Towards an integrated phylogenetic classification of the Tremellomycetes

X.-Z. Liu1,2, Q.-M. Wang1,2, M. Gőker1, M. Groenewald2, A.V. Kachalkin4, H.T. Lumbsch5, A.M. Millanes6, M. Wedin7, A.M. Yurkov3, T. Boekhout1,2,8*, and F.-Y. Bai1,2*

1State Key Laboratory for Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, PR China; 2CBS Fungal Biodiversity Centre (CBS-KNAW), Uppsalalaan & Utrecht, The Netherlands; 3Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures, Braunschweig 38124, Germany; 4Faculty of Soil Science, Lomonosov Moscow State University, Moscow 119991, Russia; 5Science & Education, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL 60605, USA; 6Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, E-28233 Móstoles, Spain; 7Department of Botany, Swedish University of Natural History, P.O. Box 50007, SE-10405 Stockholm, Sweden; 8Shanghai Key Laboratory of Molecular Medical Mycology, Changzheng Hospital, Second Military Medical University, Shanghai, PR China

Abstract: Families and genera assigned to Tremellomycetes have been mainly circumscribed by morphology and for the yeasts also by biochemical and physiological characteristics. This phylogenetic classification is largely based on the results of phylogenetic analyses from a seven-genes dataset covering the majority of tremellomycetous yeasts and closely related filamentous taxa. Circumscriptions of the taxonomic units at the order, family and genus levels were quantitatively assessed using the phylogenetic rank boundary optimisation (PRBO) and modified general mixed Yule coalescent (GMYC) tests. In addition, a comprehensive phylogenetic analysis on an expanded LSU rRNA (D1/D2 domains) gene sequence dataset covering as many as available teleomorphic and filamentous taxa within Tremellomycetes was performed to investigate the relationships between yeasts and filamentous taxa and to examine the stability of undersampled clades. Based on the results inferred from molecular data and morphological and physiochemical features, we propose an updated classification for the Tremellomycetes. We accept five orders, 17 families and 54 genera, including seven new families and 18 new genera. We propose to use the term *pro tempore* or *pro temp.* in abbreviation to indicate the species names that are temporarily maintained.

Key words: Jelly fungi, Morphology, Multigene phylogeny, Ranks, Taxonomy, Tremellomycetes, Yeasts.

Taxonomic novelties: new families: *Bulleraceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Bullerbasidiaceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Naemateliaceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Phaeotremellaceae* A.M. Yurkov & Boekhout. *Piskurozymaceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Trimmorphomycetaceae* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. New genera: *Bandonia* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Carcosoraseae* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Cutaneotrichosporon* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Dimennazyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Effusotrichosporon* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Geleiotrema* A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Genolevoriza* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Krasinikovyzma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Nielozyza* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Piskurozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Sugitzyma* A.M. Yurkov, X.Y. Bai, M. Groenew. & Boekhout. *Sativyzoma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Saccocyzma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Vishniaczyzyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. New species: *Krockovaella* prillingeri (Prillinger, G. Krape & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *New combinations: Apiothricium* brassicae (Nakase) A.M. Yurkov & Boekhout, A. cacaoisolata (J.L. Zhou, S.O. Suh & Gjuran) Kachakhlin, A.M. Yurkov & Boekhout, A. dehoogii (Middelhoven, Scorzet & Fell) A.M. Yurkov & Boekhout, A. domesticum (Sugita, A. Nishikawa & Shinoda) A.M. Yurkov & Boekhout, A. culaitum (Berkhou) A.M. Yurkov & Boekhout, A. gamitsi (Middelhoven, Scorzet, Sigler & Fell) A.M. Yurkov & Boekhout, A. gracie (Wiegmann & A. Wolff) A.M. Yurkov & Boekhout, A. laibachi (Windisch) A.M. Yurkov & Boekhout, A. ligincola (Diddens) A.M. Yurkov & Boekhout, A. loubieri (Moreno) A.M. Yurkov & Boekhout, A. montevideense (L.A. Queiroz) A.M. Yurkov & Boekhout, A. mycotoxinivorans (O. Molnár, Schatzm. & Prillinger) A.M. Yurkov & Boekhout, A. scaraebaorum (Middelhoven, Scorzet & Fell) A.M. Yurkov & Boekhout, A. siamense (Nakase, Jindam, Sugita & H. Kawan) Kachakhlin, A.M. Yurkov & Boekhout, A. sporotrichoides (van Oorschot) A.M. Yurkov & Boekhout, A. vanden (Middelhoven, Scorzet & Fell) A.M. Yurkov & Boekhout, A. vennhiis (Middelhoven, Scorzet & Fell) A.M. Yurkov & Boekhout, A. xylophil (S.O. Suh, Lee, Gjuran & Zhou) Kachakhlin, A.M. Yurkov & Boekhout, *Bandonia* marina (van Uden & Zobel) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Bullerbasidium* begoniae (Nakase, Tsuzuki, F.L. Lee & M. Takashi) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. fulicola (Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. hainanaense (Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. panici (Fungsin, M. Takash, & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. pseudovariabile (F.Y. Bai, M. Takash, & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. sanyensae (Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. setaniae (Nakase, Tsuzuki, F.L. Lee & M. Takashi) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. siamense (Fungsin, M. Takash, & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. variabile (Nakase & M. Suzuki) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, B. wuzhishanense (Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *Carcinosome* arundinariae (Fungsin, M. Takash, & Nakase) A.M. Yurkov, C. polyphyla (D.A. Reid) A.M. Yurkov, *Carcosorasea* virseae (Landell, Brandão, Saffar, Gomes, Félix, Santos, Pagani, Ramos, Broetto, Mott, Valente & Rosato) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. *Cryptococcus* depauperatus (Feltch) Boekhout, Liu, Bai & M. Groenew. *C. luteus* (Roberts) Boekhout, Liu, Bai & M. Groenew. *Cuteotrichosporon* arborformis (Sugita, M. Takash, Sano, Nishim, Kinuebuchi, S. Yamag & Osakai) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, C. curvatus (Diddens & Lodder) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, C. deummaniessum (Sugita, Takash, Nakase & Shinoda) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, C. dermatis (Sugita, Takash, Nakase, Ichikawa, Ika & Shinoda) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, C. euphorae (Middelhoven, Scorzet & Fell) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, C. hagleriorm (Middelhoven, A. Fonseca, S.C. Carreiro, Pagnocca & O.C. Bueno) X.Z. Liu, F.Y. Bai, M. Groenew. &
INTRODUCTION

Tremellomycetes is a class of Agaricomycotina (Hibbett et al. 2007, Boekhout et al. 2011a) and encompasses yeasts, dimorphic taxa and species that form hyphae and/or complex fruiting bodies. Five orders, namely Cystofilobasidiales, Filobasidiales, Holtermaniales, Tremellales and Trichosporonales, are currently recognised in Tremellomycetes based on phenotypic and phylogenic properties (Fell et al. 2000, Scorza et al. 2002, Boekhout et al. 2011a, Wuczkowski et al. 2011, Weiss et al. 2014, Liu et al. 2015). However, the separation of Trichosporonales from Tremellales remains a matter of debate (Hibbett et al. 2007, Millanes et al. 2011).

Basidiomycetous yeasts, like ascomycetous yeasts, were conventionally classified based on morphological features, including sexual and asexual reproductive structures and morphology; chemotaxonomic criteria, including cell-wall composition data and ubiquinone types; and physiologic properties characterised by standardised tests on the assimilation and fermentation of carbon and nitrogen compounds, production of starch-like compounds, and other growth tests (Lodder & Kreger-van Rij 1952, Van der Walt 1970, Van der Walt & Yarrow 1984, Boekhout et al. 1993, 2011a, Kurtzman et al. 2011b, Pillinger et al. 1993, McLaughlin et al. 1995, Sampaio & Fonseca 1995, Nguyen et al. 1998, Yarrow 1998, Takashima et al. 2000, Bauer et al. 2006, Celio et al. 2006). Basidiocarp-forming Tremellomycetes were mainly classified using morphological features, such as form and consistency of the fruiting bodies, and details of hyphae, basidia, basidiospores etc. The classification based on these phenotypic features, however, was in many cases not consistent with the results obtained from molecular phylogenetic analyses. This non-concordance is one of the most prominent problems in the classification of this group of fungi, as illustrated by the polyphylectic nature of many currently recognised genera. Bullera and Cryptococcus are just two examples of genera that are highly polyphyletic with species belonging to more than one order of Tremellomycetes (Boekhout et al. 2011b, Fonseca et al. 2011). Further discovery of new species belonging to these genera not only worsened the problem of systematics of Tremellomycetes, but also impeded the communication of researchers from different fields. For instance, a large number of environmental sequences have been obtained by microbial ecologists and were identified to species belonging to these polyphyletic genera. The NCBI GenBank database (http://www.ncbi.nlm.nih.gov) is the most widely used tool to identify these molecular reads, but the taxon names presented in the results from GenBank searches are often confusing because they refer to such non-monophyletic groups or genera.

Molecular phylogenetic analyses of multiple genes have become an effective approach to reconstruct fungal phylogenies. As the result of the Assembling the Fungal Tree of Life (AFTOL) project, James et al. (2006) used a six-gene dataset to resolve a kingdom-wide fungal phylogeny and Hibbett et al. (2007) proposed a comprehensive phylogenetic re-classification of the fungi down to the ordinal level. Yeast species formed only a small part of the nearly 200 fungal species involved in the AFTOL project. The majority of teleomorphic ascomycetous yeast taxa have independently been reclassified based on results obtained from multigene phylogenetic studies (Kurtzman 2003, Kurtzman & Robnett, 2003, 2007, Kurtzmann et al. 2007, 2008), but most basidiomycetous yeast taxa remain to be studied. In the fifth edition of ‘The Yeasts, a Taxonomic Study’ (Kurtzman et al. 2011a) many of the basidiomycetous yeast genera included are still highly polyphyletic.

The recent changes in the dual nomenclature for pleomorphic fungi prompted us to modify the classification of Tremellomycetes to fulfil the “One Fungus = One Name” principle (McNeill et al. 2012). As is the case in other groups of fungi, many species of this class have separate teleomorphic and anamorphic names. A further change in the new nomenclature is that electronic publication of new taxa and their names is permitted from 1 January 2012 in the absence of a printed hard copy (Knapp et al. 2011). So far, approximately 190 new fungal species have been e-published in Index Fungorum since then (http://www.indexfungorum.org/). The e-publication rule will accelerate the description of new fungal species, and this further urges us to revise the taxonomy of the Tremellomycetes in order to provide a stable taxonomic framework that reflects our knowledge of the phylogenetic diversity and relationships of these fungi.

Several studies across the eukaryotic tree of life have shown that there is poor equivalence of taxonomic ranks across the groups studied (Johns & Avise 1998, Avise & Johns 1999, Castresana 2001, Lumbsch 2002, Avise & Liu 2011, Talavera et al. 2013). Clades of the same rank often show high variance with regard to genetic distances and temporal aspects. Despite the arbitrary nature of taxonomic ranks above the species level, they have importance in an evolutionary framework for cataloguing and communicating about biological diversity and, hence, taxonomic decisions should be made on a consistent basis (Holt & Jonsson 2014). Different methods have been suggested to level off ranks within taxonomic groups, including a temporal approach (Hennig 1966, Farris 1976, Avise & Johns 1999, Holt & Jonsson 2014), but they have not commonly been applied in botany, mycology and zoology (Vences et al. 2013). In bacteriology, a quantitative interpretation of ranks is much more common, particularly by means of traditional (Tindall et al. 2010) or digital (Meier-Kolthoff et al. 2013) DNA:DNA hybridisation thresholds for species and 16S rRNA gene thresholds for higher ranks (Yarza et al. 2014). However, thresholds for pairwise (dis-)similarities are not a phylogenetic criterion (Wiley & Lieberman 2011) and can yield inconsistencies (Meier-Kolthoff et al. 2014). Moreover, the method used by Yarza et al. (2014) to estimate similarity thresholds does not guarantee maximum agreement with the existing assignment to ranks, which could be obtained using clustering optimisation (Göker et al. 2009, 2010, Stielow et al. 2011). Another question regarding Linnaean classification is whether higher taxa are real; this has usually been denied in the literature (Wiley & Lieberman...
Recently, we reconstructed the phylogeny of tremellomycetous yeasts and related dimorphic and filamentous Tremellomycetes by analysing sequences from seven genes (Liu et al. 2015), resulting in a relatively robust framework that allows us to update the taxonomic system of the Tremellomycetes. Here, we employed two quantitative methods, namely a phylogenetic variant of clustering optimisation (Göker et al. 2009, 2010, Stielow et al. 2011) and the iterative application of a modified general mixed Yule coalescent (GMYC) (Humphreys & Barraclough 2014), to test and circumscribe the taxonomic units at the order, family and genus levels recognised from this multigene phylogeny. Results of either method were not followed strictly, however, but were modified where necessary to decrease the number of new taxa to be introduced. Moreover, a comprehensively sampled LSU rRNA gene phylogeny, including taxa that were not studied in the seven-gene phylogeny, was constructed for Tremellomycetes integrating both yeasts and filamentous fungi, incorporating information from the seven-gene phylogeny by using backbone constraints. An updated taxonomic system for Tremellomycetes is consequently proposed based on the integrated phylogenetic evidence combined with morphological and physiological criteria.

MATERIALS AND METHODS

Organisms

A total of 294 tremellomycetous yeast strains, including the type strains of 286 currently recognised species and varieties as listed in Table 1 of Liu et al. (2015), were employed in this study. In addition, 47 tremellomycetous yeast species which were published too late to be included in the study of Liu et al. (2015) and 47 more fruiting body forming species from the genera Tremella, Syzygospora, Rhynchogasterma, Tetragoniomyces and Trimorphomyces were employed in this study (Table 1). Additionally, 23 novel but undescribed species retrieved from the public dataset were also included. Five Cryptococcus species recently described by Hagen et al. (2015) were listed in Table 1 of accepted species names but not included in the phylogenetic analyses. Large ribosomal subunit (LSU) rRNA gene sequences were additionally sampled specifically from related and filamentous taxa in Tremellomycetes, for which no culture material or other nucleotide data are available. All together, a total of 435 taxa were compared in this study.

Phylogenetic analysis

The phylogenetic analysis used for the taxonomic backbone in this study was presented in Liu et al. (2015). The phylogeny was inferred from a seven-gene dataset comprising nucleotide sequences of the internal transcribed spacer region (ITS) rRNA gene, the D1/D2 domains of the large subunit (LSU or 26S) rRNA gene, the small subunit (SSU or 18S) rRNA gene, two subunits of RNA polymerase II (RPB1 and RPB2), translation elongation factor 1-α (TEF1) and cytochrome b (CYTB), using Bayesian inference, maximum likelihood (ML) and neighbour-joining (NJ) analyses (Liu et al. 2015). The supplementary LSU rRNA gene (D1/D2 domains) sequence dataset containing newly published tremellomycetous yeast species and additional filamentous teleomorphic taxa was constructed and subjected to constrained maximum likelihood (ML) and maximum parsimony (MP) analyses based on the topology of a seven-genes dataset taken from Liu et al. (2015). The LSU sequences were aligned with MAFFT version 7 and the G-INS-i option. Constrained phylogenetic analyses were only inferring for species previously analysed using seven DNA loci. Only bipartitions that received at least 85 % bootstrap support during fast bootstrapping of the seven-genes dataset (Liu et al. 2015) conducted with Pthreads-parallelised RAxML version 8.1.24 (Stamatakis 2014) were used as a backbone constraint for LSU phylogenetic inference. Fast bootstrapping in conjunction with the autoMRE bootstopping criterion (Pattengale et al. 2009) and subsequent search for the best tree (Stamatakis et al. 2008) were conducted using the GTRCAT model approximation. MP bootstrapping with 1 000 replicates was conducted with TNT version 1.1/June 2015 (Goloboff et al. 2008).

Quantitative assessment of taxonomic ranks

Two methods were used for the assessment of taxonomic ranks on the basis of the maximum likelihood tree obtained from the concatenated sequences of the seven genes (Liu et al. 2015). Firstly, we used a phylogeny-based variant of clustering optimisation called phylogenetic rank boundary optimisation (PRBO). The goal of clustering optimisation (Göker et al. 2009, 2010, Stielow et al. 2011) is to detect distance thresholds (and clustering parameters) that yield non-hierarchical clusterings that are in maximal agreement with a given reference clustering (such as a classification into taxa of a single rank). The limitations of the approach are that it is rather a clustering method than a phylogenetic approach, even though the resulting clusters are often monophyletic, and that it estimates the boundaries for each taxonomic rank separately. PRBO instead is based on rooted phylogenies. It measures the divergence of each clade as maximum subtree height (MaSH). Taxonomic ranks are made quantitatively comparable by assigning an upper MaSH boundary to each rank, which also serves as the lower MaSH boundary of the next higher rank. Using an existing classification as template, these MaSH ranges for each rank are chosen so as to minimise the number of taxa whose MaSH is outside the MaSH range of their respective rank. Clades to which no taxon is assigned can also enter the optimisation, because their MaSH value must be higher than the upper boundary for the rank of any taxon they contain but lower than the upper boundary for the rank of the taxon assigned to the closest parent clade. This allows for estimating the boundaries for all ranks from an entire tree in a single run. Confidence intervals for the boundaries can be obtained by bootstrapping the set of clades that enters the boundary estimation. Afterwards taxa that did not enter the calculation can be judged as too large or too small, as long as their MaSH values are on the same scale.

The implementation used is the one of the forthcoming MaSH package for the R statistical software environment (R core team 2015). The boundary optimisation is done using the rpart package ( Therneau et al. 2015) with the MaSH values of each clade as dependent and the rank as independent variable. One hundred bootstrap replicates were applied to obtain 95 %
| Taxon                        | Basionym or important synonym | Strain   | LSU D1D2  |
|-----------------------------|-------------------------------|----------|-----------|
| **Cystofilobasidiales**     |                               |          |           |
| **Cystofilobasidiaceae** emend. |                               |          |           |
| C. bisporidii               |                               | CBS 6346T | EU085532  |
| C. capitatum               | Rhodosporidium capitatum      | CBS 6358T | AF075465  |
| C. fergusii                |                               | CBS 7202T | CBS database |
| C. infirmominutiatum        |                               | CBS 323T  | AF075505  |
| C. lacus-mascardi           |                               | CBS 10642T| AY158642  |
| C. macerans                | Cryptococcus macerans         | CBS 1075T | EU082225  |
| **Mrakiaeae fam. nov.**     |                               |          |           |
| Itersonilia                 |                               |          |           |
| I. pannonicus comb. nov.    | Udeniomyces pannonicus        | CBS 9123T | AB077382  |
| I. perplexans               |                               | CBS 363.85T | AJ235274 |
| **Krasilnikovozyma** gen. nov. |                               |          |           |
| K. huenpiii comb. nov.      | Candida huenpii               | CBS 8186T | AF189844  |
| C. huenpii                  | Mrakia curviuscula            |          |           |
| K. tahquamenonensis comb. nov. | C. tahquamenonensis          | CBS 13897T | KM408125  |
| **Mrakia** emend.           |                               |          |           |
| M. aquatica comb. nov.      | Mrakia aquatica               | CBS 5443T | AF075470  |
| M. biolitopsis             |                               | CBS 8921T | AY038814  |
| M. cryonitii comb. nov.     | M. cryonitii                  | CBS 10834T | GQ911524 |
| M. frigida                  | Leucosporidium frigidum       | CBS 5270T | AF075463  |
| M. gelida                   | L. gelidum                    | CBS 5272T | AF189831  |
| M. nicombssii comb. nov.    | M. nicombssii                | CBS 8917T | AY029345  |
| M. psychrophila             |                               | CBS 10828T | EU224266 |
| M. robertii                 |                               | CBS 8912T | AY038811  |
| **Phaffia** emend.          |                               |          |           |
| P. rhodozyma                | Xanthophyllomyces             | CBS 5905T | AF189871  |
| T. pamirica                 |                               | CBS 8428T | EF118825  |
| T. pullulans comb. nov.     | Guehomyces pullulans          | CBS 2532T | EF551318  |
| **Udeniomyces**             |                               |          |           |
| U. kanasensis               |                               | CBS 12488T | JQ002681 |
| U. megalosporus             |                               | CBS 7236T | AF075510  |
| U. puniceus                 |                               | CBS 5689T | AF075519  |
| U. pyricola                 |                               | CBS 6754T | AF075507  |
| **Filobasidiales**          |                               |          |           |
| **Filobasidiaceae** emend.  |                               |          |           |
| F. chernovii comb. nov.     | C. chernovii                  | CBS 8679T | AF181530  |
| F. elegans                  |                               | CBS 7640FXT | AF181548 |
| F. floriforme               |                               | CBS 6241FXT | AF075498 |
| F. globisporum             |                               | CBS 7642FXT | AF075495 |
| F. magnus comb. nov.        | C. magnus                     | CBS 140T  | AF181551  |
| F. oeirensis comb. nov.     | C. oeirensis                  | CBS 8681T | AF181519  |
| F. stepposus comb. nov.     | C. stepposus                  | CBS 10265T | DQ222456 |
| F. uniguttulatum            |                               | CBS 1730T | AF075468  |
| F. wieringae comb. nov.     | C. wieringae                  | CBS 1937T | AF181541  |

(continued on next page)
| Taxon | Basionym or important synonym | Strain | LSU D1D2 |
|-------|--------------------------------|--------|----------|
| **Goffeauzyma** gen. nov. | | | |
| G. aciditolerans comb. nov. | Cryptococcus aciditolerans | CBS 10872<sup>T</sup> | AY731790 |
| G. agrionensis comb. nov. | C. agrionensis | CBS 10799<sup>T</sup> | EU627786 |
| G. gastricus<sup>3</sup> comb. nov. | C. gastricus | CBS 2288<sup>T</sup> | AF137600 |
| G. golovkinae comb. nov. | C. golovkinae | CBS 7525<sup>T</sup> | AF181547 |
| G. ibericus comb. nov. | C. ibericus | CBS 10871<sup>T</sup> | AY731791 |
| G. metallitolerans comb. nov. | C. metallitolerans | CBS 10873<sup>T</sup> | AY731789 |
| **Heterocephalacria** emend. | | | |
| H. arrabidensis comb. nov. | C. arrabidensis | CBS 8678<sup>T</sup> | AF181535 |
| H. bachmannii comb. nov. | Syzygospora bachmannii | AM72 | JN043613 |
| H. physciacearum comb. nov. | S. physciacearum | AM17 | JN043614 |
| H. solidoides comb. nov. | S. solidoides | CBS 10505T | FJ473376 |
| **Naganishia** emend. | | | |
| N. adellensis comb. nov. | C. adellensis | CBS 8351<sup>T</sup> | AF137603 |
| N. albida comb. nov. | C. albida | CBS 142<sup>T</sup> | AF075474 |
| N. albidosimilis comb. nov. | C. albidosimilis | CBS 7711<sup>T</sup> | AF137601 |
| N. antarctica comb. nov. | C. antarctica | CBS 7687<sup>T</sup> | AF075488 |
| N. bhutanensis comb. nov. | C. bhutanensis | CBS 6294<sup>T</sup> | AF137599 |
| N. cerealis comb. nov. | C. cerealis | CBS 10505<sup>T</sup> | FJ473376 |
| N. diffuens comb. nov. | C. diffuens | CBS 160<sup>T</sup> | AF075502 |
| N. friedmannii comb. nov. | C. friedmannii | CBS 7160<sup>T</sup> | AF075478 |
| N. globosa<sup>T</sup> | C. saitoi | CBS 5106<sup>T</sup> | AF181539 |
| N. liquefaciens comb. nov. | C. liquefaciens | CBS 968<sup>T</sup> | AF181515 |
| N. onofrii comb. nov. | C. onofrii | DBVPG 5303<sup>T</sup> | KC433831 |
| N. randhawai comb. nov. | C. randhawai | CBS 10160<sup>T</sup> | AJ876599 |
| N. uzbekistanensis comb. nov. | C. uzbekistanensis | CBS 8683<sup>T</sup> | AF181508 |
| N. vaughanmartiniæ comb. nov. | C. vaughanmartiniæ | DBVPG4736<sup>T</sup> | KF861779 |
| N. vishniacii comb. nov. | C. vishniacii | CBS 7110<sup>T</sup> | AF075473 |
| **Syzygospora** | | | |
| S. alba<sup>T</sup> | AM147 | JN043616 |
| S. pallida | FO31621 | AJ406403 |
| **Piskurozymaceae** fam. nov. | | | |
| **Piskurozyma** gen. nov. | | | |
| P. capsuligenum comb. nov. | Filobasidium capsuligenum | CBS 1906<sup>T</sup> | AF363642 |
| P. cylindricus<sup>3</sup> comb. nov. | C. cylindricus<sup>T</sup> | CBS 8680<sup>T</sup> | AF181534 |
| P. fidesensis comb. nov. | C. fidesensis | CBS12705 | KC694161 |
| P. filicatus comb. nov. | C. filicatus | CBS 10874<sup>T</sup> | EU433983 |
| P. silvicola comb. nov. | C. silvicola | CBS 10099<sup>T</sup> | AY989955 |
| P. sorana comb. nov. | S. sorana | UBC_F16310 | EU541305 |
| P. taiwanensis comb. nov. | Bullera taiwanensis | CBS 9813<sup>T</sup> | AB079065 |
| **Solicoccozyma** gen. nov. | | | |
| S. aeros<sup>T</sup> comb. nov. | C. aeros | CBS 155<sup>T</sup> | AF075486 |
| S. fusescens comb. nov. | C. fusescens | CBS 7189<sup>T</sup> | AF075472 |
| S. keelungensis comb. nov. | C. keelungensis | CBS 10876<sup>T</sup> | EF621562 |
| S. phenolicus comb. nov. | C. phenolicus | CBS 8682<sup>T</sup> | AF181523 |
| S. terreus comb. nov. | C. terreus | CBS 1895<sup>T</sup> | AF075479 |
| S. terricola comb. nov. | C. terricola | CBS 4517<sup>T</sup> | AF181520 |
### Table 1. (Continued).

| Taxon | Basionym or important synonym | Strain | LSU D1D2 |
|-------|--------------------------------|--------|----------|
| **Holtermanniales** | | | |
| *Holtermannia* | | | |
| *H. corniformis* | CBS 6979<sup>T</sup> | AF189843 |
| *Holtermanniella* | | | |
| *H. festuca* | Cryptococcus festuca<sup>a</sup> | CBS 10162<sup>T</sup> | AY462119 |
| *H. mycelialis* | C. mycelialis | CBS 7712<sup>T</sup> | AJ311450 |
| *H. nyarowii* | C. nyarowii | CBS 8804<sup>T</sup> | AY006480 |
| *H. takashimae*<sup>b</sup> | | | |
| *H. wattica* | C. wattica | CBS 9496<sup>T</sup> | AY138478 |
| **Tremellales** | | | |
| *Bulleraceae* fam. nov. | | | |
| *Bullera* emend. | | | |
| *B. alba*<sup>c</sup> | B. albus | CBS 501<sup>T</sup> | AF075500 |
| *B. hannae* | CBS 8286<sup>T</sup> | AF363961 |
| *B. pennisetica* | CBS 8623<sup>T</sup> | AF363949 |
| *B. unica* | CBS 8290<sup>T</sup> | AF075524 |
| *Fonsecazyma* gen. nov. | | | |
| *F. betulae* comb. nov. | Kwoniella betulae | CBS 13896<sup>T</sup> | KM408130 |
| *F. mujuensis*<sup>c</sup> comb. nov. | C. mujuensis | CBS 10308<sup>T</sup> | DQ333884 |
| *F. tronadorensis* comb. nov. | C. tronadorensis | CBS 12691<sup>T</sup> | GU560003 |
| *Genolevuria* gen. nov. | | | |
| *G. amylolyticus*<sup>c</sup> comb. nov. | C. amylolyticus | CBS 10048<sup>T</sup> | AY562134 |
| *G. armeniacus* comb. nov. | C. armeniacus | CBS 10050<sup>T</sup> | AY562140 |
| *G. bromeliarum* comb. nov. | C. bromeliarum | CBS 10424<sup>T</sup> | DQ784566 |
| *G. tibetensis* comb. nov. | C. tibetensis | CBS 10456<sup>T</sup> | EF363143 |
| *Pseudotremella* gen. nov. | | | |
| *P. allantoinivorans* comb. nov. | C. allantoinivorans | CBS 9604<sup>T</sup> | AY315662 |
| *P. lacticolor* comb. nov. | C. lacticolor | CBS 10915<sup>T</sup> | AB375775 |
| *P. moriformis*<sup>c</sup> comb. nov. | Tremella moriformis | CBS 7810<sup>T</sup> | AF075493 |
| *P. nivalis* comb. nov. | T. nivalis | CBS 8487<sup>R</sup> | AF02232 |
| **Tremella Clade I** (Millanes et al. 2011) | | | |
| Cryptococcus cuniculi pro tem | CBS 10309<sup>T</sup> | DQ333885 |
| Sirobasidium brebeldianum | AM71 | JN043578 |
| *S. intermedium* | CBS 7805 | AF075492 |
| *Tremella caloplacae* | AM31 | JN043573 |
| *T. candelariellae* | AM34 | JN043575 |
| *T. christiansenii* | AM36 | JN043577 |
| *T. dendrographae* | AM39 | JN043576 |
| *T. exigua* | RB6623-15 | A024248 |
| **Tremella Clade III** (Millanes et al. 2011) | | | |
| Biatoropsis usnearum | Sweden, Hagner s.n. (S-F92134) | JN043592 |
| Tremella cetrariicola | Finland, Suija s.n. (S-F102413) | JN043596 |
| *T. coppinsii* | UK, Diederich 15628 (S-F102414) | JN043601 |
| *T. everniae* | USA, 2005, Kneiper s.n. (S) | JN043599 |
| *T. giraffa* | CBS 8489<sup>R</sup> | AF042271 |
| *T. huuskonenii* | Canada, B.C., Goward 11-50 (UBC), L321S/L321 | KR857095 |
| *T. hypogymniae* | Sweden, Wedin 6892 (UPS) | JN043590 |

(continued on next page)
| Taxon | Basionym or important synonym | Strain | LSU D1D2 |
|-------|-------------------------------|--------|----------|
| _T. lichenicola_ | Germany, John & Diederich s.n. (UPS-256878) | JN043611 |
| _T. pertusariae_ | France, Diederich 16331 (S-F102502) | JN043600 |
| _T. tuckerae_ | Mexico, Tucker 37335 (SBBG) | JN043588 |
| _T. wirthii_ | The Netherlands, 1996, Herb s.n. (herb. Diederich) | JN043598 |
| **Single-species lineages** | | | |
| _Tremella 'indecorata'_ pro tem | AM5 | JN043610 |
| _Tremella haematommatis_ pro tem | AM41 | JN043617 |
| _Tremella ramalinae_ pro tem | Spain, Etayo s.n. (UPS 158799) | JN043619 |

**Bulleribasidiaceae fam. nov.**

**Bulleribasidiurn** emend.

| Name | Basionym | Strain | LSU D1D2 |
|------|----------|--------|----------|
| _B. begoniae_ comb. nov. | _Bullera begoniae_ CBS 10762<sup>T</sup> | AB119462 |
| _B. foliicola_ comb. nov. | _M. foliicola_ CBS 11407<sup>T</sup> | GO438834 |
| _B. hainanense_ comb. nov. | _M. hainanensis_ CBS 11409<sup>T</sup> | GO438828 |
| _B. oberjochense_ | | | |
| _B. panici_ comb. nov. | _B. panici_ CBS 9932<sup>T</sup> | AY188387 |
| _B. pseudovariabile_ comb. nov. | _B. pseudovariabilis_ CBS 9609<sup>T</sup> | AF544247 |
| _B. sanyaense_ comb. nov. | _M. sanyaensis_ CBS 11408<sup>T</sup> | GO438831 |
| _B. setariae_ comb. nov. | _B. setariae_ CBS 10763<sup>T</sup> | AB119463 |
| _B. siamense_ comb. nov. | _M. siamensis_ CBS 9933<sup>T</sup> | AY188388 |
| _B. variabile_ comb. nov. | _B. variabilis_ CBS 7347<sup>T</sup> | AF189855 |
| _B. wuzhishanense_ comb. nov. | _M. wuzhishanensis_ CBS 11411<sup>T</sup> | GO438830 |

**Dexomyces**

| Name | Basionym | Strain | LSU D1D2 |
|------|----------|--------|----------|
| _D. amylogenes_ | CBS 12233<sup>T</sup> | HQ890372 |
| _D. anomala_ | _B. anomala_ CBS 9607<sup>T</sup> | EF682504 |
| _D. bambusicola_ | CBS 12234<sup>T</sup> | HQ890376 |
| _D. bockhoutii_ | CBS 10824<sup>T</sup> | EU517057 |
| _D. boninensis_ | _B. boninensis_ CBS 9141<sup>T</sup> | AY487568 |
| _D. corylophs_ | CBS 12299<sup>T</sup> | HQ890374 |
| _D. cylindrica_ | _B. cylindrica_ CBS 9744<sup>T</sup> | AY487563 |
| _D. hainanensis_ | CBS 10820<sup>T</sup> | EU517056 |
| _D. hubeiensis_ | _B. hubeiensis_ CBS 9747<sup>T</sup> | AY487566 |
| _D. huiaensis_ | _B. huiaensis_ CBS 8287<sup>T</sup> | AB118870 |
| _D. komagatae_ | _B. komagatae_ CBS 10153<sup>T</sup> | AF544249 |
| _D. linzihiensis_ | CBS 10827<sup>T</sup> | EU517058 |
| _D. mrakii_ | CBS 8288<sup>T</sup> | AB118871 |
| _D. nakasei_ | _B. nakasei_ CBS 9746<sup>T</sup> | AY487564 |
| _D. pseudocylindrica_ | CBS 10826<sup>T</sup> | EU517059 |
| _D. pseudohuiaensis_ | _B. pseudohuiaensis_ CBS 7364<sup>T</sup> | AF544250 |
| _D. pseudoschimicola_ | _B. pseudoschimicola_ CBS 7354<sup>T</sup> | AF416647 |
| _D. qinlingsensis_ | CBS 10818<sup>T</sup> | EU517060 |
| _D. schimicola_ | _B. schimicola_ CBS 9144<sup>T</sup> | AY487570 |
| _D. simaoensis_ | CBS 10822<sup>T</sup> | EU517062 |
| _D. waltii_ | _B. waltii_ CBS 9143<sup>T</sup> | AY487569 |
| _D. wuzhishanensis_ | CBS 10825<sup>T</sup> | EU517063 |
| _D. yunnanensis_ | CBS 10821<sup>T</sup> | EU517064 |

**Dioszegia**

| Name | Basionym | Strain | LSU D1D2 |
|------|----------|--------|----------|
| _D. antarctica_ | CBS 10920<sup>T</sup> | FJ640575 |
| _D. athyri_ | CBS 10119<sup>T</sup> | EU070931 |
| Taxon Basionym or important synonym | Strain | LSU D1D2 |
|------------------------------------------|--------|---------|
| D. aurantiaca | Bullera aurantiaca | CBS 6980<sup>T</sup> | AB104689 |
| D. buhagiarii | CBS 10054<sup>T</sup> | AY562151 |
| D. butyracea | CBS 10122<sup>T</sup> | EU070929 |
| D. catarinonii | CBS 10051<sup>T</sup> | AY562142 |
| D. changbaiensis | CBS 9608<sup>T</sup> | AY242819 |
| D. crocea | B. crocea | CBS 6714<sup>T</sup> | AF075508 |
| D. cryoxerica | CBS 10919<sup>T</sup> | FJ640562 |
| D. fristingersis | CBS 10052<sup>T</sup> | AY562146 |
| D. hungarica | Cryptococcus hungaricus | CBS 4214<sup>T</sup> | AF075503 |
| D. nishinensis | CBS 11844<sup>T</sup> | AB545810 |
| D. statzelliae | CBS 8925<sup>T</sup> | AY029341 |
| D. takashimae | CBS 10053<sup>T</sup> | AY562149 |
| D. xingshanensis | CBS 10120<sup>T</sup> | EU070928 |
| D. zsoltii | CBS 9127<sup>T</sup> | AF544245 |
| Hannaella | | | |
| H. coprosmaensis | B. coprosmae | CBS 6284<sup>T</sup> | AF363660 |
| H. kunmingensis | B. kunmingensis | CBS 8960<sup>T</sup> | AB109558 |
| H. luteola | C. luteolus | CBS 943<sup>T</sup> | AF075482 |
| H. oryzae | B. oryzae | CBS 7194<sup>T</sup> | AF075511 |
| H. pagnoccae | CBS 11142<sup>T</sup> | FJ828959 |
| H. phetchabunensis | CBS 13386<sup>T</sup> | AB922849 |
| H. phyllophila | CBS 13921<sup>T</sup> | AB934929 |
| H. siamensis | CBS 13533<sup>T</sup> | AB922844 |
| H. sinensis | | | |
| H. surugaensis | C. surugaensis | CBS 9426<sup>T</sup> | AB100440 |
| Mielozyma gen. nov. | | | |
| N. formosana comb. nov. | B. formosana | CBS 10306<sup>T</sup> | AB119465 |
| N. melostoma<sup>2</sup> comb. nov. | B. melostoma | CBS 10305<sup>T</sup> | AB119464 |
| Vishniacozyma gen. nov. | | | |
| V. camescens<sup>3</sup> comb. nov. | Torulopsis camescens | CBS 973<sup>T</sup> | AB035054 |
| V. dimennae comb. nov. | C. dimennae | CBS 5770<sup>T</sup> | AF075489 |
| V. foliicola comb. nov. | C. foliicola | CBS 9920<sup>T</sup> | AY557599 |
| V. globispora comb. nov. | B. globispora | CBS 6981<sup>T</sup> | AF075509 |
| V. heimaeyensis comb. nov. | C. heimaeyensis | CBS 8933<sup>T</sup> | DQ000317 |
| V. nebularis comb. nov. | Trimorphomyces nebularis | CBS12283 EU266921 |
| V. peneaus comb. nov. | Rhodotorula peneaus | CBS 2409<sup>T</sup> | AB035051 |
| V. psychrotolerans comb. nov. | C. psychrotolerans | CBS 12690<sup>T</sup> | JN193445 |
| V. taibaiensis comb. nov. | C. taibaiensis | CBS 9919<sup>T</sup> | AY557601 |
| V. tephrensis comb. nov. | C. tephrensis | CBS 8935<sup>T</sup> | DQ000318 |
| V. victoriae comb. nov. | C. victoriae | CBS 8685<sup>T</sup> | AF363647 |
| Carcinomycetaceae emend. | | | |
| Carcinomycetes emend. | | | |
| C. arundinariae comb. nov. | B. arundinariae | CBS 9931<sup>T</sup> | AF547661 |
| C. effibulatus<sup>1</sup> | Syzygospora effibulata | AM6 | JN043605 |
| C. polyporinus comb. nov. | Tremella polyporina | AM20 | JN043607 |
| Tremella Clade II (Millanes et al. 2011) | | | |
| Tremella cladoniae | | AM125 | JN043583 |

(continued on next page)
| Taxon                  | Basionym or important synonym | Strain       | LSU D1D2 |
|-----------------------|-------------------------------|--------------|----------|
| T. leptogii           |                               | AM81 JN043582|          |
| T. lobariacearum      |                               | AM80 JN043579|          |
| T. nephromatis        |                               | AM133 JN043581|         |
| T. phaeophysciae      |                               | AM98 JN043585|          |
| **Cryptococcaceae**   |                               |              |          |
| **Cryptococcus**      |                               |              |          |
| C. amylolentus        | Candida amylolenta            | CBS 6039⁷    | AF105391 |
| C. bacillisporus      | F. bacillispora               | CBS 6955⁷    | JN939485 |
| C. deneoformans       | F. neoformans                 | CBS 6900⁷    |          |
| C. depauperatus comb. nov. | F. depauperata               | CBS 7841⁷    | FJ534911 |
| C. gattii             | CBS 6289⁷                     | AF075526     |          |
| C. luteus comb. nov.  | F. lutea                      | CBS 8710⁷    | FJ534909 |
| C. tetratigii         | CBS 10101⁷                    |              |          |
| **Kwoniella**         |                               |              |          |
| K. bestiolae comb. nov. | C. bestiolae                 | CBS 10118⁷   | FJ534903 |
| K. botswanaensis      | CBS 12716⁷                   | HF545769     |          |
| K. dejecticola comb. nov. | C. dejecticola               | CBS 10117⁷   | AY917102 |
| K. dendrophila comb. nov. | Bullera dendrophila          | CBS 6074⁴    | AF189670 |
| K. europaea           | CBS 12714⁷                   | AY167602     |          |
| K. heveanensis        | C. heveanensis               | CBS 569⁷     | AF075467 |
| K. mangroviensis⁷     | CBS 8507⁷                    | AF444742     |          |
| K. newhampshirensensis | CBS 13917⁷                   | KM408127     |          |
| K. pinus comb. nov.   | C. pinus                     | CBS 10737⁷   | EF672245 |
| K. shandongensis      | CBS 12478⁷                   | JN160602     |          |
| K. shivaijii comb. nov. | C. shivaijii               | CBS 11374⁷   | FM212446 |
| **Cuniculitremaceae** |                               |              |          |
| **Fellomyces**        |                               |              |          |
| F. borneensis         | CBS 8282⁷                    | AF189877     |          |
| F. horovitziae        | CBS 7515⁷                    | AF189856     |          |
| F. pericillatus       | CBS 5492⁷                    | AF177405     |          |
| F. polyborus¹         | CBS 6072⁷                    | AF189859     |          |
| **Kockovaella**       |                               |              |          |
| K. barringtoniae      | CBS 9811⁷                    | AB292854     |          |
| K. calophylli         | CBS 8962⁷                    | AB292852     |          |
| K. chinensis comb. nov. | Fellomyces chinensis       | CBS 8278⁷    | AF189878 |
| K. cucphuongensis     | CBS 8959⁷                    | AB292853     |          |
| K. distylii comb. nov. | F. distylii                 | CBS 8545⁷    | AF363652 |
| K. fuzhouensis comb. nov. | F. fuzhouensis     | CBS 8243⁷    | AF363659 |
| K. imperatae          | CBS 7554⁷                    | AF189862     |          |
| K. lichenicola comb. nov. | F. lichenicola            | CBS 8315⁷    | AF363643 |
| K. litseae            | CBS 8964⁷                    | AB292850     |          |
| K. machilophila       | CBS 8607⁷                    | AF363654     |          |
| K. mexicanus comb. nov. | F. mexicanus               | CBS 8279⁷    | AJ627906 |
| Taxon                                      | Basionym or important synonym       | Strain                  | LSU D1D2   |
|-------------------------------------------|-------------------------------------|-------------------------|------------|
| K. ogasawarensis comb. nov.               | Fellomyces ogasawarensis            | CBS 8544^T              | AF363651   |
| K. phaffi                                 | CBS 8608^T                          |                         | AF363655   |
| K. prillingeri sp. nov.                   | F. thailandicus                     | CBS 8308^T              | AF363644   |
| K. sacchari                               | CBS 8624^T                          |                         | AF363650   |
| K. schimae                                | CBS 8610^T                          |                         | AF363656   |
| K. sichuanensis comb. nov.                | F. sichuanensis                     | CBS 8318^T              | AF189879   |
| K. thailandica^T                         | CBS 7552^T                          |                         | AF075516   |
| K. vietnamensis                          | CBS 8963^T                          |                         | AB292651   |
| Sterigmatosporidium                      | Cuniculitrema                       |                         |            |
| S. polymorphum^T                         | C. polymorpha                       | CBS 9644^T              | AY032662   |
| Naemateliaceae fam. nov.                  |                                     |                         |            |
| Dimennzyma gen. nov.                      |                                     |                         |            |
| D. cistialbidi^T comb. nov.               | Cryptococcus cistialbidi             | CBS 10049^T             | AY562135   |
| Naematelia                                |                                     |                         |            |
| N. aurantia                               | Tremella aurantia                   | CBS 6965^T              | AF189842   |
| N. aurantialba comb. nov.                 | T. aurantalba                       | strain9102              | EF010939   |
| N. encephala^T                           | T. encephala                        | CBS 8207^T              | AF042220   |
| N. microspora comb. nov.                  | T. microspora                       | BPI702328               | AF042253   |
| Single-species lineage                    |                                     |                         |            |
| Tremella 'decorata' II pro tem.           |                                     | CBS 6976^T              | AF042250   |
| Phaeotremellaceae fam. nov.               |                                     |                         |            |
| Gelidatrema gen. nov.                     |                                     |                         |            |
| G. spencermartiniiae^T comb. nov.         | C. spencermartiniiae                | CBS 10760^T             | DQ513279   |
| Phaeotrema emend.                         |                                     |                         |            |
| P. fagi comb. nov.                        | C. fagi                             | CBS 9964^T              | DQ054535   |
| P. mycetophiloides comb. nov.             | T. mycetophiloides                  | AM23                    | JN43608    |
| P. mycophaga comb. nov.                   | T. mycophaga                        | R86539-4                | AF042249   |
| P. neofolacea comb. nov.                  | T. neofolacea                       | CBS 8475^T              | AF042236   |
| P. pseudofolacea^T                       | T. foliacea                         | CBS 6969^P              | AF189868   |
| P. simplex comb. nov.                     | T. simplex                          | FO31782                 | AF042246   |
| P. skineri comb. nov.                     | C. skineri                          | CBS 5029^T              | AF189835   |
| Rhynchogastremaceae emend.                |                                     |                         |            |
| Papiliotrema emend.                       |                                     |                         |            |
| P. anemochoreus comb. nov.                | C. anemochoreus                     | CBS 10258^T             | DQ384929   |
| P. aspenensis comb. nov.                  | C. aspenensis                       | CBS 13867^T             | KC485500   |
| P. aureus comb. nov.                      | Torula aurea                        | CBS 318^T               | AB035041   |
| P. baii comb. nov.                        | C. bai                              | PYCC 6523^T             | LK023766   |
| P. bandeiri^T                             | CBS 9107^T                          |                         | AF146642   |
| P. flavescens comb. nov.                  | T. flavescens                       | CBS 942^T               | AB035042   |
| P. fonseca comb. nov.                     | C. fonseca                          | CBS 12692^T             | JN193447   |
| P. frias comb. nov.                       | C. frias                            | CBS 12693^T             | LK023834   |
| P. fuscus comb. nov.                      | Auriculibulla fuscus                 | CBS 9648                | AF444763   |
| P. hoabinhensis comb. nov.                | Bullera hoabinhensis                | JCM 10835^T             | AB193347   |
| P. japonica comb. nov.                    | B. japonica                         | CBS 2013^T              | AF444760   |
| P. laurentii comb. nov.                   | C. laurentii                        | CBS 139^T               | AF075469   |
| P. mangaliensis comb. nov.                | C. mangaliensis                     | CBS 10870^T             | FJ008046   |
| P. nemorosus comb. nov.                   | C. nemorosus                        | CBS 9606^T              | AF472625   |

(continued on next page)
| Taxon                                      | Basionym or important synonym | Strain       | LSU D1D2   |
|-------------------------------------------|-------------------------------|--------------|------------|
| *P. perniciosus* comb. nov. | Cryptococcus perniciosus     | CBS 9605 †  | AF472624  |
| *P. pseudoalba* comb. nov.               | Bullera pseudoalba           | CBS 7227 †  | AF075504  |
| *P. rajasthanensis* comb. nov.           | C. rajasthanensis           | CBS 10406 † | AM262324  |
| *P. ruineniae* comb. nov.                | C. ruineniae                 | PYCC 6170 † | LK023764  |
| *P. siamense*                            |                               | CBS 13330 † | AB909023  |
| *P. taeanensis* comb. nov.               | C. taeanensis                | CBS 9742 †  | AY422719  |
| *P. terrestris* comb. nov.               | C. terrestris                | CBS 10810 † | EF370393  |
| *P. wicconensis* comb. nov.              | C. wicconensis               | CBS 13895 † | KM408131  |

**Rhynchogastrema** emend.

| Taxon                                      | Basionym or important synonym | Strain       | LSU D1D2   |
|-------------------------------------------|-------------------------------|--------------|------------|
| *R. aquatica* comb. nov.                  | Bandoniozyma aquatica        | CBS 12527 † | JN979992  |
| *R. complexa* comb. nov.                  | B. complexa                  | CBS 11570 † | GU321090  |
| *R. coronatum*                           |                               | BBA 65155 † | KJ170152  |
| *R. fermentans* comb. nov.                | B. fermentans                | CBS 12399 † | HM461720  |
| *R. glucofermentans* comb. nov.           | B. glucofermentans           | CBS 10381 † | AY520334  |
| *R. nanyangensis* comb. nov.              | C. nanyangensis              | CBS 12474 † | JN564592  |
| *R. nouii* comb. nov.                     | B. nouii                     | CBS 8364 †  | AF444700  |
| *R. tunnelae* comb. nov.                  | B. tunnelae                  | CBS 6123 †  | AF444887  |
| *R. visegradiensis* comb. nov.            | B. visegradiensis            | CBS 12505 † | GU196568  |

**Sirobasidiaceae**

| Taxon                                      | Basionym or important synonym | Strain       | LSU D1D2   |
|-------------------------------------------|-------------------------------|--------------|------------|
| *F. inconspicuum*                         |                               | CBS 8237 †  | AF363641  |
| *F. murnhardtense*                        |                               | CBS 9109 †  | AF416648  |
| *F. sirobasioides*                        |                               | RJB12767     | AF416644  |

**Trimorphomycetaceae** fam. nov.

| Taxon                                      | Basionym or important synonym | Strain       | LSU D1D2   |
|-------------------------------------------|-------------------------------|--------------|------------|
| *T. brasiliensis*                         |                               | CBS 6966 †  | AF189864  |
| *T. cinnabarina*                         |                               | CBS 8234 †  | AF189866  |
| *T. coalescens*                          |                               | CBS 6967 †  | AF189865  |
| *T. flavus*                               |                               | CBS 8471 †  | AF042221  |
| *T. fusiformis*                           |                               | CBS 6970 †  | AF075476  |
| *T. globispora*                           |                               | CBS 6972 †  | AF189869  |
| *T. laurisalvae*                          | TFC Mic.24580                |              |            |
| *T. mesenterica*                          |                               | CBS 6973 †  | AF075518  |
| *T. resupinata*                           |                               | CBS 8488 †  | AF042239  |
| *T. taiwanensis*                          |                               | CBS 8479 †  | AF042230  |
| *T. tropica*                              |                               | CBS 8483 †  | AF042251  |
| *T. yokohamensis* comb. nov.              | C. yokohamensis              | JCM 16989 † | HM222927  |

**Carlosroseaec gen. nov.**

| Taxon                                      | Basionym or important synonym | Strain       | LSU D1D2   |
|-------------------------------------------|-------------------------------|--------------|------------|
| *C. vrieseae* comb. nov.                  | B. vrieseae                  | CBS 13870 † | JX280388  |

**Saitozyma** gen. nov.

| Taxon                                      | Basionym or important synonym | Strain       | LSU D1D2   |
|-------------------------------------------|-------------------------------|--------------|------------|
| *S. flavus* comb. nov.                    | C. flavus                    | CBS 331 †   | AF075497  |
| *S. ninbinbensis* comb. nov.              | B. ninbinbensis              | JCM 10836 † | AB261011  |
| *S. paraflava* comb. nov.                 | C. paraflava                 | CBS 10100 † | AY395799  |
| *S. podzolicia* comb. nov.                | C. podzolicia                | CBS 6819 †  | AF075481  |
| Taxon                          | Basionym or important synonym | Strain          | LSU D1D2   |
|-------------------------------|-------------------------------|-----------------|------------|
| **Sugitazyma** gen. nov.      |                               |                 |            |
| *S. miyagiana*\(^\d\) comb. nov. | *Bullera miyagiana*           | CBS 7526\(^T\) | AF189858   |
| **Trimorphomycetes** emend.   |                               |                 |            |
| *T. papilionaceus*\(^T\)     |                               | CBS 443.92      | AF075491   |
| *T. sakaeratica* comb. nov.   | *B. sakaeratica*              | CBS 9934\(^T\) | AY211546   |
| **Incertae sedis**            |                               |                 |            |
| *Tremella diploschistina* pro tem. |                           | AM199\(^T\)  | JN700588   |
| *Tremella pammellarum* pro tem. |                             | Spain, Diederich 16574 / (S-F102497) | JN043618 |
| **Trichosporonales**          |                               |                 |            |
| **Tetragoniomyctaceae** emend. |                               |                 |            |
| *Bandonia* gen. nov.          |                               |                 |            |
| *B. marina*\(^T\) comb. nov. | *Cryptococcus marinus*        | CBS 5235\(^T\) | AF189846   |
| **Cryptotrichosporon**        |                               |                 |            |
| *C. anacardi*\(^T\)          |                               | CBS 9551\(^T\) | AY550002   |
| *C. tibetense*               |                               | CBS 10455\(^T\) | K0020115   |
| **Takashimella**              |                               |                 |            |
| *T. formosensis*\(^T\)       | *B. formosensis*              | CBS 9812\(^T\) | AY787858   |
| *T. koratensis*              | *B. koratensis*               | CBS 10484\(^T\) | AY313006   |
| *T. lagerstroemiae*          | *B. lagerstroemiae*           | CBS 10483\(^T\) | AY313010   |
| *T. tepidarius*              | *C. tepidarius*               | CBS 9427\(^T\) | A0904046   |
| **Tetragoniomyces**           |                               |                 |            |
| *T. uliginosus*\(^T\)        | *Tremella uliginosa*          | AM186           | JN043621   |
| **Trichosporonaceae** emend.  |                               |                 |            |
| **Apiotrichum** emend.        |                               |                 |            |
| *A. brassicae* comb. nov.     | *Trichosporon brassicae*      | CBS 6382\(^T\) | AF075521   |
| *A. cacaoliposimilis* comb. nov. | *T. cacaoliposimilis*       | ATCC 20505\(^T\) | HM755978  |
| *A. dehoogii* comb. nov.      | *T. dehoogii*                 | CBS 8688\(^T\) | AF444718   |
| *A. domesticum* comb. nov.    | *T. domesticum*               | CBS 8280\(^T\) | AF075512   |
| *A. dulcitum* comb. nov.      | *Oospora dulcita*             | CBS 8257\(^T\) | AF075517   |
| *A. gamsii* comb. nov.        | *T. gamsii*                   | CBS 8245\(^T\) | AF444708   |
| *A. gracile* comb. nov.       | *Oidium gracile*              | CBS 8189\(^T\) | A053999    |
| *A. laibachii* comb. nov.     | *Endomyces laibachii*         | CBS 5790\(^T\) | AF075514   |
| *A. lignicola* comb. nov.     | *Hyalodendron lignicola*      | CBS 219.34\(^T\) | AY370685  |
| *A. loubieri* comb. nov.      | *Geotrichum loubieri*         | CBS 7065\(^T\) | AF075522   |
| *A. montevideense* comb. nov. | *Endomyccopsis montevideensis* | CBS 6721\(^T\) | AF105397   |
| *A. mycotoxinivorans* comb. nov. | *T. mycotoxinivorans*   | CBS 9756\(^T\) | A0601388   |
| *A. porosum*\(^T\)           | *T. porosum*                  | CBS 2040\(^T\) | AF189833   |
| *A. scarabaeorum* comb. nov.  | *T. scarabaeorum*             | CBS 5601\(^T\) | AF444710   |
| *A. siamense* comb. nov.      | *T. siamense*                 | JCM 12478\(^T\) | A0164370   |
| *A. sporotrichoides* comb. nov. | *T. sporotrichoides*         | CBS 8246\(^T\) | AF189885   |
| *A. vadense* comb. nov.       | *T. vadense*                  | CBS 8901\(^T\) | A093426    |
| *A. veenhuisii* comb. nov.    | *T. veenhuisii*               | CBS 7136\(^T\) | A054000    |
| *A. wieringae* comb. nov.     | *T. wieringae*                | CBS 8903\(^T\) | A0315666   |

(continued on next page)
| Taxon | Basionym or important synonym | Strain | LSU D1D2 |
|-------|------------------------------|--------|----------|
| A. xylopini comb. nov. | Trichosporon xylopini | CBS 11841<sup>T</sup> | HQ005757 |
| **Cutaneotrichosporon** gen. nov. |  |
| C. arboriformis comb. nov. | Cryptococcus arboriformis | CBS 10441<sup>T</sup> | AB260936 |
| C. curvatus comb. nov. | C. curvatus | CBS 570<sup>T</sup> | AF189834 |
| C. cutaneum<sup>2</sup> comb. nov. | Oidium cutaneum T. cutaneum | CBS 2466<sup>T</sup> | AF075483 |
| C. cyanovorans comb. nov. | C. cyanovorans | CBS 11948<sup>T</sup> | JF680899 |
| C. daszewskiae comb. nov. | C. daszewskiae | CBS 5123<sup>T</sup> | AB126588 |
| C. debeurmannianum comb. nov. | T. debeurmannianum | CBS 1896<sup>T</sup> | AY143554 |
| C. dermatis comb. nov. | T. dermatis | CBS 2043<sup>T</sup> | AY143555 |
| C. guelhoae comb. nov. | T. guelhoae | CBS 8521<sup>T</sup> | AF105401 |
| C. hagleorum comb. nov. | C. hagleorum | CBS 8902<sup>T</sup> | AF407276 |
| C. jirovecii comb. nov. | T. jirovecii | CBS 6864<sup>T</sup> | AY103598 |
| C. moniliiforme comb. nov. | O. moniliiforme T. moniliiforme | CBS 2467<sup>T</sup> | AY103592 |
| C. mucoides comb. nov. | T. mucoides | CBS 7625<sup>T</sup> | AF075515 |
| C. oleaginosus comb. nov. | T. oleaginosus ATCC 20509<sup>T</sup> | HM602135 |
| C. smithiae comb. nov. | T. smithiae | CBS 8370<sup>T</sup> | AF444706 |
| C. terricola comb. nov. | T. terricola | CBS 9546<sup>T</sup> | AB086382 |
| **Effuseotrichosporon** gen. nov. |  |
| E. vanderwaltii comb. nov. | T. vanderwaltii | CBS 12124<sup>T</sup> | JF680903 |
| **Haglerozyma** gen. nov. |  |
| H. chiarelli<sup>2</sup> comb. nov. | T. chiarelli | CBS 11177<sup>T</sup> | EU030272 |
| **Trichosporon** |  |
| T. aquatile | CBS 5973<sup>T</sup> | AF075520 |
| T. asahii | CBS 2479<sup>T</sup> | AF105393 |
| T. asteroides | CBS 2481<sup>T</sup> | AF075513 |
| T. caseorum | CBS 9052<sup>T</sup> | AJ319757 |
| T. coremiiforme | CBS 2482<sup>T</sup> | AF139983 |
| T. dohaense | CBS 10761<sup>T</sup> | FJ228471 |
| T. faecale | CBS 4828<sup>T</sup> | AF105395 |
| T. inkin | CBS 5585<sup>T</sup> | AF105396 |
| T. insectorum | CBS 10422<sup>T</sup> | AY520383 |
| T. japonicum | CBS 8641<sup>T</sup> | AF308657 |
| T. lactis | CBS 9051<sup>T</sup> | AJ319756 |
| T. ovoides<sup>7</sup> | CBS 7596<sup>T</sup> | AF075523 |
| **Vanrija** |  |
| V. albida | Sporotrichum albida | CBS 2839<sup>T</sup> | AB126564 |
| V. fragicolae comb. nov. | C. fragicolae | CBS 8898<sup>T</sup> | AB126585 |
| V. humicola<sup>9</sup> | Torula humicola | CBS 571<sup>T</sup> | AF189836 |
| V. longa | C. longus | CBS 5920<sup>T</sup> | AB126569 |
| V. meifongana comb. nov. | Asterotremella meifongana | CBS 11424<sup>T</sup> | EU289356 |
| V. musci | C. musci | CBS 8899<sup>T</sup> | AB126586 |
| V. nantouana comb. nov. | Asterotremella nantouana | CBS 10890<sup>T</sup> | EF653952 |
| V. pseudolongus | C. pseudolongus | CBS 8297<sup>T</sup> | AB126587 |
| V. thermophilia comb. nov. | C. thermophilia | CBS 10687<sup>T</sup> | AM746982 |
Table 2. PRBO results showing the divergences, if any, of the proposed taxa (except for the families) from the optimal range of divergences for their rank as inferred from the selected reference taxa.

| Taxa                          | Rank     | MaSH        | Deviation | Sigdev |
|-------------------------------|----------|-------------|-----------|--------|
| Cystofilobasidiales           | Order    | 0.7211      | -0.1226   | 0      |
| Cystofilobasidium*            | Genus    | 0.2518      | 0         | 0      |
| Krasnilkovozyma (huempi clade)| Genus    | 0.0003      | 0         | 0      |
| Itersonia*                   | Genus    | 0.0672      | 0         | 0      |
| Mrakia*                      | Genus    | 0.2071      | 0         | 0      |
| Phaffia                      | Genus    | 0.1028      | 0         | 0      |
| Tausonia                     | Genus    | –           | –         | –      |
| Udeniomyces*                 | Genus    | 0.1326      | 0         | 0      |
| Filobasidiales               | Order    | 0.5866      | -0.2570   | -0.1242|
| Filobasidium                 | Genus    | 0.2465      | 0         | 0      |
| Naganishia (albidus clade)    | Genus    | 0.1835      | 0         | 0      |
| Goffeauzymy (gastricus clade)| Genus    | 0.3281      | 0         | 0      |
| Sollicocczyma (aenius clade)  | Genus    | 0.2537      | 0         | 0      |
| Piakurozyma (cylindricus clade)| Genus | 0.1235      | 0         | 0      |
| Cryptococcus arrabidensis    | Genus    | –           | –         | –      |
| Filobasidium capsuligerum    | Genus    | –           | –         | –      |
| Holtermanniales              | Order    | 0.4607      | 0         | 0      |
| Holtermannia*                | Genus    | 0.1832      | 0         | 0      |
| Holtermannia                 | Genus    | –           | –         | –      |
| Tremellales                  | Order    | 0.9475      | 0         | 0      |
| Naemastelia (aurantia clade and C. cistialbidii)| Genus | 0.3098 | 0 | 0 |
| Rhynchogastrema              | Genus    | 0.1336      | 0         | 0      |
| Bullenbasidium*              | Genus    | 0.3380      | 0         | 0      |
| Bullera (Bullera and hannaec clades)| Genus | 0.4009 | 0.0597 | 0.0476|
| Cryptococcus                 | Genus    | 0.2325      | 0         | 0      |
| Dexomyces*                   | Genus    | 0.6263      | 0.2851    | 0.2730 |
| Dioszegia*                   | Genus    | 0.3296      | 0         | 0      |
| Genolevuaria (amyloyticus clade)| Genus | 0.1985 | 0 | 0 |
| Filomyces                    | Genus    | 0.3096      | 0         | 0      |
| Fibulobasidium*              | Genus    | 0.0971      | 0         | 0      |
| Phaeotremella (fiblcea clade)| Genus    | 0.2697      | 0         | 0      |
| Hannaela*                    | Genus    | 0.2876      | 0         | 0      |
| Kockovaella                  | Genus    | 0.3573      | 0.0161    | 0.0040 |
| Kwoniuella                   | Genus    | 0.3335      | 0         | 0      |
| Papiliotrema (areus, Auriculibul, Papiliotrema, pseuodba, lauertini clades)| Genus | 0.3345 | 0 | 0 |
| Pseudotremella (morformis clade and C. allantoinivorans)| Genus | 0.2068 | 0 | 0 |
| C. mujensis and S. intermedium| Genus | 0.2123 | 0 | 0 |
| Saltzyma (flavus clade)       | Genus    | 0.3187      | 0         | 0      |
| Nieolzyma (melastomae clade)  | Genus    | 0.1478      | 0         | 0      |
| Tremella                     | Genus    | 0.4809      | 0.1397    | 0.1276 |
| Vishniacozyma (dimennae clade)| Genus    | 0.3674      | 0.0262    | 0.0141 |

Table 2. (Continued).

| Taxa                          | Rank     | MaSH        | Deviation | Sigdev |
|-------------------------------|----------|-------------|-----------|--------|
| Trichosporaloneles            | Order    | 0.4386      | -0.4050   | -0.2722|
| Cutaneotrichosporon (cutaneeum clade and haglerorum clade)| Genus | 0.2107 | 0 | 0 |
| Takashimella (formosensis clade)| Genus | 0.1490 | 0 | 0 |
| Apatrichium (gracle/brassicaceae and Genus 0.2377 | 0 | 0 |
| Porosum clade)                | Genus    | 0.2250      | 0         | 0      |
| Vanrijia (humicola clade)     | Genus    | 0.1955      | 0         | 0      |
| Cryptotrichosporon            | Genus    | –           | –         | –      |

Note. MaSH: Maximum Subtree Height; Deviation: deviation from the point estimate for the upper (positive value) or lower (negative value) threshold of the rank of the taxon; Sigdev: significant deviation, i.e. a deviation even outside the upper or lower 95% confidence band of the upper or lower threshold, respectively. Zero indicates taxa with the appropriate divergence, negative values indicate taxa that are too small, positive values taxa that are too large. An asterisk (*) indicates the well-established taxa that were used as a reference classification for PRBO. A dash (–) indicates taxa that are monotypic in the investigated sampling, for which MaSH is not calculated. Numbers in bold indicate significant deviation from the range defined by the optimal boundaries calculated for the rank.

A confidence interval was regarded as too large or too small in a strict sense when its MaSH was outside the MaSH range of its rank, and as deviating in even a relaxed sense (i.e. significantly deviating) when its MaSH was not even located within the outer confidence bounds. Ten genera (Table 2) of tremellomycetous yeasts and their parent taxa were chosen as references. These genera are considered as being well delimited phylogenetically and because they were resolved as strongly supported monophyletic clades with stable positions in the trees derived from different datasets using different algorithms (Liu et al. 2015) and the species in each genus exhibit similar morphological or physiological properties. The resulting optimal MaSH thresholds and their 95% confidence intervals were then applied to the entire dataset.

In addition, we used a modified GMYC (generalised mixed Yule coalescent) method designed to identify evolutionary significant units (Humphreys & Barraclough 2014). The GMYC method was originally developed for species delimitation (Pons et al. 2006, Monaghan et al. 2009) and subsequently extended for identifying higher taxonomic units, also called evolutionary significant units without prior expectations, locating independently evolving lineages as a transition from intra- to intertaxa relationships on a phylogenetic tree. It aims at detecting shifts in branching rates between relationships within and among evolutionary significant units. The most recent common ancestral node at the transition point is interpreted as distinguishing taxa at a specific level. Within a likelihood framework it uses chronograms to compare two models: a) a null model under which the whole sample derives from a single evolutionary significant unit and b) an alternative GMYC model. The latter combines equations that separately describe branching patterns within and among evolutionary units. A likelihood ratio test (LRT) is used to evaluate whether the null model can be significantly rejected. If the GMYC model fits the data significantly better than the null model, the threshold T allows estimating the number of evolutionary significant units (to be interpreted as higher taxa) present in the dataset. Outgroup samples were excluded from the dataset using the drop.tip command in ape (Paradis 2006). A
Fig. 1. A taxonomic framework of genera and higher levels in Tremellomycetes based on the seven-genes phylogeny (Liu et al. 2015). The tree backbone is constructed using Bayesian analysis and branch lengths are scaled in terms of expected numbers of nucleotide substitutions per site. The Bayesian posterior probabilities (PP) and bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved. Note: ns, not supported (PP < 0.9 or BP < 50 %); nm, not monophyletic.
RESULTS AND DISCUSSION

Taxonomic units assessed by PRBO and a modified GMYC approach

A taxonomic framework was firstly proposed based on the seven-genes phylogeny (Liu et al. 2015) as shown in Fig. 1, which was the basis for further taxonomic unit assessment and expanded LSU dataset analysis. Based on the PRBO analysis including 286 taxa represented by 294 strains of tremellomycetous yeasts, strong delimitation evidence was found for the orders Cystofilobasidiales, Holtermanniales and Tremellales, which showed no significant deviation from the range defined by the optimal boundaries calculated for their rank (Table 2). The demarcation of orders Filobasidiales and Trichosporonales showed a small negative, significant deviation (Sigdev = –0.1242 and –0.2722, respectively), i.e. these orders were judged too small, most likely because of the overlap between the divergences of taxa of distinct ranks. The recognition of Filobasidiales as a distinct monophyletic lineage in Tremellomycetes is consistent in many studies (Fell et al. 2000, Scorza et al. 2002, Weiss et al. 2004, Hibbett et al. 2007, Boekhout et al. 2011a, Millanes et al. 2011, Liu et al. 2015). Therefore, and for reasons of conservatism we keep it as a single order. The recognition of Trichosporonales remains a matter of debate. Some authors placed this order within Tremellales (Weiss et al. 2004, Hibbett et al. 2007, Millanes et al. 2011), while others accepted it as a sister group to Tremellales (Scorza et al. 2002, Boekhout et al. 2011a, Weiss et al. 2014). The problem was probably caused by the unstable phylogenetic position of the foliacea clade. It appeared as an early branching clade of the Tremellales in the Bayesian tree but posterior probability (PP) support for this positioning was lacking. In the ML and NJ tree, the foliacea clade was branching before the Trichosporonales and the Tremellales lineages with strong to moderate bootstrap support values (data not shown). When the foliacea clade was considered as an independent lineage as implied by the results shown above, the monophyly of both Trichosporonales and Tremellales was resolved by Bayesian and ML analyses of a seven-genes dataset with 1.0 posterior probability and 100 % bootstrap support (Liu et al. 2015). In the LSU tree the node delimiting Tremellales was not originally constrained and received poor to moderate support in ML and MP analyses, respectively, while other nodes in Tremellales received lower support (Fig. 2). This implies that undersampling may substantially influence the delimitation of clades, and, therefore, we presently consider Trichosporonales as a distinct order based on its phylogenetic position and phenotypic characters.

Ten genera or clades of tremellomycetous yeasts which were consistently resolved as monophyletic groups with strong statistical support in the trees constructed using different datasets and algorithms (Liu et al. 2015) were used as references in the PRBO test (Table 2). Six of these genera, Bullerbasidium emend., Derxomyces, Dioszegia, Fibulobasidium, Hannaella and Holtermanniella, have been accepted as well-established genera based on their distinct morphological characters and phylogenetic positions (Bandoni 1979, Wang & Bai 2008, Wang et al. 2011, Wuczkowski et al. 2011). Of the 44 monotypic genera or clades identified in this study based on the multigene phylogeny (Liu et al. 2015), the majority (34 genera) was in agreement with the PRBO results (Table 2). Five genera showed significant deviation from the optimal range calculated for the genus rank, namely Bullera emend., Derxomyces, Kockovaella emend., Tremella sensu stricto and Vishniacozyma gen. nov. (i.e. the dimennae clade). The emended genus Bullera contains four species that were located in two clades (i.e. Bulleromyces and hannae clades) in Liu et al. (2015). The GC contents of the species in the Bulleromyces and hannae clades are 53.3–55.4 % and 42.7–44.5 %, respectively. These data support the significant deviation of the four species assigned to a single genus. We nevertheless propose to keep them in the
Fig. 2. Phylogenetic relationships of yeasts and related taxa in Tremellomycetes (major lineages) obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu et al. 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. Note: ns, not supported (BP < 50 %).
Table 3. The family identification using single thresholds model in mixed Yule coalescent method (GMYC) and its comparison with the taxonomic units delimited according to phylogeny and morphological characters.

| Order                  | Genus (or single-species clade)          | GMYC ST  | PP/BP<sup>1</sup>/BP<sup>2</sup> | Accepted Genus | PP/BP<sup>1</sup>/BP<sup>2</sup> |
|-----------------------|------------------------------------------|----------|-------------------------------|----------------|----------------------------------|
| **Cystofilobasidiales** | Cystofilobasidium                         | new family 1 | 1.0/100/100                  | Cystofilobasidaceae | 1.0/100/100                      |
|                       | Tausonia                                  | new family 2 | 0.98/ns/nm                    | Mrakia         | 0.98/ns/nm                       |
|                       | Krasinikiovozyma                          |           |                               |                 |                                  |
|                       | Itersonia                                 |           |                               |                 |                                  |
|                       | Mrakia                                    |           |                               |                 |                                  |
|                       | Udeniomyces                               |           |                               |                 |                                  |
|                       | Xanthophyllomyces                         |           |                               |                 |                                  |
| **Filibasidiales**    | Filobasidium capsuligenum                 | new family 3 | 1.0/100/99                   | Filobasidaceae | 1.0/100/95                       |
|                       | Solficocczyma                             | new family 4 | 1.0/100/85                   |                 |                                  |
|                       | Goiffeauzyma                              | new family 5 | 1.0/100/100                  | Filobasidaceae | 1.0/91/85                        |
|                       | Filobasidium                              | new family 6 | 1.0/100/100                  |                 |                                  |
|                       | Fonsecazyma                               | new family 7 | 1.0/100/100                  |                 |                                  |
|                       | Cryptococcus arrabidensis                 | Single-species clade | 1 | | |
| **Tremellales**       | Phaeotremella                             | new family 8 | 1.0/79/ns                   | Phaeotremellaceae | 1.0/79/ns                        |
|                       | C. spencermartinsiae                      |           |                               |                 |                                  |
|                       | Cryptococcus                              | new family 9 | 1.0/100/100                  | Cryptococcaceae | 1.0/100/100                      |
|                       | Kwoniella                                 | new family 10 | 1.0/100/100                |                 |                                  |
|                       | Naematiella                               | new family 11 | ns/ns/ns                 | Naematiaceae | ns/ns/ns                        |
|                       | B. arundinariae                           |           |                               |                 |                                  |
|                       | Rhynchogastrema                           | new family 12 | 1.0/100/100                | Rhynchogastremaceae | 1.0/100/100                      |
|                       | Papilotrema                               | new family 13 | 1.0/100/100                |                 |                                  |
|                       | Bullera                                   | new family 14 | nm/nm/nm                | Bulleraceae | 1.0/96/nm                       |
|                       | Genolevura                                |           |                               |                 |                                  |
|                       | Pseudotremella                            |           |                               |                 |                                  |
|                       | Cryptococcus mujensis, Sirobasidium intermedium, Tremella giraffa | | | | |
|                       | Fibulobasidium                            |           |                               |                 |                                  |
|                       | Sirobasidium magnum                       |           |                               |                 |                                  |
|                       | Fellomyces                                | new family 15 | 1.0/83/99                 | Cuniculitremaece | 1.0/83/99                       |
|                       | Kockovaella                               |           |                               |                 |                                  |
|                       | Cuniculitrema polymorpha                  |           |                               |                 |                                  |
|                       | Tremella                                  | new family 17 | 1.0/100/55                | Tremellaceae | 1.0/100/55                      |
|                       | Saitolzyma                                | new family 18 | 1.0/99/86                | Trimorphomycesae | 1.0/99/86                        |
|                       | Bullera miyagiana, B. sakaeratica, Trimorphomyces papilionaceus | | | | |
|                       | Vishniacozyma                             | new family 16 | 1.0/100/100                | Bullenbasidaceae | .99/72/51                        |
|                       | Denomyces                                 | new family 19 | 1.0/100/100                |                 |                                  |
|                       | Hannaellia                                | new family 20 | 1.0/100/100                |                 |                                  |
|                       | Bullenbasidium                            | new family 21 | 1.0/100/100                |                 |                                  |
|                       | Dioszegia                                 | new family 22 | 1.0/91/ns                 |                 |                                  |
|                       | Nielozyma                                 |           |                               |                 |                                  |
| **Trichosporonales**  | Takashimella                              | new family 23 | 1.0/88/ns                 | Tetragoniomyceace | 1.0/88/ns                        |
|                       | Cryptotrichosporon anacardi, Cryptococcus marinus | | | | |
|                       | Cutaneotrichosporon                       | new family 24 | 1.0/100/100                | Trichosporaceae | 1.0/100/100                      |
|                       | Apiotrichum                               |           |                               |                 |                                  |
|                       | Haglerozyma                               |           |                               |                 |                                  |
|                       | Trichosporon Vanniya                      |           |                               |                 |                                  |

Note. GMYC ST: the family delimitation using GMYC for single thresholds (ST) model across seven-gene ML tree; PP, Bayesian posterior probability; BP<sup>1</sup> and BP<sup>2</sup>, bootstrap values from the maximum likelihood and neighbour-joining analyses, respectively; nm: not monophyletic; ns, not supported (PP < 0.9 or BP < 50 %).
emended genus Bullera at present to accommodate their phenotypic similarity and to avoid suggesting a new genus with only two species. The significant deviation of the genus Derxomyces resulted from the inclusion of the early branching species D. anomola, which showed a remarkable divergence from the other species of the genus in the tree inferred from the seven genes (Liu et al. 2015). We prefer to maintain the current taxonomic status of this species to avoid creating a single-species clade or a monotypic genus without specific phenotypic characters. The significant deviation of the genus Kockovaella emend. was caused by the inclusion of Fellomycetes fuzhouensis in this genus. This species branches first within the Kockovaella clade with strong support (Liu et al. 2015) and is morphologically similar to the other species of the genus by forming conidia on stalks (Lopandic et al. 2011). Thus, at present we prefer to assign this species to the emended genus Kockovaella. The new genus Vishniacozyma is proposed for the strongly supported dimennae clade (Table 1, Fig. 1) (i.e. Victoriae clade in Fonseca et al. 2011) including one Bullera and six Cryptococcus species in the seven-genes tree (Fig. 1). Two strongly supported sub-clades containing two and five species, respectively, were recognised in this clade (Liu et al. 2015). The combination of these two sub-clades into a single genus is due to the consideration that they are phenotypically indistinguishable. The Tremella sensu stricto clade (i.e. the mesenterica clade in Boekhout et al. 2011a) exclusively contains Tremella species, including the type species of the genus, T. mesenterica, together with other representatives of the mesenterica and fuciformis subclades as distinguished by Chen (1998) and Liu et al. (2015). Several ecological and morphological features can be used to distinguish both subclades (Chen 1998): 1) basidiocarps are frequently associated with fungi of Russulales (Peniophora) in the mesenterica subclade, and with fungi of Xylariaceae (Hypoxilon or Xylaria) in the fuciformis subclade; 2) hymenial and subhymenial structures are loose in the mesenterica subclade in contrast to firm with numerous anastomoses present in the fuciformis subclade; 3) hyphidia are present in the mesenterica subclade but lacking in the fuciformis subclade; and 4) haustorial hyphae are not branched in the mesenterica subclade in contrast to those of the species in the fuciformis subclade. The genus Tremella containing approximately 90 species (Kirk et al. 2008) is highly polyphyletic and remains to be recircumscribed (Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015). We propose to keep the species in the Tremella sensu stricto clade in this genus at present. We also caution against the use of the generic name Tremella for newly described species outside that clade.

Phylogenetic demarcation of families in the Fungi is usually difficult due to the lack of molecular data from many taxa (Hibbett et al. 2007). This is also the case for Tremellomycetes at present because the rRNA gene sequences of many filamentous members of this class are not yet available for an integrated phylogenetic analysis (e.g. Millanes et al. 2011, Lindgren et al. 2015). The boundaries of the existing families within Tremellomycetes have not been subjected to robust phylogenetic analyses based on sufficient taxon sampling, thus family boundaries could only be derived by PRBO via interpolation, which was not applied here because the number of established genera is also small. The modified GMYC approach (Humphreys & Barraclough 2014), which does not need the reference information, was used to assign families, and the resulting taxa were then assessed using PRBO. The LRT test resulted in the recognition of two families in Cystofilobasidiales, five in Filobasidiales, 15 in Tremellales and two in Trichosporonales (Table 3). Some of the families identified in Filobasidiales and Tremellales using the GMYC approach lacked phylogenetic support. Therefore, we adjusted the family boundaries from a conservative point of view and a combined consideration on phylogenetic and phenotypic criteria, resulting in the proposal of two families in Filobasidiales and ten in Tremellales (Table 3).

The two families recognised in Cystofilobasidiales by the GMYC test are accepted here. Family 1 is equivalent to Cystofilobasidiales (Fell et al. 1999) and Mrakiaceae fam. nov. is proposed to accommodate family 2. They are supported phenotypically by the morphology and size of basidia and phylogenetically by the seven-genes Bayesian analysis. The former usually produces long and slender (up to 65 μm) holobasidia, while the teleomorph taxa of the latter usually form short and tubular (8–12 μm) holo- or phragmometabasidia. The two families recognised in Trichosporonales by the GMYC test are also accepted and are assigned to Trichosporonaceae (family 23) and Tetragononymetaceae (family 24). The majority of the taxa in the former can produce arthroconidia while the latter can not. Each of them also received strong phylogenetic support (Table 3).

The five clades resolved in the Filobasidiales obtained from the seven-genes phylogeny (Liu et al. 2015) were recognised as representing a family each (families 3–7) by the GMYC test (Table 3). However, discriminative phenotypic criteria among these clades were difficult to find from the morphological, biochemical and physiological characters that have been investigated (Kurtzman et al. 2011b). From a practical point of view, we suggest to combine families 3 and 4 (i.e. the aeriis and cylindricus clades in Fonseca et al. 2011 and Liu et al. 2015) into a single new family Piskurozymaceae fam. nov. and combine families 5–7 together with the single-species lineage Cryptococcus arrabidensis into Filobasidiales.

The family recognition in the order Tremellales was more complicated and five families (families 8, 11, 15, 17 and 18) of the 15 families recognised by the GMYC test were accepted as well delimited families with phenotypic and phylogenetic support (Table 3). The genera Cryptococcus sensu stricto (i.e. the Filobasidiella clade in Fonseca et al. 2011) and Kwoniella were identified as representing two separate families (families 9 and 10) by the GMYC test, but we suggest to combine them as a single family Cryptococcaceae in view of their close phylogenetic relationship with strong support (Liu et al. 2015) and both contain human or arthropod-associated species (Findley et al. 2009). We propose to combine families 12 and 13 (Table 3) identified by the GMYC test into a single family Auriculibulleraceae, which is phylogenetically strongly supported (Liu et al. 2015). Family 14 determined by the GMYC analysis was a paraphyletic group in the seven-genes tree (Liu et al. 2015), thus we divided it into two separate families, namely Bulleraceae and Sirobasidiales. The dimennae, Derxomyces, Hannaella, Bulleribasidium and Dioszegia (together with the melostomae clade) clades were recognised as representing a family each (families 16 and 19–22) by the GMYC test (Table 3). These clades consist of species previously belonging to the genera Bullera or Cryptococcus (Wang & Bai 2008, Fonseca et al. 2011, Wang et al. 2011), suggesting their phenotypic similarity. Therefore, we propose to combine these five clades into a single family Bulleribasidiales, which showed good support values in the seven-genes analyses, both in Bayesian and ML trees (Fig. 1).
Taxonomic impact of the expanded LSU rDNA sequence dataset analysis

The phylogenetic analysis using the seven-genes sequence dataset contained limited teleomorphic and filamentous species of Tremellomycetes. For a better understanding of the phylogenetic relationships between anamorphic (mostly well represented in the analysis in Liu et al. 2015) and teleomorphic species in Tremellomycetes, more teleomorphic species were added to the expanded LSU rDNA dataset. In public databases, these taxa are often known from a limited number of rRNA gene sequences derived from herbarium specimens. Furthermore, several recently published yeast species were also added to the LSU dataset. The constrained ML analysis of the expanded LSU dataset was used to place species known from LSU sequences in the phylogenetic clades previously recognised in the analysis of the seven genes (Fig. 1). Results from the LSU analysis were not used to challenge the results of multi-gene studies (Findley et al. 2009, Millanes et al. 2011, Liu et al. 2015), but to enlarge undersampled clades in Liu et al. (2015) and to investigate the stability of these clades.

In agreement with the few available multigene studies (Findley et al. 2009, Millanes et al. 2011, Liu et al. 2015), our results showed that LSU alone is not sufficient to resolve many clades in Tremellomycetes and the topology of the best tree from the unconstrained ML analysis (data not shown) differed from the seven-genes tree in Liu et al. (2015). Enforcing topological constraints and enlarging step-wise the dataset from 396 (data not shown) to 435 taxa, resulted in a slightly altered topology and, on average, acceptable bootstrap values (Fig. 2). Sequences containing ambiguities and missing data (e.g. from herbarium specimens) and species with unclear phylogenetic placement resulted in decreased average bootstrap values from 79.04 % in the 396-taxa-dataset (data not shown) to 69.05 % in the 435-taxa-dataset, respectively. In particular, support values of the aurantia clade comprised by Tremella aurantia, T. indecorata and T. encephala and strongly supported in Liu et al. (2015) decreased substantially, while support values for the clade containing Cryptococcus mjuensis increased. The constrained ML tree obtained from the expanded LSU rRNA gene sequence dataset did not change the main taxonomic conclusions (Fig. 2). Among the clades supported in Liu et al. (2015) poor or no support was observed for the clade (Saitozyma) comprised by C. flavus, C. parafflavus and C. podzolicus (Figs 1 and 2).

The addition of the supplemental species or strains resulted in the enlargement of several clades, especially single-species lineages recognised in the seven-genes tree, e.g. Bulliera aurundinariae, Cryptococcus arribidensis, C. mjuensis, Filobasidium capsuligenum, and Tremella giraffa (Fig. 2). In addition, a few new clades were identified (Fig. 2, Table 1). The addition of the recently described species Cryptococcus tahquamenonensis (Sylvester et al. 2015) to the monotypic Huempii clade recognised in the seven-genes dataset in the Cystofilobasidiales supports the proposal of a new genus (Krasilnikovozyma gen. nov.) for this clade (Fig. 3). Thirteen of the supplemental sequences corresponding to nine species were located in the Filobasidiales (Fig. 4). The single-species clade represented by Cryptococcus arribidensis in the seven-genes tree was expanded to contain eight species including two Syzygospora and five undescribed Cryptococcus species with high (82 % in ML and 97 % in MP, respectively) bootstrap support (Fig. 4), confirming that this clade represents a distinct genus, for which the older name Heterocephalacia is reinstated (Fig. 4, see Taxonomy section). The cylindricus clade containing two Cryptococcus species recognised in the seven-genes tree (Liu et al. 2015) was expanded to include Syzygospora sorana, Filobasidium capsuligenum and three additional Cryptococcus species. The expanded clade received 93 % and 92 % bootstrap support in the ML and MP trees, respectively (Fig. 4). The teleomorphic species Christiansenia pallida and Syzygospora alba, the type species of the genus Syzygospora, formed a distinct new clade with 100 % bootstrap support (Fig. 4). This result supports the transfer of C. pallida to the genus Syzygospora as proposed previously by Ginn (1986) and shown by Millanes et al. (2011). The remaining four clades recognised in the Filobasidiales in Liu et al. (2015) remain unchanged (Figs 1, 2 and 4).

In the Tremellales, the majority of the newly added Tremella species were located in the Tremella-containing clades recognised previously, including clades I, II and III, which were distinguished by Millanes et al. (2011) for lichenicolous taxa. These three clades exclusively or mainly contained Tremella species (Fig. 5A, B). The strongly supported aurantia clade in the seven-genes tree, comprising T. aurantia, T. indecorata and T. encephala, was expanded with two species, namely T. aurantialba and T. microspora (Fig. 5A). The phylogenetic position of T. indecorata in the LSU tree was controversial because the support for this clade was decreasing with increasing dataset size and because sequences representing this taxon appeared to be separated in the tree. Nucleotide sequences of T. indecorata derived from strains CBS 6976 (used in Liu et al. 2015) and DSM 5727 grouped together, while a sequence derived from a herbarium specimen (used in Millanes et al. 2011) was placed close to T. montformis (Fig. 5B). The latter sequence was also identical to the sequence of T. subanomala strain NBRC 9308 (collected by R.J. Bandoni), which is available in the online catalogue of the NBRC collection (NITE, Japan). Thus additional sampling is needed to assess the phylogenetic position of T. indecorata. We recognise the resolving power of multi-gene trees and despite lack of support in the LSU phylogeny, the aurantia clade will be treated as a separate genus, for which the name Naematelia is available (Fig. 5A). The foliacea clade formed by one Tremella and two Cryptococcus species recognised previously (Liu et al. 2015) was expanded to include four more Tremella species represented by eight strains with high (99 % in ML and 100 % in MP) bootstrap support (Fig. 5C). This clade will also receive generic rank and the available name Pheaeotremella will be assigned. The single-species clade Tremella moniformis recognised in Liu et al. (2015) was expanded to include three Tremella and two Cryptococcus species with moderate bootstrap support (95 % and 76 % in ML and MP analyses, respectively) and the new genus Pseudotremella is proposed to accommodate these fungi (Fig. 5B). Bulliera aurundinariae, which was placed in an isolated position in the seven-genes tree (Liu et al. 2015), joined a well-supported clade together with Tremella polyopora and Syzygospora efibulata (syn. Carcinomyces efibulatus) in the LSU analysis, for which the genus Carcinomyces is resurrected (Fig. 5D). Tremella exigua together with Sirobasidium brefeldianum and Sirobasidium intermedium formed a strongly supported new clade with a close relationship to clade I in Millanes et al. (2011). The remaining five Tremella species (T. diplochistina, T. haematommatis, T. ramalinae, T. pamelierum, and T. phaeophysciae) newly added to the LSU tree were located in independent branches in the
Fig. 3. Phylogenetic relationships of yeasts and related taxa from the order Cystofilobasidiales in Tremellomycetes obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu et al. 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. The type species of accepted genera are in bold and the taxa not included in the seven-genes dataset (Liu et al. 2015) are in red. Note: ns, not supported (BP < 50 %).
Phylogenetic classification of the Tremellomycetes

Fig. 4. Phylogenetic relationships of yeasts and related taxa from the order Filobasidiales in Tremellomycetes obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu et al. 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. The type species of accepted genera are in bold and the taxa not included in the seven-genes dataset (Liu et al. 2015) are in red. Note: ns, not supported (BP < 50 %).
Fig. 5. Phylogenetic relationships of yeasts and related taxa from the order Tremellales in Tremellomycetes obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85%) bipartitions of the topology of the seven-genes tree (Liu et al. 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. The type species of accepted genera are in bold and the taxa not included in the seven-genes dataset (Liu et al. 2015) are in red. Note: ns, not supported (BP < 50%).
Fig. 5. (Continued).
Fig. 5. (Continued).
Tremellales. The *Tremella sensu stricto* clade resolved in Liu et al. (2015) (i.e. the mesenterica clade in Boekhout et al. 2011a) containing the type species of the genus, *T. mesenterica*, was also revealed in the LSU tree and received moderate bootstrap support (64 % and 96 % in ML and MP analyses, respectively) (Fig. 5D).

The *Bandoniozyma* clade recognised in the seven-genes tree was expanded to include the sexual species *Rhynchogastremata coronatum* and a recently described *Cryptococcus* species with strong bootstrap support (99 % and 92 % in ML and MP analyses, respectively) (Fig. 5A). Hence, the *Bandoniozyma* species will be renamed as *Rhynchogastremata*.

Our analysis also cautions against the description of new species in the genus *Kwoniella* solely based on LSU sequence data. The support for this rapidly growing clade was low in all ML analyses and varied from 70 % to 64 % (data not shown). From the recently described asexual species placed in the genus based on the similarity to known *Kwoniella* species, *K. newhampshirensis* and *K. shandongensis* were grouped close to *K. heveanensis* (Fig. 5C). However, two other recently described anamorphic species, *Cryptococcus trondorenensis*, which was assigned to the *Kwoniella* clade by de Garcia et al. (2012) and *K. betulae* described by Sylvester et al. (2015) formed a separate clade together with *Cryptococcus mjuensis* with high bootstrap support (97 % in ML and 93 % in MP analyses) (Fig. 5C). These taxa were in isolated positions in Liu et al. (2015). The affinity of this clade with the *Kwoniella* clade was not supported in this study, therefore a new genus *Fonsecazyma* is proposed to accommodate these species (Fig. 5C).

The five strains of *Trimorphomyces papilionaceus*, which is the type species of the genus, clustered together and were found to be closely related to *Bullera sakaeraetica* with bootstrap support values of 86 % and 93 % in the ML and MP analyses, respectively (Fig. 5E). The close relationship of *T. papilionaceus* and *B. sakaeraetica* was also resolved in the seven-genes tree (Liu et al. 2015), suggesting that *B. sakaeraetica* has to be transferred to the genus *Trimorphomyces*. The other additional *Trimorphomyces* species employed here were placed in another well supported clade (100 % and 93 % in ML and MP analyses, respectively) with some *Cryptococcus* and *Bullera* species (Fig. 5D). This clade is also referred to as *victoriae* clade (Fonseca et al. 2011) or *dimennae* clade (Liu et al. 2015) and is not closely related to *T. papilionaceus*. The result suggests that the H-shaped conidia, as a morphological character of the genus *Trimorphomyces*, can be found in different phylogenetic clades. Thus different yeast-like taxa in Tremellomycetes may have a *Trimorphomyces*-like morph in their life cycles. In addition to the two *Trimorphomyces* strains, the *dimennae* clade originally holding six *Cryptococcus* and one *Bullera* species as recognised from the seven-genes tree (Liu et al. 2015) was expanded to contain four more *Cryptococcus* species in the tree constructed from the LSU dataset (Fig. 5D). The new *Trimorphomyces* strains were located in two subgroups in the *dimennae* clade, indicating that this clade may have a trimorphomyces-like sexual state and might be mycoparasitic.

Ten of the supplemental sequences were located in the *Trichosporonales* (Fig. 6). Two *Asterotremella* species and one recently described species *Cryptococcus thermophilus* (Vogelmann et al. 2012) clustered in the *Vanrijia* clade. The teleomorphic species, *Tetragononmyces uliginosus*, was located in this order with a phylogenetic position being in agreement with that obtained by Millanes et al. (2011) based on the combined rRNA analysis. The present and previous results suggest that *Tetragononmyces* holds an early-branching position in Trichosporonales together with the genera Cryptotrichosporon (Okoli et al. 2007) and Takashimella (Wang & Wang 2015). Three of the four newly added *Trichosporon* species were scattered in different clades formed by other species of the genus; the other species, *T. wanderwaltii*, formed a single species lineage (Fig. 6).

**TAXONOMY**

Based on 1) the multigene phylogenetic framework presented by in Liu et al. (2015), 2) the quantitative assessment of taxonomic units using the PRBO approach as well as the iterative modified GMYC tests, 3) a further phylogenetic analysis on an expanded LSU rRNA (D1/D2 domains) gene sequence dataset containing as many as available teleomorphic and filamentous taxa within Tremellomycetes, and finally 4) phenotypical criteria, we propose to update the taxonomic system for tremellomycetous yeasts and related filamentous taxa (Table 1). The phylogenetic classification includes five orders, 17 families and 54 genera. Among the genera accepted here, 18 are newly described and 18 are emended (Table 1, Figs 1 and 2). Seven of the families are newly proposed and seven are emended from existing ones. Among the accepted species, one is newly proposed and 185 are new combinations. The new and emended families and genera and new combinations are described and discussed within their respective orders. We propose to use the term *pro tempore* or *pro tem.* in abbreviation to indicate the species names that are temporarily maintained.

**Order Cystofilobasidiales** Fell, Roeijmans & Boekhout, Int. J. Syst. Bacteriol. 49: 911. 1999.

The order Cystofilobasidiales was proposed for teleomorphic yeasts with telosporcs, holobasidia and septa with dolipores, but without parentheses (Fell et al. 1999). This order was accepted as family *Cystofilobasidiales* in Filobasidiales by Wells & Bandoni (2001). Our phylogenetic analysis demonstrated the rationality of its taxonomic rank as an order (Liu et al. 2015). Accordingly a new family *Mrakiaecae* is described and family *Cystofilobasidiales* is emended to accommodate the two major lineages recognised in the order. A new genus *Kraslinikovozyigma* is described and four genera are emended.

**Mrakiaecae** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, fam. nov. MycoBank MB812173.

*Etymology*: In reference to the name of the type genus *Mrakia*.

This new family is proposed for the monophyletic group formed by the *Mrakia*, *huempii*, *Phaffia*, *Udeniomycetes*, *Iteronilia* and *Tausonia* clades recognised in the trees constructed from the Bayesian and ML analyses of the seven-gene dataset (Liu et al. 2015) as shown in Fig. 1 of this study.
Fig. 6. Phylogenetic relationships of yeasts and related taxa from the orders Trichosporonales in Tremellomycetes obtained by maximum-likelihood analysis of LSU (D1/D2 domains) rRNA gene. Tree topology was backbone-constrained with the well-supported (>85 %) bipartitions of the topology of the seven-genes tree (Liu et al. 2015). Bootstrap percentages (BP) of maximum likelihood and neighbour-joining analyses from 1 000 replicates are shown respectively from left to right on the deep and major branches resolved and in brackets following recognised clades. The type species of accepted genera are in bold and the taxa not included in the seven-genes dataset (Liu et al. 2015) are in red. Note: ns, not supported (BP < 50 %).
Type genus: *Mrakia* Y. Yamada & Komag. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Genera accepted: *Mrakia* emend., *Krasilnikovozyma* gen. nov., *Phaffia* emend., *Udeniomyces*, *Itersonilia* emend. and *Tausonia* emend.

*Mrakia* Y. Yamada & Komag., J. Gen. Appl. Microbiol. 33: 456. 1987. *emend.* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. = *Mrakia* Margesin & Fell, Int. J. Syst. Evol. Microbiol. 58: 2980. 2008.

This genus is emended to accommodate the *Mrakia* clade recognised in Liu et al. (2015) which includes five *Mrakia* and two *Mrakia*-related species in the seven-genes tree.

Basidiocarps absent. Pseudohyphae occasionally produced, branched. True hyphae occasionally produced. Clamp connections present. Sexual reproduction observed in some species. Teliospores terminal or intercalary produced, developing directly from a single cell; teliospores germination by formation of short (8–12 μm), tubular holometabasidia or phragmobasidia. Budding cells present. Chlamydospores and ballistoconidia may be present. Glucose and sucrose may be fermented. Nitrate and nitrite usually utilised. Major CoQ system CoQ-8. Glycerol and low-weight aromatic compounds are not utilised. Nitrate and nitrite usually utilised. Major CoQ systems CoQ-8, CoQ-9 or CoQ-10.

Type species: *Mrakia frigida* (Fell, Statzell, I.L. Hunter & Phaff) Y. Yamada & Komag., J. Gen. Appl. Microbiol. 33: 457. 1987.

Notes: *Mrakia curviuscula* is excluded from the emended genus *Mrakia* because this species forms a distinct clade together with the anamorphic species *Cryptococcus huempii* (Liu et al. 2015). The genus *Mrakia* was proposed for anamorphic species closely related to *Mrakia* (Margesin & Fell 2008). The three *Mrakia* species are transferred here to the genus *Mrakia*. The affinity of *Mrakia cryoconiti*, which was not included in the seven-genes phylogeny, to *Mrakia* is shown in the trees obtained from the LSU rRNA gene sequences in this study (Fig. 3) as well as in Boekhout et al. (2011a) and Weiss et al. (2014). The emended genus *Mrakia* currently contains eight species (Table 1).

New combinations for *Mrakia*

*Mrakia aquatica* (E.B.G. Jones & Slooff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB812175.

*Basionym*: Candida aquatica E.B.G. Jones & Slooff, Antonie van Leeuwenhoek 32: 223. 1966. = *Mrakia* aquatica (E.B.G. Jones & Slooff) Margesin & Fell, Int. J. Syst. Evol. Microbiol. 58: 2981. 2008.

*Mrakia cryoconiti* (Margesin & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB812176.

*Basionym*: Mrakia cryoconiti Margesin & Fell, Int. J. Syst. Evol. Microbiol. 58: 2981. 2008.

*Mrakia niccombsii* (Thomas-Hall) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB812177.

*Basionym*: Mrakia niccombsii Thomas-Hall, Extremophiles 14: 56. 2010.

Krasilnikovozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *gen. nov.* MycoBank MB812178.

Etymology: The genus is named in honour of the Russian microbiologist N.A. Krasil’nikov for his contribution to the ecology and systematics of yeasts.

This genus is proposed for the huempii clade containing *Mrakia curviuscula*, its anamorph *Cryptococcus huempii* (Liu et al. 2015) and the recently described *Cryptococcus tahquamenonensis* (Sylvester et al. 2015).

Basidiocarps absent. Pseudohyphae and true hyphae occasionally produced. Sexual reproduction observed in some species. Teliospores with pseudoclamps terminal produced; teliospores germination by formation of holometabasidia or hyphal structures. Budding cells present. Chlamydospores may be present. Fermentation absent. α-glucose, α-galactose, cellobiose, lactose, δ-xyllose, and citric acid are usually utilised. Glycerol and low-weight aromatic compounds are not utilised. Nitrate and nitrite usually utilised. Starch-like compounds can be produced. Major CoQ system CoQ-8.

Type species: *Krasilnikovozyma huempii* (C. Ramirez & A. E. González) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Notes: *Mrakia curviuscula* was considered to be the teleomorph of *C. huempii* based on similar physiological and biochemical characters (Bab’eva et al. 2002) and identical D1/D2 LSU rRNA gene sequences (Boekhout et al. 2011a, Weiss et al. 2014). Liu et al. (2015) showed that they also exhibited similar protein-coding gene sequences, confirming their conspecificity. *Cryptococcus tahquamenonensis* was recently described as a close relative of *Mrakia curviuscula* and *Cryptococcus huempii* (Sylvester et al. 2015). This relationship was confirmed in this study by the ML analysis of the D1/D2 sequence dataset (Fig. 3). Thus, *C. tahquamenonensis* is transferred here to *Krasilnikovozyma* gen. nov. Phenotypically, the species in *Krasilnikovozyma* can grow at 25 °C and thus differ from the species of the genus *Mrakia* emend., which are psychrophilic with a maximum growth temperature below 20 °C (Fell 2011). *Krasilnikovozyma* currently contains two species (Table 1) and two additional sequences representing potential new species were obtained from public databases (Fig. 3).

New combinations for *Krasilnikovozyma*

*Krasilnikovozyma huempii* (C. Ramirez & A. E. González) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB812179.

*Basionym*: Candida huempii C. Ramirez & A. E. González, Mycopathologia 88: 167. 1984. = Mrakia curviuscula Bab’eva, Lisichk., Rashetova & Danilev., Microbiology, Moscow 71: 450. 2002.

*Krasilnikovozyma tahquamenonensis* (Q.M. Wang, A.B. Hulfachor, K. Sylvester & C.T. Hittinger) A.M. Yurkov, *comb. nov.* MycoBank MB813656.

*Basionym*: Cryptococcus tahquamenonensis Wang et al., FEMS Yeast Res. 15: http://dx.doi.org/10.1093/femsyr/fov002. 2015.
**Phaffia** M.W. Mill., Yoney. & Soneda, Int. J. Syst. Bacteriol. 26: 287. 1976. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. = Xanthophyllomyces Golubev, Yeast 11: 105. 1995.

The genus *Phaffia* is emended to include the teleomorphic species *Xanthophyllomyces dendrorhous* (Golubev 1995) based on molecular phylogenetic analyses (Fell et al. 2000, Scorzetti et al. 2002, Boekhout et al. 2011a, David-Palma et al. 2014, Weiss et al. 2014, Liu et al. 2015).

Basidiocarps absent. Cultures often pigmented and pink to orange due to carotenoid pigments. Holobasidia slender cylindrical with apical basidiospores. True hyphae not produced. Rudimentary pseudohyphae occasionally produced. Budding cells present. Ballistoconidia not produced. Fermentation present. Nitrate and nitrite not utilised. Major CoQ system CoQ-10.

**Type species:** *Phaffia rhodozyma* M.W. Miller, Yoneyama & Soneda, Int. J. Syst. Bacteriol. 26: 287. 1976.

Notes: The teleomorphic genus *Xanthophyllomyces* (Golubev 1995) was described later than the anamorphic genus *Phaffia* (Miller et al. 1976), thus the name *Phaffia* has priority according to the code of nomenclature (McNeill et al. 2012). *Phaffia rhodozyma* was regarded as the anamorph of *X. dendrorhous* because the type strains of the two species had similar D1/D2 sequences (Fell et al. 2007, 2011). However, ITS and IGS sequence analyses generated by Fell & Blatt (1999) and protein-coding gene sequence comparisons performed in Liu et al. (2015) suggest that they may represent different species. A recent analysis performed by David-Palma et al. (2014) showed a rather complex population structure within the species *P. rhodozyma*. These authors also observed that the type strain of *P. rhodozyma* contains genetic material from two different populations. Thus, DNA sequencing attempts may result in two different PCR-products for marker genes, which show a substantial nucleotide difference (David-Palma et al. 2014, Liu et al. 2015). It has been suggested to consider sexual and asexual strains in a single species with four genetic lineages, and we also observed that the type strain of *P. rhodozyma* contains genetic material from two different populations. Thus, DNA sequencing attempts may result in two different PCR-products for marker genes, which show a substantial nucleotide difference (David-Palma et al. 2014, Liu et al. 2015).

*Notes*: The teleomorphic genus *Xanthophyllomyces* (Golubev 1995) was described later than the anamorphic genus *Phaffia* (Miller et al. 1976), thus the name *Phaffia* has priority according to the code of nomenclature (McNeill et al. 2012). *Phaffia rhodozyma* was regarded as the anamorph of *X. dendrorhous* because the type strains of the two species had similar D1/D2 sequences (Fell et al. 2007, 2011). However, ITS and IGS sequence analyses generated by Fell & Blatt (1999) and protein-coding gene sequence comparisons performed in Liu et al. (2015) suggest that they may represent different species. A recent analysis performed by David-Palma et al. (2014) showed a rather complex population structure within the species *P. rhodozyma*. These authors also observed that the type strain of *P. rhodozyma* contains genetic material from two different populations. Thus, DNA sequencing attempts may result in two different PCR-products for marker genes, which show a substantial nucleotide difference (David-Palma et al. 2014, Liu et al. 2015). It has been suggested to consider sexual and asexual strains in a single species with four genetic lineages, and we also observed that the type strain of *P. rhodozyma* contains genetic material from two different populations. Thus, DNA sequencing attempts may result in two different PCR-products for marker genes, which show a substantial nucleotide difference (David-Palma et al. 2014, Liu et al. 2015). It has been suggested to consider sexual and asexual strains in a single species with four genetic lineages, and we also observed that the type strain of *P. rhodozyma* contains genetic material from two different populations. Thus, DNA sequencing attempts may result in two different PCR-products for marker genes, which show a substantial nucleotide difference (David-Palma et al. 2014, Liu et al. 2015).

**Itersonilia** Derx, Bull. bot. Gdns Buitenz. 17: 471. 1948. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is emended to include the *Itersonilia* clade recognised from the rRNA and multigene sequence analyses (Niwata et al. 2002, Boekhout et al. 2011a, Weiss et al. 2014, Liu et al. 2015) and to incorporate a species previously assigned to the genus *Udeniomyces*.

Basidiocarps absent. Dikaryotic hyphae occasionally produced, regularly branched, inflated cells may be present. Monokaryotic hyphae may be present. Clamp connections present. Septa with dolipores lacking parenthesomes. Pseudohyphae without clamp connections occasionally present. Sexual reproduction not observed. Budding (monokaryotic) cells may be present. Ballistoconidia present. Chlamydospores occasionally produced. Fermentation absent. Low-weight aromatic compounds not utilised. Nitrate and nitrite utilised. Starch-like compounds may be produced. The major CoQ system CoQ-9 or CoQ-10.

**Type species:** *Itersonilia perplexans* Derx., Bull. Bot. Gdns Buitenz. 17: 471. 1948.

Notes: The species *Udeniomyces pannonicus* was separated from the *Udeniomyces* clade and located together with *Itersonilia perplexans* based on molecular data (Niwata et al. 2002, Boekhout et al. 2011a, Weiss et al. 2014, Liu et al. 2015). *I. perplexans* and *U. pannonicus* are phenotypically similar by forming greyish to yellowish colonies, whereas the other *Udeniomyces* species form pinkish-white to orange-white colonies. The emended genus *Itersonilia* currently contains two species (Table 1) and an additional sequence representing a potential new species was obtained from public databases (Fig. 3).

**New combination for *Itersonilia***

*Itersonilia pannonica* (Niwata, Tornai-Leh., T. Deák & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812189.

*Basionym*: *Udeniomyces pannonicus* Niwata et al., Int. J. Syst. Evol. Microbiol. 52: 1890. 2002.

*Tausonia* Babeva, Mikrobiologiya 67: 231. 1998. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. = Guehomyces Fell & Scorzetti, Int. J. Syst. Evol. Microbiol. 54: 997. 2004.

This genus is emended to include the monotypic genus *Guehomyces* based on rRNA sequence analyses (Boekhout et al. 2011a, Fell & Guého-Kellermann 2011, Sampaio 2011b, Liu et al. 2015).

Basidiocarps absent. Cultures may be pigmented and pinkish. Hyphae disarticulate into arthroconidia. Chlamydospores occasionally produced. Sexual reproduction not observed. Budding cells present. Fermentation present. Nitrate and nitrite utilised. Major CoQ system CoQ-9.

**Type species**: *Tausonia pamirica* Bab’eva, Mikrobiologiya 67: 232. 1998.

Notes: *Guehomyces pullulans* (formerly *Trichosporon pullulans*) and *T. pamirica* were located together in a well-supported clade named *Guehomyces* based on rRNA sequence analyses (Boekhout et al. 2011a, Fell & Guého-Kellermann 2011, Sampaio 2011b, Liu et al. 2015). *Tausonia* (Bab’eva 1998) has nomenclatural priority over *Guehomyces* (Fell & Scorzetti 2004). The two species are phenotypically similar in producing arthroconidia. The genus currently contains two species (Table 1) and an additional sequence representing a potential new species was obtained from public databases (Fig. 3).

**New combination for *Tausonia***

*Tausonia pullulans* (Lindner) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812190.
Basionym: Oidium pullulans Lindner, Mikrosk. Betriebesk. Gährung. 3te Aufl.: 286. 1901.

≡ Trichosporon pullulans (Lindner) Diddens & Lodder, Die anaskosporogenen Hefen, II Haffte: 410. 1942. MycoBank MB291956.
≡ Guiehomyces pullulans (Lindner) Fell & Scorzetti, Int. J. Syst. Evol. Microbiol. 54: 997. 2004.

Cystofilobasidiaceae K. Wells & Bandoni, The Mycota 7(B): 113. 2001. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This family is emended to include the Cystofilobasidium clade recognised from the seven-gene phylogeny (Liu et al. 2015).

Basidiocarps absent. Cultures often pink to orange due to carotenoid pigments. True hyphae produced. Pseudohyphae occasionally produced. Clamp connections may be present. Sexual reproduction observed in some species. Teliospores terminal or intercalary produced; teliospores germination by holobasidia. Budding cells present. Aromatic compounds weakly or not utilised. Nitrate and nitrite utilised by several species. The major CoQ system CoQ-8.

Type genus: Cystofilobasidium Oberw. & Bandoni.

Genus accepted: Cystofilobasidium.

Notes: The family Cystofilobasidiaceae was originally proposed within the order Filobasidiales mainly based on the morphological features of the holobasidia. Three genera Cystofilobasidium, Mrakia, and Xanthophyllomyces were included in this family (Wells & Bandoni 2001). Phylogenetic analyses suggest that this family represents an order independent of Filobasidiaceae (Fell et al. 1999, Fell et al. 2000, Scorzetti et al. 2002, Boekhout et al. 2011a, Liu et al. 2015) and support the proposal of Cystofilobasidiaceae by Fell et al. (1999). The family Cystofilobasidiaceae is emended here to include only the Cystofilobasidium clade (Fig. 1). The species in this family produce much longer (up to 65 μm) holobasidia (Fell et al. 1999, Sampaio 2011a, Weiss et al. 2014) than those (8–12 μm) produced by the teleomorphic species in the other family Mrakia-ceae within Cystofilobasidiales.

Order Filobasidiales Jülrich, Bibl. Mycol. 85: 324. 1981.

The order Filobasidiales was originally introduced to accommodate yeasts lacking basidiocarps and having holobasidia with passively released basidiospores (Jülrich 1981). Three families, namely Filobasidiaceae, Cystofilobasidiaceae and Rhynchosoustrepetaceae were included in this order by Wells & Bandoni (2001). As discussed above, the Cystofilobasidiaceae sensu Wells & Bandoni (2001) represents a distinct order and this family is emended in this study to include only the genus Cystofilobasidium. Rhynchosoustrepetaceae was monotypic, including only Rhynchosoustrema coronatum (Metzler et al. 1989). LSU rRNA sequence analyses assigned this dimorphic mycoparasite to the Tremellales as shown in Weiss et al. (2014) and this study (Fig. 5A). Molecular phylogenetic analyses showed that the order Filobasidiales without Cystofilobasidiaceae and Rhynchosoustrepetaceae represents a monophyletic lineage, which includes species from the teleomorphic genera Filobasidium and Syzygospora and the anamorphic genus Cryptococcus (Fell et al. 2000, Scorzetti et al. 2002, Boekhout et al. 2011a, Scorzetti et al. 2014, Liu et al. 2015). Three families, namely Filobasidiaceae, Syzygosporaceae and Christianseniaceae have been proposed in this order. However, they were not resolved as separate groups in the previous and present molecular phylogenetic analyses. Therefore, the families and genera within this order are recircumscribed in this study based on the phylogenetic analyses of the seven-genes (Fig. 1) and the LSU rRNA datasets (Figs 2 and 4), resulting in the recognition of two families and seven genera (Table 1).

Filobasidiaceae L.S. Olive, J. Elisha Mitchell Scienc. Soc. 84: 261. 1968. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This family is circumscribed to accommodate a monophyletic group containing the Filobasidium, albidus, gastricus, Cryptococcus arrabidensis and Syzygospora clades resolved in the trees from the seven-gene dataset (Liu et al. 2015) and the expanded LSU rRNA dataset (Figs 1 and 2).

Basidiocarps waxy to gelatinous in lichenicolous species, absent in cultures. Hyphae with clamp connection and haustorial branches may be present. Holobasidia tubular or long with terminally sessile basidiospores. Pseudohyphae and true hyphae occasionally produced. Sexual reproduction present in some species. Budding cells present. Ballistoconidia absent. Fermentation absent. Nitrate utilised by several species. The major CoQ system CoQ-9 or CoQ-10.

Type genus: Filobasidium L.S. Olive. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Genera accepted: Filobasidium, Goffeauzyma, Heterocephalaria, Nagarishia, and Syzygospora.

Notes: The family Filobasidiaceae was proposed by Olive (1968) to accommodate the species Filobasidium floriforme. Three teleomorphic genera, namely Filobasidium, Filobasidiella and Cystofilobasidium, were then included in this family (Kwon-Chung 1987). These genera share the presence of long slender holobasidia, sessile terminal basidiospores and dolipore-like septa without parenthesomes (Kwon-Chung 1987). The genera Filobasidiella and Cystofilobasidium were transferred to the Tremellales and Cystofilobasidiaceae, respectively, based on molecular phylogenetic analyses (Fell et al. 2000, Scorzetti et al. 2002). Phylogenetic analysis of the expanded LSU rRNA dataset showed that four Syzygospora species were closely related to the taxa assigned to Filobasidiaceae (Fig. 4). Therefore, the Filobasidiaceae is emended here to include Filobasidium, Nagarishia (i.e. the albidus clade), Goffeauzyma gen. nov. (i.e. the gastricus clade), Heterocephalaria (i.e. the Cryptococcus arrabidensis clade) and Syzygospora.

Filobasidium L.S. Olive, J. Elisha Mitchell Scient. Soc. 84: 261. 1968. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is emended to accommodate the species in the Filobasidium clade (floriforme clade sensu Fonseca et al.
Filobasidium

Type species: Filobasidium floriforme L.S. Olive, J. Elisha Mitchell scient. Soc. 84: 261. 1968.

Notes: Filobasidium capsuligenum is excluded from this genus because it is located outside the Filobasidium clade and is closely related to the cylindricus clade (i.e., Piskurozyma gen. nov.). The genus Filobasidium currently contains nine species (Table 1).

New combinations for Filobasidium

Filobasidium chernovii (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB812191.

Basionym: Cryptococcus chernovii Á. Fonseca et al., Can. J. Microbiol. 46: 20. 2000.

Filobasidium magnus (Lodder & Kreger-van Rij) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB812192.

Basionym: Cryptococcus laurentii var. magnus Lodder & Kreger-van Rij. Yeast, a taxonomic study, [Edn 1]: 670. 1952.

Filobasidium oeirense (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB812193.

Basionym: Cryptococcus oeirensis Á. Fonseca et al., Can. J. Microbiol. 46

Filobasidium stepposum (Golubev & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB812194.

Basionym: Cryptococcus stepposus Golubev & J.P. Samp. Mycol. Res. 110: 960. 2006.

Filobasidium wieringae (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB812195.

Basionym: Cryptococcus wieringae Á. Fonseca et al., Can. J. Microbiol. 46: 25. 2000.

Naganishia S. Goto, J. Ferment. Technology 41: 461. 1963. emend. A.M. Yurkov & T. Boekhout.

This genus is resurrected and emended here to accommodate the albidus clade comprising of 15 species that previously belonged to Cryptococcus (Fell et al. 2000, Scorzetti et al. 2002, Fonseca et al. 2011, Liu et al. 2015).

Basidiocarps absent. Hyphae and pseudohyphae usually absent. Sexual reproduction not observed. Budding cells present. Ballistoconidia absent. Fermentation absent. l-malic, vanillic, ferulic, caffeic, p-coumaric protocatechuic and hydroxybenzoic acids often utilised. Nitrate utilised. Starch-like compounds usually produced. The major CoQ system CoQ-9 or CoQ-10.

Type species: Naganishia globosa S. Goto, J. Ferment. Technology 41: 461. 1963. MycoBank MB335061.

Notes: The genus Naganishia was described to accommodate the yeast Naganishia globosaus (Goto 1963), which was later synonymised with Cryptococcus saitoi based on rRNA sequence data (Fonseca et al. 2011). Some of the other species comprising this clade were described earlier than N. globosaus, but they were originally classified in the genera Torula, Torulopsis and Rhodotorula. Since type species of these genera are placed outside Tremellomycetes, none of them can be used to reclassify the albidus clade. The generic name Naganishia also appears to be the oldest in the clade where the type species of the genus is specified and a type strain is preserved. Cryptococcus onofrii and C. vagnhammartiniae were recently described as cold-adaptive species in the albidus clade (Turchetti et al. 2015). Their affinity to the albidus clade was confirmed in this study by ML analysis using the expanded LSU rRNA gene sequence dataset (Fig. 4). Thus, these two Cryptococcus species are transferred to the genus Naganishia together with the Cryptococcus species included in the albidus clade in the seven-genes dataset (Liu et al. 2015). Fifteen species are presently accepted in the genus Naganishia (Table 1).

New combinations for Naganishia

Naganishia adeliensis (Scorzetti, I. Petrescu, Yarrow & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813139.

Basionym: Cryptococcus adeliensis Scorzetti et al., Antonie van Leeuwenhoek 77: 155. 2000.

Naganishia albidosimilis (Vishniac & Kurtzman) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813140.

Basionym: Cryptococcus albidosimilis Vishniac & Kurtzman, Int. J. Syst. Bacteriol. 42: 550. 1992.

Naganishia albida (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813140.

Basionym: Torula albida Saito, Jap. J. Bot. 1: 43. 1922.

Naganishia antarctica (Vishniac & Kurtzman) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813145.

Basionym: Cryptococcus antarcticus Vishniac & Kurtzman, Int. J. Syst. Bacteriol. 42: 548. 1992.

Naganishia bhutanensis (Goto & Sugiy.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813165.
Basionym: Cryptococcus bhutanensis Goto & Sugiy., Can. J. Bot. 48: 2097. 1970.

*Naganishia cerealis* (Passoth, A.-C. Andersson, Olstorpe, Theelen, Boekhout & Schnirrer) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813167.
Basionym: Cryptococcus cerealis Passoth et al., Antonie van Leeuwenhoek 96: 641. 2009.

*Naganishia diffuens* (Zach) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813172.
Basionym: Torulopsis diffuens Zach, Wolfram & Zach, Arch. Derm. Syph. 170: 690. 1934.

*Naganishia friedmannii* (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813177.
Basionym: Cryptococcus friedmannii Vishniac, Mycologia 77: 150. 1985.

*Naganishia liquefaciens* (Saito & M. Ota) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813177.
Basionym: Torulopsis liquefaciens Saito & M. Ota, Jozogaku Zasshi 12: 167. 1934.

*Naganishia onofrii* (Turchetti, Selbmann & Zucconi) A.M. Yurkov, *comb. nov.* MycoBank MB813182.
Basionym: Cryptococcus onofrii Turchetti et al., Extremophiles 19: 149–159. 2015.

*Naganishia randhawae* (Z.U. Khan, S.O. Suh. Ahmad, F. Hagen, Fell, Kowshik, Chandy & Boekhout) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813246.
Basionym: Cryptococcus randhawae Z.U. Khan et al., Antonie van Leeuwenhoek 97: 256. 2010.

*Naganishia uzbekistanensis* (Á. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813248.
Basionym: Cryptococcus uzbekistanensis Á. Fonseca et al., Can. J. Microbiol. 46: 25. 2000.

*Naganishia vaughanmartini* (Turchetti, Blanchette & Arenz) A.M. Yurkov, *comb. nov.* MycoBank MB813249.
Basionym: Cryptococcus vaughanmartini Turchetti et al., Extremophiles 19: 157. 2015.

*Naganishia vishniaci* (Vishniac & Hempfling) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813250.
Basionym: Cryptococcus vishniaci Vishniac & Hempfling, Int. J. Syst. Bacteriol. 29: 155. 1979.

Goffeauzyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *gen. nov.* MycoBank MB813251.

Etymology: The genus is named in honour of the yeast biologist and geneticist André Goffea, who was the initiator and coordinator of the genome sequence project of *Saccharomyces cerevisiae*.

The new genus is proposed for the *gastricus* clade recognised from the seven-genes tree (Liu et al. 2015), which consists of six species previously belonging to *Cryptococcus*.

Basidiocarps absent. True hyphae and pseudohyphae not observed. Sexual reproduction not observed. Budding cells present. Ballistoconidia absent. Fermentation absent. Low-weight aromatic compounds often not utilised. Nitrate usually not utilised. Major CoQ system CoQ-9.

Type species: Goffeauzyma gastrica (Reiersøl & di Menna) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout *comb. nov.*

Notes: The *gastricus* clade recognised in Liu et al. (2015) consists of *C. gastricus* and *C. gilvescens* isolated from soil (Fell et al. 2000, Boekhout et al. 2011a, Fonseca et al. 2011); *C. aciditolerans, C. ibericus* and *C. metaltolerans* in the *ARD ecoclade* that were obtained from acid rock drainage (Gadanho & Sampaio 2009); and *C. agrionensis* from acidic water of a volcanic environment (Russo et al. 2010). Though the species of the *ARD ecoclade* clustered together, they did not form a significantly supported clade in the seven-genes tree (Liu et al. 2015) and in the LSU rRNA gene tree (Fig. 4). The PRBO test indicated that the six species of the *gastricus* clade did not show significant deviation compared to the species in the reference clades (Table 2). Thus they are assigned to a single genus at present which currently contains six species (Table 1).

New combinations for Goffeauzyma

Goffeauzyma aciditolerans (Gadanho & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813252.
Basionym: Cryptococcus aciditolerans Gadanho & J.P. Samp., Int. J. Syst. Evol. Microbiol. 59: 2378. 2009.

Goffeauzyma agrionensis (Russo, Libkind, Samp. & van Broock) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813253.
Basionym: Cryptococcus agrionensis Russo et al., Int. J. Syst. Evol. Microbiol. 60: 998. 2010.

Goffeauzyma gastrica (Reiersøl & di Menna) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813254.
Basionym: Cryptococcus gastricus Reiersøl & di Menna, Antonie van Leeuwenhoek 24: 28. 1958.

Goffeauzyma gilvescens (Chernov & Babeva) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813255.
Basionym: Cryptococcus gilvescens Chernov & Babeva, Mikrobiologiya 57: 1032. 1988.

Goffeauzyma ibericus (Gadanho & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813256.
Basionym: Cryptococcus ibericus Gadanho & J.P. Samp., Int. J. Syst. Evol. Microbiol. 59: 2378. 2009.

Goffeauzyma metaltolerans (Gadanho & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813257.
Basionym: Cryptococcus metaltolerans Gadanho & J.P. Samp., Int. J. Syst. Evol. Microbiol. 59: 2379. 2009.

Heterocephalacria Berthier, Mycotaxon 12: 114. 1980. *emend.* A. M. Millanes, M. Wedin & A.M. Yurkov.
This genus is resurrected and emended to accommodate the clade represented by Cryptococcus arrabidensis recognised in the seven-genes tree (Liu et al. 2015) and was expanded to include two Syzygospora and five undescribed Cryptococcus species in this study (Fig. 4). The type of Heterocephaclaria, H. solida (Berthier 1980), is morphologically similar to these two lichenicolous “Syzygospora” species, viz. basidia with up to four sterigmata, spores obliquely attached to sterigmata, both spores and sterigmata refractive at the point of attachment, and most likely belongs here.

Basidiocarps waxy to gelatinous in lichenicolous species. Hyphae thin-walled with clamp connections and haustorial branches. Holobasidia tubular or long with terminal sessile basidiospores. Sexual reproduction not observed in culture. True hyphae and pseudohyphae absent in culture. Budding cells present. Fermentation absent. Nitrate utilised. Starch-like compounds usually not produced. Major CoQ system not known.

Type species: Heterocephaclaria solida Berthier, Mycotonax 12: 114. 1980.
≡ Syzygospora solida (Berthier) Ginns, Mycologia 78: 632. 1986.

Notes: The genus Heterocephaclaria with one species, H. solida, was described by Berthier (1980) for a capitulate clavarioid fungus with partially cruciately septate apices of the basidium and secondary spores (i.e. conidia). This genus was treated as a synonym of the genus Syzygospora by Ginns (1986) based on the morphological similarity of H. solida with Syzygospora species. The type species of Syzygospora, S. alba, is located in a separate clade (Fig. 4). The emended genus Heterocephaclaria currently contains four described species (Table 1) and four additional sequences representing potential new species were obtained from public databases (Fig. 4).

New combinations for Heterocephaclaria

Heterocephaclaria arrabidensis (A. Fonseca, Scorzet & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813258.
Basionym: Cryptococcus arrabidensis A. Fonseca et al., Can. J. Microbiol. 46: 20. 2000.

Heterocephaclaria bachmannii (Diederich & M.S. Christ.) Millanes & Wedin, comb. nov. MycoBank MB813259.
Basionym: Syzygospora bachmannii Diederich & M.S. Christ., Bibl. Lichenol. 61: 30. 1996.

Heterocephaclaria physciacearum (Diederich) Millanes & Wedin, comb. nov. MycoBank MB813260.
Basionym: Syzygospora physciacearum Diederich, Bibl. Lichenol. 61: 38. 1996.

Syzygospora G.W. Martin, J. Wash. Acad. Sci. 27: 112. 1937.
≡ Christiansenia Hauerslev, Friesia 9: 43. 1969.

This genus is restricted to include the species in the clade represented by Syzygospora alba, the type species of the genus, as recognised in the tree drawn from the LSU D1/D2 dataset (Fig. 4).

Basidiocarps thin, gelatinous, subhyaline on the hymenial surface of the host or a cerebriform mass up to 12 cm diam. Hyphae with clamp connections present. Haustorial branches rather frequent, typically subglobose, arising from clamp connections. Basidia suburniform to cylindrical or clavate, 50–120 × 6–8 μm, holobasidiate or incompletely septate. Basidiospores broadly ellipsoid. Zygoconidia develop as two swellings, one on each side of the transverse septum in the conidiogenous cells.

Type species: Syzygospora alba G.W. Martin, J. Wash. Acad. Sci. 27: 112. 1937.

Notes: Syzygospora proved to be polyphyletic (Sampaio 2004, Milanes et al. 2011). The phylogenetic analysis of the expanded LSU rRNA gene sequence dataset in this study showed that Syzygospora effibulata formed a strongly supported clade with Tremella polyporina in Tremellales, while the other species of Syzygospora studied occurred in three separate clades in the Filobasidiaceae. Syzygospora bachmannii and S. physciacearum were assigned to the emended genus Heterocephaclaria as discussed above. Syzygospora sorana was located in a different clade together with Cryptococcus fidesensis and Filobasidium capsuligenum (see below). The type of the genus, S. alba, formed a well supported clade with Christiansenia (Syzygospora) pallida (Fig. 4). Both species form zygoconidia and are mycoparasitic on the hymenial surface of Corticiaceae (aphyllophoralean fungi) differing from the hosts of other Syzygospora species (Ginns 1986). Thus, the genus Syzygospora currently includes only S. alba and S. pallida (Table 1).

Piskurozymaceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, fam. nov. MycoBank MB812196.

Etymology: In reference to the name of the type genus Piskurozyma gen. nov.

This family is proposed for a strongly supported monophyletic lineage including the aerius (Solicoccozyma gen. nov.) and cylindricus (Piskurozyma gen. nov.) clades and a single-species clade Filobasidium capsuligenum in Filobasidiaceae resolved by the seven-gene dataset analysis (Fig. 1).

Basidiocarps absent. Pseudohyphae and true hyphae may be present. Clamp connections on dikaryotic hyphae occasionally present. Haustorial branches not present. Sexual reproduction with holobasidia. Budding cells present. Ballistoconidia absent. Fermentation usually absent. Nitrate usually utilised. The major CoQ system CoQ-10.

Type genus: Piskurozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Genera accepted: Piskurozyma gen. nov. and Solicoccozyma gen. nov.

Piskurozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, gen. nov. MycoBank MB812206.

Etymology: The genus is named in honour of the late Jure Piškur for his contribution to yeast genetics, physiology and evolutionary biology.

This genus is proposed for the cylindricus clade (Liu et al. 2015) containing three species previously classified in the genera...
Cryptococcus or Bullera as shown in the trees obtained from the seven-genes dataset. Phylogenetic analysis of the extended LSU rRNA gene dataset suggests close relationships with the teleomorphic species Filobasidium capsuligenum and Syzygospora sorana, and two recently described cryptococci, C. filicatus and C. fidesensis (Fig. 4).

Basidiomes, if present, within the hymenium of the host. Dikaryotic hyphae with clamp connections. Haustoria not reported. In culture true hyphae occur occasionally. Pseudohyphae absent. Sexual reproduction observed for some species. Holobasidia slender with terminal sessile basidiospores. Budding cells present. Ballistoconidia may be present. Fermentation occasionally present. Nitrate may be utilised. Starch-like compounds usually produced. Major CoQ system CoQ-10.

Type species: Piskurozyma cylindrica (A. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Notes: Filobasidium capsuligenum was regarded as a single-species clade because of its unique fermentative ability. However, the close relationship of this species with the cylindricus clade was resolved in the seven-genes tree with strong support (Liu et al. 2015). In the constrained ML tree from the expanded LSU rRNA sequence dataset, F. capsuligenum clustered together with a fungicolous species, Syzygospora sorana, and two recently published Cryptococcus species, namely C. filicatus (Golubev & Sampaio 2009) and C. fidesensis (Zhang et al. 2014). Therefore these species are assigned to the genus Piskurozyma gen. nov. This genus currently contains seven described species (Table 1) and two additional sequences representing potential new species were obtained from public databases (Fig. 4).

New combinations for Piskurozyma

Piskurozyma capsuligena (Fell, Statzell, I.L. Hunter & Phaff) A.M. Yurkov, comb. nov. MycoBank MB813122.
Basionym: Leucosporidium capsuligenum Fell et al., Antonie van Leeuwenhoek 35: 444. 1969.

Piskurozyma cylindrica (A. Fonseca, Scorzetti & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB812208.
Basionym: Cryptococcus cylindricus A. Fonseca et al., Can. J. Microbiol. 46: 22. 2000.

Piskurozyma fidesensis (T. Zhang & L.-Y. Yu) A.M. Yurkov, comb. nov. MycoBank MB813124.
Basionym: Cryptococcus fidesensis T. Zhang & L.Y. Yu, Int. J. Syst. Evol. Microbiol. 64: 675–679. 2013.

Piskurozyma filicatus (Golubev & J.P. Sampa.) Kachalkin, comb. nov. MycoBank MB814788.
Basionym: Cryptococcus filicatus Golubev & J.P. Sampaio, J. Gen. Appl. Microbiol. 55: 445. 2009.

Piskurozyma silvicola (Golubev & J.P. Sampa.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB812209.
Basionym: Cryptococcus silvicola Golubev & J.P. Sampa., Antonie van Leeuwenhoek 89: 48. 2006.

Piskurozyma sorana (Hauerslev) A.M. Yurkov, comb. nov. MycoBank MB813129.
Basionym: Syzygospora sorana Hauerslev, Op. bot. 100: 113. 1989.

Piskurozyma taiwanensis (Nakase, Tsuzuki & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB812207.
Basionym: Bullera taiwanensis Nakase et al., J. Gen. Appl. Microbiol. 48: 349. 2002.

Solicoccozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, gen. nov. MycoBank MB812197.

Etymology: In reference to the ecological origin of the species in this genus that are mostly isolated from soils.

This genus is proposed for the aerius clade (Fonseca et al. 2011, Liu et al. 2015) containing six anamorphic species previously belonging to the genus Cryptococcus (Liu et al. 2015).

Basidiocarps absent. Sexual reproduction with holobasidia may be present. Pseudohyphae and true hyphae occasionally produced. Clamp connections may be present on dikaryotic hyphae. Haustorial branches not observed. Budding cells present. Ballistoconidia absent. Fermentation absent. Nitrate utilised. Starch-like compounds usually not produced. The major CoQ system CoQ-10.

Type species: Solicoccozyma aeria (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.
Notes: The aerius clade on which the new genus is based was consistently resolved and strongly supported in the trees using different datasets (Fonseca et al. 2011, Liu et al. 2015, this study). The species of this genus are usually obtained from soils (Botha 2006, Fonseca et al. 2011, Yurkov et al. 2012). They frequently produce thick polyaccharide capsules and accumulate substantial amount of lipids (Tanimura et al. 2014). They have a pronounced ability to assimilate aldaric acids and low-weight aromatic compounds, such as L-malic, L-tartaric, saccharic, mucic, caffeic, gentisic, p-coumaric, protocatechuic and hydroxybenzoic acids (Fonseca et al. 2011). This genus currently contains six described species (Table 1).

New combinations for Solicoccozyma

Solicoccozyma aeria (Saito) A.M. Yurkov, comb. nov. MycoBank MB812198.
Basionym: Torula aeria Saito, Jap. J. Bot. 1: 41. 1922.

Solicoccozyma fuscescens (Golubev) A.M. Yurkov, comb. nov. MycoBank MB812201.
Basionym: Cryptococcus fuscescens Golubev, J. Gen. Appl. Microbiol. 39: 428. 1984.

Solicoccozyma keelungensis (C.F. Chang & S.M. Liu) A.M. Yurkov, comb. nov. MycoBank MB812202.
Basionym: Cryptococcus keelungensis C.F. Chang & S.M. Liu, Int. J. Syst. Evol. Microbiol. 58: 2974. 2008.
Solicoccozyma phenolicus (Á. Fonseca, Scorzetti & Fell) A.M. Yurkov, **comb. nov.** MycoBank MB812203. 

*Basionym:* Cryptococcus phenolicus Á. Fonseca et al., Can. J. Microbiol. 46: 24. 2000.

*Solicoccozyma terreus* (Di Menna) A.M. Yurkov, **comb. nov.** MycoBank MB812204. 

*Basionym:* Cryptoccus terreus Di Menna, J. Gen. Microbiol. 11: 195. 1954. 

= Cryptococcus himalayensis Gobo & Sugiyama, Can. J. Bot. 48: 2099. 1970. 

= Cryptococcus eilinovii Golubev, Mikol. Fitopatol. 13: 466. 1979.

*Solicoccozyma terricola* (T.A. Pedersen) A.M. Yurkov, **comb. nov.** MycoBank MB812205. 

*Basionym:* Cryptoccus terricola T.A. Pedersen, Bull. Jard. Bot. État Brux. 31: 101. 1958.

**Order Holtermanniales** Libkind, Wuczkowski, Turchetti & Boekhout, Int. J. Syst. Evol. Microbiol. 61: 685. 2011.

This order was proposed by Wuczkowski et al. (2011) to include the monotypic teleomorphic genus Holtermannia and the anamorphic genus *Holtermanniella*. The latter was proposed to accommodate four *Cryptococcus* species and a new anamorphic species closely related to *Holtermannia corniformis* (Wuczkowski et al. 2011). The order *Holtermanniales* was confirmed to be a distinct lineage in the trees from the seven-gene and the expanded LSU datasets with strong support values (Figs 1 and 2). The five anamorphic *Holtermanniella* species clustered together in a robust clade separate from the teleomorphic species *Holtermannia corniformis* (Figs 1 and 2). Therefore, the two genera *Holtermanniella* with one species and *Holtermanniella* with five species are accepted here (Table 1).

**Order Tremellales** Fries, Syst. mycol. 1: 2. 1821.

Tremellales is the largest order in Tremellomycetes and six families, namely Cuniculitremaceae, Tremellaceae, Sirobasidiales, Tetragoniomycetaceae, Phragmoxenidiaceae and Rhychogastreaceae containing yeast and yeast-like taxa have been proposed within this order (Metzler et al. 1989, Bandoni 1995, Wells & Bandoni 2001, Kirschner et al. 2001). This taxonomic concept included only teleomorphic species and was circumscribed based on basidial morphology, septal pore anatomy and basidiospore production (Bandoni 1995). The monotypic family *Phragmoxenidiaceae* was tentatively assigned to the Tremellales by Oberwinkler et al. (1990). The inclusion of this family in the order is still uncertain because molecular data are not available from this family (Bandoni 1995, Wells & Bandoni 2001). The *Phragmoxenidiaceae* species is therefore not included in this study. Previous phylogenetic analyses showed the paraphyletic nature of the families in Tremellales after the inclusion of anamorphic yeast and yeast-like taxa (Fell et al. 2001, Scorzetti et al. 2002, Sampaio 2004). We re-circumscribed the families and genera in Tremellales based on the multigene phylogeny (Liu et al. 2015) and the PRBO test performed in this study. A total of 11 families and 28 genera are accepted in Tremellales here (Table 1, Figs 1, 2 and 5).

**Bulleribasidiae** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB812215.

*Etyymology:* In reference to the name of the type genus *Bulleribasidium*.

This family is proposed to accommodate the monophyletic lineage containing the *Bulleribasidium*, *Derxomyces*, *Dioszegia*, *Hannaella*, *melastomae* and *dimennae* clades in the tree obtained from the seven genes (Liu et al. 2015).

Basidiocarps not present. Pseudohyphae and true hyphae may be present. Septal pore a dolipore with poorly developed parenthesome-like structures. Sexual reproduction observed in some species. Basidia cylindrical or occasionally globose, two-celled, with transverse and occasionally longitudinal septa, and globose basidiospores. Budding cells present. Ballistoconidia occasionally present. Fermentation absent. Nitration usually not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-9 or CoQ-10.

**Type genus:* Bulleribasidium* J.P. Sampaio, emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

Genera accepted: *Bulleribasidium*, *Derxomyces*, *Dioszegia*, *Hannaella*, *Nielozyma* gen. nov., and *Vishniacozyma* gen. nov.

**Notes:** Except for one teleomorphic species, *Bulleribasidium oberjochense*, all the species included in this family are known from the asexual states only.

*Bulleribasidium* J.P. Sampaio., M. Weiss & R. Bauer, Mycologia 94: 874. 2002. **emend.** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus *Bulleribasidium* is emended to accommodate the *Bulleribasidium* clade containing *B. oberjochense* and ten anamorphic species previously belonging to *Mingxiaea* (Liu et al. 2015).

Basidiocarps not present. Pseudohyphae and true hyphae may be present. Septa with dolipores with poorly developed parenthesome-like structures. Sexual reproduction observed in some species. Basidia cylindrical or occasionally globose, two-celled, with transverse and occasionally longitudinal septa, with globose basidiospores. Budding cells present. Ballistoconidia rotationally symmetrical.

*Type species:* *Bulleribasidium oberjochense* J.P. Samp., Gadanho, M. Weiss & R. Bauer, Mycologia 94: 875. 2002.

**Notes:** The teleomorphic genus name *Bulleribasidium*, which was proposed in 2002 (Sampaio et al. 2002) has nomenclatural priority over the anamorphic genus name *Mingxiaea* proposed in 2011 (Wang et al. 2011). The species of the latter are, therefore, transferred to the genus *Bulleribasidium*. Eleven species are currently accepted in this genus (Table 1, Fig. 5E).

**New combinations for Bulleribasidium**

*Bulleribasidium begoniae* (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB812218.
**Basionym**: Bullera begoniae Nakase et al., Mycoscience 45: 290. 2004.

≡ Mingxiaea begoniae (Nakase et al.) Q.-M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 213. 2011.

*Bulleribasidium folicola* (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB812232.

*Basionym*: Mingxiaea folicola Q.M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 217. 2011.

*Bulleribasidium hainanense* (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813261.

*Basionym*: Mingxiaea hainanensis Q.M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 215. 2011.

*Bulleribasidium panici* (Fungsin, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813262.

*Basionym*: Bullera panici Fungsin et al., Microbiol. Culture Coll. 19: 27. 2003.

≡ Mingxiaea panici (Fungsin et al.) Q.-M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 213. 2011.

*Bulleribasidium pseudovariabilis* (F.Y. Bai, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813263.

*Basionym*: Bullera pseudovariabilis F.Y. Bai et al., Antonie van Leeuwenhoek 83: 261. 2003.

≡ Mingxiaea pseudovariabilis (F.Y. Bai et al.) Q.-M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 214. 2011.

*Bulleribasidium sanyaense* (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813264.

*Basionym*: Mingxiaea sanyaensis Q.M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 214. 2011.

*Bulleribasidium setariae* (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813265.

*Basionym*: Bullera setariae Nakase et al., Mycoscience 45: 292. 2004.

≡ Mingxiaea setariae (Nakase et al.) Q.-M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 213. 2011.

*Bulleribasidium siamense* (Fungsin, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813266

*Basionym*: Bullera siamensis Fungsin et al., Microbiol. Culture Coll. 19: 29. 2003.

≡ Mingxiaea siamensis (Fungsin et al.) Q.-M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 214. 2011.

*Bulleribasidium variabile* (Nakase & M. Suzuki) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813267.

*Basionym*: Bullera variabilis Nakase & M. Suzuki, J. Gen. appl. Microbiol. 33: 350. 1987.

≡ Mingxiaea variabilis (Nakase & Suzuki) Q.-M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 214. 2011.

*Bulleribasidium wuzhishanense* (Q.M. Wang, F.Y. Bai, Boekhout & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813268.

*Basionym*: Mingxiaea wuzhishanensis Q.M. Wang et al., Int. J. Syst. Evol. Microbiol. 61: 218. 2011.

*Nielozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *gen. nov.* MycoBank MB813269.

**Etymology**: The genus is named in honour of C.B. van Niel for his pioneering contributions to the study of ballistoconidium-forming yeasts.

This genus is proposed for the *melastomae* clade recognised from the seven-genes phylogeny (Liu et al. 2015).

Basidiocarps not present. Colonies usually yellowish to brownish. Pseudohyphae and true hyphae not observed. Sexual reproduction not observed. Budding cells present. Ballistoconidia present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

**Type species**: *Nielozyma melastomae* (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

**Notes**: *Nielozyma* gen. nov. is closely related to the genus *Dioszegia* (Nakase et al. 2004, Liu et al. 2015). *Nielozyma* species usually form yellowish to brownish colonies (Nakase et al. 2004), being distinct from those of *Dioszegia* species that usually are orange-coloured (Wang & Bai 2008). This genus currently contains two described species (Table 1, Fig. 5E).

**New combinations for Nielozyma**

*Nielozyma formosana* (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813270.

*Basionym*: Bullera formosana Nakase et al., Syst. Appl. Microbiol. 27: 562. 2004.

*Nielozyma melastomae* (Nakase, Tsuzuki, F.L. Lee & M. Takash.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813271.

*Basionym*: Bullera melastomae Nakase et al., Syst. Appl. Microbiol. 27: 560. 2004.

*Vishniacozyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *gen. nov.* MycoBank MB813272.

**Etymology**: The genus is named in honour of the American microbiologist Helen S. Vishniac for her contributions to the study of microbial diversity and yeast ecology, especially of cold-adapted yeasts.

This genus is proposed for the *victoriae* (sensu Fonseca et al. 2011) and *dimennae* clades recognised in Boekhout et al. (2011a) and Liu et al. (2015).
Basidiocarps gelatinous, mycoparasitic. Hyphae thin-walled with clamp connections. H-shaped conidia (e.g. zygospores) may be present. Basidia not known. Basidia subglobose to ellipsoidal or clavate, with basal clamp connections, two- to four-celled, longitudinally or obliquely septa, with ellipsoidal basidiospores. Cultures are often pigmented, pinkish-white, orange-white or yellowish-white. Hyphae not observed in culture. Poorly developed pseudohyphae present. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia occasionally produced pseudohyphae present. Sexual reproduction not observed. Nitrate not utilised. Starch-like compounds weakly produced or not produced. Major CoQ system CoQ-9 or CoQ-10. Fermentation absent. Yeasts of this genus are widespread eurybionts and are often associated with plant material (Fonseca & Inocá 2008). This genus currently contains eleven described species (Table 1) and four additional sequences representing potential new species were obtained from public databases (Fig. 5D).

**Notes:** The *victoriae* clade (sensu Fonseca et al. 2011) coincides with the *dimennae* clade as recognised in Boekhout et al. (2011a) and Liu et al. (2015) and consists of six *Cryptococcus* and one *Butlera* species. In the tree derived from the expanded LSU rRNA gene sequence dataset, two teleomorphic mycoparasites *Trimorphomyces nebularis* and *Trichomomyces* sp. CBS 200.94 (Takashima et al. 2003, Kirschner & Chen 2008) and three recently published *Cryptococcus* species were also located in this clade (Fig. 5D). Yeasts of this genus are widespread eurybionts and are often found associated with plant material (Fonseca & Inocá 2006, Fonseca et al. 2011, Yurkov et al. 2015). A possible mycoparasitic nature has been suggested for these yeasts, which may have sexual trimorphomyces-like morphs (Kirschner & Chen 2008). This genus currently contains eleven described species (Table 1) and four additional sequences representing potential new species were obtained from public databases (Fig. 5D).

**New combinations for Vishniacozyma**

*Vishniacozyma globispora* (B.N. Johri & Bandoni) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813273.

*Vishniacozyma carnescens* (Verona & Luchetti) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813274.

*Vishniacozyma dimennae* (Fell & Phaff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813275.

*Vishniacozyma foliicola* (Q.M. Wang & F.Y. Bai) A.M. Yurkov, **comb. nov.** MycoBank MB813277.

*Vishniacozyma heimaeyensis* (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813278.

*Vishniacozyma nebularis* (Vishniac) A.M. Yurkov, **comb. nov.** MycoBank MB813279.

*Vishniacozyma psychrotolerans* (V. de García, Zalar, Brizio, Gunde-Cim. & van Brooock) A.M. Yurkov, **comb. nov.** MycoBank MB813281.

*Vishniacozyma peneaus* (Phaff, Mrak & O.B. Williams) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813282.

*Vishniacozyma taibaiensis* (Q.M. Wang & F.Y. Bai) A.M. Yurkov, **comb. nov.** MycoBank MB813283.

*Vishniacozyma tephrensis* (Vishniac) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813284.

*Vishniacozyma victoriae* (M.J. Montes, Belloch, Galiana, M.D. García, C. Andrés, S. Ferrer, Torr.-Rodr. & J. Guinea) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813285.

**Tremellaceae** Fr., Syst. mycol. 1: lv. 1821.

This family is re-delimited to accommodate only the *Tremella sensu stricto* (= mesenterica) clade circumscribed by the phylogenetic analyses of seven genes (Liu et al. 2015) and consists of ten *Tremella* species previously included in the mesenterica and fuciformis groups as distinguished by Chen (1998). Additionally, *Cryptococcus yokohamensis* is included in this family based on previous phylogenetic results by Alshahni et al. (2011) and results from the analysis of the expanded LSU rRNA gene sequence dataset (Fig. 5D).

The diagnosis of the family is based on the description of the genus *Tremella* as recircumscribed below.

**Type genus:** *Tremella* Pers. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

**Genus accepted:** *Tremella*.

**Notes:** This family was created by Fries (1821) to include fungi with gelatinous fruitbodies and was later restricted by Patouillard.
(1900) to genera with tremellloid basidia. Bandoni (1984) made a major revision of this family based on the ultrastructure of the septal pore and restricted the Tremellaceae to the genera Holtermannia, Tremella and Trimorphomyces. Later, three other genera, Bulleromyces, Sirotrema and Xenolachne, were also included in this family (Bandoni 1995, Wells & Bandoni 2001). Phylogenetic analyses indicated that the genera assigned to the Tremellaceae did not form a monophyletic group but occurred scattered in different lineages (Bandoni 1984, Fell et al. 2000, Scorzetti et al. 2002, Sampaio 2004, Boekhout et al. 2011a, Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015). This family is, therefore, re-defined here to include only the Tremella sensu stricto clade as presented in Liu et al. (2015) and as shown in Fig. 1.

Tremella Pers., Neues Mag. Bot. 1: 111. 1794, emend. Z.Y. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is re-delimited to include the species in the Tremella sensu stricto clade (= mesenterica clade) including the type species of the genus, T. mesenterica. This clade is circumscribed based on the seven-genes phylogeny (Liu et al. 2015).

Basidiocarps minute (0.3–0.5 cm in diameter) to large (to 5–10 cm high). Basidiocarps variable in colour, ranging from whitish-yellow, cream, yellowish-orange to brown, reddish or black. Clamp connections and haustorial branches present in dikaryotic hyphae. Basidia globose, subglobose, ellipsoid, oval, clavate or pyriform, two- or four-celled with longitudinal or oblique septa, occasionally with transverse septa. Basidiospores globose to ellipsoid. Budding cells originate from germinating basidiospores. Fermentation absent in yeast states. Nitrate not utilised. Major CoQ systems CoQ-9 or CoQ-10.

Type species: Tremella mesenterica (Schaeff.) Retz.

Notes: The genus Tremella as traditionally circumscribed is the largest polyphyletic genus in the order Tremellales (Weiss et al. 2014). Molecular phylogenetic analyses based on LSU rRNA gene sequences showed that Tremella species occurred in several distantly related clades (Fell et al. 2000, Scorzetti et al. 2002, Sampaio 2004, Bandoni & Boekhout 2011b, Boekhout et al. 2011a, Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015, also see Fig. 2 of this study) and should be re-classified. Here we re-define the genus Tremella to include only the species in the Tremella sensu stricto clade as recognised in the tree derived from seven genes (Liu et al. 2015). As discussed above, the Tremella sensu stricto clade showed a significant deviation from the reference thresholds in the PRBO analysis (Table 2) and two subclades, mesenterica and fuciformis, with distinguishable morphological characters could be identified within the clade as shown in Chen (1998) and Liu et al. (2015). These data imply that the Tremella sensu stricto clade probably can be reclassified into two genera in the future. At present, we prefer to keep them in the genus Tremella. The reclassification of the entire Tremella genus is unfeasible at present because even the D1/D2 LSU rRNA gene sequences are only available from less than half of the described Tremella species (Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015, this study).

An anamorphic yeast species, Cryptococcus yokohamensis, was recently described and showed a close relationship to the Tremella species in the Tremella sensu stricto clade (Alshahni et al. 2011). This species exhibits phenotypic characteristics similar to those of the yeast states of Tremella. Specifically, C. yokohamensis has two major coenzymes CoQ-9 and CoQ-10, being similar to T. mesenterica and T. coalescens (Alshahni et al. 2011). Thus, C. yokohamensis represents a yeast state of a species in the Tremella sensu stricto clade and is transferred to Tremella. The re-defined genus Tremella currently contains twelve species (Table 1, Fig. 5D).

New combination for Tremella

Tremella yokohamensis (Alshahni, Satoh & Makimura) A.M. Yurkov, comb. nov. MycoBank MB813286.

Basionym: Cryptococcus yokohamensis Alshahni et al., Int. J. Syst. Evol. Microbiol. 61: 3069. 2011.

Rhynchogastremataceae (Oberw. & B. Metzler) Syst. Appl. Microbiol. 12: 283. 1989, emend. X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov.

This family is emended to accommodate the well supported monophyletic lineage consisting of the aureus, Auriculibuller, Bandoniozyma, Papiliotrema, pseudoalba and laurentii clades as recognised in Liu et al. (2015).

Basidiocarps if present, minute. Sexual reproduction present in some species. Dikaryotic hyphae with clamp connections and haustorial branches. Basidia transversely septate, cylindrical, and in small clusters. Basidiospores globose or allantoid. In culture pseudohyphae and true hyphae occasionally present. Budding cells present. Ballistoconidia may be present. Fermentation present in some species. Nitrate not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-10 as far as known.

Type genus: Rhynchogastrema B. Metzler & Oberw. emend. Z.Y. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov.

Genera accepted: Rhynchogastrea emend, and Papiliotrema emend.

Notes: The family Rhynchogastremataceae was originally proposed for a heterobasidiomycetous species Rhynchogastrema coronatum (Metzler et al. 1989). The expanded LSU rRNA gene sequence analysis located this species in the Bandoniozyma clade (Fig. 5A). Therefore, the Rhynchogastremataceae is expanded here to include the species in the Bandoniozyma and closely related clades that formed a 100 % supported monophyletic lineage (Liu et al. 2015) as shown in Fig. 1.

Papiliotrema J. P. Sampaio., M. Weiss & R. Bauer, Mycologia 94: 875. 2002, emend. X.Z. Liu, F.Y. Bai, M. Groenew, & Boekhout, MycoBank MB813287.

This genus is emended to accommodate a well-supported monophyletic clade containing teleomorphic Papiliotrema and Auriculibuller species (Liu et al. 2015) as well as anamorphic yeasts including 16 Cryptococcus and three Bullera species (Table 1, Fig. 5A).
Basidiocarps, if present, minute, ca. 0.5 mm in diameter. Dikaryotic hyphae with clamp connections and haustorial branches. Basidia cylindrical and transversely septate. Cultures pale to brownish yellow. Pseudohyphae and true hyphae may be present. Budding cells present. Ballistoconidia may be present. Sexual reproduction observed in some species. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: *Papiliotrema bandonii* J. P. Sampaio., Gadanho, M. Weiss & R. Bauer, Mycologia 94: 875. 2002.

Notes: The species assigned to the emended genus *Papiliotrema* were located in the *Aureus*, *Auriculibuller*, *laurentii*, *Papiliotrema* and *pseudoalba* clades in the seven-genes phylogenetic tree (Liu et al. 2015). In order to avoid creating genera for these small clades, we decided to combine them in a single genus. The PRBO test did not show significant deviation for the emended *Papiliotrema* generic concept (Table 2), supporting this taxonomic treatment. The genus *Papiliotrema* was proposed in 2002 (Sampaio et al. 2002), thus having nomenclature priority over *Auriculibuller*, which was proposed in 2004 (Sampaio et al. 2004). The genera *Auriculibuller* and *Papiliotrema* are morphologically similar and their sexual states form clavate basidia with transverse septa, differing clearly from those formed by *Tremella* species (Sampaio et al. 2002, 2004, Sampaio 2011c). Twenty-two species are currently accepted in the emended genus *Papiliotrema* (Table 1, Fig. 5A).

New combinations for *Papiliotrema*

*Papiliotrema anemochoreius* (C.H. Pohl, Kock, P.W.J. van Wyk & Albertyn) Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813287.

Basionym: Cryptococcus anemochoreius C.H. Pohl et al., Int. J. Syst. Evol. Microbiol. 56: 2705. 2006.

*Papiliotrema aurea* (Saito) M. Takash., Sugita, Shinoda & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813288.

Basionym: Torula aurea Saito, Mitt. Jpn. J. Bot. 1: 44. 1922. ≡ Cryptococcus aureus (Saito) M. Takash. et al., Int. J. Syst. Evol. Microbiol. 53: 1192. 2003.

*Papiliotrema aspenensis* (K. Ferreira-Paim, T.B. Ferreira, L. Andrade-Silva, D.J. Mora, D.J. Springer, J. Heitman, F.M. Fonseca, D. Matos, M.S.C. Melhem & M.L. Silva-Vergara) X.Z. Liu, F.Y. Bai, A.M. Yurkov & Boekhout *comb. nov.* MycoBank MB814710.

Basionym: Cryptococcus aspenensis K. Ferreira-Paim et al., PLoS ONE 9: e108633. 2014.

*Papiliotrema baii* (A.M. Yurkov, M.A. Guerreiro & Á. Fonseca) A.M. Yurkov, *comb. nov.* MycoBank MB813648.

Basionym: Cryptococcus baii A.M. Yurkov et al., PLoS One 10: e0120400. 2015.

*Papiliotrema flavescens* (Saito) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813289.

Basionym: Torula flavescens Saito, Jap. J. Bot. 1: 43. 1922. ≡ Cryptococcus flavescens (Saito) C.E. Skinner, Am. Midl. Nat. 43: 249. 1950.

*Papiliotrema fonsecae* (V. de Garcia, Zalar, Braizzi, Gunde-Cim. & van Brollck) A.M. Yurkov, *comb. nov.* MycoBank MB813290.

Basionym: Cryptococcus fonsecae V. de Garcia et al., FEMS Microbiol. Ecol. 82: 536. 2012.

*Papiliotrema frias* (V. de Garcia, Zalar, Braizzi, Gunde-Cim. & van Brollck) A.M. Yurkov, *comb. nov.* MycoBank MB813292.

Basionym: Cryptococcus frisae V. de Garcia et al., FEMS Microbiol. Ecol. 82: 537. 2012.

*Papiliotrema fuscus* (J.P. Samp., J. Inácio, Fonseca & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813432.

Basionym: Auriculibuller fuscus J.P. Samp. et al., Int. J. Syst. Evol. Microbiol. 54: 989. 2004.

*Papiliotrema hoabinhensis* (D.T. Luong, M. Takash., Ty. Dung & Nakase) A.M. Yurkov, *comb. nov.* MycoBank MB813293.

Basionym: Bullera hoabinhensis D.T. Luong et al., J. Gen. Appl. Microbiol. 51: 340. 2005.

*Papiliotrema japonica* (J.P. Samp., Fonseca & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813294.

Basionym: Bullera japonica J.P. Samp. et al., Int. J. Syst. Evol. Microbiol. 54: 990. 2004.

*Papiliotrema laurentii* (Kuff.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813295.

Basionym: Torula laurentii Kuff., Ann. Soc. Roy. Sci. Méd. Natur. Brux. 74: 38. 1920. ≡ Cryptococcus laurentii (Kuff). C.E. Skinner, Am. Midl. Nat. 43: 249. 1950.

*Papiliotrema mangalensis* (Fell, Statzell & Scorza) A.M. Yurkov, *comb. nov.* MycoBank MB813296.

Basionym: Cryptococcus mangalensis Fell et al., Antonie van Leeuwenhoek 99: 548. 2011.

*Papiliotrema nemorosus* (W.I. Golubev, Gadanho, J.P. Samp. & N.W. Golubev) X.Z. Liu, F.Y. Bai, A.M. Yurkov & Boekhout, *comb. nov.* MycoBank MB813298.

Basionym: Cryptococcus nemorosus W.I. Golubev et al., Int. J. Syst. Evol. Microbiol. 53: 907. 2003.

*Papiliotrema perniciosus* (W.I. Golubev, Gadanho, J.P. Samp. & N.W. Golubev) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813299.

Basionym: Cryptococcus perniciosus W.I. Golubev et al., Int. J. Syst. Evol. Microbiol. 53: 910. 2003.

*Papiliotrema pseudoalba* (Nakase & M. Suzuki) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813300.

Basionym: Bullera pseudoalba Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 32: 131. 1986. ≡ Cryptococcus celluloxyticus Nakase et al., J. Gen. Appl. Microbiol 42: 9. 1996.
**Papiliotrema ruineniae** (A.M. Yurkov, M.A. Guerreiro & Á. Fonseca) A.M. Yurkov, comb. nov. MycoBank MB813649. 
*Basionym*: Cryptococcus ruineniae A.M. Yurkov et al., PLoS One 10: e0120400. 2015.

**Papiliotrema rajasthanensis** (Saluja & G.S. Prasad) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813301.
*Basionym*: Cryptococcus rajasthanensis Saluja & G.S. Prasad, Int. J. Syst. Evol. Microbiol. 57: 417. 2007.

**Papiliotrema taeanensis** (K.S. Shin & Y.H. Park) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813302.
*Basionym*: Cryptococcus taeanensis K.S. Shin & Y.H. Park, Int. J. Syst. Evol. Microbiol. 55: 1367. 2005.

**Papiliotrema terrestris** (Crestani, Landell, Faganello, Vainstein, Vishniac & P. Valente) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813303.
*Basionym*: Cryptococcus terrestris Crestani et al., Int. J. Syst. Evol. Microbiol. 59: 635. 2009.

**Papiliotrema wisconsinensis** (K. Sylvester, Q.M. Wang & C.T. Hittinger) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB815284.
*Basionym*: Cryptococcus wisconsinensis K. Sylvester et al., FEMS Yeast Res. 15: 7. 2015.

**Rhynchogastrema** B. Metzler & Oberw., Syst. Appl. Microbiol. 12: 281. 1989. *emend.* X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov.

This genus is emended to include species classified in the anamorphic genus *Bandoniozyma* and is based on the phylogenetic analyses of the seven-gene (Liu et al. 2015) and the expanded LSU rRNA gene datasets (Fig. 5A).

Basidiocarps not present. Dikaryotic hyphae thin-walled with clamp connections and haustorial branches. Septa with doli-pores and parenthesomes of cup-shaped vesicles of the Tremella-type. Sexual reproduction observed in some species. Basidium with basally swollen probasidium, elongated to sub-globose, with apex of the neck partly cruciately septate. Budding cells present, globose, subglobose, ovoid or ellip-soidal. Ballistoconidia not produced. Pseudohyphae and true hyphae with clamp connections may be present in cultures. Fermentation of glucose usually present. Nitrate not utilised. Starch-like compounds are usually formed. Major CoQ system not known.

**Type species**: *Rhynchogastrema coronatum* B. Metzler & Oberw., Syst. Appl. Microbiol. 12: 281. 1989.

**Notes**: The species of the recently described anamorphic genus *Bandoniozyma* (Valente et al. 2012) formed a well-supported clade in the trees obtained from the analyses of the rRNA ITS (Valente et al. 2012) and the sequences of seven genes studied (Liu et al. 2015). Sequences of the D1/D2 region of the LSU rRNA gene of *Rhynchogastrema coronatum*, the type species of the teleomorphic genus (Metzler et al. 1989), were independently obtained for the type specimen BBA 65155 (GenBank KJ170152) by Weiss et al. (2014) and the ex-type culture DSM 28188 (deposited in DSMZ collection by Bertold Metzler) by Andrey Yurkov (GenBank LNB70267). The sequences derived from both sources are identical. Phylogenetic analysis showed that *Rhynchogastrema coronatum* was nested within the genus *Bandoniozyma* with 99 % and 92 % bootstrap support in ML and MP analyses, respectively (Fig. 5A), suggesting that *Bandoniozyma* species represent yeast stages of *Rhynchogastrema* species. Based on the nomenclatural priority principle, the name *Rhynchogastrema* is selected for this genus. A fermentative species, *Cryptococcus nanyangensis*, was described by Hui et al. (2012). This species was closely related to a group of unnamed *Cryptococcus* strains, which were assigned to the genus *Bandoniozyma* by Valente et al. (2012). The ML tree from the expanded LSU rRNA dataset confirmed that *C. nanyangensis* clustered together with *Bandoniozyma* and *Rhynchogastrema* species (Fig. 5A). The former is therefore transferred to the genus *Rhynchogastrema*. Nine species are currently accepted in this genus (Table 1, Fig. 5A). The yeast states of most species of this genus can ferment glucose, which is an unusual trait among basidiomyceotous yeasts.

**New combinations for *Rhynchogastrema***

**Rhynchogastrema aquatica** (Brandao, Valente, Pimenta & Rosa) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, comb. nov. MycoBank MB813305.
*Basionym*: *Bandoniozyma aquatica* Brandao et al., PLoS One 7: e46060. 2012.

**Rhynchogastrema complexa** (Landell, Pagnocca, Sette, Pas-sarin, Garcia, Ribeiro, Lee, Brandao, Rosa & Valente) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, comb. nov. MycoBank MB813306.
*Basionym*: *Bandoniozyma complexa* Landell et al., PLoS One 7: e46060. 2012.

**Rhynchogastrema fermentans** (Lee) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, comb. nov. MycoBank MB813307.
*Basionym*: *Bandoniozyma fermentans* C.F. Lee, PLoS One 7: e46060. 2012.

**Rhynchogastrema glucofermentans** (S.O. Suh & Blackwell) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, comb. nov. MycoBank MB813308.
*Basionym*: *Bandoniozyma glucofermentans* S.O. Suh & Blackwell, PLoS One 7: e46060. 2012.

**Rhynchogastrema nanyangensis** (F.L. Hui & Q.H. Niu) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, comb. nov. MycoBank MB813309.
*Basionym*: *Cryptococcus nanyangensis* F.L. Hui & Q.H. Niu, Curr. Microbiol. 65: 619. 2012.

**Rhynchogastrema nouitii** (Boekhout, Fell, Scorzzett & Theelen) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, comb. nov. MycoBank MB813304.
Basionym: Bandoniozyma noutii Boekhout et al., PLoS One 7: e46060. 2012.

Rhynchosgastrema tunnelae (Boekhout, Fell, Scorzetti & Theelen) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, comb. nov. MycoBank MB813310.
Basionym: Bandoniozyma tunnelae Boekhout et al., PLoS One 7: e46060. 2012.

Rhynchogastrema viseragradiensis (Peter & Dlauchy) X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov, comb. nov. MycoBank MB813311.
Basionym: Bandoniozyma viseragradiensis Peter & Dlauchy, PLoS One 7: e46060. 2012.

Bulleraceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, fam. nov. MycoBank MB813328.

Etymology: In reference to the name of the type genus Bullera.

This family is proposed to accommodate a monophyletic lineage formed by the *amyloyliticus* (i.e. Genolevuria gen. nov.), *Bulleromyces* and *hannae* (i.e. Bullera emend.), and *formiform* clades and four single-species lineages, namely Cryptococcus allantoinivorans (Pseudotremella), *C. mujuenis* (Fonsecazyma), *Sirobasidium intermedium* and *Tremella giraffa* in the tree obtained from the seven-genes dataset (Liu et al. 2015).

Basidiocarps tremella-like, 1–2 cm in diameter. Dikaryotic hyphae with clamp connections and haustorial branches. Sexual reproduction observed in some species. Basidia transversely, obliquely or longitudinally septate. Basidiospores globose, fusiform to narrowly clavate. Budding cells present. Pseudohyphae occasionally present. Ballistoconidia may be present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10 as far as known.

Type genus: Bullera Derr emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Genera accepted: Bullera emend., Fonsecazyma gen. nov., Genolevuria gen. nov., and Pseudotremella (Table 1, Fig. 1).

Notes: In the constrained ML tree inferred from the expanded LSU rRNA gene dataset, the *Tremella* species in Clade I of Millanes et al. (2011) were assigned to the new family Bulleraceae though bootstrap support was lacking (Figs 2 and 5B). Cryptococcus allantoinivorans was incorporated into the *formiform* clade together with two newly added species. A new genus *Pseudotremella* is proposed for this expanded clade (Fig. 5B). Cryptococcus mujuenis and the recently described species *Cryptococcus tronadorensis* and *Kwniella betulae* formed a well supported clade for which a new genus Fonsecazyma is proposed (Fig. 5B). The *Sirobasidium intermedium* lineage was expanded to contain two more species, namely *Sirobasidium brefeldianum* and *Tremella exigua*, which correspond to *Tremella clade I* in Millanes et al. (2011). The *Tremella giraffa* lineage was expanded with eight *Tremella* species corresponding to *Tremella clade III* in Millanes et al. (2011). We recommend reclassifying *Sirobasidium* and *Tremella* species in this family, as well as *Biatoropsis* (Fig 5B) when additional molecular data are available from all or the majority of the species of these three basidiocarp-forming genera.

Cryptococcus cuniculi was described by Shin et al. (2006) as a member of the *Kwniella* clade showing some relatedness to *Kwniella* (Cryptococcus) heveanensis as well as Cryptococcus tronadorensis in de Garcia et al. (2012). These results were not supported in our analyses, and *C. cuniculi* clustered close to *Tremella clade I* in Millanes et al. (2011) in the expanded LSU rRNA gene analysis (Fig. 5B). In our opinion, this species should be re-classified together with respective species of *Biatoropsis*, *Sirobasidium* and *Tremella*. Currently, we propose to keep it unclassified as Cryptococcus cuniculi pro tem. until additional molecular data is available. Similarly, two *Tremella* species were not assigned to any clade in the expanded LSU rRNA gene analysis (Fig. 5B) as well as in the combined rRNA genes analysis (Millanes et al. 2011). Thus, we recommend keeping them unclassified as *Tremella haematommati* pro tem. and *Tremella ramalinae* pro tem. until additional molecular data are available.

Bullera Derr, Annls Mycol. 28: 11. 1930. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

= Bulleromyces Boekhout & A. Fonseca, Antionie van Leeuwenhoek 59: 91. 1991.

This genus is emended to include the species in the *Bulleromyces* and *hannae* clades recognised from the multigene phylogeny (Liu et al. 2015).

Basidiocarps absent. Sexual reproduction observed in some species. Dikaryotic hyphae with clamp connections and haustorial branches. Basidia subglobose, clavate or ovoid, and transversely, obliquely or longitudinally septate. Budding cells present. Ballistoconidia rotationally or bilaterally symmetrical. Pseudohyphae not observed. Fermentation absent. Nitrate not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-10.

Type species: *Bullera alba* (W.F. Hanna) Derrx.

Notes: The genus *Bullera* as circumscribed by Boekhout et al. (2011b) contained more than 40 species, which occurred distributed in many different clades of different orders (Fell et al. 2000, Scorzetti et al. 2002, Boekhout et al. 2011a, Weiss et al. 2014, Liu et al. 2015). The sexual state of the type species *Bullera alba* was discovered by Boekhout et al. (1991) and *Bulleromyces albus* as the teleomorph of this species was consequently described. According to the “One fungus = One name” principle implemented in the Code of Nomenclature for algae, fungi, and plants (McNeill et al. 2012), the genus name *Bullera* has nomenclatural priority over *Bulleromyces*. The genus *Bullera* emend. currently includes four species (Table 1, Fig. 5B), which were located into two closely related clades in the tree obtained from the seven-genes dataset (Liu et al. 2015). Though these species show a significant deviation from the reference threshold (Table 2), they are kept in the genus *Bullera* at present to accommodate their phenotypic similarity and close phylogenetic relationship and to minimise name changes.

Fonsecazyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, gen. nov. MycoBank MB813136.

Etymology: The genus is named in honour of the Portuguese mycologist Alvaro Fonseca, for his contributions to the study of diversity and systematics of basidiomycetous yeasts.
This genus is proposed for the clade represented by Cryptococcus mjujenis, which was resolved as a single-species lineage in the seven-genes tree (Liu et al. 2015) and was supplemented by two newly described species Cryptococcus tronadorensis (de Garcia et al. 2012) and Kwonientaelae (Sylvester et al. 2015) in the LSU rRNA gene tree (Fig. 5C).

Basidiocarps unknown. Sexual reproduction has not been observed. Pseudohyphae and true hyphae have not been observed. Budding cells present. Ballistoconidia are not formed. Fermentation absent. Nitrate not utilised. Major CoQ system is CoQ-10.

**Type species: Fonsecazyma mjujenis** (K.S. Shin & Y.H. Park) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout comb. nov.

**Notes:** The phylogenetic analysis of the seven-gene dataset in Liu et al. (2015) indicated that Cryptococcus mjujenis was closely related to *Sirobasidium intermedium*. Cryptococcus tronadorensis was originally described as a new species related to the *Kwonientaelae* clade based on the LSU rRNA gene sequences similarity in de Garcia et al. (2012). Similarly, the recently described *Kwonientaelae* (Sylvester et al. 2015) was also placed in this clade. Unfortunately, *C. mjujenis* was not employed in these studies. In the tree obtained from the expanded LSU rRNA gene dataset, *C. mjujenis*, *C. tronadorensis* and *K. betulae* formed a strongly supported clade, which was only distantly related to the *Kwonientaelae* and the *S. intermedium* clades (Fig. 5C). Thus, the new genus *Fonsecazyma* is proposed to accommodate these three species (Table 1). Other sequences obtained from public databases belong to a mislabelled *K. heveanensis* (GenBank AF406890) and three undescribed *Cryptococcus* species (Fig. 5C).

**New combinations for Fonsecazyma**

*Fonsecazyma betulae* (K. Sylvester, Q.M. Wang, C. T. Hittinger) A.M. Yurkov, A.V. Kachalnik & Boekhout, **comb. nov.** MycoBank MB814752.

**Basionym:** *Kwonientaelae* K. Sylvester et al., FEMS Yeast Res. 15: 7. 2015.

*Fonsecazyma mjujenis* (K.S. Shin & Y.H. Park) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813341.

**Basionym:** *Cryptococcus mjujenis* K.S. Shin & Y.H. Park, Int. J. Syst. Evol. Microbiol. 56: 2243. 2006.

*Fonsecazyma tronadorensis* (V. de Garcia, Zalar, Brizzio, Gunde-Cim. & van Brook) A.M. Yurkov, **comb. nov.** MycoBank MB813342.

**Basionym:** *Cryptococcus tronadorensis* V. de Garcia et al., FEMS Microbiology Ecology. 82: 536. 2012.

**Genolevuria** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813329.

**Etymology:** The genus is named in honour of the French yeast genomics consortium “Genolevures” that produced high-quality yeast genome data.
connections and occasionally haustorial branches. Basidia globose, ellipsoidal, obovoid, pyriform or capitate; four-celled with longitudinal to oblique septa. Budding cells sometimes present. Poorly developed pseudohyphae sometimes present. Fermentation absent. Nitrate not utilised. Major CoQ system unknown.

**Type species:** Pseudotremella moriformis (Berk.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

**Notes:** In the tree obtained from the seven-genes dataset, Tremella moriformis and Cryptococcus allantoinivorans clustered together with strong BP and PP support values, though they were regarded as representing single-species lineages (Liu et al. 2015). In the tree from the expanded LSU rRNA gene dataset (Fig. 5B), the Tremella species in the moriformis clade recognised in Chen (1998) and Cryptococcus allantoinivorans formed a monophyletic clade together with a recently described species, Cryptococcus lacticolor (Satoh et al. 2013). Thus, we propose the new genus Pseudotremella to accommodate this clade. Four species are currently accepted in this genus (Table 1, Fig. 5B).

It should be noted that a sequence of Tremella indecorata AM5 derived from specimen Santos s.n. was located in the moriformis clade, being in agreement with Millanes et al. (2011). However, three strains obtained from different specimens of the species from different origin and hosts, CBS 6976, originated from Salix sp., HBZ194 and DSM 5727 (both from Diatrype sp. growing on Sorbus aucuparia twigs, Germany), constituted a separate clade distantly related to the moriformis clade (Fig. 5A). However, strain CBS 6976 is placed with support closely related to Pseudotremella in an unconstrained LSU-based tree – together also with strains HBZ194 and DSM 5727 (data not shown). This represents a conflict with the placement of CBS 6976 in the seven-genes tree (Liu et al. 2015), where it is located in the aurantia clade (=Naematelia). This conflict should be further investigated in the future. Specimen AM5 and strain CBS 6976 are in any case not conspecific. Strain AM5 differs from strain HBZ194 by 7 % (42/613 bp) nucleotide divergence in the LSU rRNA gene sequence, which suggest that Tremella indecorata constitutes a species complex. A taxonomic revision for T. indecorata cannot be made until the species concept of this species and the strains and sequences belonging to it are verified. Thus, we keep this species unassigned to any lineage as Tremella indecorata pro tem. (Table 1).

**New combinations for Pseudotremella**

Pseudotremella allantoinivorans (Middelhoven) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813335.

Basionym: Cryptococcus allantoinivorans Middelhoven, Antonie van Leeuwenhoek 87: 103. 2004.

Pseudotremella lacticolor (Satoh & Makimura) A.M. Yurkov, **comb. nov.** MycoBank MB813337.

Basionym: Cryptococcus lacticolor Satoh & Makimura, Antonie van Leeuwenhoek 104: 90. 2013.

Pseudotremella moriformis (Berk.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813338.

Basionym: Tremella moriformis Berk., in Smith, Engl. Fl., Fungi (Edn 2) (London) 34: tab. 2446. 1836.

Pseudotremella nivalis (Chee J. Chen) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813340.

Basionym: Tremella nivalis Chee J. Chen, Bibl. Mycol. 174: 101. 1998.

Sirobasidiaceae Lindau, Engler & Prantl, Nat. Pflanzenfam., Teil. I (Leipzig) 1: 89. 1897.

The family Sirobasidiaceae was proposed by Möller (1895) and validated by Lindau to accommodate the genus Sirobasidium. Fibulobasidium was the second genus assigned to this family (Bandoni 1979, Bandoni 1995, Wells & Bandoni 2001). Sirobasidiaceae are characterised by basidia arranged in linear chains (Sirobasidium) or in clusters (Fibulobasidium), which form passively released basidiospores. Phylogenetic studies indicated that the Fibulobasidium species formed a well-supported monophyletic clade while Sirobasidium species belonged to divergent lineages in the Tremellales (Bandoni et al. 2011, Liu et al. 2015). Sirobasidium magnun and S. japonicum formed a monophyletic lineage with the genus Fibulobasidium (Fig. 5B), whereas S. brefeldianum and S. intermedium grouped with Tremella exigua in the Buller-aceae (Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015, Fig. 5B). The phylogenetic position of the type species of Sirobasidium, S. sanguineum, is unknown because sequence data were not available for this species. Therefore, it is difficult to re-delineate the genus Sirobasidium at present. We suggest to maintain the family Sirobasidiaceae for the monophyletic lineage formed by the genus Fibulobasidium and the two Sirobasidium species (Figs 1 and 5B).

Cuniculitremaceae J.P. Sampaio., R. Kirschner & M. Weiss, Antonie van Leeuwenhoek 80: 155. 2001

Type genus: Cuniculitrema J.P. Sampaio. & R. Kirshner, Antonie van Leeuwenhoek 80: 155. 2001 (synonym of Sterigmatosporidium).

Genera accepted: Fellomyces, Kockovaella and Sterigmatosporidium (Table 1, Fig. 1).

Notes: The family Cuniculitremaceae was proposed by Kirschner et al. (2001) to accommodate the teleomorphic genus Cuniculitrema and two anamorphic genera, Fellomyces and Kockovaella, based on their close phylogenetic relationship and the common morphological feature of producing conidia on stalks. Cuniculitrema was described for the teleomorph of Sterigmatosporidium (Kirschner et al. 2001). The latter was proposed by Kraepelin & Schulze (1982) and has nomenclatural priority over the former. Therefore, Cuniculitrema is treated as a synonym of Sterigmatosporidium here.

Fellomyces Y. Yamada & I. Banno, J. Gen. Appl. Microbiol., Tokyo 30: 524. 1984.

This genus is restricted to accommodate the Fellomyces clade as recognised in Liu et al. (2015) based on the analysis of the seven-genes dataset.
Basidiocarps unknown. Sexual reproduction not observed. Pseudohyphae and true hyphae may be present. Blastocoonidia at the top of stalk-like conidiophores. Budding cells present. Ballistoconidia not present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: Fellomyces polyborus (D.B. Scott & Van der Walt) Y. Yamada & I. Banno, J. Gen. Appl. Microbiol. 30: 524. 1984.

Notes: This genus as previously delimited contained twelve species (Lopandic et al. 2011) but the Fellomyces clade recognised in Liu et al. (2015) included only four Fellomyces species. The support for the affinity of F. horovitziae to this clade in the seven-genes tree was weak (Liu et al. 2015). This species differs in physiological characteristics when compared to other Fellomyces species (Lopandic et al. 2011). We maintain this species in the emended genus Fellomyces for the time being to avoid creating a monotypic genus. This genus currently contains four species (Table 1, Fig. 5D).

Kockovaella Nakase, I. Banno & Y. Yamada, J. Gen. Appl. Microbiol., Tokyo 37: 178. 1991. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is emended to accommodate the Kockovaella clade as recognised in Liu et al. (2015), which includes non-ballistoconidium-forming species previously belonging to the genus Fellomyces.

Basidiocarps unknown. Sexual reproduction not observed. Pseudohyphae absent or poorly developed. True hyphae not observed. Blastocoonidia separate from the parental cells at the distal end of stalk-like conidiophores. Budding cells present. Ballistoconidia may be present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type species: Kockovaella thailandica Nakase, I. Banno & Y. Yamada, J. Gen. Appl. Microbiol. 37: 178. 1991.

Notes: The Kockovaella clade recognised in Liu et al. (2015) includes eight Fellomyces species and all currently recognised eleven Kockovaella species (Takahashia & Nakase 2011). As previously circumscribed, the genus Kockovaella was differentiated from the genus Fellomyces only by the production of ballistoconidia (Takahashia & Nakase 2011), a property that has since long been shown to be an unstable character (Nakase et al. 1993). The PRBO test, however, indicated that the genus is significantly more divergent than the genera that more divergent than the genera that are utilised. Major CoQ system CoQ-10.

New combinations for Kockovaella

Kockovaella chinensis (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813343.

Basionym: Fellomyces chinensis Prillinger et al., Syst. Appl. Microbiol. 20: 579. 1997.

Kockovaella distylii (Hamam., Kuroy. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813344.

Basionym: Fellomyces distylii Hamam. et al., Int. J. Syst. Bacteriol. 48: 290. 1998.

Kockovaella fuzhouensis (J.Z. Yue) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813345.

Basionym: Sterigmatomyces fuzhouensis J.Z. Yue, Acta Mycol. Sin. 1: 81. 1982.

Kockovaella lichenicola (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813346.

Basionym: Fellomyces lichenicola Prillinger et al., Syst. Appl. Microbiol. 20: 582. 1997.

Kockovaella mexicana (Lopandic, O. Molnár & Prillinger) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813347.

Basionym: Fellomyces mexicanus Lopandic et al., Microbiol. Res. 160: 8. 2005.

Kockovaella ogasawarensis (Hamam., Kuroy. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813348.

Basionym: Fellomyces ogasawarensis Hamam. et al., Int. J. Syst. Bacteriol. 48: 289. 1998.

Kockovaella sichuanensis (Prillinger, G. Kraep. & Lopandic) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813349.

Basionym: Fellomyces sichuanensis Prillinger et al., Syst. Appl. Microbiol. 20: 582. 1997.

Kockovaella prillingeri X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, sp. nov. MycoBank MB813350 Holotype: CBS 7552.

≡ Fellomyces thailandicus Prillinger et al., Syst. Appl. Microbiol. 20: 583. 1997.

Notes: The name Kockovaella thailandica, which is the type species of the genus Kockovaella, already exists. Thus a new name Kockovaella prillingeri is proposed for Fellomyces thailandicus as this species has to be transferred to the genus Kockovaella and a new combination using the epithet ‘thailandicus’ is not possible in this genus. The new name is proposed in honour of Hansjörg Prillinger who discovered and described the species Fellomyces thailandicus.

Sterigmatosporidium G. Kraep. & U. Schulze, Antonie van Leeuwenhoek 48: 479. 1963.

≡ Cuniculitrema J. P. Sampaio & R. Kirschner, Antonie van Leeuwenhoek 80: 155. 2001.

Notes: The name Sterigmatosporidium was described before Cuniculitrema and thus has nomenclatural priority. The genus has only one species, S. polymorphum with the name C. polymorpha listed as synonym (Table 1).
**Naemateliaceae** X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, fam. nov. MycoBank MB813351.

**Etymology**: In reference to the name of type genus *Naematelia*.

This family is proposed to accommodate a monophyletic lineage consisting of the *aurantia* clade formed by four *Tremella* species and a single-species clade represented by *Cryptococcus cistialbidi* as resolved in the seven-genes tree (Liu et al. 2015).

Basidiocarps when formed caespitose, tuberculate or spherical to thick foliaceous or crumpled, inorny, yellow, bright orange, reddish. Basidia subglobosse, globose to ovoid, four-celled and with vertical or occasionally transverse septa. Orange-pigmented colonies may be present. True hyphae with clamp connections and haustorial branches sometimes present. Budding cells present. Ballistoconidia sometimes present. Fermentation absent. Nitrate and nitrite not utilised. Major CoQ system CoQ-10.

**Type genus**: *Naematelia* Fr.

**Genera accepted**: *Naematelia* and *Dimennazyma*.

**Notes**: The species *Bullera arundinariae* branched before the *aurantia* clade and *Cryptococcus cistialbidi* in the seven-genes Bayesian tree, but this phylogenetic relationship was not supported (Liu et al. 2015). Thus, it is not included in the new family *Naemateliaceae*. *C. cistialbidi* occurred at different positions in the ML and NJ trees obtained from the seven-genes dataset (Liu et al. 2015). Possible relationship of the *Tremella Clade II* species (e.g. *T. cladiobae*, *T. lepogii*, *T. phaeophysci*) with the *aurantia* clade was shown in the analyses of rRNA genes (Millanes et al. 2011, Liu et al. 2015, Fig. 5A in this study). But the affinity lacked support in rRNA gene analyses. The taxonomic assignment of the Clade II species remains to be determined. A strain representing *T. indecora* in Liu et al. (2015) was placed close to Clade II species in the expanded LSU rRNA gene tree (Fig. 5A).

**Naematelia** Fr., Obs. Myc. 2: 370. 1818.

This genus is resurrected to accommodate species in the *aurantia* clade (Chen 1998, Millanes et al. 2011, Liu et al. 2015).

Basidiocarps caespitose, tuberculate or spherical to thick foliaceous or crumpled, inorny, yellow, bright orange, reddish. Basidia subglobosse, globose to ovoid, four-celled and with vertical or occasionally transverse septa. True hyphae with clamp connections and haustorial branches present. Budding cells present. Ballistoconidia sometimes present. Fermentation absent. Nitrate and nitrite not utilised. Major CoQ system CoQ-10.

**Type species**: *Naematelia encephala* (Pers.) Fr., Observ. mycol. (Havniae) 2: 370. 1818.

**Basionym**: *Tremella encephala* Pers., Syn. meth. fung. (Göttingen) 2: 623. 1801.

**Notes**: The genus contains four species previously classified as *Tremella* (Chen 1998, Millanes et al. 2011, Liu et al. 2015). These species formed a strongly supported monophyletic clade in the trees from the seven-genes (Liu et al. 2015) and expanded LSU datasets (Fig. 5A), and also in an unconstrained LSU tree (data not shown).

**New combinations for Naematelia**

*Naematelia aurantalba* (Bandoni & M. Zang) Millanes & Wedin, comb. nov. MycoBank MB813352.

Basionym: *Tremella aurantalba* Bandoni & M. Zang, Mycologia 82: 270. 1990.

*Naematelia microspora* (Lloyd) Millanes & Wedin, comb. nov. MycoBank MB813357.

Basionym: *Tremella microspora* Lloyd, Mycol. Writ. 6 (Letter 64): 991. 1920.

*Dimennazyma* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, gen. nov. MycoBank MB813339.

**Etymology**: The genus is named in honour of M. E. di Menna for her pioneering work on yeast ecology and diversity.

This genus is proposed to accommodate the single-species lineage *Cryptococcus cistialbidi* in the tree derived from the seven-genes dataset (Liu et al. 2015).

Basidiocarps not present. Colonies usually orange-coloured. Pseudohyphae occasionally present. True hyphae not observed. Budding cells present. Ballistoconidia not observed. Fermentation absent. Nitrate not utilised. Starch-like compounds weakly produced or not produced. Major CoQ system CoQ-10.

**Type species**: *Dimennazyma cistialbidi* (Â. Fonseca, J. Inácio & Spenc.-Mart.) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout comb. nov. MycoBank MB814753.

Basionym: *Cryptococcus cistialbidi* Â. Fonseca et al., FEMS Yeast Res. 5: 1177. 2005.

**Notes**: The species *Cryptococcus cistialbidi* formed a single-species branching before the *aurantia* clade (i.e. *Naematelia* gen. nov.) with strong support in the seven-genes tree (Liu et al. 2015). This species produces orange-coloured colonies as emphasised by Inácio et al. (2005), which is different from the yeast stage of the *Naematelia* species that have yellowish brown colonies. Thus *C. cistialbidi* is not assigned to *Naematelia*. The colony colour of *C. cistialbidi* is similar to those produced by the genus *Genolevuria* (i.e. the *amolylyticus* clade in Fonseca et al. 2011). However, *C. cistialbidi* was distantly related to *Genolevuria* in the seven-genes tree (Liu et al. 2015). Therefore, we propose a new genus for this single-species lineage.

**Carcinomycetaceae** Oberw. & Bandoni, Nordic Jl Bot. 2: 507. 1982. emend. A.M. Yurkov.

Basidiocarps mycoparasitic, forming a thin layer on the surface of host. Basidia subglobosse or cylindrical, longitudinally or cruciately septated, with four sterigmata. Budding cells present. Ballistoconidia occasionally present. Pseudohyphae and true hyphae not observed in culture. Sexual reproduction not
observed in culture. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type genus: Carcinomycyes Oberw. & Bandoni.

Genus accepted: Carcinomycyes.

Notes: Oberwinkler & Bandoni (1982) proposed the family Carcinomycetaceae to accommodate three mycoparasitic genera Carcinomycyes, Christiansenia and Syzygospora. While the type genus of this family is placed in the order Tremellales, two other genera are phylogenetically related to Filobasidiales (Millanes et al. 2011, Fig. 2 of this study). A close relationship between the genus Carcinomycyes (Syzygospora effulibata) and Tremella polyborina was shown previously in the analysis of the combined rRNA dataset (Millanes et al. 2011). In the present study a well-supported clade formed by Bullera arundinariae, Syzygospora effulibata and Tremella polyborina was resolved in the expanded LSU rRNA gene tree (Fig. 5D). The species B. arundinariae was the only member of this clade included in the seven-genes phylogenetic analysis in Liu et al. (2015). B. arundinariae branched before the aurantia clade (i.e. Naematelia) and Cryptococcus cistialbidi (i.e. Dimennazyma) in the seven-genes Bayesian tree, but this phylogenetic relationship was not supported (Liu et al. 2015). Thus, we prefer to classify these genera into two different families, Naematellaceae (Naematelia and Dimennazyma) and Carcinomycetaceae (Carcinomycyes).

Carcinomycyes Oberw. & Bandoni, Nordic Jl Bot. 2: 507. 1982. emend. A.M. Yurkov.

This genus is resurrected and emended to accommodate a well-supported clade formed by Bullera arundinariae, Syzygospora effulibata and Tremella polyborina in the expanded LSU rRNA gene tree (Figs 2 and 5D). The diagnosis of Carcinomycyes is based on the description of the family Carcinomycetaceae.

Type species: Carcinomycyes effulibatus (Ginns & Sunhede) Oberw. & Bandoni, Nordic Journal of Botany 2: 509. 1982.

≡ Christiansenia effulibata Ginns & Sunhede, Bot. Notiser 131: 168. 1978.
≡ Syzygospora effulibata (Ginns & Sunhede) Ginns. Mycologia 78: 626. 1986.

Notes: Carcinomycyes was proposed by Oberwinkler & Bandoni (1982) to accommodate two species transferred from Christiansenia, namely Ch. mycophila and Ch. effulibata, with the latter being the type species. Ginns (1986) treated Carcinomycyes, Christiansenia and Heterocerephalacria as synonyms of Syzygospora. Molecular phylogenetic analyses showed that the genus Syzygospora sensu Ginns (1986) was polyphyletic (Millanes et al. 2011, also see Fig. 2 of this study). As discussed above, S. alba (type of Syzygospora) and Ch. pallida (type of Christiansenia) were located in a clade within the Filobasidiales, while S. effulibata (= Ch. effulibata) was located in a well supported clade together with Bullera arundinariae and Tremella polyborina in the Tremellales (Fig. 2). Therefore, the genus Carcinomycyes is resurrected here for this clade. The taxonomic assignment of the genus Carcinomycyes in Tremellales remains to be determined as discussed above. The affinity of Carcinomycyes (Christiansenia) mycophila with this genus needs to be confirmed using molecular data.

New combinations for Carcinomycyes

Carcinomycyes arundinariae (Fungsin, M. Takash. & Nakase) A.M. Yurkov, comb. nov. MycoBank MB813361. Basionym: Bullera arundinariae Fungsin et al., Microbiol. Culture Coll. 18: 86. 2002.

Carcinomycyes polyborina (D.A. Reid) A.M. Yurkov, comb. nov. MycoBank MB813362. Basionym: Tremella polyborina D.A. Reid, Trans. Br. Mycol. Soc. 55: 416. 1970.

Trimorphomycetaceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, fam. nov. MycoBank MB813363.

Etymology: In reference to the name of the type genus Trimorphomycyes.

This family is proposed for a well-supported monophyletic lineage including the flavus clade and Trimorphomycyes papilionaceus, Bullera miyagiana and B. sakaeratica (Liu et al. 2015).

Basidiocarps minute, pubescent up to 2 mm diameter, watery-gelatinous, milky to faintly greenish. H-shaped dikaryotic conidia form dikaryotic hyphae with clamp connections and haustorial branches. Alternatively, these conidia germinate with paired blastogenous conidia. Basidia tremella-like, narrowly clavate, pyriform to stalked capitulate, and four-celled. Basidiospores bud or form ballistoconidia. In culture, true hyphae may form extensively. Budding cells present, with polar or multilateral budding. Ballistoconidia occasionally present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type genus: Trimorphomycyes Bandoni & Oberw.

Genera accepted: Trimorphomycyes, Carlosrosaea, Saitozyma and Sugitzyma.

Notes: The species assigned to Trimorphomycsetaceae also formed a monophyletic lineage in the tree obtained from the expanded LSU rRNA gene dataset, but bootstrap support was lacking (Fig. 5D). Two lichenicolous Tremella species (T. diploschistina and T. parmeilariam) are only loosely connected with other species and we therefore refrain from including them in any family until additional molecular data are available. Contrarily, Bullera ninhbinhensis clustered together with Cryptococcus podzolicus with strong support (Fig. 5E) and we thus suggest to include this species in the family. In the original description Bullera vrieseae (Landell et al. 2015) was placed together with Bullera sakaeratica and B. miyagiana in a well-supported clade, which is resolved in this study as members of the family Trimorphomycetaceae (Fig. 5E). Relationships between the three Bullera species were not supported in our analyses. Bullera sakaeratica was closely related to Trimorphomycyes papilionaceus with strong support, while B. miyagiana and B. vrieseae were located in significantly diverged branches with unresolved positions (Fig. 5E), suggesting that they represent independent lineages in the family Trimorphomycetaceae. Thus, we propose new genera for B. vrieseae and B. miyagiana. The phylogenetic relationships of Tremella diploschistina and T. parmeilariam with other species were also not resolved in our analyses. We do not reclassify the two sexual species and leave...
them temporary as *T. diploschistina* pro tem and *T. parmelianum* pro tem.

**Trimorphomyces** Bandoni & Oberw., Syst. Appl. Microbiol. 4: 106. 1983. emend. X.Z. Liu, F.Y. Bai, M. Groenew., Boekhout & A.M. Yurkov.

This genus is emended to include an anamorphic yeast species *Bullera sakaeratica*, which is closely related to the type species of *Trimorphomyces* (Liu et al. 2015, Fig. 5E in this study).

Basidiocarps mycoparasitic, small, watery-gelatinous. Hyphae with clamp connections and haustorial branches may be present. Basidia narrow clavate, pyriform to capitate, four-celled, longitudinally or obliquely septa. Basidiospores subglobose. H-shaped zygoconidia may be present. Budding cells present. Ballistoconidia occasionally present. Sexual reproduction not observed in culture. Fermentation absent. Starch-like compounds weakly produced or not formed. Major CoQ system CoQ-10.

**Type species:** *Trimorphomyces papilionaceus* Bandoni & Oberw., Syst. Appl. Microbiol. 4: 106. 1983.

**Notes:** The close relationship between *T. papilionaceus* and *B. sakaeratica* was shown in different studies (Boekhout et al. 2011a, Weiss et al. 2014, Liu et al. 2015). As discussed above, these species were treated as two single-species lineages in Liu et al. (2015) due to the consideration that the former is morphologically unique (Bandoni & Boekhout 2011a). The separation of *Trimorphomyces* species in distantly related clades and the close relationships of some *Trimorphomyces* species with some *Cryptococcus* and *Bullera* species as shown in the tree obtained from the expanded LSU rRNA gene dataset (Fig. 5D, E) suggested that the phenotypically circumscribed genus *Trimorphomyces* is polyphyletic and that *Trimorphomyces* species may have a common yeast stage. Therefore, we transfer *B. sakaeratica* to the genus *Trimorphomyces* here. Another described *Trimorphomyces* species, *T. nebularis* (Kirschner & Chen 2008), is transferred to the genus *Vishniacozyma* gen. nov. *Trimorphomyces papilionaceus* forms zygoconidia from a single conidiogenous cell, differing from *T. nebularis* (*Vishniacozyma nebularis* comb. nov.) which produces zygoconidia from two neighbouring conidiogenous cells (Bandoni & Oberwinkler 1983, Kirschner & Chen 2008). The genus *Trimorphomyces* currently contains two species (Table 1, Fig. 5E).

**New combinations for *Saitozyma***

**Saitozyma ninhibinhensis** (Luong, M. Takash., Dung & Nakase) A.M. Yurkov, **comb. nov.** MycoBank MB813370. Basionym: *Bullera ninhibinhensis* Luong et al., J. Gen. Appl. Microbiol. 6: 335–342. 2002.

**Saitozyma paraflava** (Golubev & J.P. Samp.) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813372. Basionym: *Cryptococcus paraflava* Golubev & J.P. Samp., J. Gen. Appl. Microbiol. 50: 68. 2004.

**Saitozyma podzolica** (Babeva & Reshetova) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813373. Basionym: *Candida podzolica* Babeva & Reshetova, Mikrobiologiya, Seriya B 44: 333. 1975.

**Sugitazyma** A. M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB814754. **Etymology:** The genus is named in honour of the Japanese yeast taxonomist Takashi Sugita.

This genus is proposed for the single-species lineage *Bullera miyagiana* resolved in the tree inferred from seven genes (Liu et al. 2015) and the expanded LSU rRNA gene dataset (Fig. 5E).

Basidiocarps not known. Pseudohyphae and true hyphae may be present. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia may be present. Fermentation
absent. Nitrate not utilised. Starch-like compounds produced. Major CoQ system CoQ-10.

Type species: Sugitazyma miyagiana (Nakase, Itoh, Takem. & Bandoni) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb nov. Mycobank MB814755.

Basionym: Bullera miyagiana Nakase et al., J. Gen. Appl. Microbiol. 36: 35. 1990.

Notes: Relationships between Bullera miyagiana and other Trichomycetaceae remained unclear in the expanded analysis of the LSU rRNA gene sequences (Fig. 5E). We propose to erect a new genus for this single-species lineage to restrict the genus Bullera to the type lineage in the family Bulleraceae. The genus Sugitazyma currently contains one species (Table 1).

Carlosrosaea A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, gen. nov. Mycobank MB814756.

Etymology: The genus is named in honour of the Brazilian yeast taxonomist and ecologist Carlos A. Rosa.

This genus is proposed for the single-species lineage Bullera vrieseae resolved in the tree inferred from the expanded LSU rRNA gene dataset (Fig. 5E).

Basidiocarps not known. Pseudoophyphae and true hyphae not observed in culture. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia may be observed in culture. Sexual reproduction not observed. Basidiospores not known. Pseudoophyphae and true hyphae present or not, but present after mating. Basidia one-celled, cylindrical, clavate, capitate with four chains of acropetal basidiospores, or globose to ovoid with longitudinal and transverse septa. Basidiospores passively released, variably shaped, smooth or somewhat rough bacilliform, ellipsoid, globose, oblong-pentagonal or obpyriform to cylindrical. Budding cells usually present, but may be absent. Fermentation absent. Nitrate not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-9 or CoQ-10.

Type genus: Cryptococcus Vuillemin

Genera accepted: Cryptococcus and Kwniella.

Notes: The family Cryptococcaceae was originally established to contain anamorphic tremellomycetous yeasts, including the genera Bullera, Cryptococcus, Fellomyces, Kockovaelia, Trichosphorus, Tschuchiya and Udeniomyces (Kützing 1833, Van der Walt 1987). Molecular phylogenetic studies indicated that this family and most of the genera assigned to it are not monophyletic (Wells 1994, Fell et al. 2000, Scorsetti et al. 2002, Sampaio 2004, Liu et al. 2015). Based on the seven-genes phylogeny (Liu et al. 2015), the family Cryptococcaceae is emended here to accommodate only two emended genera Cryptococcus and Kwniella (Tables 1 and 2, Fig. 1).

Cryptococcus Vuillemin, Rev. Gén. Sci. Pures Appl. 12: 741. 1901. Nomen Cons. (McNeil et al. 2006), emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout. = Filobasidiella Kwon-Chung, Mycologia 67: 1198. 1975. = Tschuchiya Yamada, Kawasaki, Itoh, Banno et Nakase, J. Gen. Appl. Microbiol. 34: 509. 1988.

This genus is emended to accommodate the Cryptococcus clade described in Findley et al. (2009), Liu et al. (2015) and the LSU rRNA gene tree (Fig. 5C), and includes the species belonging to the C. neoformans/C. gattii complex, Filobasidiella depauperata and F. lutea.

Basidiocarps not present. True hyphae may be present, but present after mating. Basidia one-celled, slender, cylindrical sphaeropedunculate. Basidiospores in four long basipetal chains, smooth, or somewhat rough bacilliform, ellipsoid, globose, oblong-pentagonal or obpyriform. Haustorial branches present or not. Budding cells usually present, but in some species also absent. Thick polysaccharide capsules may be present. Fermentation absent. Nitrate and nitrite not utilised. Starch-like compounds usually produced. Major CoQ system CoQ-9 or CoQ-10.

Type species: Cryptococcus neoformans (Sanfelice) Vuillemin, Rev. Gén. Sci. Pures Appl. 12: 747–750. 1901.

Notes: The generic name Cryptococcus was originally created by Kützing (1833) for an organism placed among the algae and only one species C. mollis was included, but the description of this species was not presented. Vuillemin (1901) recircumscribed Cryptococcus to include pathogenic yeasts and transferred Saccharomyces neoformans to this genus. The genus Cryptococcus has been conserved with C. neoformans as the type species as proposed by Fell et al. (1989). Many molecular
phylogenetic studies have shown that Cryptococcus as circum-
scribed until now (Fonseca et al. 2011) is a highly artificial genus that contains species distributed in all five major lineages of Tremellomyces (Takashima & Nakase 1999, Fell et al. 2000, Scorzetti et al. 2002, Sampaio 2004, Fonseca et al. 2011, Weiss et al. 2014, Liu et al. 2015). The teleomorphic genus Filobasidiella was described by Kwon-Chung (1975) for the perfect state of C. neoformans. Four species are currently accepted in the genus Filobasidiella (Kwon-Chung 2011). Filobasidiella bacillispora was described for the sexual stage of serotypes B and C of C. neoformans (Kwon-Chung 1976). Two other Filobasidiella species, F. depauperata and F. lutea, are mycoparasites but lack ontogenetic yeast states. The affinity of F. depauperata with the Cryptococcus/Filobasidiella clade has been shown in different studies (Sivakumaran et al. 2002, Findley et al. 2009, Rodriguez-Carres et al. 2010, Boekhout et al. 2011a, Weiss et al. 2014, Liu et al. 2015). Sequence analy-
yses of the ITS regions and SSU rRNA gene showed that F. lutea belongs to the Cryptococcus/Filobasidiella clade (Sivakumaran et al. 2002). Unfortunately, the sequence data from this species are neither available from GenBank, nor from other databases, nor from these authors. Filobasidiella xianghuijin is the fifth species described in the genus (Zang 1999), but the taxonomic and phylogenetic position of this species re-
ains to be confirmed by molecular means (Kwon-Chung 2011). Recently, a sexual cycle with a tetrapolar mating system was found in C. amylolentus (Findley et al. 2012). So far, all the species in the Cryptococcus/Filobasidiella clade have been shown to have similar sexual forms. The C. neoformans/C. gattii complex was recently revised and presently contains seven species (Hagen et al. 2015). In that paper it was also suggested that the anamorph name Cryptococcus should have priority over the teleomorph name Filobasidiella (Kwon-Chung 1975) as the former has nomenclatural priority, is much more commonly used and, importantly, refers to the name of an important infectious disease, cryptococcosis, that is caused by species of this genus (Heitman et al. 2011). Thus, the Filobasidiella species without a yeast state are transferred here to Cryptococcus. Fonseca et al. (2011) considered Tschiayea wingfieldii (basionym Ster-
gigmatomyces wingfieldii) a synonym of C. amylolentus because of similar SSU, ITS and LSU D1/D2 sequences. This point of view is supported by similar sequences of four protein-coding genes (Liu et al. 2015). Phylogenetic analysis of four MAT related genes, STE3, STE20, SX11a and LPD1 indicated minor differ-
ences between T. wingfieldii and C. amylolentus (Findley et al. 2012). Thus, further studies are needed to fully under-
stand the taxonomic relationship between these two species. Ten species are currently accepted in this genus (Table 1).

New combinations for Cryptococcus

Cryptococcus depauperatus (Petch) Boekhout, Liu, Bai & M. Groenew., comb. nov. MycoBank MB813376.
Basionym: Aspergillus depauperatus Petch, Trans. Br. Mycol. Soc. 16: 245. 1932 (‘1931’).
≡ Filobasidiella depauperata (Petch) Samson et al., Antonie van Leeuwenhoek 49: 454. 1983.
= Filobasidiella arachnophila Malloch et al., Can. J. Bot. 56: 1823. 1978.

Notes: The close relatedness between this species and C. neoformans (cited as F. neoformans) was shown by SSU rRNA gene sequence analysis (Kwon-Chung et al. 1995). Multilocus phylogenetic analysis using ITS, TEF-1 alpha and RP51 sequences corroborated these conclusions and found the species related to C. neoformans (cited as var. grubii), C. deneformans (cited as var. neoformans), C. gattii (cited as VGI) and C. deuterogatti (cited as VGI1) (Rodriguez-Carres et al. 2010). Another study using six genes (the above with addition of RP52, mitSSU and the D1/D2 domains of LSU rDNA) showed that also Tschiayea wingfieldii and Cryptococcus amylolentus were phylogenetically related (Findley et al. 2009).

Cryptococcus luteus (Roberts) Boekhout, Liu, Bai & M. Groenew., comb. nov. MycoBank MB814758.
Basionym: Filobasidiella lutea Roberts, Mycotoxan 60, 199. 1997.

Notes: This species could not be studied by molecular means due to the absence of a culture. The close relatedness between this species, C. neoformans (cited as Filobasidiella neoformans) and C. depauperatus (cited as Filobasidiella depauperata) was shown by sequence analysis of ITS and SSU rRNA gene fragments (Sivakumaran et al. 2002).

Kwoniella Statzell-Tallman & Fell, FEMS Yeast Res. 8: 107. 2008. emend. X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout.

This genus is emended to include the species of the Kwoniella clade containing K. mangroviensis and six anamorphic species previously classified in Bulliera and Cryptococcus (Liu et al. 2015).

Basidiocarps unknown. Sexual reproduction with tetrapolar mating system observed in some species. Basidia polymorphic, lageniform, globose to ovoid with longitudinal and transverse septa. Basidiospores passively released, globose, ovoid to cy-
lindrical. Pseudohyphae and true hyphae may be present. Budding cells present. Ballistoconidia occasionally present. Fermentation absent. Nitrate not utilised. Starch-like compounds are usually produced. Major CoQ system CoQ-10.

Type species: Kwoniella mangroviensis Statzell, Belloch & Fell, FEMS Yeast Res. 8: 107. 2008.

Notes: The genus Kwoniella was proposed for a teleomorphic yeast K. mangroviensis isolated from mangrove habitats (Statzell-Tallman et al. 2008). The second species of the genus, K. heveanensis, was proposed for the teleomorph of Crypto-
coccus heveanensis (Sun et al. 2011). Recently, two tele-
omorphic species, K. europaea and K. botswanensis, closely related to K. mangroviensis were described (Guerreiro et al. 2013). All sexual species displayed a tetrapolar mating sys-
tem (Guerreiro et al. 2013). Since the use of a dual nomen-
clature for classification of sexual and asexual morphs of fungi was recently terminated, three asexual species were described in the genus Kwoniella, K. shandongensis (Chen et al. 2012), K. newhampshirensis and K. betulae (Sylvester et al. 2015). The Kwoniella clade was consistently resolved in different studies (Findley et al. 2009, Boekhout et al. 2011a, Guerreiro et al. 2013, Weiss et al. 2014, Liu et al. 2015). However, the affinity of Cryptococcus cuniculi to this clade remains contro-
versial. Boekhout et al. (2011a) and Weiss et al. (2014) showed that this species belonged to the Kwoniella clade according to LSU rRNA gene sequence analyses, but Liu et al. (2015)
showed that C. cuniculi branched before the Cryptococcus and Kwoniella clades in an analysis of combined SSU, ITS and LSU rRNA gene sequences. In the tree obtained from the expanded LSU rRNA gene dataset in this study, C. cuniculi was located in a branch distantly related to the Kwoniella clade (Fig. 5B, C). Thus, the final phylogenetic position of C. cuniculi remains to be determined. The recently described K. betulae was also placed outside the genus Kwoniella in a well-supported clade (i.e. Fonsecazyma gen. nov.) containing C. mujensis and C. tronadoraes (Fig. 5C). Eleven species are accepted in Kwoniella emend. in this study (Table 1) and three sequences representing potential new species were obtained from public databases (Fig. 5C). Kwoniella species are usually saprobic and differ from the closely aligned pathogenic yeasts in the genus Cryptococcus emend. by their inability to grow at 37 °C (Findley et al. 2009).

New combinations for Kwoniella

Kwoniella dendrophila (Van der Walt & D.B. Scott) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813381.

Basionym: Bullera dendrophila Van der Walt & D.B. Scott, Antonie van Leeuwenhoek 36: 384. 1970.

Kwoniella bestiolae (Thanh, Hai & Lachance) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813383.

Basionym: Cryptococcus bestiolae Than et al., FEMS Yeast Res. 6: 301. 2006.

Kwoniella dejecticola (Thanh, Hai & Lachance) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813384.

Basionym: Cryptococcus dejecticola Than et al., FEMS Yeast Res. 6: 303. 2006.

Kwoniella pini (Golubev & Pfeiffer) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813387.

Basionym: Cryptococcus pinus Golubev & Pfeiffer, Int. J. Syst. Evol. Microbiol. 58: 1970. 2007.

Kwoniella Shivajii (S.R. Ravella, S.A. James, C.J. Bond, I.N. Roberts, K. Cross, Retter & P.J. Hobbs) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813389.

Basionym: Cryptococcus shivajii S.R. Ravella et al., Curr. Microbiol. 60: 14. 2010.

Phaeotremellaceae A.M. Yurkov & Boekhout, fam. nov. MycoBank MB813390.

Etymology: In reference to the name of the type genus Phaeotremella.

This family is proposed to accommodate the foliacea clade and a single-species lineage, Cryptococcus spencermartinsiae (Liu et al. 2015).

Basidiocarps, if present, foliaceous with caposeptate lobes, gelatinous, tan to cinnamon or light brown when fresh, drying dark brown to black. Hyphae with clamp connections; haustorial branches occasionally present. Basidia globose, subglobose, ovoid or ellipsoidal, four-celled and with longitudinal to diagonal or transverse septa. Basidiospores subglobose to broadly ellipsoid. Budding cells present in culture. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Type genus: Phaeotremella Rea

Genera accepted: Phaeotremella and Gelidatrema.

Notes: The foliacea clade was resolved as early branching Tremellales in the seven-genes Bayesian tree without PP support; however, in the seven-genomes ML and NJ trees, this clade was branching prior to the Tremellales and Trichosporonales lineages (Liu et al. 2015). The foliacea clade was also resolved as a well-supported monophyletic group in the trees constructed from rRNA genes datasets, but its position varied. In the tree from the combined SSU, ITS-5.8S and LSU datasets, the foliacea clade is branching before the Tremellales and Trichosporonales lineages in Millanes et al. (2011), but between these two lineages in Liu et al. (2015). In the trees from the LSU rRNA genes dataset containing more filamentous fruitbody-forming taxa, this clade located within the Tremellales (Boekhout et al. 2011a. Weiss et al. 2014), but as a group (equivalent to Phaeotremella) branching before the order in this study (Fig. 1). The affinity of Cryptococcus spencermartinsiae to Phaeotremellaceae fam. nov. remains to be confirmed. It branches before the foliacea clade with strong to moderate support in the Bayesian and ML trees obtained from the seven-genes dataset, but it occurred in a branch distantly related to this clade in the combined rRNA genes tree (Liu et al. 2015). In the tree from the expanded LSU dataset, C. spencermartinsiae branched more early than the foliacea (Phaeotremella) clade, but without bootstrap support (Fig. 5C). Furthermore, this species is not able to grow above 25 °C in contrast to the other species in the foliacea clade (Phaeotremella gen. nov.) that can grow at 30 °C. Thus, we propose to accommodate it in the new genus Gelidatrema gen. nov.

Phaeotremella Rea, Trans. Br. Mycol. Soc. 3: 377. 1912. emend. A.M. Yurkov & Boekhout.

Type species: Phaeotremella pseudofoliacea Rea, Trans. Br. Mycol. Soc. 3: 377. 1912.

= Tremella foliacea Pers., Observationes mycologicae 2: 98. 1800.

This genus is resurrected and emended to accommodate the foliacea clade (Chen 1998, Boekhout et al. 2011a, Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015, also see Fig. 5B).

Basidiocarps, if present, foliaceous with caposeptate lobes, gelatinous, tan to cinnamon or light brown when fresh, drying dark brown to black. Hyphae with clamp connections; haustorial branches occasionally present. Basidia globose, subglobose, ovoid or ellipsoidal, four-celled and with longitudinal to diagonal or transverse septa. Basidiospores subglobose to broadly ellipsoid. In culture budding cells sometimes present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

Notes: Phaeotremella was described by Rea (1912) including only Phaeotremella pseudofoliacea, which was considered a synonym of Tremella foliacea (Roberts 1999). As discussed
above, the foliacea clade was consistently resolved as a well-supported clade in different studies using various datasets, though its phylogenetic position varied (Chen 1998, Boekhout et al. 2011a, Millanes et al. 2011, Weiss et al. 2014, Liu et al. 2015, this study Fig. 1). Seven species, including two Cryptococcus and five Tremella species were included in this clade with 100 % bootstrap support (Fig. 1) and therefore are transferred to Phaeotremella (Table 1).

New combinations for Phaeotremella

**Phaeotremella fagi** (Middelhoven & Scorzetti) A.M. Yurkov & T. Boekhout, comb. nov. MycoBank MB813391. 
*Basionym:* Cryptococcus fagi Middelhoven & Scorzetti, Antonie van Leeuwenhoek 90: 63. 2006.

**Phaeotremella simplex** (H.S. Jacks. & G.W. Martin) Millanes & Wedin, comb. nov. MycoBank MB813392. 
*Basionym:* Tremella simplex H.S. Jacks. & G.W. Martin, Mycologia 32: 687. 1940.

**Phaeotremella skinneri** (Phaff & Carmo Souza) A.M. Yurkov & T. Boekhout, comb. nov. MycoBank MB813393. 
*Basionym:* Cryptococcus skinneri Phaff & Carmo Souza, Antonie van Leeuwenhoek 28: 205. 1962.

**Phaeotremella mycetophiloides** (Kobayasi) Millanes & Wedin, comb. nov. MycoBank MB813394. 
*Basionym:* Tremella mycetophiloides Kobayasi, Sci. Rep. Tokyo Bunrika Daig., Sect. B 4: 13. 1939.

**Phaeotremella mycophaga** (G.W. Martin) Millanes & Wedin, comb. nov. MycoBank MB813395. 
*Basionym:* Tremella mycophaga G.W. Martin, Mycologia 32: 686. 1940.

**Phaeotremella neofoliacea** (Chee J. Chen) Millanes & Wedin, comb. nov. MycoBank MB813396. 
*Basionym:* Tremella neofoliacea Chee J. Chen, Bibl. Mycol. 174: 135. 1998.

**Gelidatrema** A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, gen. nov. MycoBank MB814759. 
*Etymology:* In reference to the origin of this psychrophilic yeast and its phylogenetic relatedness to the order Tremellales.

This genus is proposed for the single-species lineage Crypto- cocci spencermartinsiae as resolved in the seven-genes tree (Liu et al. 2015) and the expanded LSU rRNA gene tree (Fig. 5C).

Basidiocarps not know. Pseudohyphae and true hyphae not observed in culture. Sexual reproduction not observed in culture. Budding cells present. Ballistoconidia absent. Fermentation absent. Nitrate not utilised. This family has a pronounced ability to assimilate aromatic compounds. Major CoQ system CoQ-9 or CoQ-10.

**Type genus:** Trichosporon Behrend.

*Genera accepted:* Trichosporon, Apiotrichum emend., Cutaneotrichospor gen. Nov., Effusiotrichospor gen. Nov., Haglerozyma gen. Nov., and Vanrij.

**Notes:** Trichosporonaceae was introduced to include the Trichosporon species that were assigned to Geotrichoides and Proteomyces (Nannizi 1934). The scope of this family has been expanded by the discovery of more Trichosporon species
(Sugita & Nakase 1998, Colombo et al. 2011), but was also reduced by the exclusion of the genus Geotrichum, an ascomycetous genus that also forms arthroconidia (Weijman 1979). Some Cryptococcus species also belonged to this clade. Thus, this family is amended to accommodate a monophyletic lineage consisting of the brassicae/gracile, cutaneum, haglerorum, humicola (i.e. Vanija pro parte), porosum, and Trichosporon clades, as well as four single-species clades of three Cryptococcus species and one Trichosporon species as recognised in Liu et al. (2015).

Trichosporon Behrend, Berliner Klin. Wochenschr. 21: 464. 1890.

This genus is re-defined to accommodate only the species in the Trichosporon clade recognised in the seven-genes phylogeny (Liu et al. 2015).

Basidiocarps not known. Septate hyphae with arthroconidia usually present. Sexual reproduction not observed. Budding cells present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-9.

Type species: Trichosporon ovoides Behrend

Notes: Pleurococcus beigelii Küchenmeister & Rabenhorst (Rabenhorst 1867) was probably the first fungus representing the current genus Trichosporon. The name Pleurococcus was rejected by Guého et al. (1992a) as it concerned a poorly described species and no material was preserved. The name Trichosporon was introduced to include only one species, T. ovoides, isolated from an infected moustache hair from Germany (Behrend 1890). Guého et al. (1992a) selected a neotype for T. ovoides, CBS 7556 isolated from capital white piedra occurring on a Caucasian, a habitat that agreed with the original description of the species by Behrend. These authors also rejected the neotypification of T. beigelii with ATCC 28592 (= CBS 2466) as proposed by McPartland & Goff (1991), but they selected this strain as neotype for T. cutaneum when using a more narrow species concept for this taxon. A major contribution to the taxonomy of the genus Trichosporon was made by Guého et al. (1992b) by recircumscribing several species using rRNA sequence analysis, nutritional physiology, electron microscopy of septal pores, and the analysis of the G+C content of the DNA and DNA–DNA hybridisation experiments. Using sequence analysis of the D2 domain of the 28S rRNA, five clusters of species were observed: 1) T. sporotrichoides, T. dulcium, T. gracile, T. multisporum, T. laibachii, and T. loubieri; 2) T. cutaneum, T. jiravecii, T. mucoides, and T. moniliiforme; 3) T. coremiiforme, T. aquatile, T. faecale, T. asahii, T. asteroids and Fissurella filamenta; 4) T. ovoides and T. inkii; and 5) T. brassicae and T. montevideenae (Guého et al. 1992b). It is interesting to note that this clustering is fully congruent with our results from the analyses of multiple genes.

Recently, many new Trichosporon species have been described or have been transferred to this genus from other genera (Guého et al. 1998, Colombo et al. 2011, Sugita 2011). According to the latest monographic treatment (Sugita 2011) the genus contains 37 species. The Trichosporon species are distributed over five clades, namely brassicae, cutaneum, gracile, porosum and Trichosporon (Middelhoven et al. 2004, Sugita et al. 2004, Sugita 2011), which are similar to those observed before in analyses of partial LSU rRNA sequences (Guého et al. 1992b). Serological characteristics correlate well with these clades and therefore were applied as a taxonomic marker in this group (Tsuchiya et al. 1974, Sugita 2011). The genus is restricted here to accommodate only the Trichosporon clade, including the neotype species T. ovoides (Liu et al. 2015). Species belonging to this newly circumscribed genus Trichosporon have serotype II. Twelve species are accepted in this genus (Table 1, Fig. 6).

Cutaneotrichosporon X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, gen. nov. MycoBank MB813397.

Etymology: In reference to the specific epithet of the type species in this genus.

This genus is proposed for the well supported monophyletic group consisting of the cutaneum and haglerorum clades together with Trichosporon guehoae, Cryptococcus curvatus, Cr. cyanovorans and Cr. daszewskae (Liu et al. 2015, Fig. 6 of this study).

Basidiocarps not known. Sexual reproduction not observed. True hyphae disarticulate into ovoid, cylindrical or cubic arthroconidia. Pseudohyphae abundant or not. Budding cells present. Fermentation absent. Nitrate not utilised, nitrite utilised or not. Major CoQ system CoQ-10.

Type species: Cutaneotrichosporon cutaneum (Beurm., Gougerot & Vaucher bis) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. Mycobank MB13398.

Notes: Close relationships between the cutaneum and haglerorum clades were supported in recent phylogenetic studies (Sugita 2011, Liu et al. 2015, Takashima et al. 2015, Fig. 6 of this study). The next well-supported node clustered with cutaneum and haglerorum clades with T. guehoae, Cr. curvatus, Cr. cyanovorans and Cr. daszewskae (Fig. 6). Since this expanded clade received strong support in multi-gene studies by Liu et al. (2015) and Takashima et al. (2015) as well as the extended LSU rRNA gene phylogeny (Fig. 6), we propose to classify the cutaneum and haglerorum clades together with T. guehoae, Cr. curvatus, Cr. cyanovorans and Cr. daszewskae (Fig. 6) in a single genus Cutaneotrichosporon gen. nov., in order to avoid proposing several small genera with only one or two species. The genus Cutaneotrichosporon currently contains 15 species (Table 1).

New combinations for Cutaneotrichosporon

Cutaneotrichosporon arboriformis (Sugita, M. Takash., Sano, Nishim., Kinebuchi, S. Yamag. & Osanai) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. Mycobank MB813407. Basionym: Cryptococcus arboriformis Sugita et al., Microbiol. Immunol. 51: 544. 2007.

Cutaneotrichosporon curvatus (Diddens & Lodder) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. Mycobank MB814761. Basionym: Candida heveanensis Diddens & Lodder var. curvata Diddens & Lodder, Beltl. Monogr. Hefenarten. II Teil. Die anas-kosporogene Hefen: 310. 1942. 

‡ Cryptococcus curvatus (Diddens & Lodder) Golubev, Mikol. Fitopatol. 15: 467. 1981.
Cutaneotrichosporon cutaneum (de Beurmann, Gougerot & Vaucher) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813398. Basionym: Oidium cutaneum de Beurmann et al., Bull. Mém. Soc. Méd. Hôpital Paris 18: 52. 1910. = Trichosporon cutaneum (de Beurmann et al.) M. Ota, Annuls Parasit. Hum. Comp. 4: 12. 1926.

Cutaneotrichosporon cyanovorans (Motaung, Albertlyn, J. L. F. Kock et Pohl) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB814762. Basionym: Cryptococcus cyanovorans Motaung et al., Int. J. Syst. Evol. Microbiol. 62: 1211. 2012.

Cutaneotrichosporon daszewskae (M. Takash., Sugita, Shinoda & Nakase) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB814763. Basionym: Cryptococcus daszewskae M. Takash.: et al., Int. J. Syst. Evol. Microbiol. 51: 2204, 2001.

Cutaneotrichosporon debeurmannianum (Sugita, M. Takash., Nakase & Shinoda) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813399. Basionym: Trichosporon debeurmannianum Sugita et al., Int. J. Syst. Evol. Microbiol. 51: 1221–1228. 2001.

Cutaneotrichosporon dermatis (Sugita, M. Takash., Nakase, Ichikawa, Ikeda & Shinoda) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813400. Basionym: Trichosporon dermatis Sugita et al., Int. J. Syst. Evol. Microbiol. 51: 1221. 2001.

Cutaneotrichosporon guehoae (Middelhoven, Scorzetti & Fell) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB814764. Basionym: Trichosporon guehoae Middelhoven et al., Can. J. Microbiol. 45: 687. 1999.

Cutaneotrichosporon jirovecii (Frágrner) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813401. Basionym: Trichosporon jirovecii Frágrner, Ceská Mykol. 23: 160. 1969.

Cutaneotrichosporon haglerorum (Middelhoven, Á. Fonseca, S.C. Carreiro, Pagnocca & O.C. Bueno) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813408. Basionym: Cryptococcus haglerorum Middelhoven et al., Antonie van Leeuwenhoek 83: 168. 2003.

Cutaneotrichosporon moniliiforme (Weigmann & A. Wolff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813403. Basionym: Oidium moniliiforme Weigmann & A. Wolff, Zentbl. Bakter. ParasitiKde, Abt. II 22: 668. 1909. = Trichosporon moniliiforme (Weigmann & A. Wolff) E. Guého & M.T. Smith, Antonie van Leeuwenhoek 61: 309. 1992.

Cutaneotrichosporon mucoides (E. Guého & M.T. Smith) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813402. Basionym: Trichosporon mucoides E. Guého & M.T. Smith, Antonie van Leeuwenhoek 61: 312. 1992.

Cutaneotrichosporon oleaginosus (J.J. Zhou, S.O. Suh & Gijjari) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB815305. Basionym: Trichosporon oleaginosus J.J. Zhou et al., Mycologia 103: 1115. 2011.

Cutaneotrichosporon smithiae (Middelhoven, Scorzetti, Sugita & Fell) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813404. Basionym: Trichosporon smithiae Middelhoven et al., Int. J. Syst. Evol. Microbiol. 54: 979. 2004.

Cutaneotrichosporon terrecola (Sugita, M. Takash. & Nakase) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813405. Basionym: Trichosporon terrecola Sugita et al., J. Gen. Appl. Microbiol. 48: 295. 2002.

Haglerozyma X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, gen. nov. MycoBank MB813406. Basionym: Trichosporon chiarelli Pagnocca, Legaspe, Rodrigues & Ruivo, Int. J. Syst. Evol. Microbiol. 60: 1457. 2010.

Etymology: The genus is named in honour of Allen N. Hagler for his work on yeast ecology and physiology.

This genus is proposed for the single-species lineage Trichosporon chiarelli, which showed some phylogenetic relatedness to the genus Cutaneotrichosporon in the seven-genes tree (Liu et al. 2015).

Basidicarps not known. Sexual reproduction not observed. True hyphae sometimes disarticulate into arthroconidia. Pseudohyphae abundant or not. Budding cells present. Fermentation absent. Nitrate and nitrite not utilised. The major CoQ system unknown.

Type species: Haglerozyma chiarelli (Pagnocca, Legaspe, Rodrigues & Ruivo) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. Mycobank MB814765.

Notes: Trichosporon chiarelli was branching earlier than the genus Cutaneotrichosporon in the seven-genes tree with strong posterior probability support from Bayesian analysis but without bootstrap support from ML and NJ analyses (Liu et al. 2015). In the expanded LSU rRNA gene analysis, T. chiarelli was located in the same position without statistical support (Fig. 6), suggesting the species represents a distinct lineage. The genus currently contains one species (Table 1).

Apiotrichum Stautz, Phytopath. Z. 3: 209. 1931. emend. A.M. Yurkov & Boekhout.

The genus Apiotrichum is resurrected and emended here for the gracile/brassicae and porosum clades containing 18 Trichosporon species (Middelhoven et al. 2004, Sugita 2011, Liu et al. 2015). Close relationships between these clades were resolved in multi-gene studies by Liu et al. (2015) and Takashima et al. (2015) as well as an extended LSU rRNA gene phylogeny (Fig. 6). Several genus names are available

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for species contained in this clade. The genus Apiotrichum was described for Apiotrichum (Trichosporon) porosum by Stautz (1931) and Hyalodendron was proposed by Diddens (1934) to accommodate Hyalodendron (Trichosporon) lignicola. The former name has nomenclature priority over the latter. Therefore, Hyalodendron is treated as a synonym of Apiotrichum.

Basidiocarps not known. Sexual reproduction not observed. Septate and branched hyphae present that form arthroconidia. Catenate or lateral conidia occasionally present. Pseudohyphae present. Budding cells present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-9.

**Type species**: Apiotrichum porosum Stautz, Phytopath. Z. 3: 209. 1931

**Notes**: The genus Apiotrichum was proposed with *A. porosum* as the type species (Stautz 1931). Though this species could not produce fragmenting mycelium, viz. arthroconidia, it was transferred to the genus *Trichosporon* based on rRNA gene sequence analysis and a similar physiology with other *Trichosporon* species (Middelhoven et al. 2001). Species belonging to this genus have serotype I and II, and their major coenzyme Q system is Q-9 (Sugita 2011, Takashima et al. 2015). Close relationships between these three clades received strong support in multi-gene studies by Liu et al. (2015) and Takashima et al. (2015) as well as the extended LSU rRNA gene phylogeny (Fig. 1). For reasons of conservatism we combine the three clades into a single genus *Apiotrichum*. The genus currently contains 20 species (Table 1).

**New combinations for Apiotrichum**

*Apiotrichum brassicae* (Nakase) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813409.

Basionym: *Trichosporon brassicae* Nakase, J. Gen. Appl. Microbiol. 17: 417. 1971.

*Apiotrichum cacaoliposimilis* (J.L. Zhou, S.O. Suh & Gujjar) Kachalkin, A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB814766.

Basionym: *Trichosporon cacaoliposimilis* J.L. Zhou et al., Mycologia 103: 1114. 2011.

*Apiotrichum dehoogii* (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813410.

Basionym: *Trichosporon dehoogii* Middelhoven et al., Int. J. Syst. Evol. Microbiol. 54: 979. 2004.

*Apiotrichum domesticum* (Sugita, A. Nishikawa & Shinoda) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813411.

Basionym: *Trichosporon domesticum* Sugita et al., J. Gen. Appl. Microbiol. 41: 431. 1995.

*Apiotrichum dulcitum* (Berkhout) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813412.

Basionym: *Oospora dulcita* Berkhout, Consid. Vég. Vosges: 50–51 + pl. 3. 1923.

≡ *Trichosporon dulcitum* (Berkhout) Weijman, Antonie van Leeuwenhoek 45: 126. 1979.

*Apiotrichum gamsii* (Middelhoven, Scorzetti, Sigler & Fell) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813413.

Basionym: *Trichosporon gamsii* Middelhoven et al., Int. J. Syst. Evol. Microbiol. 54: 982. 2004.

*Apiotrichum gracile* (Weigmann & Wolff) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813414.

Basionym: *Oidium gracile* Weigmann & A. Wolff, Zentbl. Bakt. Parasitkd. Abt. II 22: 668. 1909.

≡ *Trichosporon gracile* (Weigmann & A. Wolff) E. Guého & M.T. Smith, Antonie van Leeuwenhoek 61: 307. 1992.

*Apiotrichum laibachii* (Windisch) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813415.

Basionym: *Endomyces laibachii* Windisch, Beitr. Biol. Pfl. 41: 356. 1965.

≡ *Trichosporon laibachii* (Windisch) E. Guého & M.T. Smith, Antonie van Leeuwenhoek 61: 302. 1992.

*Apiotrichum lignicola* (Diddens) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813416.

Basionym: *Hyalodendron lignicola* Diddens, Zentbl. Bakt. Parasitkd. Abt. II 80: 317. 1934.

≡ *Trichosporon lignicola* (Diddens) Fell & Scorzetti, Int. J. Syst. Evol. Microbiol. 54: 997. 2004.

*Apiotrichum loubieri* (Morenz) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813417.

Basionym: *Geotrichum loubieri* Morenz, Mykologische Schriftenreihe, Leipzig 2: 46. 1964.

≡ *Trichosporon loubieri* (Morenz) Weijman, Antonie van Leeuwenhoek 45: 126. 1979.

*Apiotrichum montevideense* (L.A. Queiroz) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813418.

Basionym: *Endomyces montevideensis* L.A. Queiroz, Mycopath. Mycol. Appl. 51: 311. 1973.

≡ *Trichosporon montevideense* (L.A. Queiroz) E. Guého & M.T. Smith, Antonie van Leeuwenhoek 61: 301. 1992.

*Apiotrichum mycotoxinivorans* (O. Molnár, Schatzm. & Priller) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813420.

Basionym: *Trichosporon mycotoxinivorans* O. Molnár et al., Syst. Appl. Microbiol. 27: 664. 2004.

*Apiotrichum siamense* (Nakase, Jindam., Sugita & H. Kawas.) Kachalkin, A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB814767.

Basionym: *Trichosporon siamense* Nakase et al., Mycoscience 47: 107. 2006.

*Apiotrichum scarabaeorum* (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813421.

Basionym: *Trichosporon scarabaeorum* Middelhoven et al., Int. J. Syst. Evol. Microbiol. 54: 981. 2004.

*Apiotrichum sporotrichoides* (van Oorschot) A.M. Yurkov & Boekhout, **comb. nov.** MycoBank MB813422.

Basionym: *Trichosporiella sporotrichoides* van Oorschot, Stud. Mycol. 20: 66. 1980.
**Basionym:** Trichosporon vadense Middelhoven et al., Int. J. Syst. Evol. Microbiol. 54: 976. 2004.

**Apiotrichum veenhuisii** (Middelhoven, Scorzetti & Fell) A.M. Yurkov & Boekhout, *comb. nov.* MycoBank MB813424.

**Basionym:** Trichosporon veenhuisii Middelhoven et al., Int. J. Syst. Evol. Microbiol. 50: 382. 2000.

**Apiotrichum wieringae** (Middelhoven) A.M. Yurkov & Boekhout, *comb. nov.* MycoBank MB813425.

**Basionym:** Trichosporon wieringae Middelhoven, Antonie van Leeuwenhoek 86: 331. 2004.

**Apiotrichum xylopinii** (S.O. Suh, Lee, Gujji & Zhou) Kachalkin, A.M. Yurkov & Boekhout, *comb. nov.* MycoBank MB814768.

**Basionym:** Trichosporon xylopinii S.O. Suh et al., Int. J. Syst. Evol. Microbiol. 61: 2540. 2010.

**Vanrija** R.T. Moore, Bot. Mar. 23: 367. 1980.

- = Asterotremella H.J. Prillinger, K. Lopandic, K. Sterflinger, E. Metzger & R. Bauer, ScienceWeek@Austria: 11. 1993. Nomen nudum. (Note: The name Asterotremella is introduced as a nomen nudum as a description, a diagnosis, and information on a type were not provided).
- = Asterotremella Prillinger, Lopandic & Sugita, J. Gen. Appl. Microbiol. 53: 171. 2007.

The concept of this genus as emended by Weiss et al. (2014) is accepted.

Basidiocarps not known. Sexual reproduction not observed. Pseudohyphae and true hyphae present. Arthroconidia usually not present. Budding cells present. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-9 or CoQ-10.

**Type species:** Vanrija humicola (Dasz.) R.T. Moore

**Notes:** The genus Vanrija was proposed with *V. humicola* as the type strain (Moore 1980). Following suggestions made by Okoli et al. (2007) and Fonseca et al. (2011), Weiss et al. (2014) emended this genus to accommodate the *humicola* clade, including five Cryptococcus species, namely *C. ramirezgomezianus* (= *Vanrija albida*, basionym *Sporobolomyces albida*), *C. humicola*, *C. longa*, *C. musci*, and *C. pseudolongus* (Takashima et al. 2001), but they did not present an emended diagnosis for the genus. The genus *Asterotremella* and family Asterotremellaceae based on the study of yeasts isolated from Asterophora basidiocarps has been introduced by Prillinger et al. (1993) and later described (Prillinger et al. 2007), indicating in both cases close relationships with the species *C. humicola*, the type species of the genus *Vanrija* (Moore 1980). However, *Vanrija* has nomenclatural priority over *Asterotremella*. Two species, which were described as *Asterotremella*, namely *A. meifongana* and *A. nantouana* were placed in the *humicola* clade in the expanded LSU rRNA gene tree with high bootstrap support (Fig.6). *Cryptococcus fragicola*, which did not cluster in the *Vanrija* clade in Weiss et al. (2014), was shown to be closely related to this clade in the Bayesian and ML trees based on the seven-genes dataset with strong PP and BP support (Liu et al. 2015) as well as in the combined rRNA genes analysis in Wang & Wang (2015). *Cryptococcus thermophilus* was not included in the phylogenetic analysis performed by Weiss et al. (2014) and clustered loosely with the *Vanrija* core group in the LSU rRNA gene tree in Takashima et al. (2015) and Wang & Wang (2015). This species, however, clustered inside the clade delimited with *C. fragicola* in Takashima et al. (2015) and in the expanded LSU rRNA gene tree (Fig. 6). Therefore, we transfer these four species to the genus *Vanrija*. The genus currently contains nine species (Table 1).

**New combinations for Vanrija**

**Vanrija fragicola** (M. Takash., Sugita, Shinoda & Nakase) Z.X. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB814726.

**Basionym:** Cryptococcus fragicola M. Takash. et al., Int. J. Syst. Evol. Microbiol. 51: 2205. 2001.

**Vanrija meifongana** (C.F. Lee) Kachalkin, A.M. Yurkov & Boekhout, *comb. nov.* MycoBank MB814779.

**Basionym:** Asterotremella meifongana C.F. Lee, Antonie van Leeuwenhoek 99: 647. 2011.

**Vanrija nantouana** (C.F. Lee) Kachalkin, A.M. Yurkov & Boekhout, *comb. nov.* MycoBank MB814770.

**Basionym:** Asterotremella nantouana C.F. Lee, Antonie van Leeuwenhoek 99: 648. 2011.

**Vanrija thermophila** (Vogelmann, Chaves & Hertel) Kachalkin, A.M. Yurkov & Boekhout, *comb. nov.* MycoBank MB814772.

**Basionym:** Cryptococcus thermophilus Vogelmann et al., Int. J. Syst. Evol. Microbiol. 62: 1719. 2012.

**Effuseotrichosporon** A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *gen. nov.* MycoBank MB814773.

**Etymology:** In reference to the widespread distribution (Lat. effuse) of the species.

This genus is proposed for the single-species lineage formed by *Trichosporon vanderwaltii* in *Trichosporonaceae* (Figs 2 and 6).

Basidiocarps not known. Sexual reproduction not observed. True hyphae disarticulate into arthroconidia. Pseudohyphae abundant or not. Budding cells present. Fermentation absent. Nitrate and nitrite sometimes utilised. The major CoQ system unknown.

**Type species:** Effuseotrichosporon vanderwaltii (Motaung, Albertyn, Kock, C.F. Lee, S.O. Suh, M. Blackwell & C.H. Pohl) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB814774.

**Basionym:** Trichosporon vanderwaltii Motaung et al., Antonie van Leeuwenhoek. 103: 315. 2013.

**Notes:** *Trichosporon vanderwaltii* was described for a group of strains from different sources (Motaung et al. 2013). These strains formed a sister clade to the *brassicae/porosum* clades (i.e. *Apiotrichum* gen. nov.) in the tree drawn from the ITS and LSU D1/D2 sequences but statistical support for this phylogeny was lacking (Motaung et al. 2013). The affinity of *T. vanderwaltii* to the family *Trichosporonaceae* was resolved in this study but its phylogenetic relationships to other clades of the family remained
unclear (Fig. 6). This species showed wide geographic distribution and we expect more species to be described in the future. Currently the genus contains one species (Table 1).

**Tetragoniomycetaceae** Oberw. & Bandoni, Can. J. Bot. 59: 1039. 1981. *emend.* X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

This family is emended to accommodate the monophyletic lineage comprising *Tetragoniomyces*, *Takashimella* (i.e. the *formosensis* clade), *Cryptocotrichosporon* and *Cryptococcus marinus* recognised in *Liu et al.* (2015) and the present study (Figs 1, 2 and 6).

Basidiocarps not known or growing as a thin film on sclerotia of a basidiomycetous host. Sexual reproduction unknown or by basidia that occur terminally on hyphae; initially thin-walled, ellipsoid to globose, becoming thick-walled and four-celled; mature basidia deciduous, rhomboidal; germination by dikaryotic hyphae or germ tubes that may conjugate. In culture pseudohyphae and true hyphae present or not. Budding cells present or absent. Ballistoconidia bilaterally symmetrical. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

**Type genus:** *Tetragoniomyces* Oberw. & Bandoni

**Genera accepted:** Bandonia, Cryptotrichosporon, Takashimella and Tetragoniomyces.

**Notes:** The family *Tetragoniomycetaceae* was established for a single species, *Tetragoniomyces uliginosus* (Oberwinkler & Bandoni 1981). This species produces unusual deciduous basidia that germinate directly into a filamentous phase and does not have a unicellular yeast phase. Molecular phylogenetic analysis indicated that *T. uliginosus* is an early-branching member of Trichosporonales with loose connection to *Cryptotrichosporon anacardi* (Millanes et al. 2011, Weiss et al. 2014). The latter is branching before the *formosensis* clade (i.e. *Takashimella*) with strong support in the Bayesian and ML trees obtained from the seven-genes dataset (*Liu et al.* 2015). The tree inferred from the expanded LSU rRNA gene dataset confirmed this phylogenetic relationship (Fig. 6). A new *Cryptotrichosporon* species, *C. tibetensi* that is able to form ballistoconidia was described recently and the genus description emended consequently (*Wang & Wang* 2015). The close phylogenetic relationship between *Cryptotrichosporon* and *Tetragoniomyces* was supported in *Wang & Wang* (2015). The genus *Tetragoniomyces* remains monotypic and the genera *Cryptotrichosporon* (Okoli et al. 2007) and *Takashimella* (*Wang & Wang* 2015) contain two and four species, respectively (Table 1). *Cryptococcus marinus* was branching more early than this family in the Bayesian and ML trees derived from the seven-genes dataset, but its position was not resolved in the seven-genes NJ tree and the combined rRNA genes tree (*Liu et al.* 2015). In all molecular phylogenetic studies performed to date this species occurred as a single long-branch lineage (Fell et al. 2000, Scorzetti et al. 2002). Below we propose a new genus *Bandonia* to accommodate this species.

**Bandonia** A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *gen. nov.* MycoBank MB814775.

**Etymology:** In honour of Robert J. Bandoni for his valuable contribution to the studies of Tremellomycetes.

The genus is proposed to accommodate the single-species lineage *Cryptococcus marinus*, which was placed in *Tetragoniomycetaceae* (*Liu et al.* 2015, Fig. 6 of this study).

Basidiocarps not known. Sexual reproduction not observed. Pseudohyphae present or not. Budding cells present or absent. Ballistoconidia not observed. Fermentation absent. Nitrate not utilised. Major CoQ system CoQ-10.

**Type species:** *Bandonia marina* (van Uden & Zobell) A.M. Yurkov, X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB814776.

**Basionym:** *Candida marina* van Uden & Zobell, Antonie van Leeuwenhoek. 28: 278. 1962.

**Notes:** The phylogenetic position of *Cryptococcus marinus* in Tremellomycetes remained unclear (e.g. Fonseca et al. 2011) before the seven-genes phylogenetic analysis (*Liu et al.* 2015). The latter analysis placed the species in Trichosporonales with some affinity to the genera *Cryptotrichosporon* and *Takashimella*. The species is known from a single strain only and is characterised by several unusual physiological properties (Fonseca et al. 2011).

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