

Pietro Buzzini · Marc-André Lachance  
Andrey Yurkov *Editors*

# Yeasts in Natural Ecosystems: Ecology

 Springer

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*Editors*

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# Preface

Yeasts are the smallest eukaryotic organisms. They are fungi that share the unique morphological adaptation of growing as predominantly unicellular organisms and multiplying through budding. Since their first discovery as the fermentative agent in wine and beer, yeasts have been used widely for the production of beverages, food, organic acids, enzymes, proteins, lipids, and pigments. However, unlike the domesticated yeast *Saccharomyces cerevisiae* (baker's yeast), other species do have habitats in nature. Ecology explores organisms in the context of their environment. This includes the chemical, physical, and psychological properties which together describe habitats in which an organism can live. However, successful colonization and persistence in a habitat depends on other organisms and their interactions. Each species constantly modifies the environment through its own activities that make a habitat a dynamic system. Accordingly, a yeast does not occur as a pure culture but coexists with other species in a microbial community or microbiome. Although yeasts are among the earlier colonizers of nutrient-rich substrates, their role in ecosystem processes is not limited to the consumption and transformation of simple sugars. Yeasts participate in the degradation of complex organic substances and also synthesize, accumulate, and release organic molecules into the environment. They also act as primary and secondary decomposers in ecosystems and serve as a source of nutrients for micro- and macroorganisms in the food web.

Why did we decide to assemble this book? Almost every book dealing with the biology of yeasts also introduces the reader to ecology. The large taxonomic compendium *The Yeasts: A Taxonomic Study* included in its more recent editions a chapter on yeast ecology. Several books and book series such as *The Life of Yeasts* (Phaff, Miller, Mraz), *The Yeasts* (Rose and Harrison), *Yeasts in Natural and Artificial Habitats* (Spencer and Spencer), and *Biodiversity and Ecophysiology of Yeasts* (Rosa and Peter) published in the last four decades covered major advances in the ecology of yeasts. With this book, we attempt to give an update on topics covered in previous books, introduce new subjects, and provide novel views on selected aspects of yeast ecology.

Our knowledge of yeast ecology derives from studies of yeast properties and available records of isolation sources. Research on applications of yeasts in food production and biotechnology or as model organisms in science overshadows ecological studies. As a result, the physiological properties of yeast species are better known than their habitats. Many species are documented from only a limited number of strains, and their original taxonomic descriptions do not always describe the habitat or community and biotic interactions. Yeasts constantly interact with animals, plants, and other fungi in the environment. They also engage in close relationships with other living organisms as mutualists, competitors, parasites, and pathogens. Thus, alterations of the environment may lead to rapid changes in local yeast communities—for example, a yeast species may become extinct in the absence of its host or vector. Indirect effects of climate and vegetation type on belowground yeast communities have been also demonstrated.

The book presents a comprehensive overview on different aspects of yeast ecology and constitutes the first volume of a whole monograph on *Yeasts in Natural Ecosystems*, of which the second volume (assembled by the same editors) is dedicated to yeast diversity. It shows how views on yeasts have changed with the discovery of new species and new methods to study them. All chapters review the knowledge accumulated during research carried out in the past decades. Yeast species cited in these works were often identified by different techniques and criteria that may not be as accurate as the current sequence-based approaches. Many species names cited in the early literature are not current. Accordingly, all original taxonomic designations reported in the cited references were checked and, if necessary, updated following the latest taxonomic guidelines published in Kurtzman et al. (2011), Liu et al. (2015), Wang et al. (2015a, 2015b), or more recent literature. A unified list of abbreviations was prepared to assist readers in following species names throughout the book.

The selection of topics and invitation of potential contributors were made by the three editors. Chapters were edited and managed by P. Buzzini and A. Yurkov. The editors thank all the authors for their excellent contributions. We also acknowledge researchers for granting access to public repositories of publications and sharing unpublished results.

P. Buzzini is grateful to Ann Vaughan-Martini and dedicates this book to the memory of his teacher (and friend) Alessandro Martini.

A. Yurkov is grateful to his teachers, soil microbiologists, and yeast ecologists Inna Babjeva and Ivan Chernov. A few sections of the book review their work and are dedicated to the memory of Ivan Chernov, who studied the distribution of yeasts across many terrestrial biomes.

A. Yurkov acknowledges the research network of yeast scientists promoted by the van Uden International Advanced Course on Molecular Ecology, Taxonomy and Identification of Yeasts. Many of the authors of this book were participants and later lecturers in this course in various years.

M. A. Lachance is grateful to P. Buzzini and A. Yurkov for their invitation to join the editorial team in a mostly advisory capacity.

Finally, the editors would like to thank the Springer team, especially Isabel Ullmann and Dr. Andrea Schlitzberger, for their valuable and continuous support during the preparation of this book.

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# Abbreviations

The following abbreviations are used for names of microbial genera (including synonyms) cited in the text.

<i>Acinetobacter</i>	<i>Acin.</i>
<i>Anthracocystis</i>	<i>Anthr.</i>
<i>Apiotrichum</i>	<i>Ap.</i>
<i>Babjeviella</i>	<i>Bab.</i>
<i>Candida</i>	<i>C.</i>
<i>Clavispora</i>	<i>Cl.</i>
<i>Colacogloea</i>	<i>Col.</i>
<i>Cryptococcus</i>	<i>Cr.</i>
<i>Cutaneotrichosporon</i>	<i>Cut.</i>
<i>Cyberlindnera</i>	<i>Cyb.</i>
<i>Debaryomyces</i>	<i>Deb.</i>
<i>Dioszegia</i>	<i>Di.</i>
<i>Eremothecium</i>	<i>Er.</i>
<i>Filobasidiella</i>	<i>Fil.</i>
<i>Filobasidium</i>	<i>F.</i>
<i>Goffeauzyma</i>	<i>Goff.</i>
<i>Hanseniaspora</i>	<i>H'spora</i>
<i>Hansenula</i>	<i>H.</i>
<i>Itersonilia</i>	<i>It.</i>
<i>Kluyveromyces</i>	<i>K.</i>
<i>Kodamaea</i>	<i>Kod.</i>
<i>Komagataella</i>	<i>Kom.</i>
<i>Leucosporidium</i>	<i>Leuc.</i>
<i>Macrorhabdus</i>	<i>Mac.</i>
<i>Malassezia</i>	<i>Mal.</i>
<i>Metschnikowia</i>	<i>M.</i>
<i>Meyerozyma</i>	<i>Mey.</i>

<i>Millerozyma</i>	<i>Mill.</i>
<i>Mycosarcoma</i>	<i>Mycos.</i>
<i>Naganishia</i>	<i>Na.</i>
<i>Ogataea</i>	<i>O.</i>
<i>Phaffia</i>	<i>Ph.</i>
<i>Phaffomyces</i>	<i>Phaff.</i>
<i>Pichia</i>	<i>P.</i>
<i>Pleurococcus</i>	<i>Pl.</i>
<i>Pseudomonas</i>	<i>Pseudom.</i>
<i>Rhodotorula</i>	<i>Rh.</i>
<i>Saccharomyces</i>	<i>S.</i>
<i>Saccharomycopsis</i>	<i>Sacch.</i>
<i>Saitozyma</i>	<i>Sa.</i>
<i>Solicoccozyma</i>	<i>Sol.</i>
<i>Sporobolomyces</i>	<i>Sp.</i>
<i>Starmerella</i>	<i>Starmer.</i>
<i>Streptococcus</i>	<i>Str.</i>
<i>Takashimella</i>	<i>Tak.</i>
<i>Taphrina</i>	<i>Taph.</i>
<i>Tausonia</i>	<i>Ta.</i>
<i>Tetragoniomyces</i>	<i>Tetrag.</i>
<i>Tilletiopsis</i>	<i>Till.</i>
<i>Trichosporon</i>	<i>Tr.</i>
<i>Ustilago</i>	<i>U.</i>
<i>Ustilentyloma</i>	<i>Ust.</i>
<i>Vanrija</i>	<i>Va.</i>
<i>Vishniacozyma</i>	<i>Vishn.</i>
<i>Wickerhamiella</i>	<i>Wick.</i>
<i>Wickerhamomyces</i>	<i>W.</i>
<i>Zygosaccharomyces</i>	<i>Zygosacch.</i>

# Chapter 1

## Yeasts as Distinct Life Forms of Fungi

Cletus P. Kurtzman and Teun Boekhout

**Abstract** Detection, identification, and classification of yeasts have undergone major changes since application of gene sequence analyses and genome comparisons. Development of a database of barcodes consisting of easily determined DNA sequences from domains 1 and 2 (D1/D2) of the nuclear large subunit rRNA gene and from ITS now permits many laboratories to identify species quickly and accurately, thus replacing the laborious and often inaccurate phenotypic tests previously used. Phylogenetic analysis of gene sequences is leading to a major revision of yeast systematics that will result in redefinition of nearly all genera. This new understanding of species relationships has prompted a change of rules for naming and classifying yeasts and other fungi, and these new rules were recently implemented in the *International Code of Nomenclature for algae, fungi, and plants* (Melbourne Code). The use of molecular methods for species identification and the impact of Code changes on classification will be discussed.

**Keywords** Yeasts • Taxonomy • Molecular systematics • Evolution

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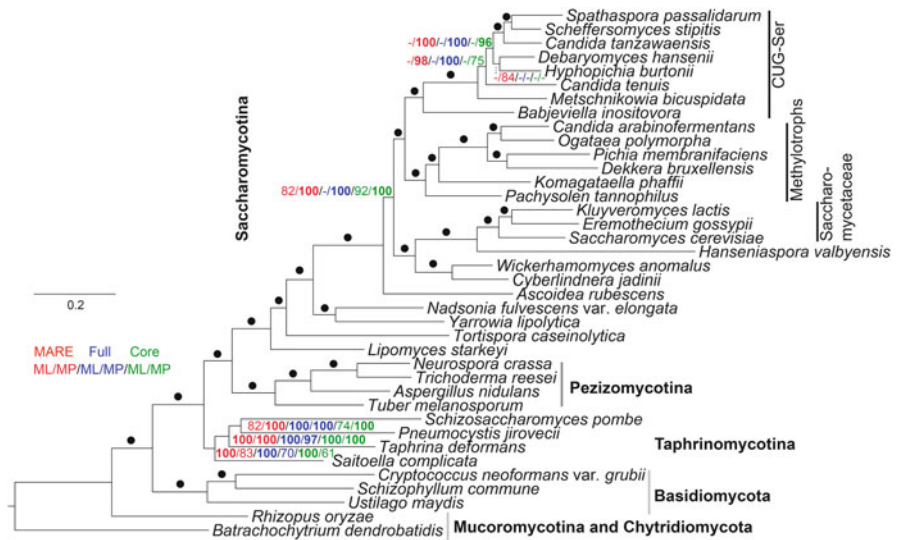
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## 1.1 Introduction

The title of this chapter, “Yeasts as Distinct Life Forms of Fungi,” challenges us to ask if yeasts represent a unique phylogenetic group or whether the yeast morphotype is common in many lineages of the Mycota. The most commonly known yeast, the ascomycete *Saccharomyces cerevisiae*, is widely used for production of bread, beer, wine, and many other fermentation products. The simplicity of its life cycle, asexual reproduction by budding and a sexual cycle represented by ascospore formation in a single cell ascus, suggests that it must be a primitive fungus (Guilliermond 1912), or could it be a reduced form among more mycelial taxa, as proposed by Cain (1972) and von Arx and van der Walt (1987)? Initially, it appeared that all yeasts were ascomycetes, but that belief changed with the discovery that some yeasts are basidiomycetes (Kluyver and van Niel 1924, 1927; Banno 1967; Nyland 1949).

The first indication of the phylogenetic placement of ascomycete yeasts among the fungi came from the study of Walker (1985), who proposed from analysis of 5S rRNA sequences that Ascomycota is comprised of three major groups: (1) *Schizosaccharomyces* and *Protomyces* (Taphrinomycotina), (2) budding yeasts (Saccharomycotina), and (3) the “filamentous fungi” (Pezizomycotina). Some species of the Pezizomycotina are dimorphic, but have sexual states that are formed in or on a fruiting body, which is typical of this subphylum. A multitude of additional studies, ranging from single genes to whole genomes, have shown these same basic relationships among the Ascomycota (e.g., Kurtzman and Robnett 1998, 2013; Fitzpatrick et al. 2006; James et al. 2006; Hittinger et al. 2015; Shen et al. 2016). For the Basidiomycota, single gene sequences and whole genome analyses have demonstrated placement of yeast forms in all of the major lineages. An overview of the phylogeny of the Mycota that was determined from whole genome analyses is given in Fig. 1.1.

In an effort to explain the basis for budding versus filamentous growth, Nagy et al. (2014) compared 59 genomes of filamentous, dimorphic, and yeast-forming fungi. It appears that expression of the zinc cluster transcription factors regulates which morphotype predominates. This mechanism may have arisen at the base of the *Dikarya* and shows varying expression in different lineages of the Mycota. However, this finding alone does not explain why yeasts of various lineages form sexual states not enclosed in a fruiting body, whereas dimorphic fungi in nearby



**Fig. 1.1** Phylogenetic tree inferred from the MARE-filtered supermatrix (364,126 aligned amino acid residues) using maximum likelihood (ML) and rooted with *Batrachochytrium*. Numbers on the branches indicate ML and maximum parsimony (MP) bootstrap support values for the MARE-filtered (red), full (blue), and core genes (green) supermatrices. Values less than 60% are shown as dashes; dots indicate branches with maximum support under all settings. Yeasts in the CUG-Ser clade use an altered genetic code in which CUG codons are translated as serine rather than the canonical leucine (Santos et al. 1997, 2011). One further modification was found for *Pachysolen tannophilus*, in which CUG codes for alanine (Riley et al. 2016). (Modified from Riley et al. 2016, with permission)

lineages do form fruiting bodies. Because yeasts can occur in various lineages of the Mycota, the definition of yeasts is presently based on morphology and has become fungi, ascomycetes or basidiomycetes, that asexually reproduce by budding or fission and that have a sexual state not enclosed in a fruiting body.

In the following sections, we will discuss placement of yeasts within the taxonomic framework of the Ascomycota and Basidiomycota. Application of molecular methods for species identification has resulted in discovery of a large number of new species and genera. For comparison, the fourth edition of *The Yeasts: A Taxonomic Study* (Kurtzman and Fell 1998) listed 97 genera and 700 species, whereas the fifth edition (Kurtzman et al. 2011a) includes 150 genera and 1500 species. Since the publication of the fifth edition in 2011, many new species and genera of both ascomycetes and basidiomycetes have been described.

In addition to the substantial changes in classification brought by DNA sequence comparisons, recent changes in the rules for classification of fungi are having a major impact on naming of taxa. The classification of yeasts and other fungi previously was governed by the rules of the *International Code of Botanical Nomenclature* (e.g., McNeill et al. 2006), which based taxonomy on sexual states of fungi and required separate names for asexual “form genera.” The ability to

group sexual and asexual states within a clade using DNA characters eventually led to a logical change in the rules of nomenclature, and the latest edition of the Code (*International Code of Nomenclature for algae, fungi, and plants*) (McNeill et al. 2012) ends “dual” nomenclature for fungi and requires inclusion of sexual and asexual states within monophyletic groups, which then have a common genus name.

## 1.2 Ascomycota

### 1.2.1 *Saccharomycotina*

For the Ascomycota, yeast species are found exclusively in the subphyla Saccharomycotina and Taphrinomycotina (Fig. 1.1), and a listing of currently accepted genera is given in Table 1.1. Phylogenetic relatedness among genera was examined by Kurtzman and Robnett (2013) from analysis of concatenated sequences from the nearly entire genes for nuclear large subunit rRNA, nuclear small subunit rRNA, translation elongation factor EF-1 $\alpha$ , and RNA polymerase II subunit 1 and subunit 2 for type species (Fig. 1.2). Not surprisingly, the five-locus dataset shows much lower bootstrap support of basal branches than seen in whole genome analyses (e.g., Fig. 1.1), but the overall topology is similar for both trees, although many species are not represented in the whole genome tree. In both trees, *Lipomyces* is the earliest diverging genus in the Saccharomycotina, and perhaps of significance, species of *Lipomyces* are predominantly isolated from soil.

One of the most urgent problems for classification of ascomycete yeasts is the asexual genus *Candida*, which has over 400 described species (Lachance et al. 2011; Daniel et al. 2014). The genus was circumscribed on *Candida vulgaris* (= *Candida tropicalis*), although the majority of *Candida* species are not members of this clade, which also includes *Candida albicans* and *Candida dubliniensis*. Previously, many unrelated yeasts without known sexual reproduction were placed in *Candida*, often because of lack of taxonomic characters needed to group related species. Phylogenetic analyses of molecular characters led to the early recognition that species of the genus *Candida* are distributed throughout the Saccharomycotina with some species as members of ascosporic (sexual) clades, whereas others form isolated lineages that appear to correspond to independent genera without known sexual states (Kurtzman and Robnett 1998). Where sufficient DNA data are available, some divergent species already have been assigned to new genera (Table 1.1), such as *Alloascoidea*, *Danielozyma*, *Deakozyma*, *Diddensiella*, *Diutina*, *Groenewaldozyma*, *Hagleromyces*, *Hemisphaericaspora*, *Martiniozyma*, *Middelhovenomyces*, *Spencermartinsiella*, *Suhomyces*, *Teunomyces*, *Tortispora*, and *Yueomyces*, and other species await transfer as more robust datasets are developed. It is anticipated that a recircumscribed *Candida* will include the approximately 40 species that now form the *C. tropicalis* clade.

**Table 1.1** Presently accepted genera of Saccharomycotina and Taphrinomycotina

<b>Subphylum Saccharomycotina<sup>a</sup></b>	
<i>Aciculoconidium</i> D.S. King & S.-C. Jong (1976)	<i>Metschnikowia</i> Kamienski (1899)
<i>Alloascoidea</i> Kurtzman & Robnett (2013)	<i>Meyerozyma</i> Kurtzman & M. Suzuki (2010)
<i>Ambrosiozyma</i> van der Walt (1972)	<i>Middelhovenomyces</i> Kurtzman & Robnett (2014)
<i>Ascoidea</i> Brefeld & Lindau (1891)	<i>Milleroyzyma</i> Kurtzman & M. Suzuki (2010)
<i>Babjeviella</i> Kurtzman & M. Suzuki (2010)	<i>Myxozyma</i> van der Walt, Weijman & von Arx (1981)
<i>Barnettozyma</i> Kurtzman, Robnett & Basehoar-Powers (2008)	<i>Nadsonia</i> Sydow (1912)
<i>Blastobotrys</i> von Klopotek (1967)	<i>Nakaseomyces</i> Kurtzman (2003)
<i>Botryozyma</i> Shann & M.Th. Smith emend. Lachance & Kurtzman (2013)	<i>Nakazawaea</i> Y. Yamada, Maeda & Mikata (1994)
<i>Brettanomyces</i> Kufferath & van Laer (1921)	<i>Naumovozyma</i> Kurtzman (2008)
<i>Candida</i> Berkhout (1923)	<i>Ogataea</i> Y. Yamada, K. Maeda & Mikata (1994)
<i>Cephaloascus</i> Hanawa (1920)	<i>Pachysolen</i> Boidin & Adzet (1957)
<i>Citeromyces</i> Santa María (1957)	<i>Peterozyma</i> Kurtzman & Robnett (2010)
<i>Clavispora</i> Rodrigues de Miranda (1979)	<i>Phaffomyces</i> Y. Yamada (1997)
<i>Coccidiascus</i> Chatton emend. Lushbaugh, Rowton & McGhee (1976)	<i>Phialoascus</i> Redhead & Malloch (1977)
<i>Cyberlindnera</i> Minter (2009)	<i>Pichia</i> E.C. Hansen (1904)
<i>Cyniclomyces</i> van der Walt & D.B. Scott (1971)	<i>Priceomyces</i> Kurtzman & M. Suzuki (2010)
<i>Danielozyma</i> Kurtzman & Robnett (2014)	<i>Saccharomyces</i> Meyen (1870)
<i>Deakozyma</i> Kurtzman & Robnett (2014)	<i>Saccharomycodes</i> E.C. Hansen (1904)
<i>Debaryomyces</i> Lodder & Kreger-van Rij (1952)	<i>Saccharomycopsis</i> Schiöningg (1903)
<i>Diddensiella</i> Péter, Dlačuchy & Kurtzman (2012)	<i>Saprochaete</i> Coker & Shanor ex D.T.S. Wagner & Dawes (1970)
<i>Dipodascopsis</i> Batra & P. Millner emend. Kurtzman, Albertyn & Basehoar-Powers (2007)	<i>Saturnispora</i> Liu & Kurtzman (1991)
<i>Dipodascus</i> de Lagerheim (1892)	<i>Scheffersomyces</i> Kurtzman & M. Suzuki (2010)
<i>Diutina</i> Khunnamwong, Lertwattanasakul, Jindamorakot, Limtong & Lachance (2015)	<i>Schwanniomyces</i> Klöcker emend. M. Suzuki & Kurtzman (2010)
<i>Endomyces</i> Reess (1870)	<i>Spathaspora</i> N.-H. Nguyen, S.-O. Suh & M. Blackwell (2006)
<i>Eremothecium</i> Borzi emend. Kurtzman (1995)	<i>Spencermartinsiella</i> Péter, Dlačuchy, Tornai-Lehoczki, M. Suzuki & Kurtzman (2011)
<i>Galactomyces</i> Redhead & Malloch (1977)	<i>Sporopachydermia</i> Rodrigues de Miranda (1978)
<i>Geotrichum</i> Link:Fries (1832)	<i>Starmera</i> Y. Yamada, Higashi, Ando & Mikata (1997)
<i>Groenewaldozyma</i> Kurtzman (2016)	<i>Starmerella</i> Rosa & Lachance (1998)
<i>Hagleromyces</i> Sousa, Morais, Lachance & Rosa (2014)	<i>Sugiyamaella</i> Kurtzman & Robnett (2007)

(continued)

**Table 1.1** (continued)

<i>Hanseniaspora</i> Zikes (1912)	<i>Suhomyces</i> M. Blackwell & Kurtzman (2016)
<i>Helicogonium</i> W.L. White (1942)	<i>Tetrapisispora</i> Ueda-Nishimura & Mikata emend. Kurtzman (2003)
<i>Hemisphaericaspora</i> Hui, Ren, Chen, Li, Zhang & Niu (2014)	<i>Teunomyces</i> Kurtzman & M. Blackwell (2016)
<i>Hyphopichia</i> von Arx & van der Walt (1976)	<i>Tortispora</i> Lachance & Kurtzman (2013)
<i>Kazachstania</i> Zubkova (1971)	<i>Torulaspora</i> Lindner (1904)
<i>Kluyveromyces</i> van der Walt (1971)	<i>Trichomonascus</i> H.S. Jackson emend Kurtzman & Robnett (2007)
<i>Kodamaea</i> Y. Yamada, T. Suzuki, Matsuda & Mikata emend. Rosa, Lachance, Starmer, Barker, Bowles & Schlag-Edler (1999)	<i>Trigonopsis</i> Schachner emend. Kurtzman & Robnett (2007)
<i>Komagataella</i> Y. Yamada, Matsuda, Maeda & Mikata (1995)	<i>Vanderwaltozyma</i> Kurtzman (2003)
<i>Kregervanrija</i> Kurtzman (2006)	<i>Wickerhamia</i> Soneda (1960)
<i>Kuraishia</i> Y. Yamada, Maeda & Mikata (1994)	<i>Wickerhamiella</i> van der Walt (1973)
<i>Kurtzmaniella</i> Lachance & Starmer (2008)	<i>Wickerhamomyces</i> Kurtzman, Robnett & Basehoar-Powers (2008)
<i>Lachancea</i> Kurtzman (2003)	<i>Yamadazyma</i> Billon-Grand (1989)
<i>Lipomyces</i> Lodder & Kreger-van Rij (1952)	<i>Yarrowia</i> van der Walt & von Arx (1980)
<i>Lodderomyces</i> van der Walt (1971)	<i>Yueomyces</i> Q.M. Wang, L. Wang, M. Groenewald & T. Boekhout (2015)
<i>Macrorhabdus</i> Tomaszewski, Logan, Snowden, Kurtzman & Phalen (2003)	<i>Zygoascus</i> M.Th. Smith (1986)
<i>Magnusiomyces</i> Zender (1977)	<i>Zygosaccharomyces</i> Barker (1901)
<i>Martiniomyces</i> Kurtzman (2015)	<i>Zygotorulaspora</i> Kurtzman (2003)
<b>Subphylum Taphrinomycotina</b>	
<i>Archaeorhizomyces</i> Rosling & T. James (2011)	<i>Saitoella</i> S. Goto, Sugiyama, Hamamoto & Komagata (1987)
<i>Burenia</i> M.S. Reddy & C.L. Kramer (1975)	<i>Schizosaccharomyces</i> Lindner (1893)
<i>Neolecta</i> Spegazzini (1881)	<i>Taphridium</i> Lagerheim & Juel ex Juel (1902)
<i>Pneumocystis</i> Delanoë & Delanoë (1912)	<i>Taphrina</i> Fries (1832)
<i>Protomyces</i> Unger (1833)	<i>Volkartia</i> Maire (1907)
<i>Protomyopsis</i> Magnus (1905)	

<sup>a</sup>Recent and expected transfer of species to comply with the Melbourne Code:

*Trichomonascus* species to *Blastobotrys*

*Ascobotryozyma* species to *Botryozyma*

*Dekkera* species to *Brettanomyces*

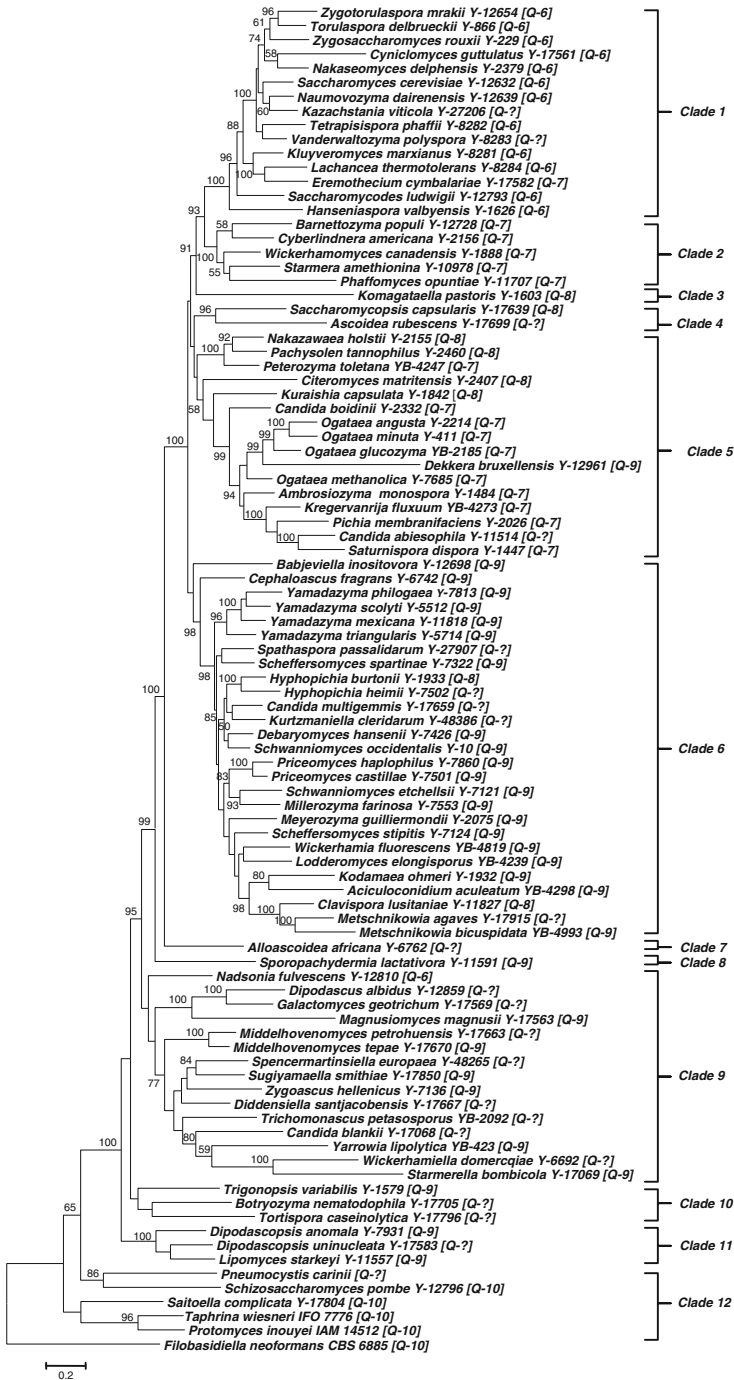
*Kloeckera* species to *Hanseniaspora*

*Schizoblastosporion* species to *Nadsonia*

*Candida* to be comprised of species of the *Candida tropicalis* clade

*Saprochaete* species to *Magnusiomyces*





**Fig. 1.2** Phylogenetic relationships among type species of ascomycete yeast genera and reference taxa determined from ML analysis using concatenated gene sequences for LSU rRNA, SSU rRNA, EF-1 $\alpha$ , RPB1, and RPB2. *Filobasidiella neoformans* was the designated outgroup species in the

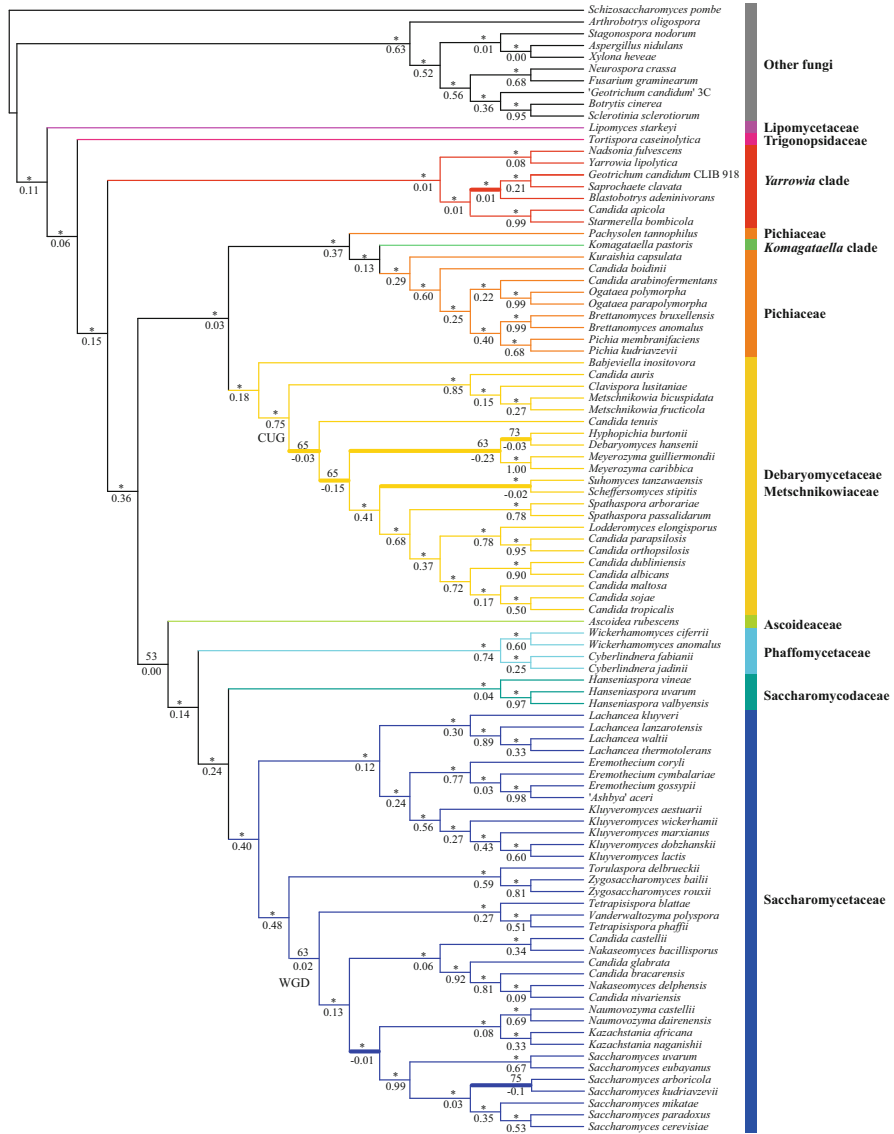
In addition to identifying clades of related species, the question arises as to which of these monophyletic lineages represent genera and families. Species in Fig. 1.3 are grouped from whole genome analysis, and this analysis presents a preview of what we might expect to see following more inclusive sequencing. For example, in this analysis Pichiaceae includes the genera *Pachysolen*, *Komagataella*, *Kuraishia*, *Ogataea*, *Brettanomyces*, and *Pichia*. The currently described Saccharomycetaceae shows a noticeable dichotomy, which may indicate that *Lachancea*, *Eremothecium*, and *Kluyveromyces* belong in a separate family sister to the Saccharomycetaceae. It is anticipated that whole genome sequencing of all known species will allow a better prediction of generic and family boundaries. Another issue is placement of newly described species in the correct genus. When these species clearly fall within the confines of a described genus by virtue of being closely related to known species, genus assignment should not be a problem. For more divergent species, the sequence from the commonly used D1/D2 domains of the nuclear large subunit rRNA gene that is used for species identification may not have enough resolution for genus assignment. Most taxonomists are unlikely to determine the genome sequence of each new species, so perhaps a selection of 5–10 genes would suffice for reliable genus placement of divergent species.

### 1.2.2 *Taphrinomycotina*

A major surprise from DNA sequence comparisons was the discovery that the genus *Schizosaccharomyces* is not in the same subphylum as *Saccharomyces cerevisiae* (e.g., Fig. 1.1). Besides *Schizosaccharomyces*, the subphylum Taphrinomycotina includes such diverse genera as *Taphrina*, *Protomyces*, *Pneumocystis*, and *Archaeorhizomyces*, the latter a slow-growing fungus associated with pine rootlets (Rosling et al. 2011) but previously detected in soil through metagenomic analyses. Many of the genera (Table 1.1, Kurtzman et al. 2011a) assigned to Taphrinomycotina are plant pathogens, but *Pneumocystis* is a common cause of pneumonia in HIV/AIDS patients. In contrast to Saccharomycotina, relatively few species of Taphrinomycotina are known, which suggests that many more species may yet be found in this earlier diverging subphylum.

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**Fig. 1.2** (continued) analysis. *Names in bold font* are type species of currently recognized genera, whereas names in standard font are not type species. Data for *Pneumocystis*, *Protomyces*, and *Taphrina* are from James et al. (2006). *Pneumocystis* is represented by the type species, but not the type strain. *Protomyces* and *Taphrina* are not represented by type species. Bootstrap values (1000 replicates) >50% are given at branch nodes. Strain accession numbers are NRRL unless otherwise indicated. *Designations in brackets* indicate the coenzyme Q value for each species. (from Kurtzman and Robnett 2013)



**Fig. 1.3** The phylogenetic relationships of Saccharomycotina yeasts inferred from the coalescence-based analysis of a 1233 single-copy BUSCO gene amino acid (AA) data matrix. The coalescence-based phylogeny estimation was conducted using ASTRAL version 4.7.7 (Mirarab et al. 2014). Branch support values near internodes are indicated as bootstrap support value (*above*) and internode certainty (*below*), respectively. Asterisk indicates bootstrap support values greater than or equal to 95%. *Thicker branches* show conflicts between coalescence-based phylogeny and concatenation-based phylogeny (Shen et al. 2016, with permission)

### 1.3 Basidiomycota

The basidiomycetous nature of some yeasts was first suggested by the presence of ballistoconidia in the red yeast *Sporobolomyces* (Kluyver and van Niel 1924, 1927), later by the presence of budding cells, ballistoconidia, clamp connections, and smut-like teliospores in *Sporidiobolus* (Nyland 1949), and convincingly by the discovery of mating and a sexual state in *Rhodotorula glutinis* (Banno 1967). Unicellular stages, or yeasts, occur in all three lineages of phylum Basidiomycota, namely, Agaricomycotina, Pucciniomycotina, and Ustilaginomycotina (Hibbett et al. 2007; Boekhout et al. 2011). Many species are dimorphic and alternate yeast and hyphal stages throughout their life cycle (Bandoni 1995). Today the recognition of a yeast as belonging to the Basidiomycota is mainly done by the analysis of gene sequences, most notably the D1/D2 domains of the large subunit rDNA (LSU rDNA), the internal transcribed spacers 1 and 2 (ITS) of rDNA, or the small subunit (SSU) rDNA. A number of morphological, biochemical, ultrastructural, and physiological criteria indicate basidiomycetous affinity as well, such as a positive diazonium blue B reaction, urease activity, enteroblastic budding, presence of ballistoconidia and/or red carotenoid pigments, a lamellate cell wall ultrastructure, presence of a dolipore septum, the biochemical composition of the cell wall, and a high mol% G + C of genomic DNA (usually  $>50\%$ ) with the majority of basidiomycetous yeasts above 50% (see Boekhout et al. 2011).

Early molecular evolutionary studies of 5S rRNA indicated two phylogenetic lineages that correlated with septal ultrastructure (Walker and Doolittle 1982; Templeton 1983). This was confirmed by the observation made by Blanz and Gottschalk (1984) who distinguished a lineage that is now recognized as Pucciniomycotina and a second one now known as Agaricomycotina. Molecular phylogenetic studies using SSU rDNA revealed one more lineage (Swann and Taylor 1995; Sugiyama 1998) that is presently known as Ustilaginomycotina. Thus, these early molecular evolutionary studies revealed the presence of yeast and yeastlike fungi in all three domains of Basidiomycetes. The presence of these three subphyla in Basidiomycota and the presence of yeasts, therein, are widely accepted and supported by many molecular phylogenetic studies (Fell et al. 1995, 2000; Begerow et al. 1997; Scorzetti et al. 2002; James et al. 2006; Liu et al. 2015a, b; Wang et al. 2014, 2015a, b, c). All three subphyla are species rich and show a great amount of organismal complexity that ranges from unicellular yeasts to hyphally growing or multicellular life forms, such as mushrooms, and the plant pathogenic rusts and smuts. With respect to the taxonomy of the basidiomycetous yeasts, the most important observation resulting from these molecular studies was the lack of concordance between the previously recognized taxa, especially genera, and the molecularly defined clades. Notably, many so-called anamorphic (=asexual) genera, such as *Cryptococcus*, *Bullera*, *Sporobolomyces*, *Bensingtonia*, and *Rhodotorula* were highly polyphyletic. Therefore, a multigene-based effort was made to bring the taxonomy in line with the results of molecular phylogeny studies (Wang et al. 2014, 2015a, b, c; Liu et al. 2015a, b). Probably the most relevant

taxonomic rearrangements relate to the reclassification of species of these previously highly polyphyletic genera, such as *Rhodotorula* and *Bensingtonia*.

Pucciniomycotina seem ancestral to both the Ustilaginomycotina and Agaricomycotina (James et al. 2006). Yeast taxa form a minor part of the ca. 8000 species described (Kirk et al. 2001) with the majority (ca. 95%) known as the rusts (Pucciniales). Species in this lineage also show a great diversity of ecological interactions. As indicated, the majority of species are plant pathogens, but others are mycoparasites, insect pathogens, or saprotrophs. Until recently, eight major clades were recognized as classes (Weiss et al. 2004; Aime et al. 2006; Bauer et al. 2006; Hibbett et al. 2007), but recently a new class Spiculogloeomycetes was added (Wang et al. 2015b). Classes Agaricostilbomycetes, Spiculogloeomycetes, Cystobasidiomycetes, Microbotryomycetes, and Mixiomycetes contain yeast taxa. Mixiomycetes contain only one species, *Mixia osmundae*, that is a fern parasite that forms cream yeast colonies in culture (Nishida et al. 1995).

Spiculogloeomycetes contain three genera (Table 1.2) with yeast taxa, *Spiculogloea*, *Mycogloea* (in part), and *Phyllozoma* (Wang et al. 2015b). Agaricostilbomycetes contain ten genera with yeasts belonging to four families, Agaricostilbaceae, Chionosphaeraceae, Kondoaceae, and Ruineniaceae (Wang et al. 2015b). The phylogenetic affiliation of the genus *Jianyunia* within Agaricostilbomycetes is not yet solved (Wang et al. 2015b). Cystobasidiomycetes contain 11 genera with yeast taxa classified in seven families, Cystobasidiaceae, Erythrobasidiaceae, Naohideaceae, Symmetrosporaceae, Buckleyzymaceae, Microsporomycetaceae, and Sakaguchiaceae (Wang et al. 2015b). Several species are able to form mycosporines, which are low molecular weight water-soluble pigments that are capable of absorbing UV radiation (Libkind et al. 2005). Most pucciniomycetous yeasts belong to class Microbotryomycetes that contains 25 genera affiliated to six families, namely, Kriegeriaceae, Campotbasidiaceae, Leucosporidiaceae, Sporidiobolaceae, Colacogloeaceae, and Chrysozymaceae (Wang et al. 2015b). Yeast forms occur in the orders Kriegeriales, Leucosporidiales and Sporidiobolales (Wang et al. 2015b), whereas plant and mycoparasitism mainly belong to orders Microbotryales and Heterogastridiales, respectively.

Agaricomycotina contains five classes, viz., Agaricomycetes, Dacrymycetes, Tremellomycetes, Wallemiomycetes, and Geminibasidiomycetes (Zalar et al. 2005; Hibbett 2006; Matheny et al. 2006; Hibbett et al. 2007; Nguyen et al. 2015). In Tremellomycetes, yeasts or dimorphic taxa occur only in five orders, Cystofilobasidiales, Filobasidiales, Holtermanniales, Tremellales, and Trichosporonales (Fell et al. 2000; Sampaio 2004; Wuczkowski et al. 2011; Liu et al. 2015a, b; Table 1.3). Trichosporonales, however, is not accepted as a separate order from Tremellales by some authors (Weiss et al. 2004; Hibbett et al. 2007), but recent multigene-based phylogenies suggested otherwise (Liu et al. 2015a, b). Similar to Pucciniomycotina, the reclassifications made of highly polyphyletic genera, such as *Cryptococcus* and *Bullera*, can be seen as the most significant contribution to the restructuring of the taxonomy of yeasts in Agaricomycotina (Tables 1.3 and 1.5; Liu et al. 2015b). Within Tremellales, Cystofilobasidiales

Table 1.2 Accepted yeast genera of Pucciniomycotina

Class	Order	Family	Genus	Type species	Other (yeast) species
Agaricostilbomycetes	Agaricostilbales	Agaricostilbaceae	<i>Sterigmatomyces</i>	<i>Sterigmatomyces halophilus</i>	
			<i>Pseudobensingtonia</i>	<i>Pseudobensingtonia ingoldii</i>	
		Chionosphaeraceae	<i>Ballistosporomyces</i>	<i>Ballistosporomyces xanthus</i>	
			<i>Chionosphaera</i>	<i>Chionosphaera apobasidialis</i>	
			<i>Cystobasidiopsis</i>	<i>Cystobasidiopsis nirenbergiae</i>	
			<i>Kurtzmanomyces</i>	<i>Kurtzmanomyces neclairi</i>	<i>Mycogloea nipponica</i>
		<i>Incertae sedis</i> Chionosphaeriaceae			
		Kondoaceae	<i>Bensingtonia</i>	<i>Bensingtonia ciliata</i>	
			<i>Kondoa</i>	<i>Kondoa mahinella</i>	
		Ruineniaceae	<i>Ruinenia</i>	<i>Ruinenia rubra</i>	
			<i>Jianyunia</i>	<i>Jianyunia sakaguchii</i>	
Spiculogloeomycetes	Spiculogloales	Spiculogloeaceae	<i>Spiculogloea</i>	<i>Spiculogloea occulta</i>	
			<i>Mycogloea</i> (pro parte)	<i>Mycogloea carnosa</i>	
			<i>Phyllozyma</i>	<i>Phyllozyma subbrunnea</i>	
Cystobasidiomycetes	Cystobasidiales	Cystobasidiaceae	<i>Cystobasidium</i>	<i>Cystobasidium finetarium</i>	
			<i>Occultifur</i>	<i>Occultifur internus</i>	
	Erythrobasidiales	Erythrobasidiaceae	<i>Bannoa</i>	<i>Bannoa hajajimensis</i>	
			<i>Erythrobasidium</i>	<i>Erythrobasidium hasegawianum</i>	

	<i>Incertae sedis</i> Erythrobasidiales		<i>Cyrenella</i>	<i>Cyrenella elegans</i>
			<i>Hasegawazyma</i>	<i>Hasegawazyma lactosa</i>
	Naohideales	Naohideaceae	<i>Naohidea</i>	<i>Naohidea sebacea</i>
<i>Incertae sedis</i> Cystobasidiomycetes		Symmetrosporaceae	<i>Symmetrospora</i>	<i>Symmetrospora gracilis</i>
		Buckleyzymaceae	<i>Buckleyzyma</i>	<i>Buckleyzyma aurantitaca</i>
		Microsporomyetaceae	<i>Microsporomyces</i>	<i>Microsporomyces magnisporus</i>
		Sakaguchiaceae	<i>Sakaguchia</i>	<i>Sakaguchia dacryoidea</i>
Microbotryomycetes	Kriegeriales	Kriegeriaceae	<i>Kriegeria</i>	<i>Kriegeria eriophori</i>
			<i>Meredithblackwellia</i>	<i>Meredithblackwellia eburnea</i>
			<i>Phenoliferia</i>	<i>Phenoliferia psychrophenolica</i>
			<i>Yamadamyces</i>	<i>Yamadamyces rosulatus</i>
		Camptobasidiaceae	<i>Camptobasidium</i>	<i>Camptobasidium hydrophilum</i>
			<i>Glaciozyma</i>	<i>Glaciozyma antarctica</i>
	Leucosporidiales	Leucosporidiaceae	<i>Leucosporidium</i>	<i>Leucosporidium scottii</i>
	Sporidiobolales	Sporidiobolaceae	<i>Rhodotorula</i>	<i>Rhodotorula glutinis</i>
			<i>Rhodospiridiobolus</i>	<i>Rhodospiridiobolus nylandii</i>
			<i>Sporobolomyces</i>	<i>Sporobolomyces roseus</i>
<i>Incertae sedis</i> Microbotryomycetes		Colacogloaceae	<i>Colacogloea</i>	<i>Colacogloea penitiphorae</i>
		Chrysozymaceae	<i>Bannozyma</i>	<i>Bannozyma yamatoana</i>
			<i>Chrysozyma</i>	<i>Chrysozyma griseoflava</i>
			<i>Fellozyma</i>	<i>Fellozyma inositophila</i>

(continued)

Table 1.2 (continued)

Class	Order	Family	Genus	Type species	Other (yeast) species
			<i>Hamamotoa</i>	<i>Hamamotoa singularis</i>	
			<i>Pseudohyphozyma</i>	<i>Pseudohyphozyma buffonii</i>	
			<i>Pseudoleucosporidium</i>	<i>Pseudoleucosporidium fasciculatum</i>	
			<i>Oberwinklerozyma</i>	<i>Oberwinklerozyma yarrowii</i>	
			<i>Sampaiozyma</i>	<i>Sampaiozyma ingeniosa</i>	
			<i>Spencerozyma</i>	<i>Spencerozyma crocea</i>	
			<i>Slooffia</i>	<i>Slooffia tsugae</i>	
			<i>Trigonosporomyces</i>	<i>Trigonosporomyces hylophilus</i>	
			<i>Yunzhangia</i>	<i>Yunzhangia auriculariae</i>	
			<i>Vanudentiozyma</i>	<i>Vanudentiozyma ferulica</i>	
			<i>Vonarxula</i>	<i>Vonarxula javanica</i>	
Mixiomycetes	Mixiales	Mixiaceae	<i>Mixia</i>	<i>Mixia osmundae</i>	



Table 1.3 Accepted yeast genera of Agaricomycotina

Class	Order	Family	Genus	Type species	Other (yeast) species	
Tremellomycetes	Cystoflobasidiales	Mrakiaceae	<i>Itersoniella</i>	<i>Itersoniella perplexans</i>		
			<i>Krasilnikovozyma</i>	<i>Krasilnikovozyma huempfi</i>		
			<i>Mrakia</i>	<i>Mrakia frigida</i>		
			<i>Phaffia</i>	<i>Phaffia rhodozyma</i>		
			<i>Tausonia</i>	<i>Tausonia pamirica</i>		
			<i>Udentomyces</i>	<i>Udentomyces pyriticola</i>		
				Cystoflobasidiaceae	<i>Cystoflobasidium capitatum</i>	
				Filobasidiaceae	<i>Filobasidium floriforme</i>	
					<i>Goffeauzyma gastrica</i>	
					<i>Heterocephalacria solida</i>	<i>Heterocephalacria arrabidensis</i>
Holtermanniales	Not assigned		<i>Naganishia</i>	<i>Naganishia globosa</i>		
			<i>Szygospora</i>	<i>Szygospora alba</i>		
			<i>Piskurozyma</i>	<i>Piskurozyma cylindrica</i>		
			<i>Solicocozyma</i>	<i>Solicocozyma aerea</i>		
			<i>Holtermannia</i>	<i>Holtermannia corniformis</i>		
			<i>Holtermanniella</i>	<i>Holtermanniella takashimae</i>		
			Bulleribasidiaceae	<i>Bulleribasidium oberjochense</i>		
				<i>Dexomyces mirakii</i>		
				<i>Dioszegia hungarica</i>		

(continued)

Table 1.3 (continued)

Class	Order	Family	Genus	Type species	Other (yeast) species
			<i>Hannaella</i>	<i>Hannaella sinensis</i>	
			<i>Nielozyma</i>	<i>Nielozyma melastomae</i>	
			<i>Vishniacozyma</i>	<i>Vishniacozyma carnescens</i>	
		Tremellaceae	<i>Tremella</i>	<i>Tremella mesenterica</i>	
		Rhynchoastromataceae	<i>Papiliotrema</i>	<i>Papiliotrema bandonii</i>	
			<i>Rhynchoastroma</i>	<i>Rhynchoastroma coronatum</i>	
		Bulleraceae	<i>Bullera</i>	<i>Bullera alba</i>	
			<i>Fonsecazyma</i>	<i>Fonsecazyma mujuensis</i>	
			<i>Genolevuria</i>	<i>Genolevuria amylyolytica</i>	
			<i>Pseudotremella</i>	<i>Pseudotremella moriformis</i>	
			Tremella clade I		<i>Cryptococcus cuniculi</i> pro tem.
		Sirobasidiaceae	<i>Fibulobasidium</i>	<i>Fibulobasidium inconspicuum</i>	
		<i>Incertae sedis</i> Sirobasidiaceae			<i>Sirobasidium japonicum</i> pro tem.; <i>Sirobasidium magnum</i> pro tem.
		Cuniculitremaeae	<i>Fellomyces</i>	<i>Fellomyces polyborus</i>	
			<i>Kockovaella</i>	<i>Kockovaella thailandica</i>	
			<i>Sterigmatosporidium</i>	<i>Sterigmatosporidium polymorphum</i>	
		Naemateliaceae	<i>Naematelia</i>	<i>Naematelia encephala</i>	

		Carcinomycetaceae	<i>Carcinomyces</i>	<i>Carcinomyces effibulatus</i>
		Trimorphomycetaceae	<i>Saitozyma</i> <i>Sugitazyma</i>	<i>Saitozyma flava</i> <i>Sugitazyma miyagiana</i>
			<i>Trimorphomyces</i>	<i>Trimorphomyces papilionaceus</i>
		Cryptococcaceae	<i>Cryptococcus</i>	<i>Cryptococcus neoformans</i>
			<i>Kwonieella</i>	<i>Kwonieella mangroviensis</i>
		Phaeotremellaceae	<i>Gelidatrema</i> <i>Phaeotremella</i>	<i>Gelidatrema spencermartinsiae</i> <i>Phaeotremella pseudofoliacea</i>
	Trichosporonales	Trichosporonaceae	<i>Apiotrichum</i> <i>Cutaneotrichosporon</i>	<i>Apiotrichum porosum</i> <i>Cutaneotrichosporon cutaneum</i>
			<i>Haglerozyma</i>	<i>Haglerozyma haglerorum</i>
			<i>Trichosporon</i>	<i>Trichosporon ovoides</i>
			<i>Vanrija</i>	<i>Vanrija humicola</i>
		Tetragoniomycetaceae	<i>Bandonia</i> <i>Cryptotrichosporon</i>	<i>Bandonia marina</i> <i>Cryptotrichosporon anacardii</i>
			<i>Takashimella</i>	<i>Takashimella formosensis</i>
			<i>Tetragoniomyces</i>	<i>Tetragoniomyces uliginosus</i>

Pro tem. = pro tempore, indicating that the final taxonomic placement of the species is not yet known and, hence, it is left in the polyphyletic genus from where it should be removed when more evidence becomes available

forms the basal lineage (Liu et al. 2015a, b) with yeast taxa belonging to eight genera of two families, Mrakiaceae and Cystofilobasidiaceae (Liu et al. 2015b). Species of *Mrakia* and *Phaffia* are able to ferment, and the latter forms astaxanthin (Johnson 2003; Johnson and Echavarri-Erasun 2011) that is widely used as a colorant for salmon grown in aquaculture. The elongate basidia of *Phaffia* species are formed after cell-bud mating and produce apical basidiospores (Golubev 1995). Strains of *Phaffia* came from tree sap in temperate regions of the Northern Hemisphere and from the sugar-rich stromata of *Cyttaria* spp. that parasitize *Nothofagus* trees in the Southern Hemisphere (Libkind et al. 2007). Species of *Mrakia* may also cause spoilage of refrigerated citrus juice that may cause significant economic damage (Houbraken, unpublished data). Filobasidiales has seven yeast species containing genera that cluster into two families, Filobasidiaceae and Piskurozymaceae (Liu et al. 2015b). Holtermanniales has only two genera, namely, *Holtermannia* that forms mushroom-like gelatinous fruiting bodies formed by aggregates of erect, simple, or branched teeth of which the basidiospores germinate with yeast cells and *Holtermanniella* that contains only yeasts and one filamentous growing species.

Most yeast containing genera belong to Tremellales, namely, 28 that are classified into 11 families (Table 1.3; Liu et al. 2015b). Note that *Tremella*, a genus containing highly typical mushroom-like fruiting bodies known as jelly fungi, turned out to be polyphyletic (Chen 1998; Scorzetti et al. 2002; Liu et al. 2015a, b) with clades belonging to different families. Hence, these clades were assigned to different genera (Liu et al. 2015b), but some lineages still remain to be reclassified due to uncertainties in the phylogenetic positions of key species that may only be available as herbarium specimens. Mycoparasitism seems to occur commonly in this order based on the presence of so-called haustorial branches in many genera and species, e.g., *Papiliotrema flavescens* (cited as *Cryptococcus laurentii*, Kurtzman 1973), *Auriculibuller* (Sampaio et al. 2004), *Bulleromyces* (Boekhout et al. 1991), *Sterigmatosporidium* (cited as *Cuniculitrema*, Kirschner et al. 2001), and *Bulleribasidium* and *Papiliotrema* (Sampaio et al. 2002). Due to the recent update on its taxonomy, the previously highly polyphyletic genus *Cryptococcus* is presently confined to the human pathogens *Cryptococcus neoformans* and *Cryptococcus gattii* and related species (Hagen et al. 2015; Liu et al. 2015a, b). Next to the dimorphic yeast species, this clade also contains some filamentous growing species, previously classified in *Filobasidiella*, namely, *Cryptococcus depauperatus* and *Cryptococcus luteus* (Liu et al. 2015b). *Filobasidiella* is now considered a synonym under *Cryptococcus*. The basidia formed by *Cryptococcus sensu stricto* species are elongated holobasidia with terminal sessile basidiospores in basipetal chains and occur in both the filamentous and dimorphic representatives. Order Trichosporonales contains members of the anamorphic genus *Trichosporon* that to a large extent forms true hyphae and arthroconidia (Fell et al. 2000). Over time, several species of *Cryptococcus*, *Bullera*, and *Cryptotrichosporon* were added (Sugita et al. 2001; Takashima et al. 2001; Nakase et al. 2002; Middelhoven et al. 2003; Fungsin et al. 2006; Okoli et al. 2007) thus questioning the circumscription of genera in this order. Prillinger et al. (2007) proposed *Asterotremella* to

accommodate *Cryptococcus* species belonging to the *Humicola* clade. However, from a nomenclatural point of view, the use of the name *Vanrija* has priority over *Asterotremella* (Okoli et al. 2007; Liu et al. 2015b). A recent reclassification resulted in the recognition of nine genera that belong to the families Trichosporonaceae and Tetragonomycetaceae (Liu et al. 2015b; Tables 1.3 and 1.5).

The subphylum Ustilaginomycotina currently comprises four classes, namely, Ustilaginomycetes and Exobasidiomycetes (Begerow et al. 2000; Hibbett et al. 2007) and the recently added Malasseziomycetes and Moniliellomycetes (Wang et al. 2014). Classes Ustilaginomycetes and Exobasidiomycetes comprise mainly plant pathogens, but asexual states of some of these may grow on agar media. Classes Malasseziomycetes and Moniliellomycetes comprise the genera *Malassezia* and *Moniliella*, respectively. A recent multigene-based phylogenetic analysis of asexual growing yeasts and yeastlike fungi from the four classes and a comparison with LSU rDNA data from sexually growing taxa, mainly plant pathogens, indicated that several asexual species belong to genera of Exobasidiomycetes and Ustilaginomycetes (Wang et al. 2015c; Tables 1.4 and 1.5). Thus, similar to the situation in Pucciniomycotina and Agaricomycotina, the polyphyletic nature of genera such as *Pseudozyma* and *Tilletiopsis* was largely reduced. Next to containing plant pathogens, some of the asexual genera previously classified in *Pseudozyma*, *Tilletiopsis*, *Meira*, and *Acaromyces ingoldii* showed biocontrol capabilities (Urquhart et al. 1994; Belang er et al. 1998; Boekhout et al. 2003). Ustilaginomycotina are also highly polyphyletic, and this prompted the reclassification of the well-known model organism *Ustilago maydis*, as *Mycosarcoma maydis* (McTaggart et al. 2016). Among Ustilaginomycotina two orders have yeasts or yeastlike species, namely, Urocystales (genus *Fereydounia*) and Ustilaginales with the genera *Farysia*, *Anthracoystis*, *Dirkmeia*, *Kalmanozyma*, *Langdonia*, *Moesziomyces*, *Ustilago*, *Mycosarcoma*, and some single species lineages (Table 1.4; Wang et al. 2015c). Note that *Fereydounia khargensis*, the first yeast found in Urocystales and originally described from soil in Iran (Nasr et al. 2014), has been found as an emerging human pathogen in Malaysia (Tap et al. 2016). Many anamorphic *Pseudozyma* species could be transferred to plant pathogenic teleomorphic genera of smuts (Tables 1.4 and 1.5), but five species could not yet be ascribed to any teleomorphic smut genus, and these were *Pseudozyma alboarmeniaca*, *Pseudozyma hubeiensis*, *Pseudozyma pruni*, *Pseudozyma thailandica*, and *Pseudozyma tsukubaensis*. These were left provisionally in the genus *Pseudozyma*, despite that the type species of the genus, *Pseudozyma prolifica*, was made a synonym of *Mycos. maydis* (Wang et al. 2015c; McTaggart et al. 2016). In the Exobasidiomycetes, yeastlike species belonged to six orders, Entylomatales, Exobasidiales, Georgefischeriales, Golubeviales, Microstromatales, and Robbauerales, and two genera, *Jaminaea* and *Sympodiomyopsis*, remained *incertae sedis* in Microstromatales (Tables 1.3 and 1.4; Wang et al. 2015c). Some anamorphic *Tilletiopsis* species could be transferred to teleomorphic genera, such as *Gjaerumia*, *Phragmotonium*, and *Tilletiaria* (Wang et al. 2015c). Only the *Tilletiopsis washingtonensis* complex remained in

**Table 1.4** Accepted genera of Ustilaginomycotina with yeast or yeastlike stages

Class	Order	Family	Genus	Type species	Other (yeast) species
Exobasidiomycetes	Entylomatales	Entylomataceae	<i>Tilletiopsis</i>	<i>Tilletiopsis washingtonensis</i>	
	Exobasidiales	Brachybasidiaceae	<i>Meira</i>	<i>Meira geulakonigii</i>	
		Cryptobasidiaceae	<i>Acaromyces</i>	<i>Acaromyces ingoldii</i>	
	Georgisphaerales	Gjaerumiaceae	<i>Gjaerumia</i>	<i>Gjaerumia minor</i>	
		Tilletiariaceae	<i>Phragmotaelium</i>		<i>Phragmotaelium derxii</i> , <i>Phragmotaelium fubescens</i> , <i>Phragmotaelium flavum</i> , <i>Phragmotaelium oryzicola</i>
			<i>Tilletiaria</i>	<i>Tilletiaria anomala</i>	
	Golubeviales	Golubeviaceae	<i>Golubevia</i>	<i>Golubevia pallescens</i>	
	Microstromatales	Microstromataceae	<i>Microstroma</i>	<i>Microstroma album</i>	
	Microstromatales <i>incertae sedis</i>		<i>Jaminaea</i>	<i>Jaminaea angkorensis</i>	
			<i>Sympodiomyces</i>	<i>Sympodiomyces paphiopedili</i>	
	Robbaurales	Robbauraceae	<i>Robbaura</i>	<i>Robbaura albescens</i>	
Ustilaginomycetes	Urocystales	Fereydouniaceae	<i>Fereydounia</i>	<i>Fereydounia khargensis</i>	
	Ustilaginales	Anthracoideaceae	<i>Farysia</i>	<i>Farysia javanica</i>	<i>Farysia acheniorum</i> , <i>Farysia chardoniana</i> , <i>Farysia itapuensis</i> , <i>Farysia setubalensis</i> , <i>Farysia taiwaniana</i>
		Melanotaeniaceae	<i>Anthracoecystis</i>	<i>preceed name with 'Pseudozyma', flocculosa</i>	
		Ustilaginaceae	<i>Dirkmeia</i>	<i>Dirkmeia churashimaensis</i>	