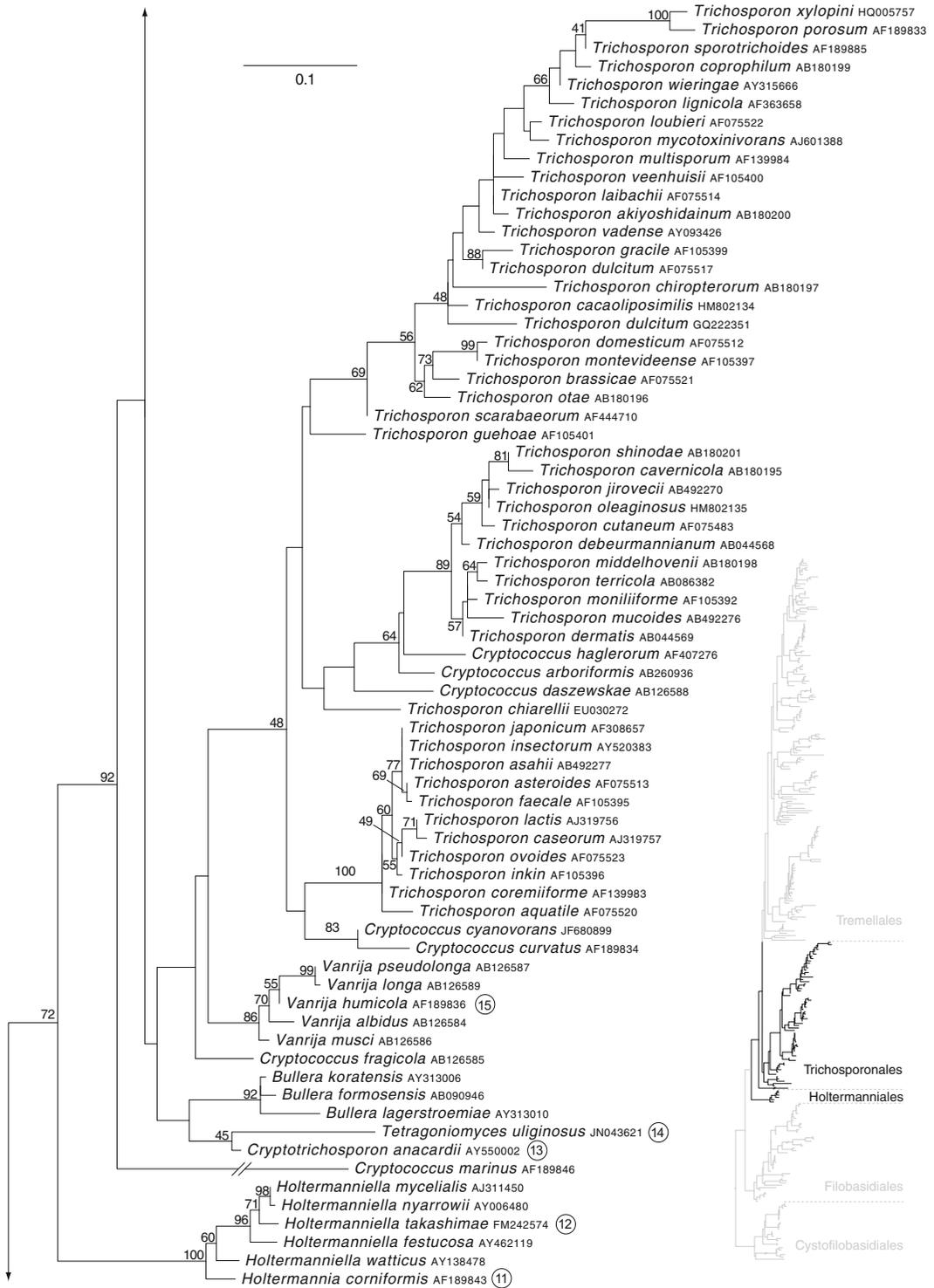


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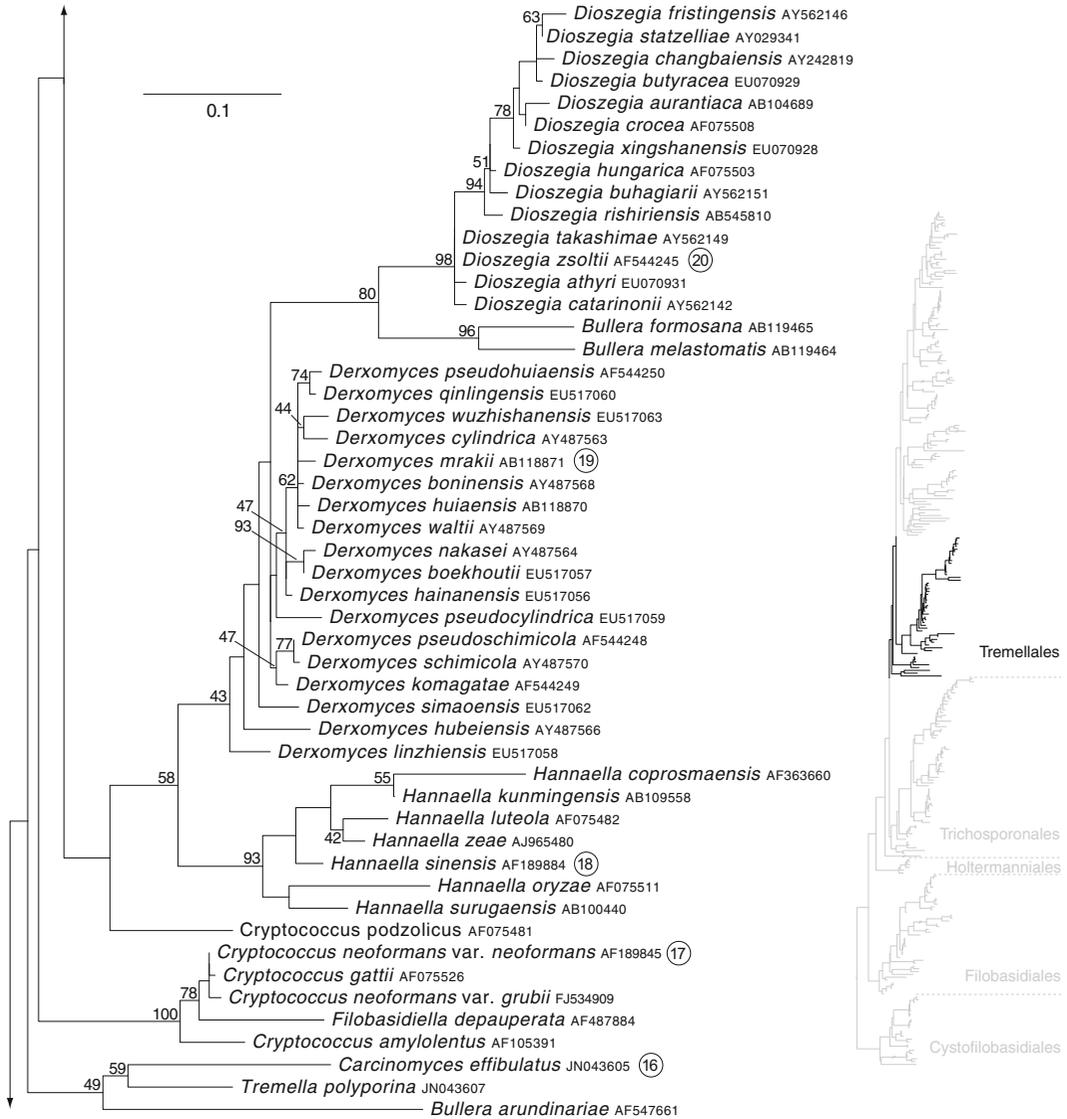


Fig. 12.7 (continued)

methane seep at a water depth of 640 m in the Pacific Ocean (Takishita et al. 2006). For some species ecological trends are visible. Psychrophilic species, such as members of *Mrakia*, have been isolated in Antarctica or Greenland or from glaciers but were also reported from refrigerated food (Fell 2011). *Bullera alba* is frequently isolated from the phylloplane (Sampaio 2004). *Xanthophyllumycetes dendrorhous* is known from the sap of various tree species (David-Palma et al. 2014; Fell et al. 2011).

Some species of *Fellomyces* have only been found on lichen thalli (Lopandic et al. 2011).

For many, if not most, of the known species, however, data are still too sparse to estimate distribution and ecology with confidence. Additionally, it may be problematic to integrate data based on morphological and physiological species determination with data based on sequence-based identification. Since all known tremellomycetous yeast species have been DNA-barcoded, analysis of environmental

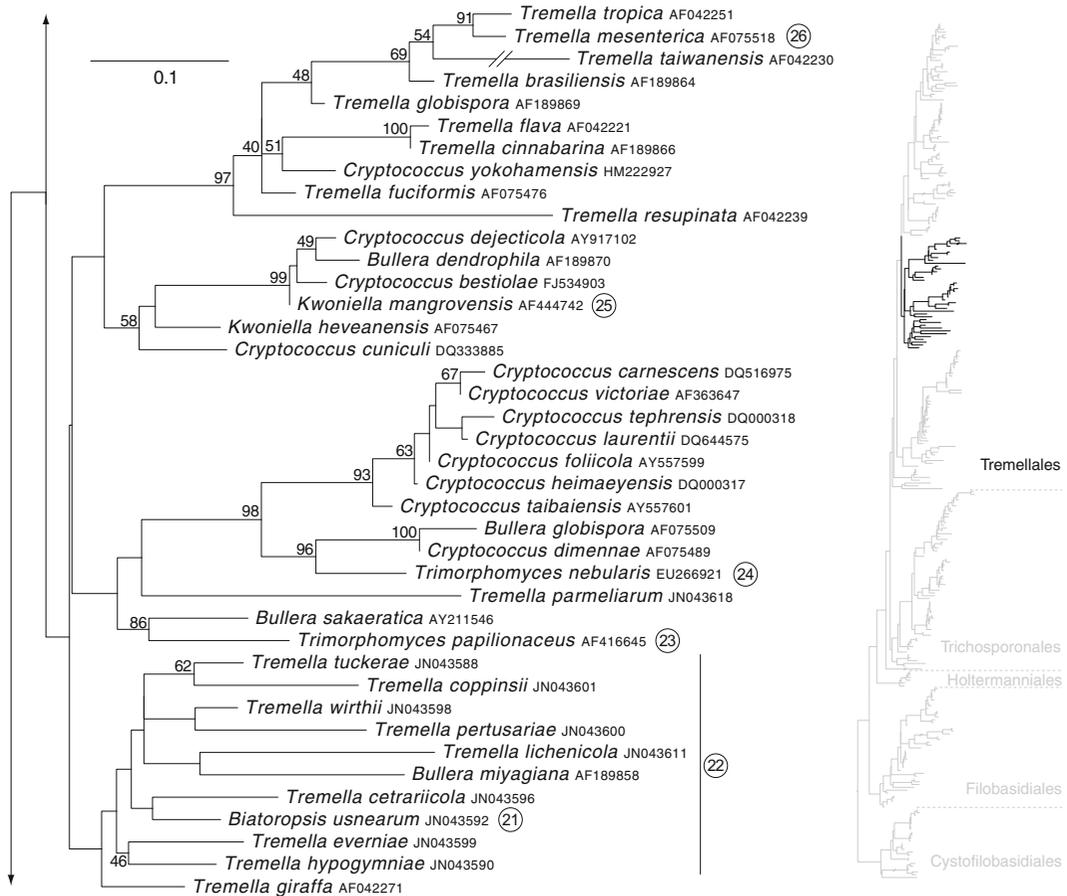


Fig. 12.7 (continued)

high-throughput sequencing data should refine our estimates about biogeography and ecology in the future.

C. Animal and Human Pathogens

C. neoformans, the yeast stage of *F. neoformans*, is an opportunistic pathogen in immunocompromised humans and animals around the world. The fungus is able to infest immunocompetent individuals without causing noticeable disease symptoms. However, in immunocompromised individuals, for example, those with an HIV infection, it may disseminate from a local infection to any organ of a patient and in particular invade the central nervous system. Today, *C. neoformans* is one

of the leading pathogens worldwide that can be grown from cerebrospinal fluid (Perfect 2005). Each year cryptococcal meningoencephalitis is diagnosed in nearly a million individuals and accounts for more than 600,000 deaths (Park et al. 2009). Even if treated with state-of-the-art therapy, cryptococcosis is fatal in ca. 20 % of cases (Desnos-Ollivier et al. 2010). As the closely related *Cryptococcus gattii* (anamorph of *Filobasidiella bacillispora*), *C. neoformans* apparently has a wide spectrum of potential host taxa, including both vertebrate and invertebrate species and even protozoans [see Kwon-Chung (2011)].

The genus *Trichosporon* contains many known pathogens of animals and humans, and more than 30 % of *Trichosporon* species were found to be correlated with human infections

Tremellomycetes and Related Groups

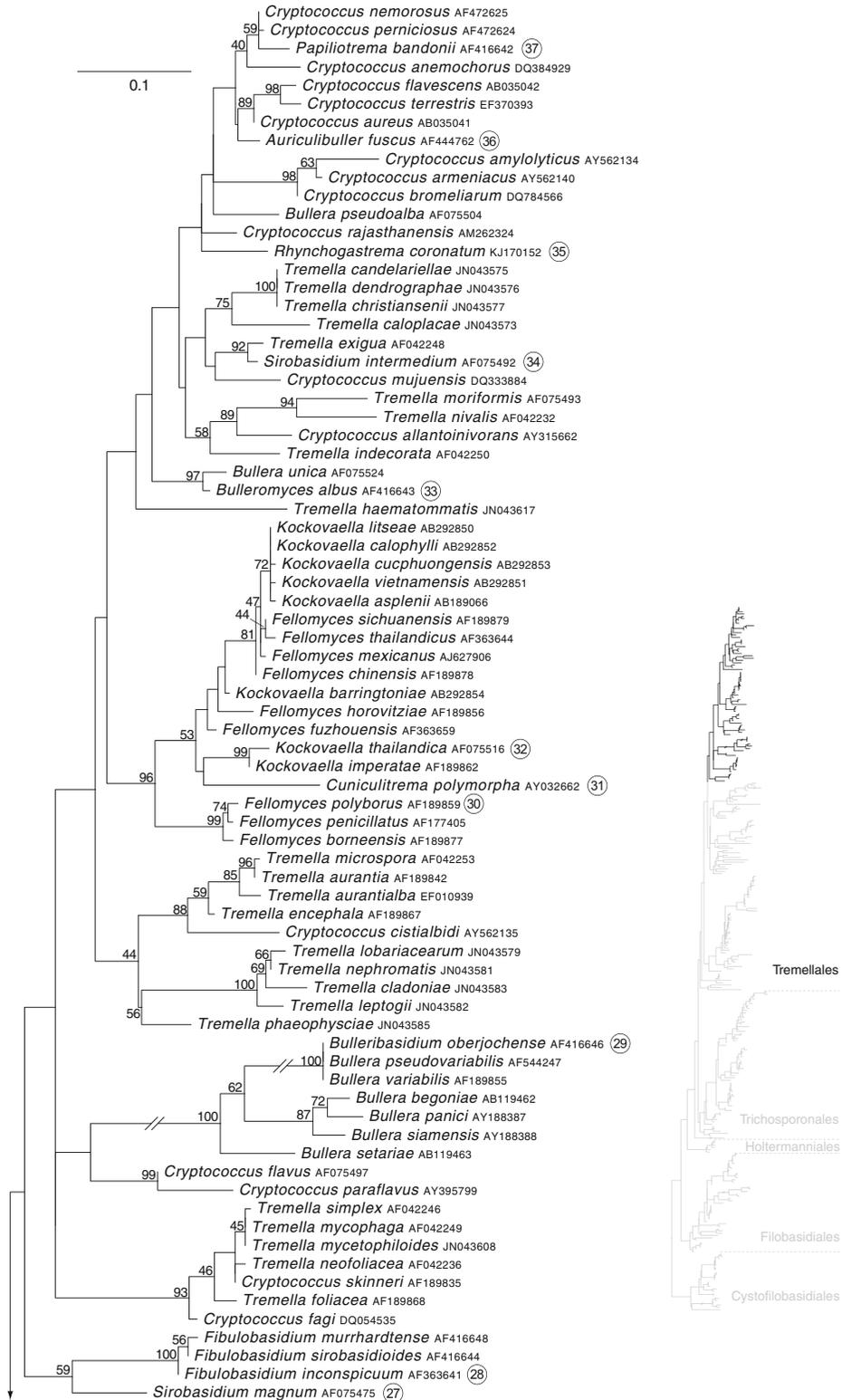


Fig. 12.7 (continued)

or allergies. *Trichosporon* infections are particularly threatening for immunodeficient patients suffering from leukemia or lymphoma. Species often seen associated with patients with a deep-seated, and potentially fatal, trichosporonosis include *T. asahii*, *T. asterioides*, *T. debeurmanianum*, *T. inkin*, *T. loubieri*, and *T. mucoides* [see Sugita (2011)]. *Trichosporon* species have also been shown to be involved in summer-type hypersensitivity pneumonitis (SHP), an allergic disease occurring in hot and humid seasons in Asia that is caused by inhalation of *Trichosporon* arthroconidia. Causative species include *T. dermatis* (Sugita 2011), a taxon that has also been isolated from hydrothermal fields in the Mid-Atlantic Ridge (Gadanhó and Sampaio 2005). Finally, *Trichosporon* species can cause infections on skin and hair, for example, white piedra.

A prerequisite for a fungal species that is potentially pathogenic for humans is its ability to grow at 37 °C. This criterion is used as a routine test in classical yeast taxonomy. That growth at 37 °C is not sufficient to prove pathogenicity may be illustrated by *Trichosporon loubieri*, a species not known as a pathogen, which is able to grow even at 42 °C but that has been reported from soils in Antarctic Dry Valleys (Fell et al. 2006).

V. Biotechnological Applications

Biotechnological applications have been reported for a number of tremellomycetous yeasts. Some examples are provided here. *Cryptococcus terreus* and *Cryptococcus terricola* may be useful in the biodegradation of phenolic compounds,

even in cold environments (Bergauer et al. 2005). Other species can be used as sources of enzymes with particular characteristics, for example, cold- and high-pressure-tolerant polygalacturonases from the deep-sea yeast *C. liquefaciens* (Abe et al. 2006). Tremellomycetous yeasts, for example *C. albidus* and *C. laurentii*, may be used in the biocontrol of plant-pathogenic fungi, for example *Botrytis*, and to reduce postharvesting decay of fruits (Fonseca et al. 2011). *C. curvatus* can use celluloses and hemicelluloses to produce triglycerides and accumulates these lipids at levels of 60 % cell dry weight [see Fonseca et al. (2011) for detailed references], which makes this species interesting for biomass conversion.

X. dendrorhous is cultured industrially for its ability to produce carotenoids, predominantly astaxanthin, which can be used, for example, as a dietary additive for mariculture of crustaceans or salmonids to enhance these animals pigmentation.

VI. Phylogenetic Relationships

Based on morphological, ultrastructural, chemical, and ecological data, the monophyly of Tremellomycetes as conceived here has been suggested by various authors, for example, Wells (1994, as Tremellales) and Wells and Bandoni (2001, as Tremellomycetidae). Molecular phylogenetic analyses have supported this hypothesis, for example, Matheny et al. (2006) and Weiß and Oberwinkler (2001). However, some molecular studies based on nrDNA have yielded alternative topologies, in which tremellomycetous taxa form a grade, with a more basal Cystofilobasidiales separated from the

Fig. 12.7 Phylogenetic relationships in Tremellomycetes, as estimated from nuclear rDNA sequences coding for 5' terminal domain of ribosomal large subunit (nLSU). Sequence sampling based on comprehensive search of GenBank nucleotide collection (<http://www.ncbi.nlm.nih.gov/>), yielding preliminary set of ca. 1,700 sequences, which was gradually pruned by eliminating duplicate and dubious sequences after preliminary phylogenetic analyses. Sequences were aligned with MAFFT v7.045b (Kato and Standley 2013), a maximum-likelihood tree was derived with RAxML

v7.3.2 (Stamatakis et al. 2008) in a parallelized version at Bioportal (Kumar et al. 2009) using GTR+CAT model of DNA substitution and with heuristic searches starting from bootstrap trees (Stamatakis et al. 2008). Branch support was calculated from 1,000 bootstrap replicates; values below 40 % omitted. The tree was rooted with Cystofilobasidiales. Branch lengths are in terms of number of expected substitutions per alignment site (see bar); intersected branches were reduced in length by half for graphical presentation. Numbers in circles referenced in text

remaining taxa (Bauer et al. 2006; Matheny et al. 2006; Millanes et al. 2011). Within Agaricomycotina, Tremellomycetes obtains a basal position (Floudas et al. 2012; James et al. 2006; Weiß et al. 2004).

The phylogenetic tree derived for this review from a comprehensive sampling of nrLSU data is shown in Fig. 12.7. We did not test whether or not Cystofilobasidiales is part of a monophyletic Tremellomycetes and so did not include any outgroup sequences, which increased alignment quality. Consistent with the current literature, our tree was rooted with Cystofilobasidiales. Filobasidiales branches next, followed by Holtermanniales, which is consistent with Millanes et al. (2011) and Wuczkowski et al. (2011), but in contrast to the analysis by Boekhout et al. (2011), where a sister-group relationship of Holtermanniales and Filobasidiales received high bootstrap support. The most basal branch in the remaining subtree is occupied by *Cryptococcus marinus*, a species that was found in an isolated position in several studies, for example, Boekhout et al. (2011) and Scorzetti et al. (2002). Trichosporonales and Tremellales appear as sister groups, consistent with Boekhout et al. (2011) but in contrast to other analyses where Trichosporonales cluster nested within Tremellales (Millanes et al. 2011; Sampaio 2004).

VII. Taxonomy

A. Taxonomy in Flow

Among all groups of Agaricomycotina, Tremellomycetes is particularly prone to future taxonomic changes. First, molecular phylogenetic studies strongly suggest that *Tremella*, the largest teleomorphic genus in this group, is non-monophyletic (Fig. 12.7) (Boekhout et al. 2011; Millanes et al. 2011). The same is true for the main anamorphic genera, *Bullera* and *Cryptococcus* (Fig. 12.7). Accordingly, segregation of subgroups of these catch-all genera is being or already has been implemented (e.g., *Deroxomyces*, *Dioszegia*, *Hannaella*, *Vanrija*). Second, the International Code of Nomenclature for algae, fungi, and plants (ICN) (McNeill et al.

2012) has abandoned taxonomic priority for teleomorphic stages, principally rendering obsolete taxa that had been established for teleomorphic stages detected in groups that formerly only contained anamorphic species, for example, *Bulleromyces*, *Bulleribasidium*, and *Cuniculitrema*. Likewise, it is no longer necessary to keep genera for anamorphs in originally solely teleomorphic groups, for example, *Holtermanniella* and *Mrakiella*. Some of these more recently created names for teleomorphic or anamorphic genera may be used to define appropriate monophyletic subgroups in the future. Ongoing discussions in the mycological community will yield proposals about which of the competing names to conserve or abandon.

B. Taxonomic Synopsis

What follows is a synopsis of generic names in the Tremellomycetes that are currently in use. As of this writing, questions regarding the taxonomic priority of names versus names to be conserved that have emerged as a result of the ICN (McNeill et al. 2012) (see the discussion in the previous section) have not been resolved. Therefore, we include both anamorph- and teleomorph-derived names for groups in which one or the other will probably be eliminated in the future. Taxa typified with a teleomorph are designated by an asterisk (*).

Cystofilobasidiales Fell, Roeijmans & Boekhout 1999

Cryptococcus Vuill. 1901 p.pte (type *C. neoformans*) (Fig. 12.7: 17)

*Cystofilobasidium** Oberw. & Bandoni 1983 (type *C. capitatum*) (Fig. 12.7: 2)

Guehomyces Fell & Scorzetti 2004 (type *G. pullulans*) (Fig. 12.7: 4)

Itersonilia Derx 1948 (type *I. perplexans*) (Fig. 12.7: 5)

*Mrakia** Y. Yamada & Komag. 1987 (type *M. frigida*) (Fig. 12.7: 7)

Mrakiella Margesin & Fell 2008 (type *M. cryoconiti*) (Fig. 12.7: 8)

Phaffia M.W. Mill., Yoney. & Soneda 1976 (type *P. rhodozyma*) (Fig. 12.7: 1)

Tausonia Babeva 1998 (type *M. pamirica*) (Fig. 12.7: 3)

Udeniomyces Nakase & Takem. 1992 (type *U. pyricola*) (Fig. 12.7: 6)

*Xanthophyllomyces** Golubev 1995 (type *X. dendrorhous*; teleomorph of *Phaffia rhodozyma*) (Fig. 12.7: 1)

Filobasidiales Jülich 1981

- Bullera* Derx 1930 p.pte (type *B. alba*) (Fig. 12.7: 33)
Cryptococcus Vuill. 1901 p.pte (type *C. neoformans*) (Fig. 12.7: 17)
*Filobasidium** L.S. Olive 1968 (type *F. floriforme*) (Fig. 12.7: 10)
*Syzygospora** G.W. Martin 1937 (type *S. alba*) (Fig. 12.7: 9)

Holtermanniales

- Holtermannia** Sacc. & Traverso 1910 (type *H. pinguis*) (Fig. 12.7: 11)
Holtermanniella Libkind, Wuczkowski, Turchetti & Boekhout 2010 (type *H. takashimae*) (Fig. 12.7: 12)

Trichosporonales Boekhout & Fell 2001

- Bullera* Derx 1930 p.pte (type *B. alba*) (Fig. 12.7: 33)
Cryptococcus Vuill. 1901 pro parte (type *C. neoformans*) (Fig. 12.7: 17)
Cryptotrichosporon Okoli & Boekhout 2007 (type *C. anacardii*) (Fig. 12.7: 13)
*Tetragoniomyces** Oberw. & Bandoni 1981 (type *T. uliginosus*) (Fig. 12.7: 14)
Trichosporon Behrend 1890 (type *T. beigeli*)
Vanrija R.T. Moore 1980 (type *V. humicola*) (Fig. 12.7: 15)

Tremellales Fr. 1821

- Auriculibuller** J.P. Samp. & Fonseca 2004 (type *A. fuscus*) (Fig. 12.7: 36)
Bandoniozyma P. Valente, Pagnocca, C.A. Rosa, C.F. Lee, S.O. Suh, M. Blackw., G. Péter & Fell 2012 (type *B. noutii*)
*Biatoropsis** Räsänen 1934 (type *B. usnearum*) (Fig. 12.7: 21)
Bullera Derx 1930 p.pte (type *B. alba*) (Fig. 12.7: 33)
*Bulleribasidium** J.P. Samp., M. Weiß & R. Bauer 2002 (type *B. oberjochense*) (Fig. 12.7: 29)
*Bulleromyces** Boekhout & A. Fonseca 1991 (type *B. albus*) (Fig. 12.7: 33)
*Carcinomyces** Oberw. & Bandoni 1982 (type *C. mycetophilus*) (Fig. 12.7: 16)
Cryptococcus Vuill. 1901 p.pte (type *C. neoformans*) (Fig. 12.7: 17)
*Cuniculitrema** J.P. Samp. & R. Kirschner 2001 (type *C. polymorpha*; teleomorph of *Sterigmatosporidium polymorphum*) (Fig. 12.7: 31)
Derxomyces F.Y. Bai & Q.M. Wang 2008 (type *D. mra-kii*) (Fig. 12.7: 19)
Dioszegia Zsolt 1957 (type *D. hungarica*) (Fig. 12.7: 20)
Fellomyces Y. Yamada & I. Banno 1984 (type *F. polyborus*) (Fig. 12.7: 30)
*Fibulobasidium** Bandoni 1979 (type *F. inconspicuum*) (Fig. 12.7: 28)

- Filobasidiella** Kwon-Chung 1976 (type *F. neoformans*, teleomorph of *Cryptococcus neoformans*) (Fig. 12.7: 17)
Hannaella F.Y. Bai & Q.M. Wang 2008 (type *H. sinensis*) (Fig. 12.7: 18)
Kockovaella Nakase, I. Banno & Y. Yamada 1991 (type *K. thailandica*) (Fig. 12.7: 32)
*Kwoniella** Statzell-Tallman, Belloch & J.W. Fell 2008 (type *K. mangrovensis*) (Fig. 12.7: 25)
*Papiliotrema** J.P. Samp., M. Weiß & R. Bauer 2002 (type *P. bandonii*) (Fig. 12.7: 37)
*Phragmoxenidium** Oberw. 1990 (type *Phragmoxenidium mycophilum*; no DNA data available)
*Phyllogloea** Lowy 1961 (type *P. singeri*; no DNA data available)
*Rhynchogastrema** B. Metzler & Oberw. 1989 (type *R. coronatum*) (Fig. 12.7: 35)
*Signogloea** Bandoni & J.C. Krug 2000 (type *S. tremelloidea*; no DNA data available)
*Sirobasidium** Lagerh. & Pat. 1892 (type *S. sanguineum*) (Fig. 12.7: 27, 34)
*Sirotrema** Bandoni 1986 (type *S. pusilla*; no DNA data available)
Sterigmatosporidium G. Kraep. & U. Schulze 1983 (type *S. polymorphum*, the anamorph of *Cuniculitrema p.*) (Fig. 12.7: 31)
*Tremella** Pers. 1794 (type *T. mesenterica*) (Fig. 12.7: 26)
Tremellina Bandoni 1986 (type *T. pyrenophila*; no DNA data available)
*Trimorphomyces** Bandoni & Oberw. 1983 (type *T. papilionaceus*) (Fig. 12.7: 23, 24)
*Xenolachne** D.P. Rogers 1947 (type *X. flagellifera*; no DNA data available)

Incertae sedis

- Dictyotremella* Kobayashi 1971 (type *Dictyotremella novoguineensis*; no DNA data available)
Heteromycophaga P. Roberts 1997 (type *H. glandulosa*; no DNA data available)
Hyalococcus Schroeter 1889
Neotremella Lowy 1979 (type *N. guzmanii*; no DNA data available)
Bartheletia (type *B. paradoxa*)
Wallemia (type *W. ichthyophaga*)

C. Key Groups

1. Cystofilobasidiales

Whether this is the most basal group in the Tremellomycetes or whether Cystofilobasidiales should be excluded from Tremellomycetes in order to assure its monophyly has not yet been answered with certainty (see preceding

Sect. VI). According to molecular phylogenetic analyses [e.g., Boekhout et al. (2011); this study, Fig. 12.7] the order splits into *Cystofilobasidium*, *Xanthophyllomyces* (both with slender holobasidia), and a clade containing *Mrakial*/*Mrakiella* and several anamorphic species of *Tausonia*/*Guehomyces*, *Itersonilia*, and *Udeniomyces*. A characteristic trait of the order, which is absent in all other groups of the Tremellomycetes, is the formation of teliospores, which can be observed in species of *Cystofilobasidium* and *Mrakia*. Teleomorphs are holobasidiate producing sessile basidiospores. Dolipores lack parentheses (Fig. 12.5a); basidiomes are not known in this group. Species of *Cystofilobasidium* and *Xanthophyllomyces* produce carotenoids, a trait that is commercially used in *X. dendrorhous*, where the carotenoid astaxanthin produced by an optimized strain is used in industrial mariculture (Johnson and Schroeder 1995). Biogeographically, some species of the Cystofilobasidiales, for example, *Cystofilobasidium bisporidii*, and the species of *Mrakial*/*Mrakiella* are clearly cold-adapted and have been found in Arctic environments.

2. Filobasidiales

Filobasidiales contains a taxonomically heterogeneous assemblage of species. Teleomorphic species have been assigned to the morphogenera *Filobasidium* and *Syzygospora*, neither of which seems to represent monophyletic taxa in their current circumscription (Fig. 12.7) (Boekhout et al. 2011; Millanes et al. 2011). Teleomorphic species have holobasidia; spores are sessile in most species. Species of *Filobasidium* have characteristically elongate slender basidia bearing apically a whorl of sessile basidiospores (Fig. 12.2b). Macroscopically visible fruiting bodies may be present (*Syzygospora alba*, *Syzygospora pallida*) (Fig. 12.1k) or absent. Parentheses are lacking in *S. pallida* (Oberwinkler et al. 1984). Species of *Syzygospora* parasitize fruiting bodies of asco- or basidiomycetes or lichen thalli (Diederich 1996; Oberwinkler et al. 1984). The ecology of most other Filobasidiales species is not known; strains have been isolated from different sources such as plants, animals, or soils.

3. Holtermanniales

Holtermanniales is the most understudied order in the Tremellomycetes. It currently contains the teleomorphic species of *Holtermannia* and some yeast species, for which the genus *Holtermanniella* was recently established (Wuczowski et al. 2011). The only *Holtermannia* species that has been cultured and sequenced is *Holtermannia corniformis*, with small clavarioid and anatomically complex basidiomes reminiscent of *Calocera* (Bandoni et al. 2011) and tremelloid basidia. Since *H. corniformis* grows on ascomycetous stromata on dead wood and possesses tremelloid haustoria, it is probably a mycoparasitic species. Based on the available morphological data the other six described species of *Holtermannia* do not seem to be closely related to *H. corniformis* (Bandoni et al. 2011); thus, detailed morphological studies and analyses of sequence data are needed to clarify their phylogenetic position. While species of *Holtermannia* are only known from Southeast Asia and Brazil (Kirk et al. 2008), *Holtermanniella* species have been reported from Europe and North America.

4. Trichosporonales

This order nearly exclusively comprises anamorphic species, most of which are characterized by the formation of hyphae and arthroconidia (*Trichosporon*) and the lack of a yeast stage. If merged with some yeast species that probably secondarily lost the ability to form arthroconidia and are still classified in *Cryptococcus*, *Trichosporon* may represent a monophyletic group (Fig. 12.7). Roughly one-third of all described *Trichosporon* species are associated with human infections or allergic diseases (Sugita 2011).

Following Fonseca et al. (2011) and Sugita (2011) we give *Vanrija* (Moore 1980) nomenclatural priority over *Asterotremella* (Prillinger et al. 2007) for a monophyletic group of yeasts closely related to *Trichosporon* that lack arthroconidia and formerly were classified in *Cryptococcus* (*humicola* group) (Fig. 12.7: 15). Thus, we restrict the original concept of *Vanrija* (Moore 1980, 1987) to the *humicola* clade of the Trichosporonales and add some species that were described later. Our emended concept includes the new combinations *Van-*

rija albida (C. Ramírez) M. Weiß, *Vanrija longa* (M. Takash., Sugita, Shinoda & Nakase) M. Weiß, *Vanrija musci* (M. Takash., Sugita, Shinoda & Nakase) M. Weiß, and *Vanrija pseudolonga* (M. Takash., Sugita, Shinoda & Nakase) M. Weiß based on *Sporobolomyces albidus* C. Ramírez (Ramírez Gómez 1957, p. 238), *Cryptococcus longus* M. Takash., Sugita, Shinoda & Nakase (Takashima et al. 2001, p. 2207), *Cryptococcus musci* M. Takash., Sugita, Shinoda & Nakase (Takashima et al. 2001, p. 2207), and *Cryptococcus pseudolongus* M. Takash., Sugita, Shinoda & Nakase (Takashima et al. 2001, p. 2208), respectively.

Interestingly, in our molecular phylogenetic analysis, as well as in Millanes et al. (2011), *Tetragoniomyces uliginosus* (Fig. 12.7: 14) seems to be a basal member of the Trichosporonales. If this position is verified in future analyses, this species would be the only member of this order for which a sexual stage is known. Like most species of *Trichosporon*, but in contrast to the majority of species in Tremellomycetes, *Tetragoniomyces* lacks a yeast stage. *Tetragoniomyces* basidia detach, and compatible basidial compartments fuse either directly or via germination tubes to establish a new dikaryotic hyphal cell (Fig. 12.2c).

5. Tremellales

Tremellales is the largest group in the Tremellomycetes and shows a high diversity of features regarding life cycles and morphology. Within the Tremellomycetes, Tremellales harbors most of the teleomorphs with conspicuous basidiocarps, most of which are still classified in the genus *Tremella* [ca. 90 species; Kirk et al. (2008)]. However, according to molecular phylogenetic analyses (e.g., Boekhout et al. 2011; Millanes et al. 2011; this study) (Fig. 12.7), *Tremella* seems to be polyphyletic and, consequently, will have to be split into monophyletic subgroups in future classifications. Obviously it will also be necessary to include anamorphic yeast species (in current taxonomy mostly still assigned to *Cryptococcus* or *Bullera*) in most of these subgroups to render them monophyletic. Judging from published sequence data, yeast stages of sequenced *Tremella* species have not yet been isolated from environmental samples; however,

since most described species of *Tremella* are still without sequence data, this may be a preliminary observation.

Other teleomorphic genera of the Tremellales with sequenced members include *Auriculibuller*, *Biatoropsis*, *Bulleribasidium*, *Bulleromyces*, *Carcinomyces*, *Cuniculitrema*, *Fibulobasidium*, *Filobasidiella*, *Kwoniella*, *Papiliotrema*, *Rhynchogastrema*, *Sirobasidium*, and *Trimorphomyces*. In current molecular phylogenetic analyses (e.g., Boekhout et al. 2011; Millanes et al. 2011; this study) (Fig. 12.7), these taxa appear scattered over the Tremellales tree. Since backbone resolution is still poor, we will not speculate about phylogenetic relationships here. Basidial morphology in these taxa varies from longitudinally to obliquely to transversely or irregularly septate to nonseptate (see Micromorphology in Sect. II). Species of *Carcinomyces* and *Filobasidiella* have holobasidia; basidia in *Rhynchogastrema* are apically partially septate. In many instances teleomorphic species appear closely related to yeast species for which teleomorphic stages have not yet been observed.

Some parts of the tree contain monophyletic clades that are currently exclusively composed of yeast species. Some of these have recently been transferred from *Cryptococcus* or *Bullera* into genera of their own, for example, *Dioszegia* and *Hannaella*.

Of the various families that have been proposed in Tremellales in the past, only two, Cuniculitremales and Sirobasidiaceae, seem to represent monophyletic groups. A typical feature present in Cuniculitremales (*Fellomyces*, *Kockovaella*, *Cuniculitrema*) is the production of ballistoconidia on elongate conidiophores. Members of Sirobasidiaceae (*Fibulobasidium*, *Sirobasidium*) form cylindrical to fusiform and passively released basidiospores that are possibly homologous to the epibasidial tubes in *Tremella* (Wells and Bandoni 2001).

The production of basidiospores in chains is a unique feature of the species of *Filobasidiella*. Teleomorphs of this genus have never been reported from natural environments and are only known from in vitro fusion of compatible yeast strains. Since *C. neoformans*, the most virulent pathogen in the Tremellomycetes (see Animal and Human Pathogens in Sect. IV),

is the type species of its genus, *Cryptococcus* may in the future be restricted to species now known as *Filobasidiella*.

In recent molecular phylogenetic studies (Millanes et al. 2011; this study) (Fig. 12.7: 16), *Carcinomyces effibulatus*, a holobasidiate species parasitizing the agaric *Gymnopus dryophilus* and inducing the formation of characteristic tumors in the host basidiomes, was found to be included in Tremellales. Preliminary sequence data (M. Weiß, unpublished) suggest that this taxon is conspecific with *Carcinomyces mycetophilus* and *Carcinomyces tumefaciens*. We thus reinstall *Carcinomyces* (Oberwinkler and Bandoni 1982), a genus apparently well separated from species of *Syzygospora* (Filobasidiales) (Fig. 12.7, part 1), with which *Carcinomyces* had been merged earlier (Ginns 1986).

D. Possibly Related Taxa *Incertae Sedis*

1. *Bartheletia*

In molecular phylogenetic analyses Scheuer et al. (2008) found that *Bartheletia paradoxa*, the only species of *Bartheletia*, is a member of the Agaricomycotina, but they were unable to assign it to any particular subgroup of this subphylum. *B. paradoxa* is a dimorphic fungus that rapidly develops on fallen *Ginkgo biloba* leaves in its filamentous conidiogenous anamorphic state in autumn. Later, resting teliospores are formed that germinate a year later into longitudinally septate basidia. Since all other teliospore-generating taxa in the Agaricomycotina belong to the *Cystofilobasidiales*, Scheuer et al. (2008) speculated about a possible relationship of *Bartheletia* to the Tremellomycetes. However, unlike most members of the Tremellomycetes, *B. paradoxa* lacks a yeast stage. In addition, that fungus differs from all other known members of the Agaricomycotina by the absence of dolipores. Instead, *Bartheletia* has multiple plasmodesmalike perforations in its hyphal septa (Scheuer et al. 2008).

2. *Wallemia*

The hyphomycete genus *Wallemia* includes three described species that can tolerate osmotic

stress and are hence regularly detected as contaminants of low-moisture foods (Zalar et al. 2005). Ultrastructural data have shown the basidiomycetous nature of *Wallemia sebi* (Moore 1986). However, molecular phylogenetic analyses could not unambiguously assign it to any of the major basidiomycetous clades (Matheny et al. 2006). Recent phylogenomic studies with limited taxon sampling placed *Wallemia* in a basal position within the Agaricomycotina (Padamsee et al. 2012; Zajc et al. 2013). The septal pore apparatus of *W. sebi* resembles that of Tremellales (Fig. 12.5d) (Padamsee et al. 2012).

VIII. Conclusions

We have provided an overview of Tremellomycetes, a basal group in the Agaricomycotina. For most of its species, knowledge of ecology and phylogeography is still sparse. A particular problem for the taxonomy of this group is the fact that teleomorphs and anamorphs have mostly been studied by different scientific communities using different taxonomic methods. Polymerase chain reaction-based advances in molecular biology have triggered an integration of these two taxonomic approaches into a consistent classification system, yet a sound phylogenetic classification is only just emerging. We expect that most of the open systematic questions will be solved in the near future by phylogenomic analyses, when more genomes in the Tremellomycetes will be available (as of writing this chapter, genome data are only available for *C. neoformans* and *T. mesenterica*). We hope that, along with the progress in molecular techniques and data, a rising number of mycologists will be interested in and capable of studying these fascinating fungi in the field, to shed light on the biodiversity still unknown.

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Chapter No.: 12

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