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# Phylogenetic classification of yeasts and related taxa within *Pucciniomycotina*

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**Abstract:** Most small genera containing yeast species in the *Pucciniomycotina* (*Basidiomycota*, *Fungi*) are monophyletic, whereas larger genera including *Bensingtonia*, *Rhodosporidium*, *Rhodotorula*, *Sporidiobolus* and *Sporobolomyces* are polyphyletic. With the implementation of the “One Fungus = One Name” nomenclatural principle these polyphyletic genera were revised. Nine genera, namely *Bannoa*, *Cystobasidiopsis*, *Colacogloea*, *Kondoa*, *Erythrobasidium*, *Rhodotorula*, *Sporobolomyces*, *Sakaguchia* and *Sterigmatomyces*, were emended to include anamorphic and teleomorphic species based on the results obtained by a multi-gene phylogenetic analysis, phylogenetic network analyses, branch length-based methods, as well as morphological, physiological and biochemical comparisons. A new class *Spiculogloeomycetes* is proposed to accommodate the order *Spiculogloeales*. The new families *Buckleyzymaceae* with *Buckleyzyma* gen. nov., *Chrysozymaceae* with *Chrysozyma* gen. nov., *Microsporomycetaceae* with *Microsporomyces* gen. nov., *Ruineniaceae* with *Ruinenia* gen. nov., *Symmetrosporaceae* with *Symmetrospora* gen. nov., *Colacogloeaceae* and *Sakaguchiaceae* are proposed. The new genera *Bannozyma*, *Buckleyzyma*, *Fellozyma*, *Hamamotoa*, *Hasegawazyma*, *Jianyunia*, *Rhodosporidiobolus*, *Oberwinklerozyma*, *Phenoliferia*, *Pseudobensingtonia*, *Pseudohyphozyma*, *Sampaiozyma*, *Slooffia*, *Spencerozyma*, *Trigonosporomyces*, *Udeniozyma*, *Vonarxula*, *Yamadamyces* and *Yunzhangia* are proposed to accommodate species segregated from the genera *Bensingtonia*, *Rhodosporidium*, *Rhodotorula*, *Sporidiobolus* and *Sporobolomyces*. *Ballistosporomyces* is emended and reintroduced to include three *Sporobolomyces* species of the **sasicola** clade. A total of 111 new combinations are proposed in this study.

**Key words:** *Fungi*, GMYC approach, Molecular phylogeny, Phylogenetic rank boundary optimisation, *Pucciniomycotina*, Taxonomy, Yeasts.

**Taxonomic novelties: New class:** ***Spiculogloeomycetes*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout; **New families:** ***Buckleyzymaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Chrysozymaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Colacogloeaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Microsporomycetaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Ruineniaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Sakaguchiaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Symmetrosporaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout; **New genera:** ***Bannozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Buckleyzyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Chrysozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Fellozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Hamamotoa*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Hasegawazyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Jianyunia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Microsporomyces*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Oberwinklerozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Phyllozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Phenoliferia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Pseudobensingtonia*** F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, ***Pseudohyphozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Rhodosporidiobolus*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Ruinenia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Sampaiozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Slooffia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Spencerozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Symmetrospora*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Trigonosporomyces*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Udeniozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Vonarxula*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Yamadamyces*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Yunzhangia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout; **New combinations:** ***Ballistosporomyces*** *sasicola* (Nakase & M. Suzuki) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, *B. taupoensis* (Hamam. & Nakase) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, ***Bannoa*** *bischofiae* (Hamam., Thanh & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *B. syzygii* (Hamam., Thanh & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *B. ogasawarensis* (Hamam., Thanh & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Bannozyma*** *arctica* (Vishniac & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *B. yamatoana* (Nakase, M. Suzuki & M. Itoh) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Buckleyzyma*** *armeniaca* (R.G. Shivas & Rodr. Mir.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *B. aurantiaca* (Saito) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *B. kluyveri-nielii* (van der Walt) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *B. phyllomatis* (van der Walt & Y. Yamada) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *B. salicina* (B.N. Johri & Bandoni) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Chrysozyma*** *fushanensis* (Nakase, F.L. Lee & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. griseoflava* (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Colacogloea*** *cycloclastica* (Thanh, M.S. Smit, Moleleki & Fell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. diffluens* (Ruinen) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. eucalyptica* (C.H. Pohl, M.S. Smit & Albertyn) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. falcata* (Nakase, M. Itoh & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. foliorum* (Ruinen) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. philyla* (van der Walt, Klift & D.B. Scott) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. retinophila* (Thanh, M.S. Smit, Moleleki & Fell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. terpenoidalis* (Thanh, M.S. Smit, Moleleki & Fell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Cystobasidiopsis*** *lactophilus* (Nakase, M. Itoh, M. Suzuki & Bandoni) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *C. lophatheri* (Nakase, Tsuzuki, F.L. Lee, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Cystobasidium*** *portillonense* (F. Laich, I. Vaca & R. Chávez) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Erythrobasidium*** *elongatum* (R.G. Shivas & Rodr. Mir.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *E. yunnanense* (F.Y. Bai, M. Takash., Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Fellozyma*** *inositophila* (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Hamamotoa*** *lignophila* (Dill, C. Ramírez & González) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *H. singularis* (Phaff & do Carmo-Sousa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Hasegawazyma*** *lactosa* (Hasegawa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Jianyunia*** *sakaguchii* (Sugita, M. Takash., Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Kondoa*** *changbaiensis* (F.Y. Bai & Q.M. Wang) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, *K. miscanthi* (Nakase & M. Suzuki) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, *K. phyllada* (van der Walt & Y. Yamada) Q.M.

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Fonseca & van Uden) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Phenoliferia*** *psychrophenolica* (Margesin & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. psychrophila* (Margesin & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. glacialis* (Margesin & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. himalayensis* (Shivaji, Bhadra & Rao) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Phyllozyma*** *coprosmicola* (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. corallina* (N. Furuya & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. dimennae* (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. linderae* (Nakase, M. Takash. & Hamam.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. novozealandica* (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. producta* (N. Furuya & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. subbrunnea* (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Pseudobensingtonia*** *ingoldii* (Nakase & Itoh.) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, *P. musae* (M. Takash., S.O. Suh & Nakase) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, ***Pseudohyphozyma*** *bogoriensis* (Deinema) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. buffonii* (C. Ramírez) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *P. pustula* (Buhagiar) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Rhodotorula*** *alborubescens* (Derx) Q.M. Wang, F.Y. Bai, Groenew. & Boekhout, *R. babjevae* (Golubev) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. diobovata* (S.Y. Newell & I.L. Hunter) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. kratochvilovae* (Hamam., Sugiy. & Komag.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. paludigena* (Fell & Tallman) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. sphaerocarpa* (S.Y. Newell & Fell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. toruloides* (I. Banno) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Rhodosporidiobolus fluvialis* (Fell, Kurtzman, Tallman & J.D. Buck) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. azoricus* (J.P. Samp. & Gadanho) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. microsporus* (Higham ex Fell, Blatt & Statzell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. nylandii* (M. Takash. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. ruineniae* (Holzschu, Tredick & Phaff) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. lusitaniae* (Á. Fonseca & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. colostri* (T. Castelli) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. odoratus* (J.P. Samp., Á. Fonseca & Valério) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. poonsookiae* (M. Takash. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Ruinenia*** *clavata* (F.Y. Bai & Q.M. Wang) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. diospyroris* (Nakase, Tsuzuki, F.L. Lee, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. dracophylli* (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. pyrrosiae* (Nakase, Tsuzuki, F.L. Lee, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *R. rubra* (Nakase, Oakada & Sugiy.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Sakaguchia*** *cladiensis* (Fell, Statzell & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. lamellibrachiae* (Nagah., Hamam., Nakase & Horikoshi) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. meli* (Libkind, van Broock & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. oryzae* (F.Y. Bai & Y.M. Cai) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Sampaiozyma*** *ingeniosa* (Di Menna) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. vanillica* (J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Slooffia cresolica* (Middelhoven & Spaaij) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. pilati* (F.H. Jacob, Faure-Raynaud & Berton) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***S. tsugae*** (Phaff & do Carmo-Sousa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Spencerozyma*** *crocea* (Shifrine & Phaff) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Sporobolomyces*** *longiusculus* (Libkind, van Broock & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. johnsonii* (Nyland) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Sterigmatomyces*** *hyphaenes* (Har. & Pat.) F.Y. Bai, Q.M. Wang, Groenewald & Boekhout, *S. pulcherrima* (J.E. Wright) F.Y. Bai, Q.M. Wang, Groenewald & Boekhout, *S. novozelandica* (W.B. Kendr. & X.D. Gong) F.Y. Bai, Q.M. Wang, Groenewald & Boekhout, ***Symmetrospora*** *coprosmae* (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. foliicola* (R.G. Shivas & Rodr. Mir.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. gracilis* (Derx) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. vermiculata* (M. Takash. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. marina* (Phaff, Mrak & Williams) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *S. symmetrica* (F.Y. Bai & Q.M. Wang) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Trigonosporomyces*** *hylophilus* (van der Walt, van der Klift & D.B. Scott) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Ustilentyloma*** *graminis* (Rodr. Mir. & Diem) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Udeniozyma*** *ferulica* (J.P. Samp. & van Uden) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Vonarxula*** *javanica* (Ruinen) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Yamadamyces*** *rosulatus* (Golubev & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, ***Yunzhangia*** *auriculariae* (Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Y. sonckii* (Hopsu-Havu, Tunnela & Yarrow) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

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## INTRODUCTION

The subphylum *Pucciniomycotina* (Phylum *Basidiomycota*, Kingdom *Fungi*) presently includes eight classes, and four of these, namely the *Agaricostilbomycetes*, *Cystobasidiomycetes*, *Microbotryomycetes* and *Mixiomycetes*, contain taxa with a dominant yeast stage (Aime *et al.* 2006, 2014, Bauer *et al.* 2006, Hibbett *et al.* 2007, Boekhout *et al.* 2011, Wang *et al.* 2015a). So far 28 genera with yeast states have been proposed within *Pucciniomycotina* (Boekhout *et al.* 2011, Turchetti *et al.* 2011, Toome *et al.* 2013). Most of these genera are monophyletic, whereas five genera, namely *Bensingtonia*, *Rhodosporidium*, *Rhodotorula*, *Sporidiobolus* and *Sporobolomyces* are polyphyletic (Fell *et al.* 2000, Scorzetti *et al.* 2002, Boekhout *et al.* 2011, Wang *et al.* 2015a, b). *Bensingtonia*, *Rhodotorula* and *Sporobolomyces* species are placed in various classes of *Pucciniomycotina* (Fell *et al.* 2000, Scorzetti *et al.* 2002, Boekhout *et al.* 2011, Hamamoto *et al.* 2011, Sampaio 2011, Yurkov *et al.* 2015). Species of the teleomorphic genera *Rhodosporidium* and *Sporidiobolus* together with some asexual *Rhodotorula* and *Sporobolomyces* species are nested within *Sporidiobolales* (Fell *et al.* 2000, Scorzetti *et al.* 2002, Boekhout *et al.* 2011, Sampaio 2011). With the implementation of the “One Fungus = One Name” nomenclatural principle (Hawksworth 2011, Taylor 2011, McNeill *et al.* 2012) these five polyphyletic genera need to be revised.

Several studies using molecular analyses of ribosomal DNA sequences have provided a detailed grouping of species in clades among the four classes that contain yeast and yeast-like species (Hamamoto & Nakase 2000, Nakase 2000, Fell *et al.* 2000, Scorzetti *et al.* 2002, Boekhout *et al.* 2011), but many species remained unassigned (Boekhout *et al.* 2011). Thus the boundaries of the clades and genera have to be reassessed by analysing a robust molecular dataset. In another study we analysed seven gene fragments, namely SSU (18S) rRNA, LSU (26S/28S) rRNA D1/D2 domains, the ITS region (including the 5.8S rRNA), *RPB1* (the largest subunit of DNA polymerase II), *RPB2* (the second largest subunit of DNA polymerase II), *TEF1* (translation elongation factor 1-α) and *CYTB* (cytochrome *b*) that placed most pucciniomycetous yeast species into 51 well-supported clades (Wang *et al.* 2015a). These data are used here to address the taxonomic affiliations of those fungi. We propose 26 of the 51 recognised clades as new taxa at the genus, family and class levels based on a phylogenetic and taxonomic analysis of the combined seven genes-based and the enlarged LSU rRNA gene datasets. The assessment of taxonomic ranks followed the branch length-based methods as described in Liu *et al.* (2015).

## MATERIALS AND METHODS

### Strains and molecular phylogenetic analyses

Multi-gene data of the yeast strains used were taken from a previous study (Wang *et al.* 2015a). As described previously (Wang *et al.* 2015a) multi-gene phylogenetic trees constructed from Maximum likelihood (ML), Maximum parsimony (MP) and Bayesian inference (BI) analyses of a dataset comprising nucleotide sequences of the ITS region (including the 5.8S rRNA), the D1/D2 domains of the LSU rRNA, the SSU rRNA, and the *RPB1*, *RPB2*, *TEF1* and *CYTB* genes is used here to address the taxonomy of the pucciniomycetous yeasts. Fifty-one clades that may be equal to the generic rank, including 16 single-species lineages, were recognised among the pucciniomycetous yeasts used in the previous study with strong statistical support values in all trees drawn using different phylogenetic algorithms (Wang *et al.* 2015a). In order to detect the reliability of those 51 clades, a phylogenetic network approach was employed to infer the relationships between those pucciniomycetous yeasts. The seven genes-based phylogenetic network was constructed in SplitsTree4 (Huson & Bryant 2006) using the ConsensusNetwork algorithm with default parameter settings. The seven single-gene ML trees used in the phylogenetic network analysis were constructed using RAxML-HPC 7.2.8 (Stamatakis 2006) using the parameter settings described previously (Wang *et al.* 2015a).

The supplementary LSU rRNA gene (D1/D2 domains) sequence dataset containing data from newly published pucciniomycetous yeast species and a few 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-based dataset taken from Wang *et al.* (2015a). The LSU sequences were aligned with MAFFT version 7 and the G-INS-i option (Standley K 2013). Constrained phylogenetic analyses were only inforced for species previously analysed using seven DNA loci. Only bipartitions that received at least 85% bootstrap support during fast bootstrapping of the seven genes-based dataset (Wang *et al.* 2015a) 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). The alignments and trees were deposited in TreeBASE (No. 18537).

### Quantitative assessment of taxonomic ranks

The modified Generalized Mixed Yule Coalescent (GMYC) method (Humphreys & Barraclough 2014) was applied iteratively to identify higher evolutionary significant units (higher ESUs) above the species levels in the pucciniomycetous yeasts as done before for tremellomycetous fungi (Liu *et al.* 2015). Firstly, the overall GMYC analysis was carried out for the simulation at class level, and secondly nested analyses were run for the higher ESUs identification at family level for each clade. Outgroup samples were excluded from the dataset using the drop.tip command in ape (Paradis 2006). A chronogram was calculated from the ML-based tree using the penalised likelihood method (Sanderson 2002) as implemented in the chronopl command in ape (Paradis 2006). The chronogram was then analysed using a modified GMYC package in SPLITS in R (version 2.10, www.cran.r-project.org) using the single threshold method. In the case of clades with a small number of samples the modified GMYC approach would not result in significant differences simply because of sampling size: these were marked as ‘NA’ (not analysed).

Phylogenetic rank boundary optimisation (PRBO), a phylogenetic variant of clustering optimisation (Göker *et al.* 2009, 2010, Stielow *et al.* 2011), was conducted based on taxonomy-based reference information as described in Liu *et al.* (2015). A reduced classification including twelve putatively reliable genera of pucciniomycetous yeasts was chosen as reference taxonomy. The resulting optimal upper boundaries for the divergence of each taxonomic rank were then applied back to the entire dataset. These boundaries for each taxonomic rank were compared with boundaries estimated from the entire classification (Table 1). For each newly proposed or already established taxon, maximum subtree height (MaSH) of its corresponding clade, absolute deviation and significant deviation (Sigdev) from the threshold optimal for the reliable taxa were calculated. One hundred bootstrap replicates were applied to obtain the 95% confidence intervals for the boundaries to detect the significances of the divergences from the optimal range for each taxonomic rank.

The seven genes-based ML tree used in Wang *et al.* (2015a) was employed as the basis for the PRBO and iterative modified GMYC analyses. The taxa within *Ustilaginomycotina* were used as outgroup and taxa within *Pucciniomycetes* were used as ingroup in the above two analyses. Note that none of the two methods was followed strictly in the current study. Where possible, wider circumscriptions of taxa were chosen to lower the number of taxonomic changes suggested; moreover, where possible, clades with distinct phenotypic or ecological features were proposed as new taxa (Liu *et al.* 2015). Additionally, already established taxa were kept unless they appeared evidently non-monophyletic.

## RESULTS AND DISCUSSION

### Taxonomic units addressed by the iterative modified GMYC and PRBO analyses

The pucciniomycetous yeast species belong to four recognised classes, namely *Agaricostilbomycetes*, *Cystobasidiomycetes*, *Microbotryomycetes* and *Mixiomycetes* (Bauer *et al.* 2006, Hibbett *et al.* 2007, Boekhout *et al.* 2011). The overall modified GMYC analysis supported the *Agaricostilbomycetes* without *Spiculogloeales* as a class in agreement with the indication that *Spiculogloeales* may represent a new class within *Pucciniomycotina* based on the seven genes-based phylogenetic analyses (Wang *et al.* 2015a). Thus *Spiculogloeomycetes* is proposed as a new class to accommodate the order *Spiculogloeales*.

The nested analyses of the GMYC approach identified five families in the class *Agaricostilbomycetes* (Table 2), including the

**Table 1.** PRBO results showing the divergences, if any, of the proposed genera from the optimal range of divergences for their rank as inferred from selected reference data.

| Taxa | Rank | MaSH | Deviation | Sigdev |
|---|---|---|---|---|
| ***Agaricostilbomycetes*** | Class | 0.71223 | 0.07318 | 0 |
| *Agaricostilbum* clade | Genus | 0.22827 | 0 | 0 |
| ingoldii clade | Genus | 0.14859 | 0 | 0 |
| *Chionosphaera** | Genus | 0.29924 | 0 | 0 |
| *Kurtzmanomyces** | Genus | 0.33350 | 0.02844 | 0 |
| lactophilus clade | Genus | 0.25804 | 0 | 0 |
| sasicola clade | Genus | 0.15364 | 0 | 0 |
| *Kondoa* clade* | Genus | 0.28874 | 0 | 0 |
| *Bensingtonia** | Genus | 0.24787 | 0 | 0 |
| ruber clade | Genus | 0.29828 | 0 | 0 |
| subbrunneus clade | Genus | 0.39731 | 0.09225 | 0 |
| ***Cystobasidiomycetes*** | Class | 0.51968 | 0 | 0 |
| *Erythrobasidium* clade* | Genus | 0.16907 | 0 | 0 |
| *Bannoa* clade* | Genus | 0.15301 | 0 | 0 |
| aurantiaca clade | Genus | 0.16265 | 0 | 0 |
| marina clade | Genus | 0.23897 | 0 | 0 |
| *Sakaguchia* clade* | Genus | 0.29017 | 0 | 0 |
| magnisporus clade | Genus | 0.33920 | 0.03414 | 0 |
| *Cystobasidium* (minuta) clade* | Genus | 0.18036 | 0 | 0 |
| ***Microbotryomycetes*** | Class | 0.72324 | 0.08419 | 0 |
| *Sporidiobolus* clade | Genus | 0.34525 | 0.04020 | 0 |
| *Rhodosporidium* clade | Genus | 0.40759 | 0.10253 | 0 |
| mixed *Rhodosporidium*/*Sporidiobolus* clade | Genus | 0.16275 | 0 | 0 |
| *Kriegeria** | Genus | 0.21892 | 0 | 0 |
| glacialis clade | Genus | 0.16560 | 0 | 0 |
| buffonii clade | Genus | 0.10602 | 0 | 0 |
| yarrowii clade | Genus | 0.09543 | 0 | 0 |
| tsugae clade | Genus | 0.23831 | 0 | 0 |
| singularis clade | Genus | 0.05035 | 0 | 0 |
| yamatoana clade | Genus | 0.06763 | 0 | 0 |
| griseoflavus clade | Genus | 0.16370 | 0 | 0 |
| *Curvibasidium* clade* | Genus | 0.04099 | 0 | 0 |
| *Colacogloea* clade* | Genus | 0.23771 | 0 | 0 |
| sonckii clade | Genus | 0.06955 | 0 | 0 |
| vanillica clade | Genus | 0.07445 | 0 | 0 |
| *Leucosporidium* clade* | Genus | 0.15399 | 0 | 0 |
| *Microbotryum* clade | Genus | 0.14270 | 0 | 0 |

*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.

recognised families *Agaricostilbaceae*, *Chionosphaeraceae* and *Kondoaceae*, a new *Agaricostilbales* family 1 (**ruber** clade) and a new *Agaricostilbales* family 2 (***Bensingtonia sakaguchii*** lineage). Because only *B. sakaguchii* occurs in the new *Agaricostilbales* family 2, this family is not proposed in this study. Consequently, *B. sakaguchii* is placed into a new genus (see Taxonomy), which is presently treated as '*incertae sedis*' in the *Agaricostilbales*.

Nine clades were indentified at the family level within *Cystobasidiomycetes* by the nested analyses of GMYC (Table 2). The presently accepted families *Cystobasidiaceae*, *Erythrobasidiaceae* and *Naohideaceae* belong to *Cystobasidiales*, *Erythrobasidiales* and *Naohideales*, respectively. The genus *Occultifur* is separated from *Cystobasidiaceae* as a family in the GMYC analyses, but we presently prefer to keep this genus in the *Cystobasidiaceae* due to the low number of taxa in this genus. The ***Cyrenella*** and ***Rhodotorula lactosa*** lineages were suggested as two new families in the *Erythrobasidiales* by the GMYC nested analyses, however, these two lineages represent single species each, and, therefore, we temporarily placed them as '*incertae sedis*' in the *Erythrobasidiales*. The **aurantiaca** and **marina** clades were grouped into one family in the GMYC nested analyses, which is not supported by the phylogenetic analysis of seven genes that showed the two clades as a paraphyletic group (Wang *et al.* 2015a). The **magnisporus** and ***Sakaguchia*** clades were identified as families in agreement with the phylogenetic analysis of seven genes (Wang *et al.* 2015a).

Within *Microbotryomycetes* two families, namely *Leucosporidiaceae* and *Microbotryaceae*, were supported by the nested analyses of GMYC approach (Table 2). The family *Sporidiobolaceae* in the *Sporidiobolales* was divided into three families represented by the ***Sporidiobolus*** clade, the ***Rhodosporidium*** clade and the mixed ***Rhodosporidium***/***Sporidiobolus*** clade, respectively. We preserve the current taxonomic status of *Sporidiobolaceae* because the phenotype of these three clades is similar and it forms a strongly supported lineage in the phylogenetic analysis of seven genes (Wang *et al.* 2015a). The *Kriegeriaceae* and *Camptobasidiaceae* in the *Kriegeriales* were grouped into a single family in the nested GMYC analyses. However, the *Camptobasidiaceae*, including *Glaciozyma antarctica*, clustered together with the *Kriegeriaceae* lacking support value in the ML analysis and they did not occur in the same cluster in the MP and BI analyses (Wang *et al.* 2015a, Fig. 1 of this study). Consequently the two families are maintained in this study.

Ten clades and seven single-species lineages in *Microbotryomycetes* could not be assigned to presently recognised families and orders (Wang *et al.* 2015a). These clades are strongly divergent from each other and seem to have a sister relationship to the known families and orders within *Microbotryomycetes* (Fig. 1). The species *Rhodotorula hylophila*, *R. javanica*, *R. crocea* and *Reniforma strues* were not included in the nested GMYC analyses because they occurred outside the *Microbotryomycetes* in the overall GMYC analysis. In the nested GMYC analyses, the **griseoflavus**, **yamatoana**, **singularis** clades and *Sporobolomyces inositophilus* were identified as one family that was supported by the phylogenetic analysis of seven genes with strong support values (Wang *et al.* 2015a); the **buffonii**, **tsugae** and **yarrowii** clades were assigned to one family, but this was weakly supported by the seven genes ML analysis (57 % BP), lacking support in the BI analysis and were not supported by the MP analysis (Fig. 1), and consequently, they are not treated as a single family in this study; the other clades and the single-species lineages were identified as separate families in the nested GMYC analyses (Table 2).

Among 51 pucciniomycetous yeast clades suggested as genera in the previous multi-gene phylogenetic study (Wang

**Table 2.** Analyses with the modified GMYC approach showing the supported classification of the pucciniomycetous yeast at family and class levels.

| Class/Order | family | Genus | GMYC |
|---|---|---|---|
| ***Agaricostilbomycetes*** | | | supported |
| ***Agaricostilbales*** | | | |
| | ***Kondoaceae*** | | supported |
| | | ***Kondoa*** | |
| | | ***Bensingtonia*** | |
| | ***Agaricostilbaceae*** | | supported |
| | | ***Sterigmatomyces*** (*Agaricostilbum* clade) | |
| | | ***Pseudobensingtonia*** (ingoldii clade) | |
| | ***Chionosphaeraceae*** | | supported |
| | | ***Chionosphaera*** | |
| | | ***Kurtzmanomyces*** | |
| | | ***Mycogloea nipponica*** | |
| | | ***Ballistosporomyces*** (sasicola clade) | |
| | | ***Cystobasidiopsis*** (lactophilus clade) | |
| | ***Ruineniaceae*** | | new family |
| | | ***Ruinenia*** (ruber clade) | |
| | ***incertae sedis* in the *Agaricostilbales*** | ***Jianyunia*** (*Bensingtonia sakaguchii*) | new family |
| ***Spiculogloeomycetes*** | | | not supported |
| ***Spiculogloeales*** | | | |
| | ***Spiculogloeaceae*** | | supported |
| | | ***Phyllozyma*** (subbrunneus clade) | |
| ***Cystobasidiomycetes*** | | | not supported |
| ***Cystobasidiales*** | | | |
| | ***Cystobasidiaceae*** | | not supported |
| | | ***Occultifur*** | |
| | | ***Cystobasidium*** (minuta clade) | |
| ***Erythrobasidiales*** | | | |
| | ***Erythrobasidiaceae*** | | supported |
| | | ***Erythrobasidium*** | |
| | | ***Bannoa*** | |
| | ***incertae sedis* in the *Erythrobasidiales*** | ***Hasegawazyma*** (*Rhodotorula lactosa*) | new family |
| | | ***Cyrenella*** | new family |
| ***Naohideales*** | | | |
| | ***Naohideaceae*** | | supported |
| | | ***Naohidea*** | |
| *incertae sedis* in the ***Cystobasidiomycetes*** | | | |
| | ***Buckleyzymaceae*** | | not supported |
| | | ***Buckleyzyma*** (aurantiaca clade) | |
| | ***Symmetrosporaceae*** | | not supported |
| | | ***Symmetrospora*** (marina clade) | |
| | ***Sakaguchiaceae*** | | new family |
| | | ***Sakaguchia*** | |
| | ***Microsporomycetaceae*** | | new family |
| | | ***Microsporomyces*** (magnisporus clade) | |
| ***Microbotryomycetes*** | | | not supported |
| ***Sporidiobolales*** | | | |

(*continued on next page*)

**Table 2.** (Continued).

| Class/Order | family | Genus | GMYC |
|---|---|---|---|
| | ***Sporidiobolaceae*** | | not supported |
| | | ***Rhodotorula*** (*Rhodosporidium* clade) | new family |
| | | ***Rhodosporidiobolus*** (mixed *Rhodosporidium*/*Sporidiobolus* clade) | new family |
| | | ***Sporobolomyces*** (*Sporidiobolus* clade) | new family |
| ***Kriegeriales*** | | | |
| | ***Kriegeriaceae*** | | not supported |
| | | ***Kriegeria*** | |
| | | ***Meredithblackwellia*** | |
| | | ***Phenoliferia*** (glacialis clade) | |
| | | ***Yamadamyces*** (*Rhodotorula rosulata*) | |
| | ***Camptobasidiaceae*** | | not supported |
| | | ***Glaciozyma*** | |
| ***Leucosporidiales*** | | | |
| | ***Leucosporidiaceae*** | | supported |
| | | ***Leucosporidium*** | |
| ***Microbotryales*** | | | |
| | ***Microbotryaceae*** | | supported |
| | | ***Microbotryum*** | |
| | ***Ustilentylomataceae*** | | supported |
| | | ***Ustilentyloma*** | |
| ***Heterogastridiales*** | | | |
| | ***Heterogastridiaceae*** | | supported |
| | | ***Heterogastridium*** | |
| *incertae sedis* in the ***Microbotryomycetes*** | | | |
| | ***Chrysozymaceae*** | | new family |
| | | ***Chrysozyma*** (griseoflavus clade) | |
| | | ***Bannozyma*** (yamatoana clade) | |
| | | ***Hamamotoa*** (singularis clade) | |
| | | ***Fellozyma*** (*Sporobolomyces inositophilus*) | |
| | ***Colacogloeaceae*** | | new family |
| | | ***Colacogloea*** | |
| Genera *incertae sedis* in the ***Microbotryomycetes*** | | | |
| | | ***Pseudohyphozyma*** (buffonii clade) | new family |
| | | ***Slooffia*** (tsugae clade) | |
| | | ***Oberwinklerozyma*** (yarrowii clade) | |
| | | ***Sampaiozyma*** (vanillica clade) | new family |
| | | ***Yunzhangia*** (sonckii clade) | new family |
| | | ***Curvibasidium*** | new family |
| | | ***Pseudoleucosporidium*** (*Leucosporidium fasciculatum*) | |
| | | ***Udeniozyma*** (*Rhodotorula ferulica*) | new family |
| | | ***Reniforma*** | new family |
| | | ***Trigonosporomyces*** (*Rhodotorula hylophila*) | new family |
| | | ***Vonarxula*** (*Rhodotorula javanica*) | new family |
| | | ***Spencerozyma*** (*Rhodotorula crocea*) | |
| ***Mixiomycetes*** | | | not supported |
| ***Mixiales*** | | | |
| | ***Mixiaceae*** | | NA |
| | | ***Mixia*** | |

*Note*: NA means "not analysed". In the overall GMYC analysis, *Naohideales* is a separate class from *Cystobasidiomycetes*; *Spiculogloмycetes* and *Mixiomycetes* were identified as one class; *Heterogastridium*, *Rhodotorula hylophila*, and *Reniforma* form a separate class from *Microbotryomycetes*; *Rhodotorula javanica* and *Rhodotorula crocea* form another separate class from *Microbotryomycetes*.

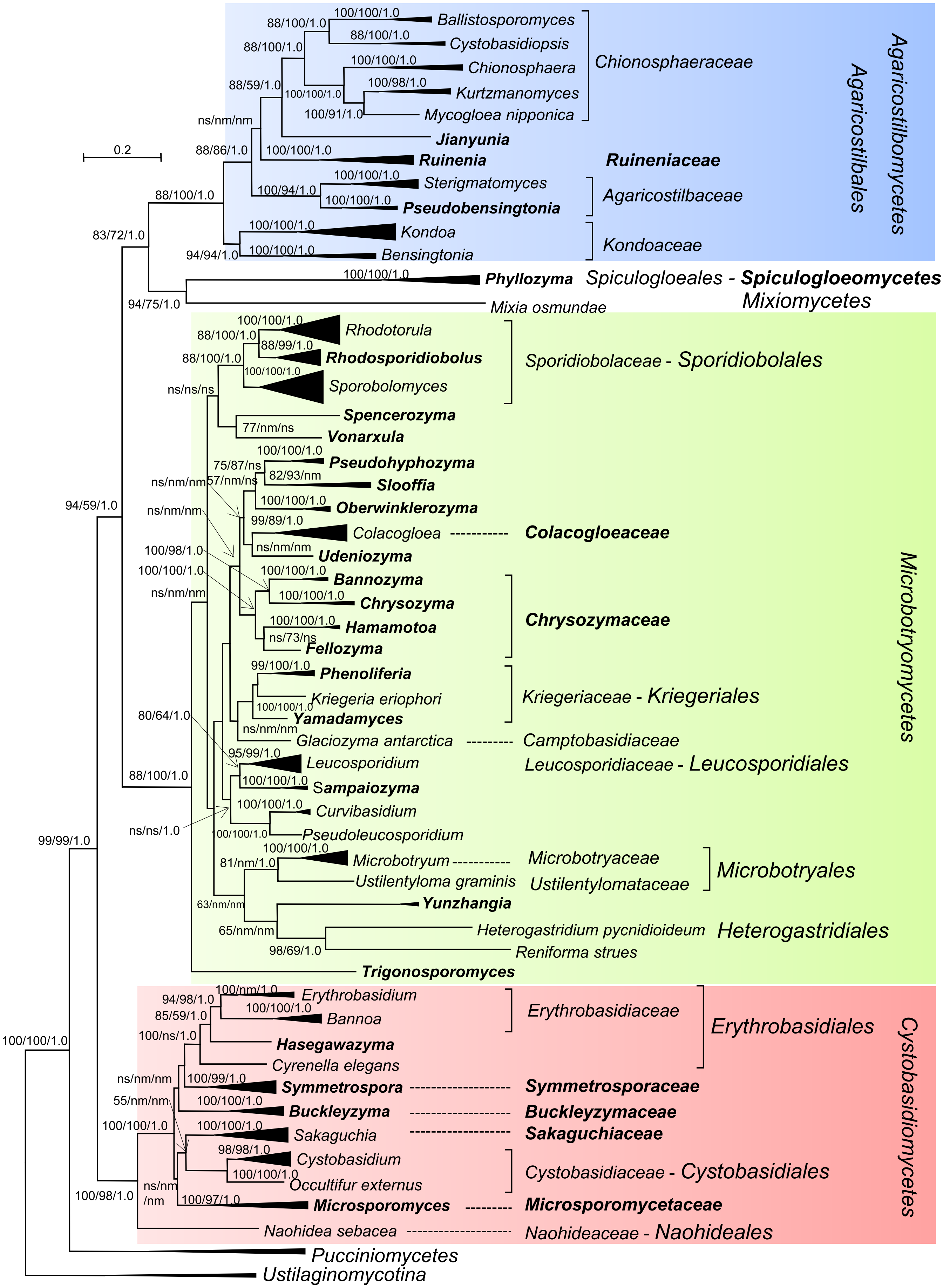

**Fig. 1.** Phylogenetic tree inferred using the combined sequences of SSU rRNA, LSU rRNA D1/D2 domains, ITS regions (including 5.8S rRNA), *RPB1*, *RPB 2*, *TEF1* and *CYTB*, depicting the phylogenetic positions of existing yeast taxa and new genera (in bold) within *Pucciniomycotina*. The tree backbone was constructed using maximum likelihood analysis. Bootstrap percentages of maximum likelihood and maximum parsimony analyses over 50 % from 1 000 bootstrap replicates and posterior probabilities of Bayesian inference above 0.95 are shown respectively from left to right on the deep and major branches. Bar = 0.2 substitutions per nucleotide position. *Note*: ns, not supported (BP < 50 % or PP < 0.9); nm, not monophyletic. The new taxa are in bold.

*et al.* 2015a), only few were found to deviate from the optimal range of divergences as determined in the PRBO analysis, and were found to significantly deviate (Table 1), which supports the preliminary taxonomic conclusions from the multi-gene phylogenetic analysis. Twenty-six of them represent currently described genera. The others are proposed as new genera (Fig. 1) based on the phylogenetic analyses, PRBO analysis and phenotypic comparisons (Table 1, Table 3 and Figs 2, 3) presented in this study.

## Phylogenetic analyses

Only 156 species from 184 ones used in the seven genes-based tree (Wang *et al.* 2015a) were selected to construct the phylogenetic network, because some protein genes were not available for all species. As a result all clades recognised in the seven genes-based tree could be recognised in the network approach. The network result showed that the five classes containing yeast species, viz. *Agaricostilbomycetes*, *Cystobasidiomycetes*, *Microbotryomycetes*, *Mixiomycetes* and *Spiculogloeomycetes*, remain separated (Fig. 2A). The 51 clades in the seven genes-based tree are also separated without any reticulation (Fig. 2B–D). This result confirmed the reliability of the combined phylogenetic analysis of the seven genes.

For a better understanding of the phylogenetic relationships between *Agaricostilbomycetes*, *Cystobasidiomycetes*, *Microbotryomycetes*, *Mixiomycetes* and *Spiculogloeomycetes*, and to include recently described species, an enlarged LSU rRNA gene dataset was analysed. Thereby, the LSU dataset analysed by Wang *et al.* (2015a) was enlarged from 184 to 242 sequences containing both sexual (e.g. *Camptobasidium*, *Cystobasidium*, *Glaciozyma*, *Kondoa* and *Ustilentyloma*) and asexual (e.g. *Rhodotorula*, *Sporobolomyces* and *Occultifur*) genera and species (Figs 4–8). The constrained ML analysis of the enlarged LSU dataset was used to place species known from LSU rRNA gene sequences in the phylogenetic clades previously recognised in the analysis based on the seven DNA-loci. Results from the LSU analysis were not used to challenge the results of the multi-gene study (Wang *et al.* 2015a), but to investigate the stability of the taxonomy in undersampled clades.

The enlarged analysis of the LSU rRNA gene dataset suggests that the number of single-species lineages in *Microbotryomycetes* is likely to increase in the future, since many sequences representing potentially new species could not be assigned to any of the clades recognised (Figs 4–8). In agreement with previous studies (Scorzetti *et al.* 2002, Weiß *et al.* 2004, Boekhout *et al.* 2011, Wang *et al.* 2015a), our results showed that LSU alone is not sufficient to resolve many clades in *Microbotryomycetes* (Fig. 6).

The addition of the supplemental species or sequences representing potential new species resulted in the enlargement of several clades, especially single species lineages recognised in the phylogenetic analysis of seven genes (Wang *et al.* 2015a), e.g. *Fellozyma*, *Glaciozyma*, *Occultifur* and *Rhodotorula hordea* (Figs 5–7). In addition, a few new clades and single-species lineages were identified such as *Camptobasidium hydrophilum*, *Meredithblackwellia eburnea* and *Rhodotorula svalbardensis* (Fig. 6). Most supplemental sequences (34 out of 58) were located in *Microbotryomycetes* (Figs 6, 7). The following type species were added to the dataset, namely *Cystobasidium fimetarium*, *Camptobasidium hydrophilum*, *Meredithblackwellia eburnea* and *Microbotryozyma collariae* (Figs 5–7). Newly added sequences substantially expanded the following clades recognised in Wang *et al.* (2015a), viz. *Curvibasidium* (Fig. 7), *Glaciozyma* (Fig. 6), *Ruinenia* (Fig. 4) and *Slooffia* (Fig. 6).

# TAXONOMY

**Class *Agaricostilbomycetes*** R. Bauer *et al.*, Mycol. Progr. 5: 45. 2006.

*Type order*: *Agaricostilbales* Oberw. & R. Bauer

This class contains the order *Agaricostilbales*. Our previous multi-gene sequence analyses indicated that nine well support clades, namely ***Agaricostilbum***, ***Bensingtonia***, ***Chionosphaera***, ***Kondoa***, ***Kurtzmanomyces***, **ingoldii**, **lactophilus**, **ruber**, **sasicola**, and two species *Bensingtonia sakaguchii* and *Mycogloea nipponica*, occurred in the *Agaricostilbales* (Wang *et al.* 2015a). These clades which are delimited at the generic rank are supported by the PRBO analysis (Table 1), the phylogenetic network analysis (Fig. 2B), and the analysis of the enlarged LSU rRNA gene dataset (Fig. 4). The genera *Chionosphaera* and *Kurtzmanomyces* are well-established genera. The genera *Sterigmatomyces*, *Cystobasidiopsis* and *Kondoa* are emended to include both teleomorphic and anamorphic species in the *Agaricostilbum*, lactophilus and *Kondoa* clades, respectively. *Ballistosporomyces* is emended and reintroduced to include species in the **sasicola** clade. *Jianyunia* gen. nov., *Pseudobensingtonia* gen. nov. and *Ruinenia* gen. nov. are proposed to accommodate the species in the ***Bensingtonia sakaguchii***, **ingoldii** and **ruber** clades, respectively. *Ruineniaceae* fam. nov. is proposed to accommodate the genus *Ruinenia* based on results from the phylogenetic analysis of seven genes (Fig. 1) and GMYC analyses (Table 2).

**Order *Agaricostilbales*** Oberw. & R. Bauer, Sydowia 41: 240. 1989.

*Type family*: *Agaricostilbaceae* Oberw. & R. Bauer.

This order was proposed to accommodate the family *Agaricostilbaceae* (Oberwinkler & Bauer 1989). The *Agaricostilbaceae*, *Chionosphaeraceae* and *Kondoaceae* were accepted in this order by Bauer *et al.* (2006). Here we propose *Ruineniaceae* and *Jianyunia* as '*incertae sedis*' in the *Agaricostilbales*.

**Family *Agaricostilbaceae*** Oberw. & R. Bauer, Sydowia 41: 240. 1989.

*Type genus*: *Agaricostilbum* J.E. Wright.

This family is characterised by septal pores without microbodies, aseptate basidiospores produced in a yeast-like manner and lack of tremelloid haustorial cells (Oberwinkler & Bauer 1989, Bauer *et al.* 2006).

**Table 3.** Selected physiological and biochemical characteristics of different clades within the *Pucciniomycotina*.

| **Genus or species** | Sucrose | Raffinose | Lactose | Trehalose | Maltose | Melezitose | Methyl-α-D-glucoside | Soluble Starch | L-Arabinose | D-Arabinose | Glycerol | *myo* -Inositol | DL-glucoside | Nitrate | Nitrite | CoQ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Agaricostilbomycetes*** | | | | | | | | | | | | | | | | |
| ***Agaricostilbales*** | | | | | | | | | | | | | | | | |
| ***Kondoaceae*** | | | | | | | | | | | | | | | | |
| ***Kondoa*** | v | v | v | + | v | v | v | v | v | v | + | − | v | v | v | 9 |
| ***Bensingtonia*** | v | v | v | v | v | v | − | v | v | v | + | − | v | + | v | 9 |
| ***Agaricostilbaceae*** | | | | | | | | | | | | | | | | |
| ***Sterigmatomyces*** (*Agaricostilbum* clade) | v | v | v | + | − | v | v | − | v | + | + | − | v | v | v | 9 |
| ***Pseudobensingtonia*** (ingoldii clade) | v | v | v | + | − | v | − | v | v | + | + | − | v | v | v | 9 |
| ***Chionosphaeraceae*** | | | | | | | | | | | | | | | | |
| ***Ballistosporomyces*** (sasicola clade) | + | v | v | + | + | v | v | + | v | − | − | − | − | v | v | 10 |
| ***Cystobasidiopsis*** (lactophilus clade) | + | v | v | + | + | v | v | + | v | + | + | − | + | v | v | 10 |
| ***Kurtzmanomyces*** | v | v | v | v | v | v | − | − | v | v | v | v | v | + | + | 10 |
| ***Chionosphaera*** | − | − | − | v | v | − | − | v | v | v | v | v | v | − | − | 10 |
| ***Jianyunia*** (*Bensingtonia sakaguchii*) | − | − | + | + | + | + | v | + | − | − | − | − | − | − | − | 9 |
| ***Ruinenia*** (ruber clade) | + | + | v | v | v | + | v | v | v | − | v | − | − | − | − | 10 |
| ***Spiculogloeales*** | | | | | | | | | | | | | | | | |
| ***Phyllozyma*** (subbrunneus clade) | v | v | v | v | − | − | − | − | − | v | v | − | v | + | v | 10 |
| ***Cystobasidiomycetes*** | | | | | | | | | | | | | | | | |
| ***Cystobasidiales*** | | | | | | | | | | | | | | | | |
| ***Cystobasidium*** (minuta clade) | v | v | v | v | v | v | v | v | v | v | + | v | v | − | − | 9,10 |
| ***Occultifur externus*** | + | − | + | + | + | + | − | − | + | + | + | − | + | − | − | n |
| ***Erythrobasidiales*** | | | | | | | | | | | | | | | | |
| ***Erythrobasidium*** | + | − | − | + | + | + | − | v | + | + | + | − | v | v | v | 10($H_2$) |
| ***Bannoa*** | + | + | v | + | + | + | v | + | v | v | + | v | v | − | − | 10 ($H_2$) |
| ***Hasegawazyma*** (*Rhodotorula lactosa*) | + | + | + | + | + | + | − | + | + | + | + | − | + | + | + | 9 |
| ***Cyrenella elegans*** | + | + | − | + | + | + | − | + | + | − | + | − | − | + | + | n |
| ***Microsporomyces*** (magnisporus clade) | v | v | v | + | v | + | v | v | v | v | v | v | v | v | v | 10 |
| ***Buckleyzyma*** (aurantiaca clade) | v | v | − | v | v | v | − | − | + | + | + | − | v | v | v | 10 |

(*continued on next page*)

**Table 3.** (Continued).

| **Genus or species** | Sucrose | Raffinose | Lactose | Trehalose | Maltose | Melezitose | Methyl-α-D-glucoside | Soluble Starch | L-Arabinose | D-Arabinose | Glycerol | *myo* -Inositol | DL-glucoside | Nitrate | Nitrite | CoQ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Symmetrospora*** (marina clade) | v | v | v | v | v | v | v | v | v | v | + | − | v | v | v | 10 |
| ***Sakaguchia*** | v | v | − | + | v | v | − | v | v | v | + | − | v | − | − | 10 |
| ***Naohideales*** | | | | | | | | | | | | | | | | |
| ***Naohidea sebacea*** | − | − | − | − | − | − | − | − | − | − | + | − | + | − | − | n |
| ***Mixiomycetes*** | | | | | | | | | | | | | | | | |
| ***Mixia osmundae*** | − | − | − | − | − | − | − | + | − | v | − | − | − | − | − | 10 |
| ***Microbotryomycetes*** | | | | | | | | | | | | | | | | |
| ***Sporidiobolales*** | | | | | | | | | | | | | | | | |
| ***Rhodotorula*** (*Rhodosporidium* clade) | + | v | − | + | v | v | v | − | v | v | + | − | v | v | v | 9,10 |
| ***Rhodosporidiobolus*** (mixed *Rhodosporidium*/*Sporidiobolus* clade) | v | v | − | + | v | v | v | v | v | v | + | − | v | + | + | 9,10 |
| ***Sporobolomyces*** (*Sporidiobolus* clade) | + | v | − | v | v | v | v | v | v | v | v | − | v | v | v | 10 |
| ***Leucosporidiales*** | | | | | | | | | | | | | | | | |
| ***Leucosporidium*** | v | v | − | v | v | v | v | − | v | v | + | − | v | v | v | 9,10 |
| ***Kriegeriales*** | | | | | | | | | | | | | | | | |
| ***Kriegeriaceae*** | | | | | | | | | | | | | | | | |
| ***Phenoliferia*** (glacialis clade) | + | + | − | − | − | + | − | n | − | − | − | − | − | + | − | n |
| ***Meredithblackwellia eburnea*** | + | − | − | + | + | + | + | − | w | + | + | − | + | − | − | n |
| ***Yamadamyces*** (*Rhodotorula rosulata*) | + | − | − | w | + | + | − | w | − | − | w | + | d | + | + | n |
| ***Kriegeria eriophori*** | + | − | − | + | + | + | + | − | + | v | + | − | + | + | + | n |
| ***Camptobasidiaceae*** | | | | | | | | | | | | | | | | |
| ***Glaciozyma antarctica*** | v | − | − | − | v | − | − | v | − | − | v | − | − | + | + | 10 |
| ***Sampaiozyma*** (vanillica clade) | + | + | + | + | + | + | v | + | − | v | + | − | + | + | + | 10 |
| ***Curvibasidium*** | v | v | v | v | v | v | − | − | + | v | v | v | v | − | − | 9 |
| ***Chrysozyma*** (griseoflavus clade) | v | − | − | + | + | + | v | v | − | v | v | − | − | v | v | 10 |
| ***Bannozyma*** (yamatoana clade) | + | − | − | + | v | + | − | v | − | − | + | − | − | − | − | 9 |
| ***Hamamotoa*** (singularis clade) | − | − | + | + | − | − | − | − | v | v | + | − | + | − | − | n |
| ***Fellozyma*** (*Sporobolomyces inositophilus*) | + | − | − | + | + | + | − | − | − | − | + | + | − | + | + | 10 |
| ***Colacogloea*** | v | v | − | + | v | v | v | − | − | v | v | − | v | v | v | 10 |
| ***Udeniozyma*** (*Rhodotorula ferulica*) | + | − | + | + | + | + | + | − | − | + | + | − | v | + | + | 10 |
| ***Pseudohyphozyma*** (buffonii clade) | − | − | − | v | v | v | − | v | v | + | + | − | v | v | v | 10 |

**Table 3.** (Continued).

| **Genus or species** | Sucrose | Raffinose | Lactose | Trehalose | Maltose | Melezitose | Methyl-α-D-glucoside | Soluble Starch | L-Arabinose | D-Arabinose | Glycerol | *myo*-Inositol | DL-glucoside | Nitrate | Nitrite | CoQ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Slooffia*** (tsugae clade) | + | - | v | + | + | + | v | - | - | v | + | - | + | + | + | 10 |
| ***Oberwinklerozyma*** (yarrowii clade) | + | + | - | + | + | + | v | v | - | v | + | + | + | + | + | 9 |
| ***Microbotryum*** | + | - | + | + | + | + | + | + | - | - | + | - | + | + | + | n |
| ***Ustilentyloma graminis*** (*Rhodotorula hordea*) | + | - | + | + | + | + | + | + | - | - | + | - | + | + | + | n |
| ***Yunzhangia*** (sonckii clade) | v | - | - | + | v | v | - | - | - | - | + | - | v | v | v | n |
| ***Trigonosporomyces*** (*Rhodotorula hylophila*) | - | - | - | - | - | - | - | - | - | - | + | - | + | - | - | n |
| ***Vonarxula*** (*Rhodotorula javanica*) | - | + | - | + | + | - | - | + | + | + | + | - | - | + | + | 9 |
| ***Spencerozyma*** (*Rhodotorula crocea*) | + | - | - | + | + | + | - | - | v | v | + | - | - | + | + | 10 |
| ***Reniforma strues*** | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | 7 |

*Note*: V: variable; +: positive; −: negative; w: weak; d: delay; n: not tested.

*Genera accepted*: *Sterigmatomyces* Fell, *Pseudobensingtonia* F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout.

***Sterigmatomyces*** Fell, Antonie van Leeuwenhoek 32: 101. 1966. **emend.** F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout.

= *Agaricostilbum* J.E. Wright, Mycologia 62: 679. 1970.

*Type species*: *Sterigmatomyces halophilus* Fell.

This genus is emended to include species of *Agaricostilbum* and *Sterigmatomyces*, which occurred as a well supported ***Agaricostilbum*** clade within *Agaricostilbaceae* (Figs 1, 4). The name *Sterigmatomyces* was published before *Agaricostilbum* (Fell 1966, 2011, Wright 1970, Bandoni & Boekhout 2011), so the merged genus is named *Sterigmatomyces*.

Sexual reproduction observed in some species. Basidia occur predominantly in synnemata-like basidiomata. Hyphae, basidia and basidiospores relatively thick-walled. Basidiospores often attached to a budding locus (Bandoni & Boekhout 2011). Colonies cream and butyrous. Budding cells present or not, some of them produce one or more stalk-like conidiophores with blastoconidia separating at a septum in the mid-region of the stalk on the parent cell. Ballistoconidia not produced. Major CoQ system Q-9.

*Species accepted*:

1) *Sterigmatomyces elviae* Sonck & Yarrow, Antonie van Leeuwenhoek 35: 172. 1969.
2) *Sterigmatomyces halophilus* Fell, Antonie van Leeuwenhoek 32: 101. 1966.
3) ***Sterigmatomyces hyphaenes*** (Har. & Pat.) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813385.

   *Basionym*: *Pilacre hyphaenes* Har. & Pat., Bull. Mus. Hist. Nat. 17: 370. 1911.

   ≡ *Agaricostilbum hyphaenes* (Har. & Pat.) Oberw. & Bandoni.
4) ***Sterigmatomyces pulcherrimus*** (J.E. Wright) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813386.

   *Basionym*: *Isaria pulcherrima* Berk. & Broome, J. Linn. Soc. Bot. 14: 96. 1873.

   ≡ *Agaricostilbum pulcherrimum* (Berk. & Broome) B.L. Brady, B. Sutton & Samson.

   = *Agaricostilbum palmicola* J.E. Wright.
5) ***Sterigmatomyces novozelandicus*** (W.B. Kendr. & X.D. Gong) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813388.

   *Basionym*: *Agaricostilbum novozelandicum* (as *novazelandica*) W.B. Kendr. & X.D. Gong, Mycotaxon 54: 21. 1995.

***Pseudobensingtonia*** F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813078.

*Etymology*: The genus is named because of a similar morphology as present in the genus *Bensingtonia*.

This genus is proposed to accommodate the *ingoldii* clade containing two species that previously belonged to the genus *Bensingtonia* (Wang *et al.* 2015a). Member of the *Agaricostilbaceae*. The genus is mainly circumscribed by the

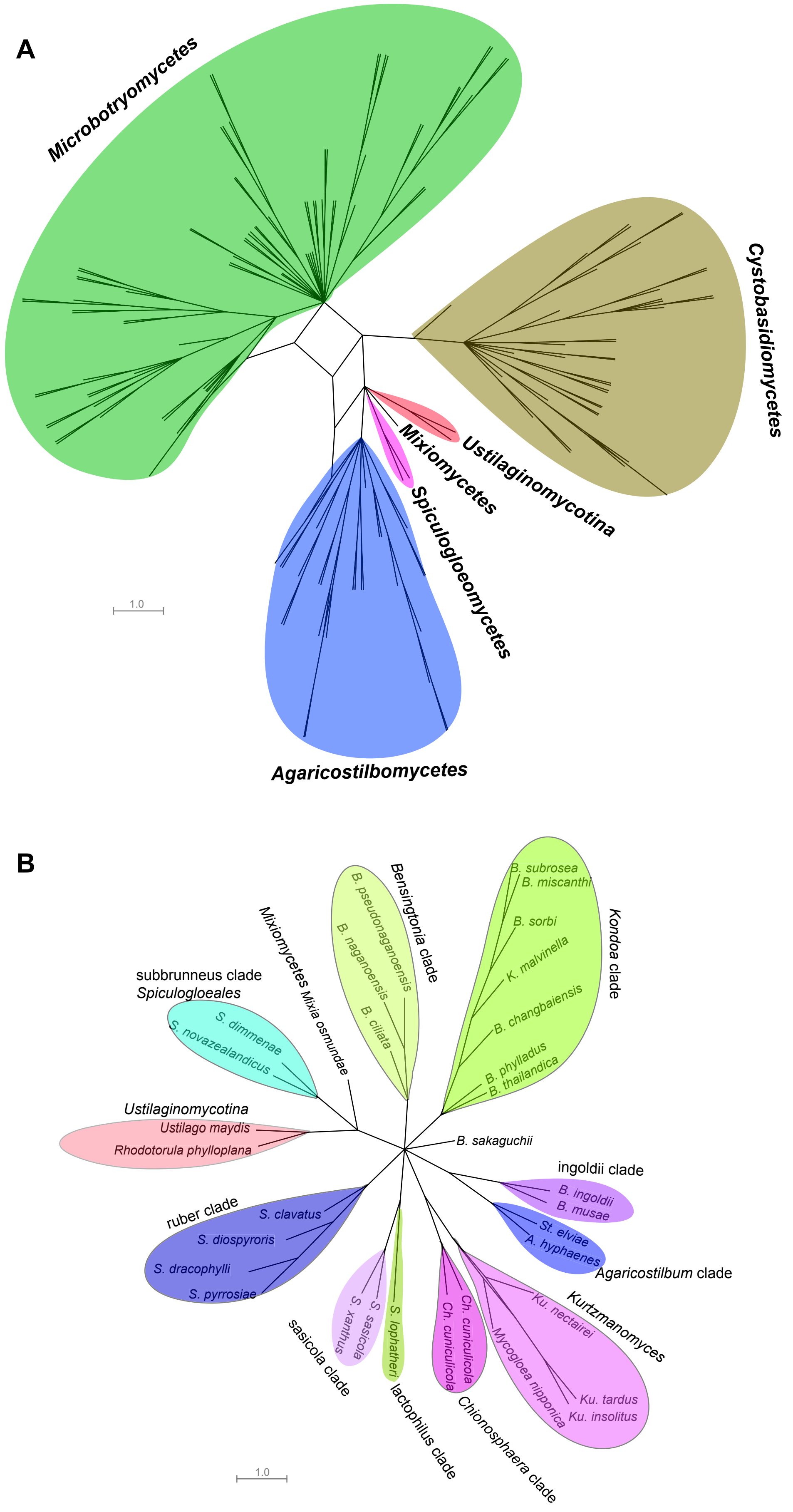

**Fig. 2.** Phylogenetic network of the yeast species within *Pucciniomycotina*. Single gene ML trees inferred with RAxML were investigated in Splitstree 4.13.1 using the ConsensusNetwork algorithm under default settings. A): the phylogenetic network of the *Agaricostilbomycetes*, *Mixiomycetes*, *Microbotryomycetes*, *Cystobasidiomycetes* and *Spiculogloeomycetes*; B): the phylogenetic network of *Agaricostilbomycetes*, *Mixiomycetes* and *Spiculogloeomycetes*; C): the phylogenetic network of *Cystobasidiomycetes*; D): the phylogenetic network of *Microbotryomycetes*. Abbreviations: *A*: *Agaricostilbum*; *B*: *Bensingtonia*; *C*: *Curvibasidium*; *Ch*: *Chionosphaera*; *K*: *Kondoa*; *Ku*: *Kurtzmanomyces*; *L*: *Leucosporidium*; *Le*: *Leucosporidiella*; *M*: *Microbotryum*; *Ma*: *Mastigobasidium*; *R*: *Rhodotorula*; *Rh*: *Rhodosporidium*; *S*: *Sporobolomyces*; *Sa*: *Sakaguchia*; *Sp*: *Sporidiobolus*; *Sph*: *Sphacelotheca*; *Ster*: *Sterigmatomyces*.

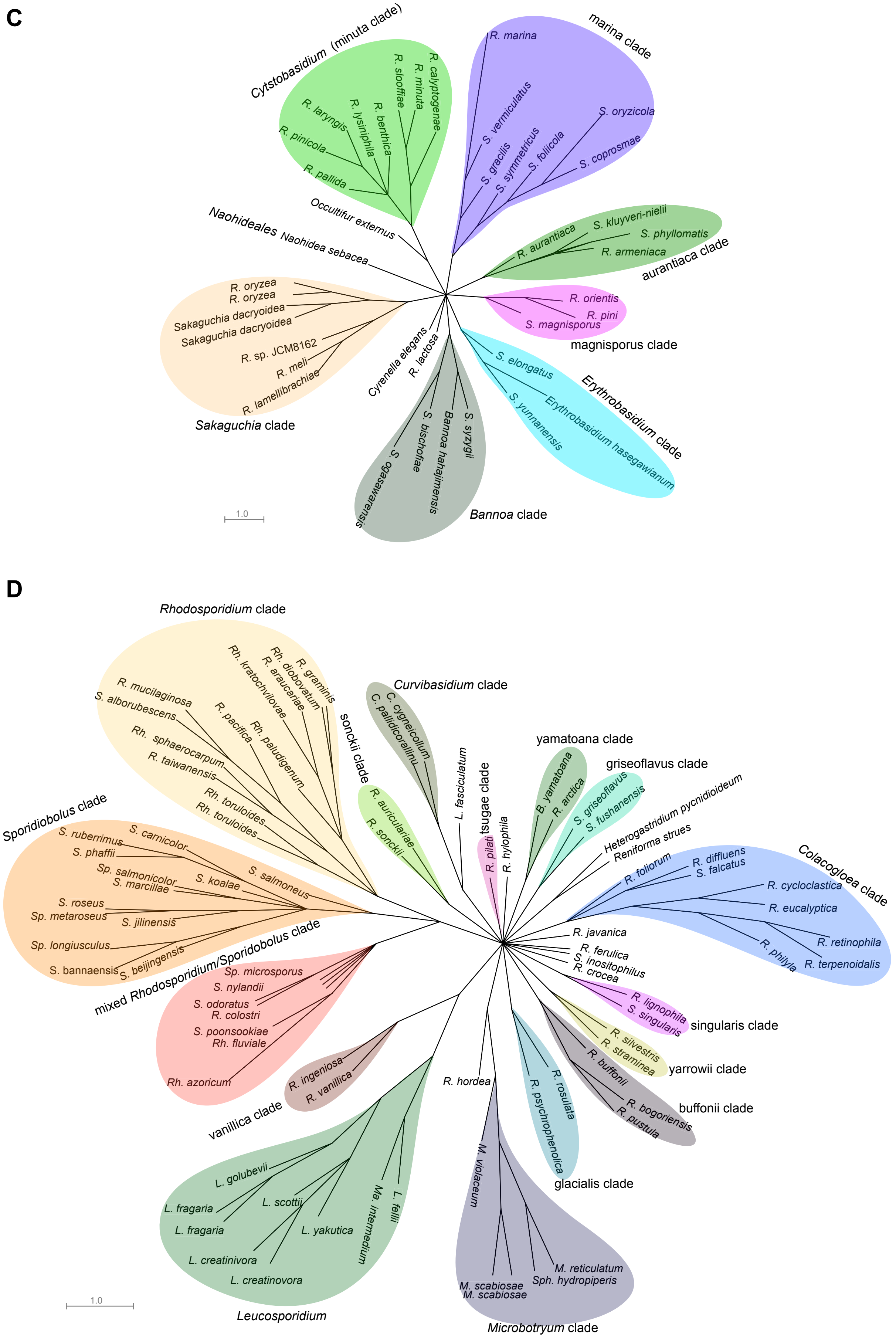

**Fig. 2.** (Continued).

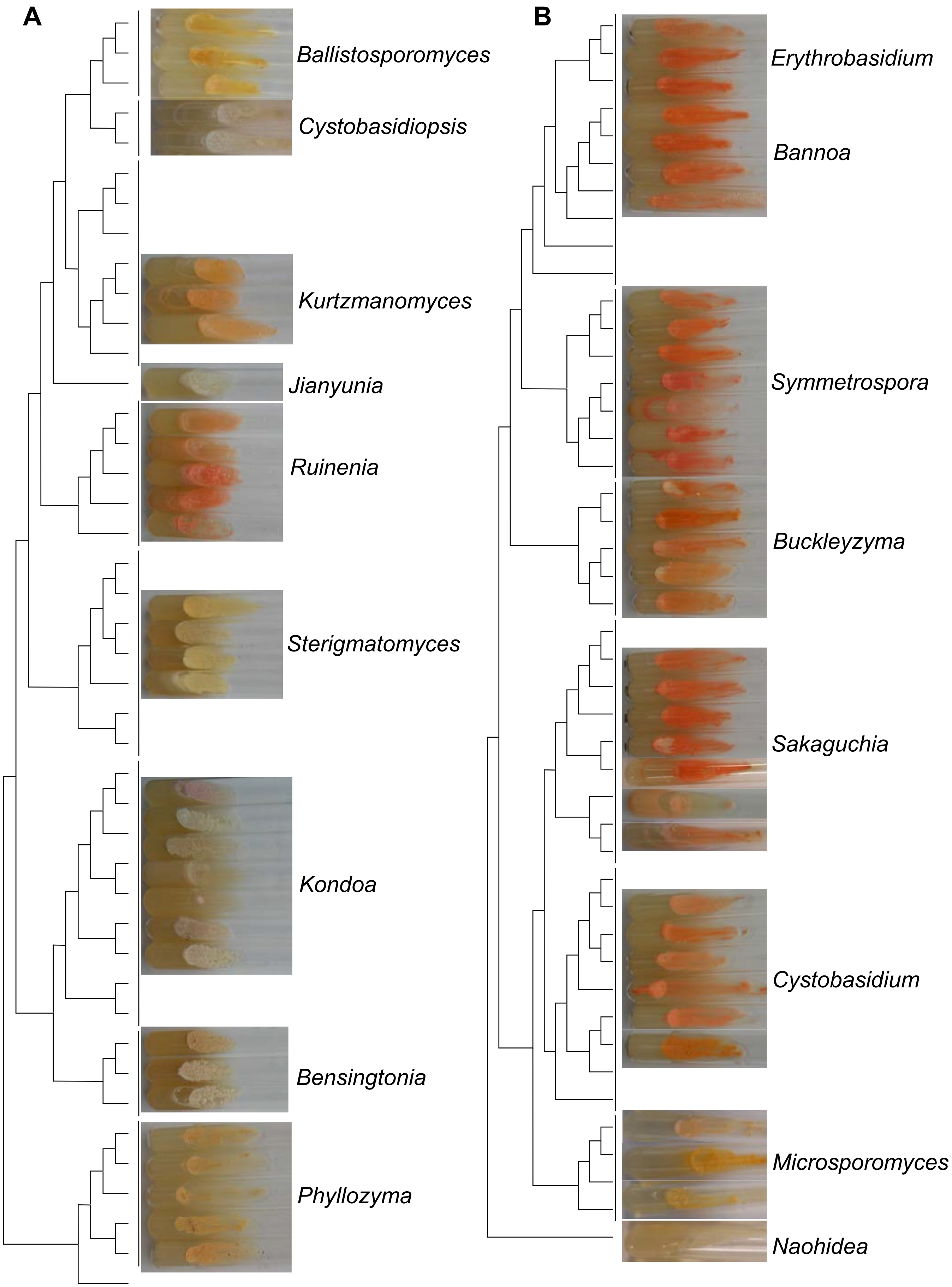

**Fig. 3.** Comparison of the colony characteristics in different clades within the *Pucciniomycotina*. All strains were cultured on slants with potato dextrose agar (PDA) medium for one month at 17 °C. The tree was inferred using maximum likelihood analysis from the combined seven genes (Wang *et al.* 2015a). A): The colony characteristics in different clades of the classes *Agaricostilbomycetes* and *Spiculogloeomycetes*; B): The colony characteristics in different clades of the class *Cystobasidiomycetes*; C): The colony characteristics in different clades of the order *Sporidiobolales* of *Microbotryomycetes*; D): The colony characteristics in different clades of the class *Microbotryomycetes*, except those belonging to order *Sporidiobolales*.

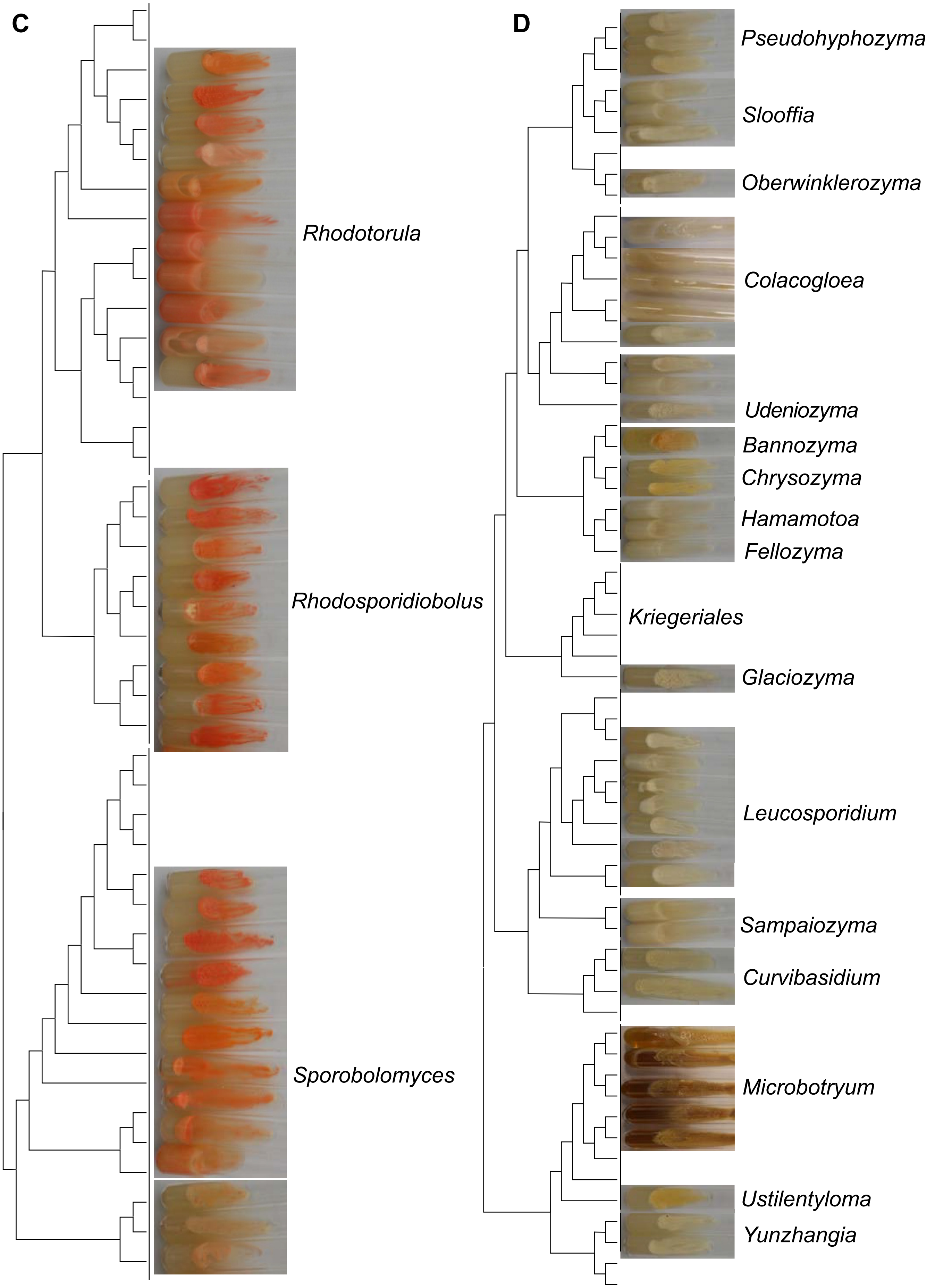

**Fig. 3.** (Continued).

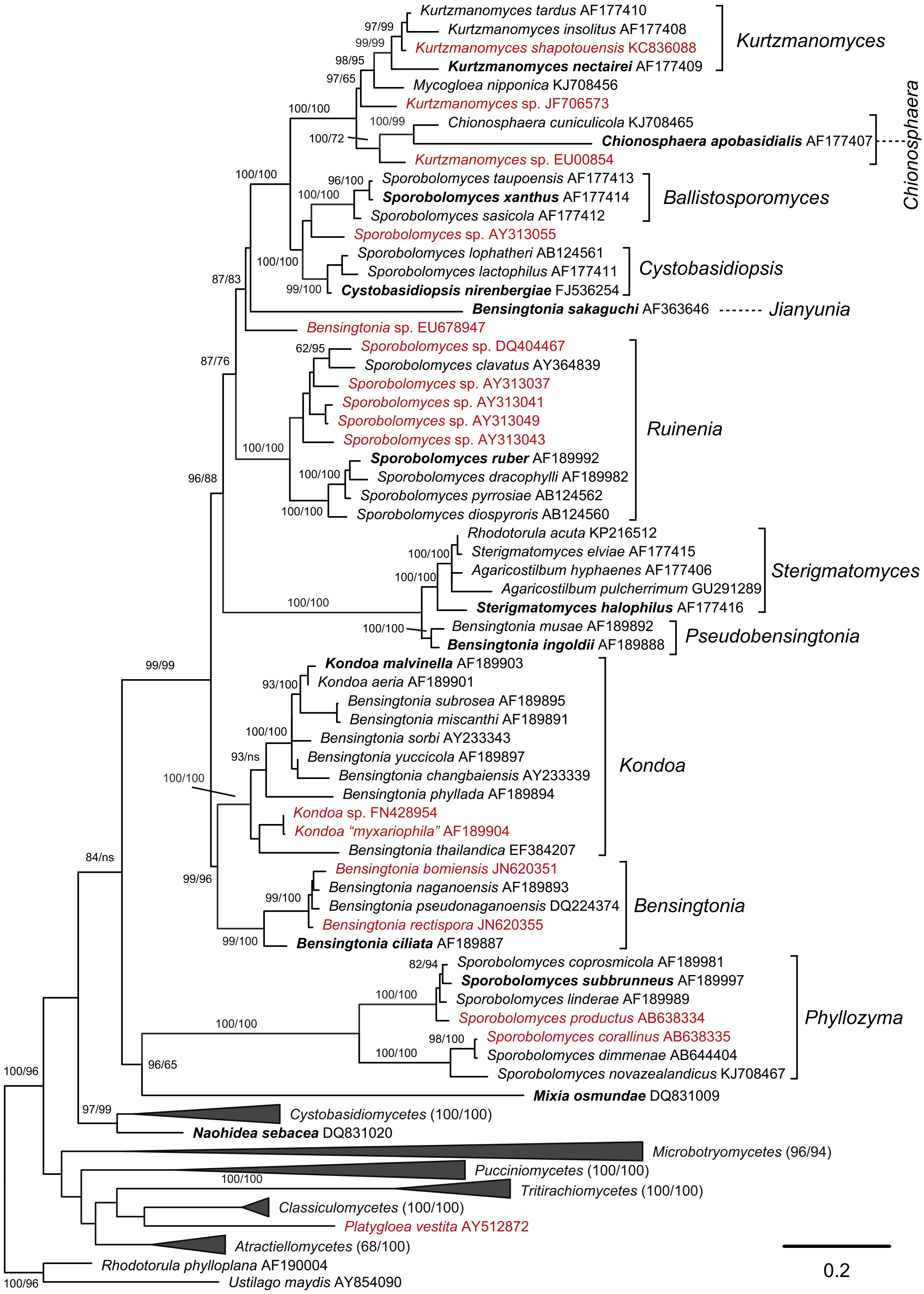

**Fig. 4.** Phylogenetic relationships of yeasts and related taxa from the *Agaricostilbomycetes* and *Mixiomycetes* lineages obtained by Maximum-Likelihood analysis of the LSU (D1/D2 domains) rRNA gene. Tree topology was constrained according to the topology of the seven genes-based tree (Wang *et al.* 2015a) with nodes showing bootstrap values >85 % inforced to be monophyletic. The type species of each genus is in bold. Taxa not included in the phylogenetic analysis of the seven genes (Wang *et al.* 2015a) are indicated in red. *Note*: ns, not supported (BP < 50 %).

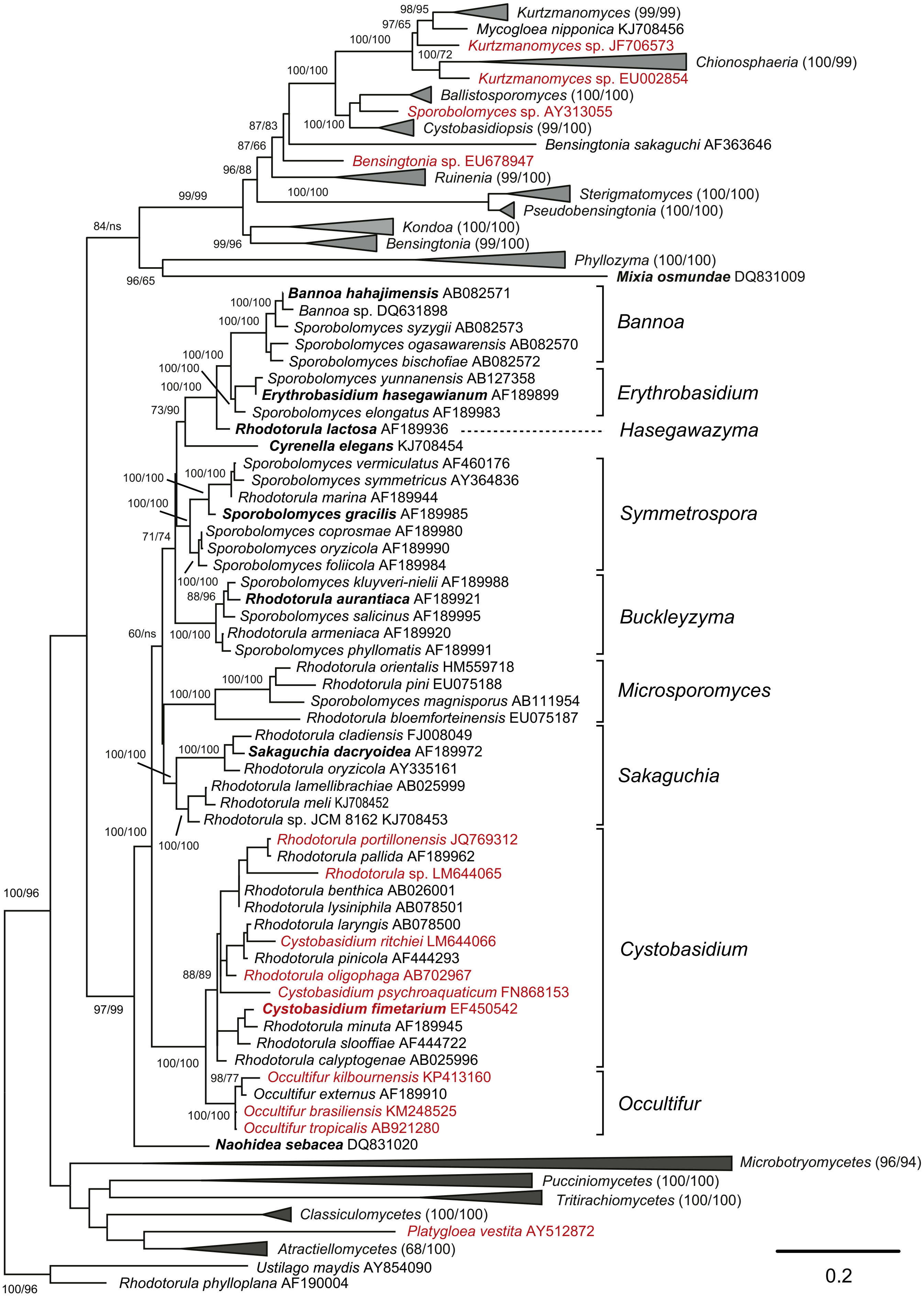

**Fig. 5.** Phylogenetic relationships of yeasts and related taxa from the *Cystobasidiomycetes* lineage obtained by Maximum-Likelihood analysis of the LSU (D1/D2 domains) rRNA gene. Tree topology was constrained according to the topology of the seven genes-based tree (Wang *et al.* 2015a) with nodes showing bootstrap values >85 % inforced to be monophyletic. The type species of each genus is in bold. Taxa not included in the phylogenetic analysis of the seven genes (Wang *et al.* 2015a) are indicated in red. *Note*: ns, not supported (BP < 50 %).

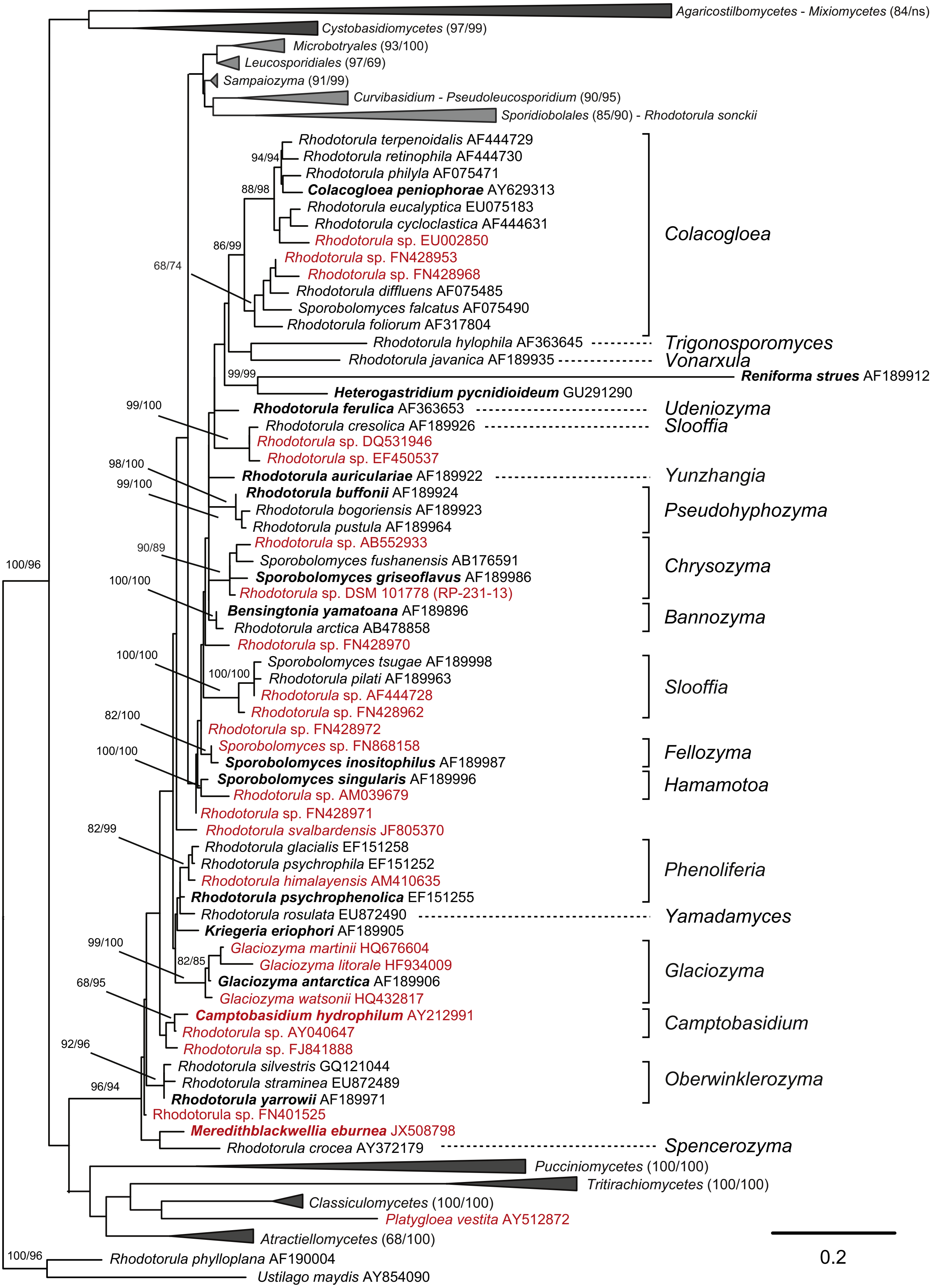

**Fig. 6.** Phylogenetic relationships of yeasts and related taxa from the *Microbotryomycetes* ('*incertae sedis*' lineages) obtained by Maximum-Likelihood analysis of the LSU (D1/D2 domains) rRNA gene. Tree topology was constrained according to the topology of the seven genes-based tree (Wang *et al.* 2015a) with nodes showing bootstrap values >85 % inforced to be monophyletic. The type species of each genus is in bold. Taxa not included in the phylogenetic analysis of the seven genes (Wang *et al.* 2015a) are indicated in red. *Note*: ns, not supported (BP < 50 %).

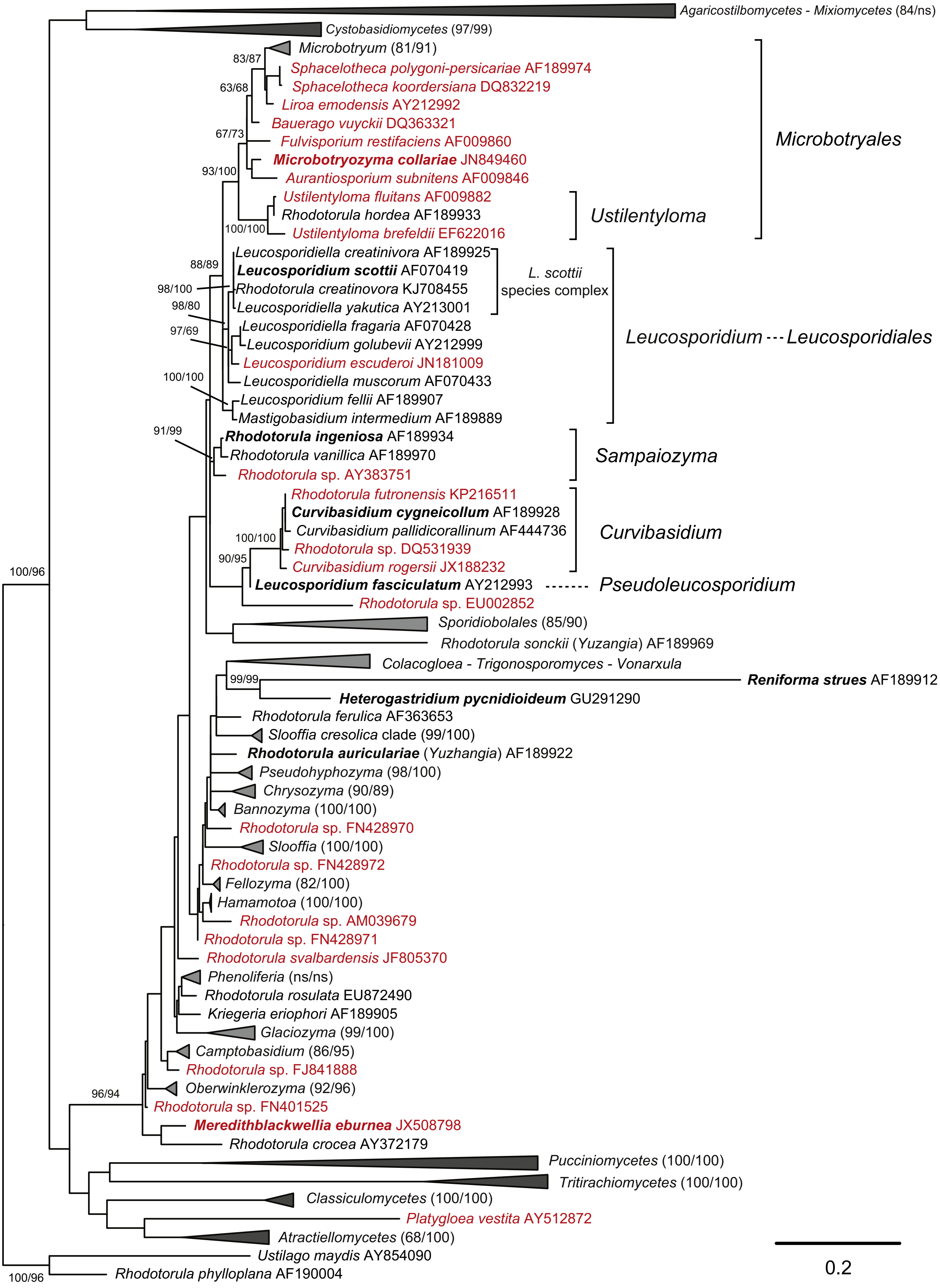

**Fig. 7.** Phylogenetic relationships of yeasts and related taxa from the *Microbotryomycetes* (*Microbotryales*, *Leucosporidiales* and related '*incertae sedis*' lineages) obtained by Maximum-Likelihood analysis of the LSU (D1/D2 domains) rRNA gene. Tree topology was constrained according to the topology of the seven genes-based tree (Wang *et al.* 2015a) with nodes showing bootstrap values >85 % inforced to be monophyletic. The type species of each genus is in bold. Taxa not included in the phylogenetic analysis of the seven genes (Wang *et al.* 2015a) are indicated in red. *Note*: ns, not supported (BP < 50 %).

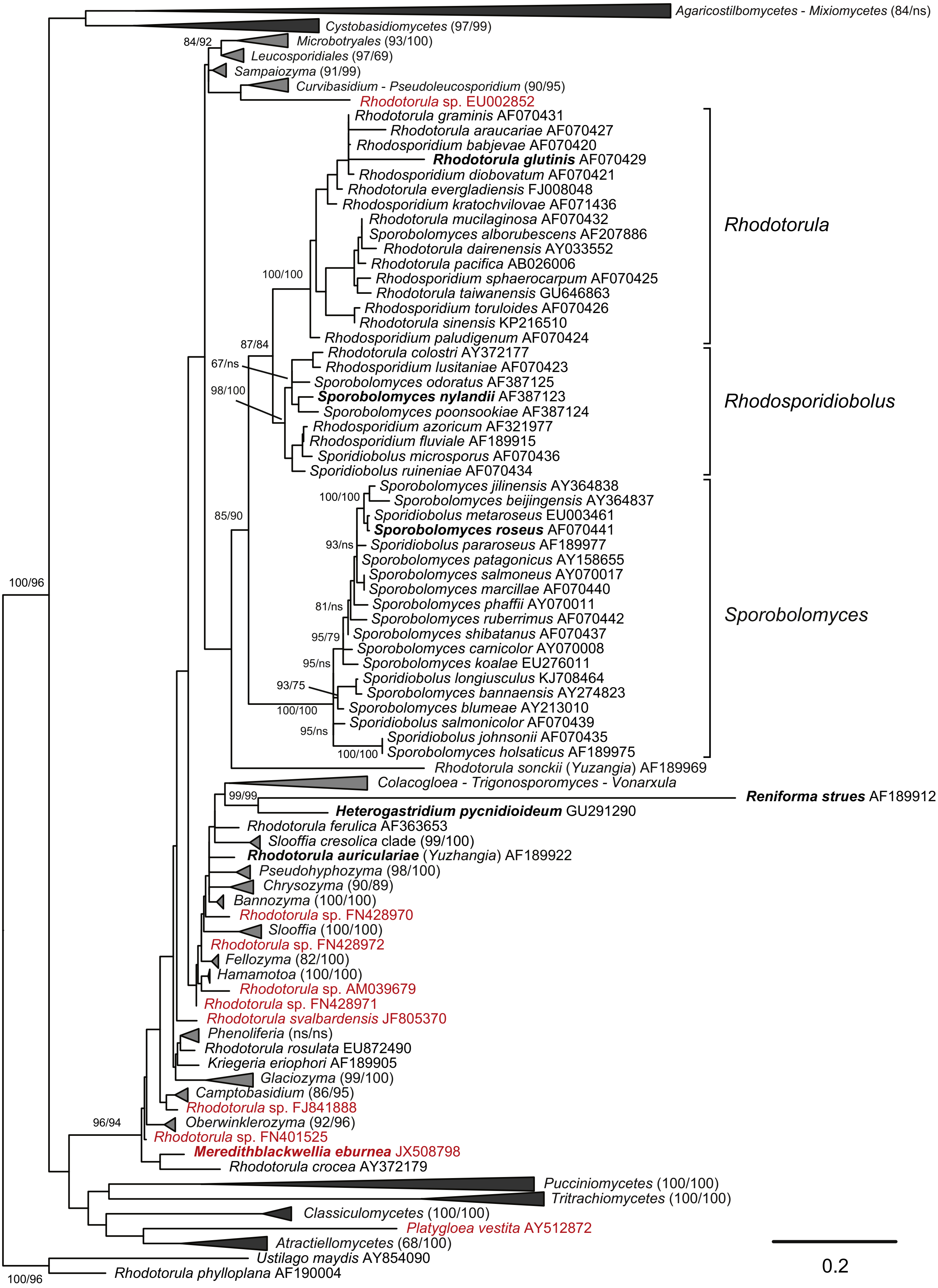

**Fig. 8.** Phylogenetic relationships of yeasts and related taxa from the *Microbotryomycetes* (*Sporidiobolales* and selected '*incertae sedis*' lineages) obtained by Maximum-Likelihood analysis of the LSU (D1/D2 domains) rRNA gene. Tree topology was constrained according to the topology of the seven genes-based tree (Wang *et al.* 2015a) with nodes showing bootstrap values >85 % inforced to be monophyletic. The type species of each genus is in bold. Taxa not included in the phylogenetic analysis of the seven genes (Wang *et al.* 2015a) are indicated in red. *Note*: ns, not supported (BP < 50 %).

phylogenetic analysis of seven genes, in which it formed a sister lineage to the genus *Sterigmatomyces* within *Agaricostilbaceae* (Figs 1, 4). This genus is phylogenetically distinct from the ***Bensingtonia*** clade that contains the type species of *Bensingtonia*, *B. ciliata*, that belongs to the family *Kondoaceae* (Wang *et al.* 2015a, Fig. 4 of this study).

Sexual reproduction not known. Colonies greyish-yellow or dark yellow and butyrous. Budding cells present. Pseudohyphae present or not. Ballistoconidia present, ellipsoidal or kidney-shaped. Major CoQ system Q-9.

*Type species*: *Pseudobensingtonia ingoldii* (Nakase & Itoh.) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout.

*Note*: The species of *Pseudobensingtonia* do not form conidiogenous stalks, which are present in the anamorphic species of *Sterigmatomyces* (Nakase *et al.* 1989, 2011, Takashima *et al.* 1995).

*Species accepted*:

1) ***Pseudobensingtonia ingoldii*** (Nakase & Itoh.) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813079.
   *Basionym*: *Bensingtonia ingoldii* Nakase & Itoh., J. Gen. Appl. Microbiol. 35: 53. 1989.
2) ***Pseudobensingtonia musae*** (M. Takash., S.O. Suh & Nakase) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813080.
   *Basionym*: *Bensingtonia musae* M. Takash. *et al.*, J. Gen. Appl. Microbiol. 41: 143. 1995.

**Family *Chionosphaeraceae*** Oberw. & Bandoni, Can. J. Bot. 60: 1732. 1982.

*Type genus*: *Chionosphaera* D.E. Cox.

This family is characterised by teleomorphic members with gasteroid basidia with simultaneous basidiospore production per basidium (Oberwinkler & Bandoni 1982, Bauer *et al.* 2006).

*Genera accepted*: *Ballistosporomyces* Nakase *et al.* emend. F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, *Chionosphaera* D.E. Cox, *Cystobasidiopsis* R. Bauer *et al.* emend. F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, *Kurtzmanomyces* Y. Yamada *et al.*, *Stilbum* Tode.

*Notes*: *Mycogloea nipponica* was placed in this family based on a multi-gene analyses (Wang *et al.* 2015a) and an analysis of the enlarged LSU rRNA gene dataset (Fig. 4). The species of the genus *Stilbum* are not listed here because living cultures of *Stilbum* are not available at present.

***Ballistosporomyces*** Nakase *et al.*, J. Gen. Appl. Microbiol. 35: 291. 1989. **emend.** F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout.

*Type species*: *Ballistosporomyces xanthus* Nakase *et al.*

This genus is emended and reintroduced to include species of the **sasicola** clade (Wang *et al.* 2015a), which occurred as a well-supported clade related to the genus *Cystobasidiopsis* within *Chionosphaeraceae* (Figs 1, 4). The genus *Ballistosporomyces* was erected by Nakase *et al.* (1989) and included *Ba. xanthus* (= *Sporobolomyces xanthus*), the type of *Ballistosporomyces*, and *Ba. ruber* (= *Sporobolomyces ruber*). This genus was treated as a synonym of *Sporobolomyces* (Boekhout 1991). Our analyses showed that *Ba. xanthus* (*S. xanthus*) is located in the **sasicola** clade, whereas *Ba. ruber* (*S. ruber*) occurs in the **ruber** clade that is phylogenetically distinct from the family *Chionosphaeraceae* (Fig. 1). Thus, here we emend and reintroduce *Ballistosporomyces* as a genus to include the species of the **sasicola** clade.

Sexual reproduction unknown. Colonies orange to pale yellowish-brown and butyrous. Budding cells present. Hyphae and pseudohyphae not formed. Ballistoconidia present, allantoid. Major CoQ system Q-10.

*Note*: *Sporobolomyces ruber* (*Ba. ruber*), which is located in the **ruber** clade (Fig. 1), is proposed as a new combination in *Ruinenia* (Fig. 4).

*Species accepted*:

1) ***Ballistosporomyces sasicola*** (Nakase & M. Suzuki) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813081.
   *Basionym*: *Sporobolomyces sasicola* Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 33: 171. 1987.
2) ***Ballistosporomyces taupoensis*** (Hamam. & Nakase) F.Y. Bai, Q.M. Wang, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813082.
   *Basionym*: *Sporobolomyces taupoensis* Hamam. & Nakase, Antonie van Leeuwenhoek 67: 163. 1995.
3) *Ballistosporomyces xanthus* Nakase *et al.*, J. Gen. Appl. Microbiol. 35: 292. 1989.

***Chionosphaera*** D.E. Cox, Mycologia 68: 503. 1976.

*Type species*: *Chionosphaera apobasidialis* D.E. Cox.

*Species accepted*:

1) *Chionosphaera apobasidialis* D.E. Cox, Mycologia 68: 503. 1976.
2) *Chionosphaera coppinsii* P. Roberts, Mycotaxon 63: 195. 1997.
3) *Chionosphaera cuniculicola* R. Kirschner *et al.*, Mycol. Res. 105: 1404. 2001.
4) *Chionosphaera erythrinae* (Hansf.) R. Kirschner, Fungal Science Taipei 23: 50. 2008.
5) *Chionosphaera lichenicola* Alstrup *et al.*, Graphis Scripta 5: 97. 1993.
6) *Chionosphaera phylaciicola* (Seifert & Bandoni) R. Kirschner & Oberw., Mycol. Res. 105: 1406. 2001.

*Note*: Living cultures have been obtained only from *Ch. apobasidialis* and *Ch. cuniculicola*, which have an asexual yeast stage.

***Cystobasidiopsis*** R. Bauer *et al.*, Mycol. Res. 113: 962. 2009. **emend.** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Type species*: *Cystobasidiopsis nirenbergiae* R. Bauer *et al.*

This genus is emended to include species of *Cystobasidiopsis* and anamorphic species of the **lactophilus** clade (Wang *et al.* 2015a), which occurred as a well supported clade related to the genus *Ballistosporomyces* within *Chionosphaeraceae* (Figs 1, 4).

Sexual reproduction observed in some species. Teleomorphic taxa produce probasidia with stipitate, transversely septate basidia. Basidiospores sessile. Colonies cream white and butyrous. Budding cells present or not. Ballistoconidia present or not, ellipsoidal, amygdaliform or falcate. Major CoQ system Q-10.

*Species accepted*:

1) ***Cystobasidiopsis lactophilus*** (Nakase, M. Itoh, M. Suzuki & Bandoni) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813083.
   *Basionym*: *Sporobolomyces lactophilus* Nakase *et al.*, Trans. Mycol. Soc. 31: 161. 1990.
2) ***Cystobasidiopsis lophatheri*** (Nakase, Tsuzuki, F.L. Lee, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813084.
   *Basionym*: *Sporobolomyces lophatheri* Nakase *et al.*, J. Gen. Appl. Microbiol. 51: 282. 2005.
3) *Cystobasidiopsis nirenbergiae* R. Bauer *et al.*, Mycol. Res. 113: 962. 2009.

*Note*: The emended genera *Cystobasidiopsis* and *Ballistosporomyces* can be distinguished by colony morphology and some physiological characteristics (Table 3, Fig. 3A). The species of *Cystobasidiopsis* form white colonies and assimilate D-arabinose, glycerol and DL-lactate, whereas the species of *Ballistosporomyces* form yellow-brown colonies and do not assimilate these three carbon sources.

***Kurtzmanomyces*** Y. Yamada *et al.*, J. Gen. Appl. Microbiol. 34: 505. 1988.

*Type species*: *Kurtzmanomyces nectairei* (Rodr. Mir.) Y. Yamada *et al.*

*Species accepted*:

1) *Kurtzmanomyces insolitus* J.P. Samp. & Fell, Syst. Appl. Microbiol. 22: 62. 1999.
2) *Kurtzmanomyces nectairei* (Rodr. Mir.) Y. Yamada *et al.*, J. Gen. Appl. Microbiol. 34: 505. 1988.
3) *Kurtzmanomyces shapotouensis* T. Zhang & L.Y. Yu, Int. J. Syst. Evol. Microbiol. 63: 3894. 2013.
4) *Kurtzmanomyces tardus* Gim.-Jurado & van Uden, Antonie van Leeuwenhoek 58: 130. 1990.

*Note*: *Kurtzmanomyces shapotouensis* was not included in our previous phylogenetic study (Wang *et al.* 2015a); the sequence analysis of the LSU rRNA D1/D2 domains and ITS (including 5.8S rRNA) region indicated that it belongs to the genus *Kurtzmanomyces* (Zhang *et al.* 2013, Fig. 4 of this study).

**Family *Kondoaceae*** R. Bauer *et al.*, Mycol. Progr. 5: 45. 2006.

*Type genus*: *Kondoa* Y. Yamada *et al.*

This family was proposed to accommodate the genus *Kondoa* that has ballistosporic phragmobasidia, as well as members of the genus *Bensingtonia* (Bauer *et al.* 2006).
*Genera accepted*: *Bensingtonia* Ingold, *Kondoa* Y. Yamada *et al.* emend. Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout.

***Bensingtonia*** Ingold, Trans. Br. mycol. Soc. 86: 325. 1986.

*Type species*: *Bensingtonia ciliata* Ingold

*Species accepted*:

1) *Bensingtonia bomiensis* F.Y. Bai & Q.M. Wang, Int. J. Syst. Evol. Microbiol. 62: 2043. 2012.
2) *Bensingtonia ciliata* Ingold, Trans. Br. mycol. Soc. 86: 325. 1986.
3) *Bensingtonia naganoensis* (Nakase & M. Suzuki) Nakase & Boekhout, J. Gen. Appl. Microbiol. 34: 435. 1988.
4) *Bensingtonia pseudonaganoensis* F.Y. Bai & Q.M. Wang, Antonie van Leeuwenhoek 89: 262. 2006.
5) *Bensingtonia rectispora* F.Y. Bai & Q.M. Wang, Int. J. Syst. Evol. Microbiol. 62: 2042. 2012.

*Note*: *B. rectispora* and *B. bomiensis* were not included in our previous phylogenetic study (Wang *et al.* 2015a), but the ITS and the D1/D2 domains of LSU rRNA sequences analysis demonstrated that they belong to *Bensingtonia* (Wang *et al.* 2012, Fig. 4 of this study).

***Kondoa*** Y. Yamada *et al.*, J. Gen. Appl. Microbiol. 35: 383. 1989. **emend.** Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout.

*Type species*: *Kondoa malvinella* (Fell & Hunter) Y. Yamada *et al.*

This genus is emended to include species of the genera *Kondoa* and *Bensingtonia* hitherto classified in the ***Kondoa*** clade (Wang *et al.* 2015a), which occurred as a well supported clade that is phylogenetically distinct from the genus *Bensingtonia* within *Kondoaceae* (Figs 1, 4). Thus all *Bensingtonia* species included in the ***Kondoa*** clade will be transferred into the genus *Kondoa* based on the "One Fungal = One Name" principle (Hawksworth 2011, Taylor 2011, McNeill *et al.* 2012).

Sexual reproduction observed in some species. Transversely septate basidia arise directly on the hyphae. Sexual structures not known on agar media. Teliospores are not formed. Colonies cream to pinkish-cream and butyrous. Budding cells present. Pseudohyphae or true hyphae present or not. Septal pores in true hyphae 'simple' and uniperforate. Major CoQ system Q-9.

*Species accepted*:

1) *Kondoa aeria* Á. Fonseca, J.P. Samp. & Fell, Antonie van Leeuwenhoek 77: 295.
2) ***Kondoa changbaiensis*** (F.Y. Bai & Q.M. Wang) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, **comb. nov.** MycoBank MB813085.

*Basionym*: *Bensingtonia changbaiensis* F.Y. Bai & Q.M. Wang, Int. J. Syst. Evol. Microbiol. 53: 2086. 2003.

3) *Kondoa malvinella* (Fell & Hunter) Y. Yamada *et al.*, J. Gen. Appl. Microbiol. 35: 384. 1989.

4) ***Kondoa miscanthi*** (Nakase & M. Suzuki) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, **comb. nov.** MycoBank MB813086.

*Basionym*: *Sporobolomyces miscanthi* Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 33: 183. 1987.

≡ *Bensingtonia miscanthi* (Nakase & M. Suzuki) Nakase & Boekhout.

5) ***Kondoa phyllada*** (van der Walt & Y. Yamada) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, **comb. nov.** MycoBank MB813087.

*Basionym*: *Sporobolomyces phylladus* van der Walt & Y. Yamada, Antonie van Leeuwenhoek 55: 190. 1989.

≡ *Bensingtonia phyllada* (van der Walt & Y. Yamada) van der Walt *et al.* ex Boekhout.

≡ *Bensingtonia phylladus* (van der Walt & Y. Yamada) van der Walt *et al.*, Nom. inval.

6) ***Kondoa sorbi*** (F.Y. Bai & Q.M. Wang) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, **comb. nov.** MycoBank MB813088.

*Basionym*: *Bensingtonia sorbi* F.Y. Bai & Q.M. Wang, Int. J. Syst. Evol. Microbiol. 53: 2087. 2003.

7) ***Kondoa subrosea*** (Nakase & M. Suzuki) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, **comb. nov.** MycoBank MB813089.

*Basionym*: *Sporobolomyces subroseus* Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 33: 186. 1987.

≡ *Bensingtonia subrosea* (Nakase & M. Suzuki) Nakase & Boekhout.

8) ***Kondoa thailandica*** (Fungsin, Hamam. & Nakase) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, **comb. nov.** MycoBank MB813090.

*Basionym*: *Bensingtonia thailandica* Fungsin *et al.*, Int. J. Syst. Evol. Microbiol. 51: 1209. 2001.

9) ***Kondoa yuccicola*** (Nakase & M. Suzuki) Q.M. Wang, M. Groenew., F.Y. Bai & Boekhout, **comb. nov.** MycoBank MB813091.

*Basionym*: *Sporobolomyces yuccicola* Nakase & M. Suzuki, Antonie van Leeuwenhoek 54: 48. 1988.

≡ *Bensingtonia yuccicola* (Nakase & M. Suzuki) Nakase & Boekhout.

*Note*: Two sequences representing the not yet described species *Kondoa myxariophila* (Scorzetti *et al.* 2002, Fonseca 2011) were obtained from public databases (Fig. 4).

**Family *Ruineniaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813092.

Member of *Agaricostilbales* (*Agaricostilbomycetes*). The diagnosis of the family *Ruineniaceae* is based on the description of the genus *Ruinenia*. The nomenclature of the family is based on the genus *Ruinenia*.

*Type genus*: *Ruinenia* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Genus accepted*: *Ruinenia* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

***Ruinenia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813093.

*Etymology*: The genus is named in honour of J. Ruinen for her contributions to the biology of yeasts from the phyllosphere.

This genus agrees with the **ruber** clade (Wang *et al.* 2015a). Member of *Ruineniaceae* (*Agaricostilbales*, *Agaricostilbomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes, in which it occurred as a well supported clade distinct from the other genera within *Agaricostilbales* (Figs 1, 4).

Sexual reproduction not known. Colonies orange-red or salmon-pink, and butyrous. Budding cells present. Hyphae and pseudohyphae present or not. Ballistoconidia present, ellipsoidal, reniform to falcate. Major CoQ system Q-10.

*Type species*: *Ruinenia rubra* (Nakase, Oakada & Sugiy.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Ruinenia clavata*** (F.Y. Bai & Q.M. Wang) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813094.

*Basionym*: *Sporobolomyces clavatus* F.Y. Bai & Q.M. Wang, FEMS Yeast Res. 4: 583. 2004.

2) ***Ruinenia diospyroris*** (Nakase, Tsuzuki, F.L. Lee, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813095.

*Basionym*: *Sporobolomyces diospyroris (as diospyri)* Nakase *et al.*, J. Gen. Appl. Microbiol. 51: 280. 2005.

3) ***Ruinenia dracophylli*** (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813096.

*Basionym*: *Sporobolomyces dracophylli* (as *dracophyllus*) Hamam. & Nkase, Antonie van Leeuwenhoek 67: 168. 1995.

4) ***Ruinenia pyrrosiae*** (Nakase, Tsuzuki, F.L. Lee, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813097.

*Basionym*: *Sporobolomyces pyrrosiae* Nakase *et al.*, J. Gen. Appl. Microbiol. 51: 284. 2005.

5) ***Ruinenia rubra*** (Nakase, G. Oakada & Sugiy.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813098.

*Basionym*: *Ballistosporomyces ruber* Nakase *et al.*, J. Gen. Appl. Microbiol. 35: 295. 1989.

≡ *Sporobolomyces ruber* (Nakase *et al.*) Boekhout.

*Note*: The species of *Ruinenia* (i.e. **ruber** clade) form salmon-orange to red colonies, which are a unique feature in the *Agaricostilbomycetes* (Fig. 3A). Additionally, five sequences representing potential new species of this genus were obtained from public databases (Fig. 4).

## Taxa *incertae sedis* in the *Agaricostilbales*

***Jianyunia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813099.

*Etymology*: The genus is named in honour of Jian-Yun Zhuang, former professor at the Institute of Microbiology, Chinese Academy of Sciences, for his contributions to the taxonomic study of *Pucciniales* in China.

This genus agrees with the ***Bensingtonia sakaguchii*** lineage (Wang *et al.* 2015a). Member of *Agaricostilbales* (*Agaricostilbomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes, in which it occurred as a single-species lineage distinct from the other genera within *Agaricostilbales* (Figs 1, 4).

Sexual reproduction not known. Colonies ivory and butyrous. Budding cells present. Pseudohyphae present. Ballistoconidia present, kidney-shaped. Major CoQ system Q-9.

*Type species*: *Jianyunia sakaguchii* (Sugita, M. Takash., Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Jianyunia sakaguchii*** (Sugita, M. Takash., Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813100.
   *Basionym*: *Bensingtonia sakaguchii* Sugita *et al.*, J. Gen. Appl. Microbiol. 43: 232. 1997.

**Class *Spiculogloeomycetes*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **class. nov.** MycoBank MB813101.

*Type order*: *Spiculogloeales* R. Bauer *et al.*

Member of *Pucciniomycotina*. The class is mainly circumscribed by the phylogenetic analysis of seven genes, in which it formed a deep well supported lineage with affinity to *Mixiomycetes* within *Pucciniomycotina* (Fig. 1). The diagnosis of the class *Spiculogloeomycetes* is based on the description of the order *Spiculogloeales* (Bauer *et al.* 2006). The nomenclature of this class is based on the *Spiculogloeales*.

This class contains species of *Spiculogloea* and some species of *Mycogloea* and *Sporobolomyces* (Aime *et al.* 2006, 2014, Bauer *et al.* 2006, Wang *et al.* 2015a). *Phyllozyma* gen. nov. is proposed to accommodate the *Sporobolomyces* species in the **subbrunneus** clade based on the phylogenetic analysis of seven genes (Fig. 1), PRBO (Table 1), phylogenetic network analysis (Fig. 2B) and the analysis of the enlarged LSU rRNA gene dataset (Fig. 4).

**Order *Spiculogloeales*** R. Bauer *et al.*, Mycol. Prog. 5: 41. 2006.

*Type family*: *Spiculogloeaceae* Denchev.

This order is characterised by teleomorphic members that may form tremelloid haustorial cells (nanometer-fusion mycoparasitism) and includes species of the sexual genera *Spiculogloea* and *Mycogloea*, as well as asexual species previously classified in the genus *Sporobolomyces* (Bauer *et al.* 2006).

***Spiculogloeaceae*** Denchev, Mycol. Balcanica 6: 87. 2009.

*Type genus*: *Spiculogloea* P. Roberts.

The name *Spiculogloeaceae* was validated by Denchev (2009) to include the taxa of *Spiculogloeales* (Bauer *et al.* 2006).

*Genera accepted*: *Spiculogloea* P. Roberts, *Phyllozyma* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Mycogloea* L.S. Olive (*pro parte*).

*Note*: The species of the genus *Spiculogloea* and *Mycogloea* are not listed here because cultures of *Spiculogloea* and *Mycogloea*, except for *Mycogloea nipponica* that is located in the *Chionosphaeraceae*, are presently not available. Moreover, nucleotide sequence data for type species of these genera are not available from public databases.

***Phyllozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813102.

*Etymology*: The genus is named based on the habitat as all species from this clade were isolated from the leaves of plants.

This genus agrees with the **subbrunneus** clade (Wang *et al.* 2015a). Member of the *Spiculogloeaceae* (*Spiculogloeales*, *Spiculogloeomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade (Figs 1, 4). Species in the **subbrunneus** clade are associated with plant leaves (Hamamoto *et al.* 2011) and are ecologically different from the teleomorphic species *Spiculogloea* spp. and *Mycogloea* spp., which are mycoparasites with tremelloid haustorial cells (Roberts 1996, Bauer 2004, Weiß *et al.* 2004).

Sexual reproduction not known. Colonies pale yellowish-brown, reddish-orange and butyrous. Budding cells present. Hypha and pseudohyphae present or not. Ballistoconidia present, ellipsoidal, fusiform or sickle-shaped. Major CoQ system Q-10.

*Type species*: *Phyllozyma subbrunnea* (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

*Species accepted*:

1) ***Phyllozyma coprosmicola*** (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813103.
   *Basionym*: *Sporobolomyces coprosmicola* Hamam. & Nakase, Antonie van Leeuwenhoek 67: 162. 1995.
2) ***Phyllozyma corallina*** (N. Furuya & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813321.
   *Basionym*: *Sporobolomyces corallinus* N. Furuya & M. Takash., Mycoscience 53: 261. 2012.
3) ***Phyllozyma dimennae*** (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813104.
   *Basionym*: *Sporobolomyces dimennae* Hamam. & Nakase, Antonie van Leeuwenhoek 67: 159. 1995.
4) ***Phyllozyma linderae*** (Nakase, M. Takash. & Hamam.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813105.

*Basionym*: *Sporobolomyces linderae* Nakase *et al.*, J. Gen. Appl. Microbiol. 40: 98. 1994.

5) ***Phyllozyma novozealandica*** (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813106.
*Basionym*: *Sporobolomyces novazealandicus* Hamam. & Nakase, Antonie van Leeuwenhoek 67: 156. 1995.

6) ***Phyllozyma producta*** (N. Furuya & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813322.
*Basionym*: *Sporobolomyces productus* N. Furuya & M. Takash., Mycoscience 53: 261. 2012.

7) ***Phyllozyma subbrunnea*** (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813107.
*Basionym*: *Sporobolomyces subbrunneus* Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 31: 468. 1985.

*Note*: *S. productus* and *S. corallinus* were not included in our previous phylogenetic study (Wang *et al.* 2015a). These two species were placed in the **subbrunneus** lineage closely related to *S. subbrunneus* and *S. dimnenae* based on the sequence analysis of the D1/D2 domains of LSU rRNA (Furuya *et al.* 2012, Fig. 4 of the present study), and hence, they are recombined in the genus *Phyllozyma*.

**Class *Cystobasidiomycetes*** R. Bauer *et al.*, Mycol. Progr. 5: 46. 2006.

*Type order*: *Cystobasidiales* R. Bauer *et al.*

Three orders, namely *Cystobasidiales*, *Erythrobasidiales* and *Naohideales*, as well as the **aurantiaca**, **magnisporus**, **marina** and ***Sakaguchia*** clades occur within *Cystobasidiomycetes* (Wang *et al.* 2015a). As the relative positioning of these five groups could not be resolved with certainty (Fig. 1) we suggest to treat the four clades as families but not to assign them to any order. Instead, we place them as '*incertae sedis*' within *Cystobasidiomycetes*.

*Buckleyzymaceae* fam. nov. with *Buckleyzyma* gen. nov, *Microsporomycetaceae* fam. nov. with *Microsporomyces* gen. nov., *Symmetrosporaceae* fam. nov. with *Symmetrospora* gen. nov., and *Sakaguchiaceae* fam. nov. are proposed to accommodate the taxa in the **aurantiaca**, **magnisporus**, **marina** and ***Sakaguchia*** clades, respectively (Figs 1, 5).

**Order *Cystobasidiales*** R. Bauer *et al.*, Mycol. Progr. 5: 46. 2006.

*Type family*: *Cystobasidiaceae* Gäum.

This order was proposed to accommodate the family *Cystobasidiaceae* that is characterised by nanometer-fusion mycoparasitism with tremelloid haustorial cells and septal pores with cystosomes (Bauer *et al.* 2006).

**Family *Cystobasidiaceae*** Gäum., Vergl. Morph. Pilze (Jena): 411. 1926.

*Type genus*: *Cystobasidium* Lagerh. emend. A.M. Yurkov *et al.*

The family comprises the genera *Occultifur* and *Cystobasidium*, as well as species previously classified in the genus *Rhodotorula* in Bauer *et al.* (2006).

*Genera accepted*: *Cystobasidium* Lagerh. emend. A.M. Yurkov *et al.*, *Occultifur* Oberw.

***Cystobasidium*** (Lagerh.) emend. A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 179. 2015.
= *Jola* subgen. *Cystobasidium* Lagerh., Bihang till Kungliga svenska Vetenskaps-Akademiens Handlingar 24: 15. 1898.

*Type species*: *Cystobasidium fimetarium* (Schumach.) P. Roberts

*Species accepted*:
1) *Cystobasidium benthicum* (Nagah. *et al.*) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 180. 2015.
2) *Cystobasidium calyptogenae* (Nagah. *et al.*) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 181. 2015.
3) *Cystobasidium fimetarium* (Schumach.) P. Roberts, Mycologist 13: 171. 1999.
4) *Cystobasidium hypogymniicola* Diederich & Ahti, Biblthca Lichenol. 61: 21. 1996.
5) *Cystobasidium laryngis* (Reiersöl) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 181. 2015.
6) *Cystobasidium lysinophilum* (Nagah. *et al.*) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 181. 2015.
7) *Cystobasidium minuta* (Saito) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 180. 2015.
8) *Cystobasidium oligophagum* (Satoh & Makimura) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 181. 2015.
9) *Cystobasidium pallidum* (Lodder) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 181. 2015.
10) *Cystobasidium pinicola* (F.Y. Bai *et al.*) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 181. 2015.
11) ***Cystobasidium portillonense*** (F. Laich, I. Vaca & R. Chávez) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout **comb. nov.** MycoBank MB813108.
*Basionym*: *Rhodotorula portillonensis* F. Laich *et al.*, Int. J. Syst. Evol. Microbiol. 63: 3889. 2013.
12) *Cystobasidium proliferans* L.S. Olive, Mycologia 44: 564. 1952.
13) *Cystobasidium psychroaquaticum* A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 181. 2015.
14) *Cystobasidium ritchiei* A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 182. 2015.
15) *Cystobasidium sebaceum* G.W. Martin, Mycologia 31: 507. 1939.
16) *Cystobasidium slooffiae* (E.K. Novák & Vörös-Felkai) A.M. Yurkov *et al.*, Antonie van Leeuwenhoek 107: 180. 2015.
17) *Cystobasidium usneicola* Diederich & Alstrup, Biblthca Lichenol. 61: 25. 1996.

*Note*: *R. portillonensis* that is phylogenetically located in the *Cystobasidium* clade was recently proposed by Laich *et al.* (2013). This species was placed in this genus in the analysis of the enlarged LSU rRNA gene dataset (Fig. 5) and we transfer *R. portillonensis* to the genus *Cystobasidium*.

***Occultifur*** Oberw., Rep. Tottori Mycol. Inst. 28: 119. 1990.

*Type species*: *Occultifur internus* (L.S. Olive) Oberw.

*Species accepted*:

1) *Occultifur brasiliensis* Gomes *et al.*, Antonie van Leeuwenhoek 107: 608. 2015.
2) *Occultifur corticiorum* P. Roberts, Mycotaxon 63: 202. 1997.
3) *Occultifur externus* J.P. Samp. *et al.*, Mycologia 91: 1095. 1999.
4) *Occultifur internus* (L.S. Olive) Oberw., Rep. Tottori Mycol. Inst. 28: 120. 1990.
5) *Occultifur kilbournensis* Kurtzman & Robnett, Antonie Van Leeuwenhoek 107: 1325. 2015.
6) *Occultifur tropicalis* Khunnamwong *et al.*, Int. J. Syst. Evol. Microbiol. 65: 1580. 2015.

*Notes*: Three species of the genus *Occultifur*, *O. corticiorum*, *O. externus* and the generic type *O. internus*, were accepted by Sampaio & Oberwinkler (2011), but only *O. externus* was included in our previous phylogenetic study (Wang *et al.* 2015a) as neither living cultures nor molecular data are available for the other two species. Three new asexual members of the genus *Occultifur* (Fig. 5), namely *O. brasiliensis*, *O. kilbournensis* and *O. tropicalis*, were recently described by Gomes *et al.* (2015), Kurtzman & Robnett (2015) and Khunnamwong *et al.* (2015), respectively.

**Order *Erythrobasidiales*** R. Bauer *et al.*, Mycol. Progr. 5: 46. 2006.

*Type family*: *Erythrobasidiaceae* Denchev.

This order accommodates the genera *Erythrobasidium* and *Bannoa* that have non-tremelloid haustorial cells, septal pores without cystosomes, and coenzyme CoQ10 (H2), as well as some *Rhodotorula* and *Sporobolomyces* species (Bauer *et al.* 2006). The genus *Cyrenella* was not placed in this order by Aime *et al.* (2006), Bauer *et al.* (2006) and Hibbett *et al.* (2007). This genus, however, formed a well supported clade with the genera *Erythrobasidium* and *Bannoa*, and *Rhodotorula lactosa*, which is placed in a new genus *Hasegawazyma* (Fig. 1). Thus, this order includes the family *Erythrobasidiaceae* and the genera *Cyrenella* and *Hasegawazyma*, which are treated as '*incertae sedis*' in the *Erythrobasidiales*.

**Family *Erythrobasidiaceae*** Denchev, Mycol. Balcanica 6: 87. 2009.

*Type genus*: *Erythrobasidium* Hamam. *et al.*

The name *Erythrobasidiaceae* was validated by Denchev (2009) to include the taxa of *Erythrobasidiales* (Bauer *et al.* 2006).

*Genera accepted*: *Bannoa* Hamam., *Erythrobasidium* Hamam. *et al.*

***Bannoa*** Hamam., Int. J. Syst. Evol. Microbiol. 52: 1027. 2002. **emend.** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Type species*: *Bannoa hahajimensis* Hamam. *et al.*

This genus is emended to include species of *Bannoa* and related *Sporobolomyces* species that hitherto were classified in the ***Bannoa*** clade (Wang *et al.* 2015a), which occurred as a well supported clade related to *Erythrobasidium* within *Erythrobasidiales* (Figs 1, 5).

Sexual reproduction observed in some species. Clamp connections present. Teliospores not formed. Unicellular basidia arise laterally on a clamp connection, or terminally at the hyphae. Cells of the basidia germinate with hyphae, from which yeast cells originate. Colonies orange to salmon-red. Budding cells present. Pseudohyphae absent. Ballistoconidia present or not, ovoid and ellipsoidal. Major CoQ system Q-10(H2).

*Species accepted*:

1) ***Bannoa bischofiae*** (Hamam., Thanh & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813109.
   *Basionym*: *Sporobolomyces bischofiae* Hamam. *et al.*, Int. J. Syst. Evol. Microbiol. 52: 1029. 2002.
2) *Bannoa hahajimensis* Hamam. *et al.*, Int. J. Syst. Evol. Microbiol. 52: 1028. 2002.
3) ***Bannoa syzygii*** (Hamam., Thanh & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813110.
   *Basionym*: *Sporobolomyces syzygii* Hamam. *et al.*, Int. J. Syst. Evol. Microbiol. 52: 1031. 2002.
4) ***Bannoa ogasawarensis*** (Hamam., Thanh & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813111.
   *Basionym*: *Sporobolomyces ogasawarensis* Hamam. *et al.*, Int. J. Syst. Evol. Microbiol. 52: 1030. 2002.

*Note*: Our analyses suggest that *Bannoa* sp. MP3490 (AFTOL-ID 1921) represents a potentially new species of this genus (Wang *et al.* 2015a, Fig. 5 of this study).

***Erythrobasidium*** Hamam., Sugiy. & Komag., J. Gen. Appl. Microbiol. 34: 285. 1988. **emend.** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

*Type species*: *Erythrobasidium hasegawianum* Hamam. *et al.*

This genus is emended to include species of *Erythrobasidium* and related *Sporobolomyces* species that hitherto were classified in the ***Erythrobasidium*** clade (Wang *et al.* 2015a), which occurred as a well supported clade closely related to *Bannoa* within *Erythrobasidiales* (Figs 1, 5).

Sexual reproduction observed in some species. Hyphae form from single cells without mating. Clamp connections present or absent. Septal pores 'simple'. Teliospores not formed. Unicellular basidia (holobasidia) arise by the formation of lateral protrusions on the hyphae. Sessile basidiospores produced terminally on the holobasidia and not forcibly discharged. Colonies orange-red. Budding cells present. Pseudohyphae absent. Ballistoconidia present or not, ellipsoidal or ovoid. Major CoQ system Q-10(H2).

*Species accepted*:

1) ***Erythrobasidium elongatum*** (R.G. Shivas & Rodr. Mir.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813112.
   *Basionym*: *Sporobolomyces elongatus* R.G. Shivas & Rodr. Mir., Antonie van Leeuwenhoek 49: 160. 1983.
2) *Erythrobasidium hasegawianum* Hamam. *et al.*, J. Gen. Appl. Microbiol. 37: 131. 1991.

3) ***Erythrobasidium yunnanense*** (F.Y. Bai, M. Takash., Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813113.
*Basionym*: *Sporobolomyces yunnanensis* F.Y. Bai *et al.*, Int. J. Syst. Evol. Microbiol. 51: 234. 2001.

## Taxa *incertae sedis* in the *Erythrobasidiales*

***Cyrenella*** Goch., Mycotaxon 13: 268. 1981.

*Type species*: *Cyrenella elegans* Goch.

*Species accepted*:
1) *Cyrenella elegans* Goch., Mycotaxon 13: 268. 1981.

***Hasegawazyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813114.

*Etymology*: The genus is named in honour of T. Hasegawa who firstly described the species *Rhodotorula lactosa*.

This genus corresponds to the ***Rhodotorula lactosa*** lineage (Wang *et al.* 2015a, Fig. 5 of this study). Member of *Erythrobasidiales* (*Cystobasidiomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a single-species lineage distinct from the other genera within *Cystobasidiomycetes* (Figs 1, 5). This genus differs from *Bannoa*, *Cyrenella* and *Erythrobasidium* by having ubiquinone Q-9.

Sexual reproduction not known. Colonies pink-coloured and butyrous. Budding cells present. Pseudohyphae and true hyphae not observed. Ballistoconidia absent. Major CoQ system Q-9.

*Type species*: *Hasegawazyma lactosa* (Hasegawa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

*Species accepted*:
1) ***Hasegawazyma lactosa*** (Hasegawa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813115.
*Basionym*: *Rhodotorula lactosa* Hasegawa, J. Gen. Appl. Microbiol. 5: 31. 1959.

**Order *Naohideales*** R. Bauer *et al.*, Mycol. Progr. 5: 46. 2006.

*Type family*: *Naohideaceae* Denchev

This order was proposed to accommodate the genus *Naohidea*, which is characterised by nanometer-fusion mycoparasitism with intracellular haustoria (tremelloid) and septal pores without cystosomes (Bauer *et al.* 2006).

**Family *Naohideaceae*** Denchev, Mycol. Balcanica 6: 87. 2009.

*Type genus*: *Naohidea* Oberw.

The name *Naohideaceae* was validated by Denchev (2009) to include the taxa of *Naohideales* (Bauer *et al.* 2006).

*Genus accepted*: *Naohidea* Oberw.

***Naohidea*** Oberw., Rep. Tottori Mycol. Inst. 28: 114. 1990.

*Type species*: *Naohidea sebacea* (Berk. & Broome) Oberw.

The genus *Naohidea*, representing the order *Naohideales*, produces cream-coloured cultures that are different from all other taxa in the *Cystobasidiomycetes*, which form pink to orange-red pigmented colonies (Sampaio & Chen 2011, Fig. 3B of this study).

*Species accepted*:
1) *Naohidea sebacea* (Berk. & Broome) Oberw., Rep. Tottori Mycol. Inst. 28: 114. 1990.

## Taxa *incertae sedis* in the *Cystobasidiomycetes*

**Family *Symmetrosporaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813116.

Member of the *Cystobasidiomycetes*. The diagnosis of the family *Symmetrosporaceae* is based on the description of the genus *Symmetrospora*. The nomenclature of the family is based on the genus *Symmetrospora*.

*Type genus*: *Symmetrospora* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Genus accepted*: *Symmetrospora* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

***Symmetrospora*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813117.

*Etymology*: The genus is named by the (almost) symmetrical ballistoconidia that are formed by ballistoconidia-forming species of this clade.

This genus agrees with the **marina** clade (Wang *et al.* 2015a). Member of the *Symmetrosporaceae* (*Cystobasidiomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a sister clade to *Erythrobasidiales* within *Cystobasidiomycetes* (Figs 1, 5).

Sexual reproduction not known. Colonies orange-red and butyrous. Budding cells present. Hypha and pseudohyphae not observed. Ballistoconidia present or not, symmetrical or nearly symmetrical, ellipsoidal or ovoidal. Major CoQ system Q-10.

*Type species*: *Symmetrospora gracilis* (Derx) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

*Species accepted*:
1) ***Symmetrospora coprosmae*** (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813118.
*Basionym*: *Sporobolomyces coprosmae* Hamam. & Nakase, Antonie van Leeuwenhoek 67: 166. 1995.
2) ***Symmetrospora foliicola*** (R.G. Shivas & Rodr. Mir.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813119.

*Basionym*: *Sporobolomyces foliicola* R.G. Shivas & Rodr. Mir., Antonie van Leeuwenhoek 49: 162. 1983.

3) ***Symmetrospora gracilis*** (Derx) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813120.

*Basionym*: *Sporobolomyces gracilis* Derx, Annls mycol. 28: 18. 1930.

4) ***Symmetrospora vermiculata*** (M. Takash. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813121.

*Basionym*: *Sporobolomyces vermiculatus* M. Takash. & Nakase, Mycoscience 41: 367. 2000.

5) ***Symmetrospora marina*** (Phaff, Mrak & Williams) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813123.

*Basionym*: *Rhodotorula marina* Phaff *et al.*, Mycologia 44: 436. 1952.

6) ***Symmetrospora symmetrica*** (F.Y. Bai & Q.M. Wang) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813125.

*Basionym*: *Sporobolomyces symmetricus* F.Y. Bai & Q.M. Wang, FEMS Yeast Res. 4: 584. 2004.

**Family *Buckleyzymaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MB813126.

Member of the *Cystobasidiomycetes*. The diagnosis of the family *Buckleyzymaceae* is based on the description of the genus *Buckleyzyma*. The nomenclature of the family is based on the genus *Buckleyzyma*.

*Type genus*: *Buckleyzyma* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Genus accepted*: *Buckleyzyma* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

***Buckleyzyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813127.

*Etymology*: The genus is named in honour of Helen R. Buckley for her contributions to yeast taxonomy.

This genus agrees with the **aurantiaca** clade (Wang *et al.* 2015a). Member of *Buckleyzymaceae* (*Cystobasidiomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a sister clade to *Erythrobasidiales* and *Symmetrospora* within *Cystobasidiomycetes* (Figs 1, 5).

Sexual reproduction not known. Colonies brownish-orange or orange and butyrous. Budding cells present. Hyphae and pseudohyphae present or not. Ballistoconidia present or not, ellipsoidal allantoid to amygdaliform. Major CoQ system Q-10.

*Type species*: *Buckleyzyma aurantiaca* (Saito) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

*Species accepted*:

1) ***Buckleyzyma armeniaca*** (R.G. Shivas & Rodr. Mir.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813133.

*Basionym*: *Rhodotorula armeniaca* R.G. Shivas & Rodr. Mir., Antonie van Leeuwenhoek 49: 163. 1983.

2) ***Buckleyzyma aurantiaca*** (Saito) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813128.

*Basionym*: *Torula aurantiaca* Saito, Jap. J. Bot. 1: 45. 1922.

≡ *Rhodotorula aurantiaca* (Saito) Lodder

3) ***Buckleyzyma kluyveri-nielii*** (van der Walt) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813130.

*Basionym*: *Sporobolomyces kluyveri-nielii* van der Walt, Antonie van Leeuwenhoek 52: 432. 1986.

4) ***Buckleyzyma phyllomatis*** (van der Walt & Y. Yamada) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813131.

*Basionym*: *Sporobolomyces phyllomatis* van der Walt & Y. Yamada, Antonie van Leeuwenhoek 54: 202. 1988.

5) ***Buckleyzyma salicina*** (B.N. Johri & Bandoni) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813132.

*Basionym*: *Bullera salicina* B.N. Johri & Bandoni, Taxonomy of Fungi (Proc. int. Symp. Madras 1973) Part 2 (Madras) 2: 544. 1984.

≡ *Sporobolomyces salicinus* (B.N. Johri & Bandoni) Nakase & M. Itoh

**Family *Microsporomycetaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813134.

Member of *Cystobasidiomycetes*. The diagnosis of the family *Microsporomycetaceae* is based on the description of the genus *Microsporomyces*. The nomenclature of the family is based on the genus *Microsporomyces*.

*Type genus*: *Microsporomyces* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Genus accepted*: *Microsporomyces* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

***Microsporomyces*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813135.

*Etymology*: The genus name relates to the type species, *Sporobolomyces magnisporus* that produces small (micro-) ballistoconidia.

This genus agrees with the **magnisporus** clade (Wang *et al.* 2015a). Member of the *Microsporomycetaceae* (*Cystobasidiomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a sister clade to *Cystobasidiales* and *Sakaguchia* within the *Cystobasidiomycetes* (Figs 1, 5).

Sexual reproduction not known. Colonies orange or salmon-coloured and butyrous. Budding cells present. Pseudohyphae present or not. Ballistoconidia present or not, ellipsoidal, allantoid to amygdaliform. Major CoQ system Q-10.

*Type species*: *Microsporomyces magnisporus* (Nakase, Tsuzuki, F.L. Lee, Sugita, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Microsporomyces bloemfonteinensis*** (Pohl, M.S. Smit & Albertyn) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB814789.
   *Basionym*: *Rhodotorula bloemfonteinensis* Pohl *et al.*, Int. J. Syst. Evol. Microbiol. 61: 2324. 2011.
2) ***Microsporomyces magnisporus*** (Nakase, Tsuzuki, F.L. Lee, Sugita, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813137.
   *Basionym*: *Sporobolomyces magnisporus* Nakase *et al.*, J. Gen. Appl. Microbiol. 49: 341. 2003.
3) ***Microsporomyces pini*** (Pohl, M.S. Smit & Albertyn) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813138.
   *Basionym*: *Rhodotorula pini* Pohl *et al.*, Int. J. Syst. Evol. Microbiol. 61: 2323. 2011.
4) ***Microsporomyces orientalis*** (Pohl, M.S. Smit & Albertyn) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813327.
   *Basionym*: *Rhodotorula orientalis* (as *orientis*) Pohl *et al.*, Int. J. Syst. Evol. Microbiol. 61: 2325. 2011.

**Family *Sakaguchiaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813142.

Member of the *Cystobasidiomycetes*. The diagnosis of the family *Sakaguchiaceae* is based on the description of the genus *Sakaguchia*. The nomenclature of the family is based on the genus *Sakaguchia*.

*Type genus*: *Sakaguchia* Y. Yamada *et al.*

*Genus accepted*: *Sakaguchia* Y. Yamada *et al.* emend. Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

***Sakaguchia*** Y. Yamada *et al.*, Biosc. Biotechn. Biochem. 58: 102. 1994. **emend.** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Type species*: *Sakaguchia dacryoidea* (Fell *et al.*) Y. Yamada *et al.*

This genus is emended to include *Sakaguchia dacryoidea* and related *Rhodotorula* species that hitherto were classified in the ***Sakaguchia*** clade (Wang *et al.* 2015a), which occurred as a well supported clade within the *Cystobasidiomycetes* (Figs 1, 5).

Sexual reproduction in some species. Clamp connections present. Teliospores laterally or terminally on the hyphae. Teliospores germinate with two- to four-celled metabasidium with lateral and terminal basidiospores. Colonies red or orange-red and butyrous. Budding cells present. Pseudohyphae or true hyphae present or not. Ballistoconidia not produced. Major CoQ system Q-10.

*Species accepted*:

1) ***Sakaguchia cladiensis*** (Fell, Statzell & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813144.
   *Basionym*: *Rhodotorula cladiensis* Fell *et al.*, Antonie van Leeuwenhoek 99: 546. 2011.
2) *Sakaguchia dacryoidea* (Fell *et al.*) Y. Yamada *et al.*, Biosc. Biotechn. Biochem. 58: 102. 1994.
3) ***Sakaguchia lamellibrachiae*** (Nagah., Hamam., Nakase & Horikoshi) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813147.
   *Basionym*: *Rhodotorula lamellibrachiae* (as *lamellibrachii*) Nagah. *et al.*, Antonie van Leeuwenhoek 80: 320. 2001.
4) ***Sakaguchia meli*** (Libkind, van Broock & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813148.
   *Basionym*: *Rhodotorula meli* Libkind *et al.*, Int. J. Syst. Evol. Microbiol. 60: 2253. 2010.
5) ***Sakaguchia oryzae*** (F.Y. Bai & Y.M. Cai) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813150.
   *Basionym*: *Rhodotorula oryzae* F.Y. Bai & Y.M. Cai, Antonie van Leeuwenhoek 86: 296. 2004.

*Note*: Our analyses suggest that *Rhodotorula* sp. JCM 8162 represents a potential new species of this genus, as revealed by the multi-gene analyses (Wang *et al.* 2015a) and the analysis of the enlarged LSU rRNA gene dataset (Fig. 5).

**Class *Microbotryomycetes*** R. Bauer *et al.*, Mycol. Progr. 5: 47. 2006.

*Type order*: *Microbotryales* R. Bauer & Oberw.

This class presently contains four orders that contain yeast species, namely *Kriegeriales*, *Leucosporidiales*, *Microbotryales* and *Sporidiobolales* (Aime *et al.* 2006, 2014, Bauer *et al.* 2006, Hibbett *et al.* 2007, Toome *et al.* 2013). Ten clades and seven single-species lineages do not belong to the above listed orders (Wang *et al.* 2015a), and they may be assigned into eleven families based on modified GMYC analysis (Table 2) in conjunction with the phylogenetic analysis of seven genes (Fig. 1). However, most of these suggested families are monotypic or poorly sampled (Table 2). Thus, we propose *Chrysozymaceae* fam. nov. to accommodate the **griseoflavus**, **yamatoana**, **singularis** and ***Sporobolomyces inositophilus*** clades, and *Colacogloeaceae* fam. nov. to cover the ***Colacogloea*** clade because these two proposed families have more taxa than the other clades and have strong support values (Fig. 1). The other six clades and six single-species lineages are proposed to be included in twelve genera that at the higher rank are considered as '*incertae sedis*' within the *Microbotryomycetes* at present. The species *Rhodotorula svalbardensis* (Singh *et al.* 2014) was not included in the seven genes-based phylogenetic analysis (Wang *et al.* 2015a) and has no proper placement in the constrained LSU analysis (Fig. 6). The phylogenetic placement of this species needs to be addressed by a robust molecular analysis. Thus, we leave it as *Rhodotorula svalbardensis pro tem.* in this study. The term "*pro tem.*" (*pro tempore*) was proposed in Wang *et al.* (2015b) and indicates a temporary taxonomic placement.

**Order *Kriegeriales*** Toome & Aime, Mycologia 105: 489. 2013.

*Type family*: *Kriegeriaceae* Toome & Aime.

This order was proposed to contain the families *Kriegeriaceae* and *Camptobasidiaceae* (Toome *et al.* 2013). The teleomorphic members of this order are characterised by the presence of 'simple' septal pores and subgloboid spindle pole bodies (Toome *et al.* 2013).

**Family *Kriegeriaceae*** Toome & Aime, Mycologia 105: 489. 2013.

*Type genus*: *Kriegeria* Bres.

This family was proposed to accommodate the sexual plant parasite *Kriegeria,* the asexual genus *Meredithblackwellia*, and six related *Rhodotorula* species (Toome *et al.* 2013). The species *R. pilati* was placed in the *Kriegeriaceae* by Toome *et al.* (2013), but this affiliation was not supported in the muligene study by Wang *et al.* (2015a). This species was located in the **tsugae** clade (Wang *et al.* 2015a). The other five *Rhodotorula* species in the *Kriegeriaceae* are reclassified into two new genera *Phenoliferia* and *Yamadamyces*.

*Genera accepted*: *Kriegeria* Bres., *Meredithblackwellia* Toome & Aime, *Phenoliferia* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Yamadamyces* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

***Kriegeria*** Bres., Revue mycol. Toulouse 13: 14. 1891.

= *Zymoxenogloea* D.J. McLaughlin & Doublés, Mycologia 84: 671. 1992.

*Type species*: *Kriegeria eriophori* Bres.

*Species accepted*:

1) *Kriegeria eriophori* Bres., Revue mycol. Toulouse 13: 14. 1891.

***Meredithblackwellia*** Toome & Aime, Mycologia 105: 490. 2013.

*Type species*: *Meredithblackwellia eburnea* Toome & Aime.

*Species accepted*:

1) *Meredithblackwellia eburnea* Toome & Aime, Mycologia 105: 491. 2013.

***Phenoliferia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813152.

*Etymology*: The genus is named because the species in this clade can assimilate phenol.

This genus agrees with the **glacialis** clade (Wang *et al.* 2015a). Member of the *Kriegeriaceae* (*Kriegeriales*, *Microbotryomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade related to the genus *Kriegeria* within *Kriegeriaceae* (Figs 1, 6).

Sexual reproduction not known. Colonies creamy-white and butyrous. Budding cells present. Pseudomycelium or true hyphae not observed. Ballistoconidia not produced. Major CoQ system unknown.

*Type species*: *Phenoliferia psychrophenolica* (Margesin & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

*Species accepted*:

1) ***Phenoliferia psychrophenolica*** (Margesin & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813153.
*Basionym*: *Rhodotorula psychrophenolica* Margesin & J.P. Samp., Int. J. Syst. Evol. Microbiol. 57: 2183. 2007.

2) ***Phenoliferia psychrophila*** (Margesin & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813154.
*Basionym*: *Rhodotorula psychrophila* Margesin & J.P. Samp., Int. J. Syst. Evol. Microbiol. 57: 2181. 2007.

3) ***Phenoliferia glacialis*** (Margesin & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813155.
*Basionym*: *Rhodotorula glacialis* Margesin & J.P. Samp., Int. J. Syst. Evol. Microbiol. 57: 2183. 2007.

4) ***Phenoliferia himalayensis*** (Shivaji, Bhadra & Rao) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813156.
*Basionym*: *Rhodotorula himalayensis* Shivaji *et al.*, Extremophiles 12: 380. 2008.

*Notes*: Species of *Phenoliferia* (i.e. the **glacialis** clade) have similar assimilation patterns of carbon and nitrogen compounds (Margesin *et al.* 2007). They share the ability to grow on raffinose as the sole carbon source but not on maltose. In contrast, closely related taxa, such as *Kriegeria eriophori* and *Rhodotorula rosulata*, have different assimilation properties and are able to utilise maltose, but not raffinose (Table 3). *R. himalayensis* was not included in our previous phylogenetic study (Wang *et al.* 2015a). This species was found to be closely related to *R. psychrophila* and *R. glacialis* based on the sequence analyses of LSU rRNA D1/D2 domains and ITS (Shivaji *et al.* 2008, Turchetti *et al.* 2011, Toome *et al.* 2013, Singh *et al.* 2014, Fig. 6 of this study), and, hence, it is recombined in the genus *Phenoliferia*.

***Yamadamyces*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813326.

*Etymology*: The genus is named in honour of Y. Yamada because of his contributions to the taxonomy of yeasts.

This genus corresponds to the ***Rhodotorula rosulata*** lineage (Wang *et al.* 2015a). Member of the *Kriegeriaceae* (*Kriegeriales*, *Microbotryomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a single-species lineage within the *Kriegeriaceae* (Figs 1, 6).

Sexual reproduction not known. Colonies greyish-cream and butyrous. Budding cells present. Pseudomycelium present. Ballistoconidia not produced. Major CoQ system unknown.
*Type species*: *Yamadamyces rosulatus* (Golubev & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Yamadamyces rosulatus*** (Golubev & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813578.

*Basionym*: *Rhodotorula rosulata* Golubev & Scorzetti, Int. J. Syst. Evol. Microbiol. 60: 2503. 2010.

*Notes*: The species *R. rosulata* was found to differ from *K. eriophori* in the utilisation of three carbon sources, namely methyl-α-D-glucoside, L-arabinose and *myo*-inositol (Table 3). The micromorphology of the species resembles that of *Me. eburnea* and *K. eriophori* with budding cells remaining connected to each other at the base and forming clusters (or rosettes) of cells.

**Family *Camptobasidiaceae*** R.T. Moore, Mycotaxon 59: 8. 1996.

*Type genus*: *Camptobasidium* Marvanová & Suberkr.

The family *Camptobasidiaceae* was described to accommodate a teleomorphic aquatic fungus *Camptobasidium* (Marvanová & Suberkropp 1990) that was placed in the *Atractiellales* (*Atractiellomycetes*) by Moore (1996). Aime *et al.* (2006) indicated that *Camptobasidium* belongs to *Microbotryomycetes* rather than *Atractiellomycetes* based on rRNA sequence analysis.

*Genera accepted*: *Camptobasidium* Marvanová & Suberkr., *Glaciozyma* Turchetti *et al.*

*Note*: Our previous study (Wang *et al.* 2015a) did not support the family *Camptobasidiaceae* as belonging to the *Kriegeriales*, and, therefore, we consider the family as '*incertae sedis*' in *Microbotryomycetes*.

***Camptobasidium*** Marvanová & Suberkr., Mycologia 82: 209. 1990.

= *Crucella* Marvanová & Suberkr., Mycologia 82: 212. 1990.

*Type species*: *Camptobasidium hydrophilum* Marvanová & Suberkr.

*Species accepted*:
1) *Camptobasidium hydrophilum* Marvanová & Suberkr., Mycologia 82: 209. 1990.

*Notes*: *Camptobasidium hydrophilum* is a slow-growing psychrophilic fungus without a yeast stage but with a tetraradiate anamorph, *Crucella subtilis*. In co-culturing experiments with aquatic hyphomycetes *Camptobasidium hydrophilum* behaves like a contact biotrophic mycoparasite and its hyphae coil around host hyphae or conidia. The penetration of the host by hyphae has, however, not been reported (Marvanová & Suberkropp 1990).

***Glaciozyma*** Turchetti *et al.*, Extremophiles 15: 579. 2011.

*Type species*: *Glaciozyma antarctica* (Fell *et al.*) Turchetti *et al.*

*Species accepted*:
1) *Glaciozyma antarctica* (Fell *et al.*) Turchetti *et al.*, Extremophiles 15: 579. 2011.
2) *Glaciozyma litoralis* A.V. Kachalkin, Antonie van Leeuwenhoek 105: 1080. 2014.
3) *Glaciozyma martinii* Turchetti *et al.*, Extremophiles 15: 579. 2011.
4) *Glaciozyma watsonii* Turchetti *et al.*, Extremophiles 15: 582. 2011.

*Note*: Only one species of the genus *Glaciozyma*, namely *G. antarctica*, was employed in our previous study (Wang *et al.* 2015a) because *G. litoralis*, *G. martini* and *G. watsonii* were only recently published (Turchetti *et al.* 2011, Kachalkin 2014). These species were included in the analysis of the enlarged LSU rRNA gene dataset (Fig. 6), and the genus *Glaciozyma* received high support in ML and MP analyses.

**Order *Leucosporidiales*** J.P. Samp. *et al.*, Mycol. Prog. 2: 61. 2003.

*Type family*: *Leucosporidiaceae* J.P. Samp. *et al.*

This order was proposed to accommodate the asexual or sexual, non-phytoparasitic members of the *Microbotryomycetidae* with white to cream-coloured colonies (Sampaio *et al.* 2003). The order includes *Mastigobasidium* and *Leucosporidium fellii*, and the family *Leucosporidiaceae* in Sampaio *et al.* (2003). Members of this order have colacosomes (lenticular bodies) and represent potential mycoparasites (Sampaio *et al.* 2003).

**Family *Leucosporidiaceae*** J.P. Samp. *et al.*, Mycol. Prog. 2: 63. 2003.

*Type genus*: *Leucosporidium* Fell *et al.* emend. V. de Garcia *et al.*

This family was proposed to accommodate the genera *Leucosporidiella* and *Leucosporidium* excluding the species *L. fellii* and *L. fasciculatum*, and *Mastigobasidium* (Sampaio *et al.* 2003). The genera *Mastigobasidium* and *Leucosporidiella* were recently proposed as a synonym of *Leucosporidium* (de García *et al.* 2015). Thus, the family *Leucosporidiaceae* presently includes only the genus *Leucosporidium* (Fig. 7).

*Genus accepted*: *Leucosporidium* Fell *et al.* emend. V. de Garcia *et al.*

***Leucosporidium*** Fell *et al.*, Antonie van Leeuwenhoek 35: 438. 1969. emend. V. de Garcia *et al.*, FEMS Yeast Res. 15: 9. 2015.

= Mastigobasidium Golubev, Int. J. Syst. Bacter. 49: 49. 1999

= Leucosporidiella Sampaio, Mycol. Progr. 2: 63. 2003

*Type species*: *Leucosporidium scottii* Fell *et al.*

*Species accepted*:
1) *Leucosporidium creatinivorum* (Golubev) V. de Garcia *et al.*, FEMS Yeast Res. 15: 9. 2015.
2) *Leucosporidium drummii* A.M. Yurkov *et al.*, Int. J. Syst. Evol. Microbiol. 62: 730. 2012.
3) *Leucosporidium escuderoi* Vaca *et al.*, Antonie van Leeuwenhoek 105: 599. 2013.
4) *Leucosporidium fellii* Gim.-Jurado & Uden, Antonie van Leeuwenhoek 55: 134. 1989.
5) *Leucosporidium golubevii* Gadanho *et al.*, Mycol. Progr. 2: 57. 2003.
6) *Leucosporidium scottii* Fell *et al.*, Antonie van Leeuwenhoek 35: 440. 1969.
7) *Leucosporidium yakuticum* (Golubev) V. de Garcia *et al.*, FEMS Yeast Res. 15: 9. 2015.
8) *Leucosporidium muscorum* (Di Menna) V. de Garcia *et al.*, FEMS Yeast Res. 15: 9. 2015.
9) *Leucosporidium intermedium* (Golubev) V. de Garcia *et al.*, FEMS Yeast Res. 15: 9. 2015.

10) *Leucosporidium fragarium* (J.A. Barnett & Buhagiar) V. de Garcia *et al.*, FEMS Yeast Res. 15: 9. 2015.

**Order *Microbotryales*** R. Bauer & Oberw., Can. J. Bot. 75: 1309. 1997.

*Type family*: *Microbotryaceae* R.T. Moore.

This order was proposed to accommodate phytoparasitic taxa lacking colacosomes (lenticular bodies) and teliospores (Bauer *et al.* 1997, Bauer *et al.* 2006). The order includes the families *Microbotryaceae* and *Ustilentylomataceae*. No yeast species are included in the family *Microbotryaceae*, but yeast stages of taxa in this family occur (Fig. 3D).

**Family *Ustilentylomataceae*** R. Bauer & Oberw., Can. J. Bot. 75: 1311. 1997.

*Type genus*: *Ustilentyloma* Savile.

This family was proposed to include taxa with 'simple' septal pores in the *Microbotryales* (Bauer *et al.* 1997).

*Genera accepted*: *Aurantiosporium* M. Piepenbr. *et al.*, *Fulvisporium* Vánky, *Ustilentyloma* Savile, *Microbotryozyma* S.O. Suh *et al.*

*Note*: The species of the genera *Aurantiosporium* and *Fulvisporium* are not listed here because no yeast phase has been observed in these two genera. Representatives of these genera were included in the analysis of the enlarged LSU rRNA gene dataset (Fig. 7).

***Microbotryozyma*** S.O. Suh *et al.*, Antonie van Leeuwenhoek 102: 102. 2012.

*Type species*: *Microbotryozyma collariae* S.O. Suh *et al.*

*Species accepted*:
1) *Microbotryozyma collariae* S.O. Suh *et al.*, Antonie van Leeuwenhoek 102: 103. 2012.

*Note*: *Mi. collariae* is a yeast species within *Ustilentylomataceae*, which was recently described to accommodate two strains isolated from the intestine of a plant bug (*Collaria oleosa*, *Miridae*, *Heteroptera*, *Insecta*) by Suh *et al.* (2012). This anamorphic species is distantly related to any teleomorphic parasitic taxa in this family (Fig. 7).

***Ustilentyloma*** Savile, Can. J. Bot. 42: 708. 1964. **emend.** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Type species*: *Ustilentyloma pleuropogonis* Savile.

This genus was originally described for teleomorphic fungi occurring on *Poaceae* (Savile & Parmelee 1964, Vánky 2002). Here it is emended to include free-living yeast species with unknown sexual states.

*Species accepted*:
1) *Ustilentyloma pleuropogonis* Savile, Can. J. Bot. 42: 708. 1964.
2) *Ustilentyloma brefeldii* (Krieg.) Vánky, Mycotaxon 41: 491. 1991.
   *Basionym*: *Entyloma brefeldii* Krieg., Hedwigia 35(Beibl.): 145. 1896.
3) *Ustilentyloma fluitans* (Liro) Vánky, Microbiologia Bucuresti 1: 328. 1970.
4) *Ustilentyloma oreochloae* (Durrieu) Vánky, Mycotaxon 78: 319. 2001.
5) ***Ustilentyloma graminis*** (Rodr. Mir. & H.G. Diem) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813157.
   *Basionym*: *Candida graminis* Rodr. Mir. & H.G. Diem, Can. J. Bot. 52: 279. 1974.
   = *Rhodotorula hordea* Rodr. Mir. & Weijman.

*Notes*: The close relatives of *R. hordea* are plant parasite species of *Ustilentyloma* based on the sequence analysis of the D1/D2 domains of the LSU rRNA (Sampaio 2011, Fig. 7 of this study) and the ITS (including 5.8S rRNA) region. Nucleotide sequences of *R. hordea* differ from *Ustilentyloma fluitans* (GenBank number: AF009882 and KC994459) and *Ustilentyloma brefeldii* (GenBank number: EF622016) by 1 and 15 positions in the D1/D2 domains of the LSU rRNA, respectively. However, *R. hordea* differs from *U. fluitans* by 78 mismatches and gaps (12 %) in the ITS region (GenBank number: AY212990 and KC994460), and by the assimilation of D-galactose, L-sorbose, D-ribose, lactose, erythritol, ribitol and protocatechuic acid (Sampaio 2011). The genus *Ustilentyloma* established by Savile & Parmelee (1964) contains *U. brefeldii*, *U. fluitans*, *U. oreochloae* and *U. pleuropogonis*. All species of this genus are parasites infecting leaves of *Poaceae*. *R. hordea* isolated from the leaves of six-row barley (*Hordeum vulgare subsp. hexastichium*, *Poaceae*) may have a similar ecology as a phyllosphere inhabitant as the species of *Ustilentyloma*, although it is not known to be a parasite on barley. One possibility may be that *R. hordea* represents a yeast stage of a dimorphic phytoparasite that is distinct from *U. fluitans*. Sequences of *U. pleuropogonis*, the type species of *Ustilentyloma*, are not available at present, but the above mentioned sequence analysis of *U. brefeldii* and *U. fluitans* indicated that this genus may be monophyletic (Fig. 7). The morphological characters of this genus also support its monophyletic nature (Vánky 2002). Based on the above discussion we prefer to propose *R. hordea* as a new combination of *Ustilentyloma*. The name *Rhodotorula hordea* was chosen to replace *Candida graminis* when it was transferred to *Rhodotorula* by Weijman *et al.* (1998) because the specific epithet '*graminis'* was already used for the species *Rhodotorula graminis*. Here we reuse this epithet for *Ustilentyloma graminis*.

**Order *Sporidiobolales*** J.P. Samp. *et al.*, Mycol. Progr. 2: 66. 2003.

*Type family*: *Sporidiobolaceae* (R.T. Moore) J.P. Samp. *et al.*

This order was proposed to include the family *Sporidiobolaceae* (Sampaio *et al.* 2003).

**Family *Sporidiobolaceae*** R.T. Moore, Bot. Mar. 23: 361. 1980. emend. J.P. Samp. *et al.*, Mycol. Progr. 2: 66. 2003.

*Type genus*: *Sporidiobolus* Nyland.

This family was emended to include *Sporidiobolus* and *Rhodosporidium* that have colacosomes (lenticular bodies), 'simple' septal pores and teliospores, and some species that are hitherto classified in *Sporobolomyces* and *Rhodotorula* (Sampaio *et al.* 2003). All known species in this family have pink-coloured cultures (Sampaio *et al.* 2003, Fig. 3C of this study).

*Genera accepted*: *Rhodotorula* F.C. Harrison emend. Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Rhodosporidiobolus* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Sporobolomyces* Kluyver & C.B. Niel emend. Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

***Rhodotorula*** F.C. Harrison, Proc. & Trans. Roy. Soc. Canada ser. 3 21: 349. 1927. **emend.** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

= *Rhodosporidium* I. Banno, J. Gen. Appl. Microbiol. 13: 192. 1967.

*Type species*: *Rhodotorula glutinis* (Fresen.) F.C. Harrison.

This genus is emended to include *Rhodotorula* species and their sexual counterpart *Rhodosporidium* in the ***Rhodosporidium*** clade (Wang *et al.* 2015a), which is a well supported clade within *Sporidiobolaceae* (*Sporidiobolales*). The ***Rhodosporidium*** clade is composed of *Rhodotorula glutinis*, the type species of *Rhodotorula*, and *Rhodosporidium toruloides*, the type species of *Rhodosporidium* (Figs 1, 8). The name *Rhodotorula* is older than *Rhodosporidium*, and has taxonomic priority over the latter.

Sexual reproduction observed in some species. Clamp connections present. Teliospores may be formed and produce transversely septate basidia. The basidiospores ovoid, passively released and germinate by budding. Colonies red and butyrous. Budding cells present. Pseudohyphae or true hyphae present or not. Ballistoconidia formed or not, ellipsoidal. Major CoQ systems Q-9 or Q-10.

*Species accepted*:

1) ***Rhodotorula alborubescens*** (Derx) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813323.
   *Basionym*: *Sporobolomyces alborubescens* Derx, Annls mycol. 28: 15. 1930.
2) *Rhodotorula araucariae* Grinb. & Yarrow, Antonie van Leeuwenhoek 36: 455. 1970.
3) ***Rhodotorula babjevae*** (Golubev) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813324.
   *Basionym*: *Rhodosporidium babjevae* Golubev, Syst. Appl. Microbiol. 16: 445. 1993.
4) *Rhodotorula dairenensis* (T. Haseg. & I. Banno) Fell, J.P. Samp. & Gadanho, FEMS Yeast Res. 2: 56. 2002.
5) ***Rhodotorula diobovata*** (S.Y. Newell & I.L. Hunter) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813325.
   *Basionym*: *Rhodosporidium diobovatum* S.Y. Newell & I.L. Hunter, J. Bact. 104: 504. 1970.
   = *Rhodotorula glutinis* (Fresenius) Harrison var. *lusitanica* Marcilla.
6) *Rhodotorula evergladensis* Fell, Statzell & Scorzetti, Antonie van Leeuwenhoek 99: 547. 2011.
7) *Rhodotorula glutinis* (Fresen.) F.C. Harrison, Proc. & Trans. Roy. Soc. Canada ser. 3 21: 349. 1928.
8) *Rhodotorula graminis* Di Menna, J. Gen. Microbiol. 18: 270. 1958.
9) ***Rhodotorula kratochvilovae*** (Hamam., Sugiy. & Komag.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813353.
   *Basionym*: *Rhodosporidium kratochvilovae* Hamam. *et al.*, J. Gen. Appl. Microbiol. 34: 122. 1988.
10) *Rhodotorula mucilaginosa* (A. Jörg.) F.C. Harrison, Proc. & Trans. Roy. Soc. Canada ser. 3 21: 349. 1928.
11) *Rhodotorula pacifica* Nagah. & Hamam., Int. J. Syst. Evol. Microbiol. 56: 297. 2006.
12) ***Rhodotorula paludigena*** (Fell & Tallman) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813354.
   *Basionym*: *Rhodosporidium paludigenum* Fell & Tallman, Int. J. Syst. Bacteriol. 30: 658. 1980.
13) ***Rhodotorula sphaerocarpa*** (S.Y. Newell & Fell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813356.
   *Basionym*: *Rhodosporidium sphaerocarpum* S.Y. Newell & Fell, Mycologia 62: 276. 1970.
14) *Rhodotorula taiwanensis* F.L. Lee & C.H. Huang, Antonie van Leeuwenhoek 99: 300. 2011.
15) ***Rhodotorula toruloides*** (I. Banno) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813358.
   *Basionym*: *Rhodosporidium toruloides* I. Banno, J. Gen. Appl. Microbiol. 13: 193. 1967.

***Rhodosporidiobolus*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813359.

*Etymology*: The genus name refers to the fact that the species were hitherto classified in the genera *Rhodosporidium* or *Sporidiobolus*.

This genus agrees with the mixed ***Rhodosporidium/Sporidiobolus*** clade (Wang *et al.* 2015a) and includes asexual states classified in the genera *Rhodotorula* and *Sporobolomyces*, and their sexual counterparts *Rhodosporidium* and *Sporidiobolus* (Fig. 8). Member of the *Sporidiobolaceae* (*Sporidiobolales*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade within *Sporidiobolales* (Figs 1, 8). Because the type species of the genera *Rhodotorula*, *Rhodosporidium*, *Sporobolomyces* and *Sporidiobolus* are located in other clades, species in this clade will be transferred into a new genus.

Sexual reproduction observed in some species. Clamp connections present. Teliospores may be formed and produce transversely septate basidia. Colonies pink to red and butyrous. Budding cells present. Pseudohyphae or true hyphae present or not. Ballistoconidia formed or not, ellipsoidal, allantoid or amygdaliform. Major CoQ systems Q-9 or Q-10.

*Type species*: *Rhodosporidiobolus nylandii* (M. Takash. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Rhodosporidiobolus fluvialis*** (Fell, Kurtzman, Tallman & J.D. Buck) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813360.

*Basionym*: *Rhodosporidium fluviale* Fell *et al.*, Mycologia 80: 562. 1988.

2) ***Rhodosporidiobolus azoricus*** (J.P. Samp. & Gadanho) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813364.

*Basionym*: *Rhodosporidium azoricum* J.P. Samp. & Gadanho, Can. J. Microbiol. 47: 214. 2001.

3) ***Rhodosporidiobolus microsporus*** (Higham ex Fell, Blatt & Statzell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813366.

*Basionym*: *Sporidiobolus microsporus* Higham ex Fell *et al.*, Antonie van Leeuwenhoek 74: 268. 1998.

4) ***Rhodosporidiobolus nylandii*** (M. Takash. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813369.

*Basionym*: *Sporobolomyces nylandii* M. Takash. & Nakase, Mycoscience 41: 364. 2000.

5) ***Rhodosporidiobolus ruineniae*** (Holzschu, Tredick & Phaff) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813371.

*Basionym*: *Sporidiobolus ruineniae* Holzschu *et al.*, Curr. Microbiol. 5: 75. 1981.

6) ***Rhodosporidiobolus lusitaniae*** (Á. Fonseca & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813374.

*Basionym*: *Rhodosporidium lusitaniae* Á. Fonseca & J.P. Samp., Syst. Appl. Microbiol. 15: 48. 1992.

7) ***Rhodosporidiobolus colostri*** (T. Castelli) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813375.

*Basionym*: *Mycotorula colostri* T. Castelli, Giorn. Biol. App. alla Indust. Chim. ad Alm. 2: 1. 1932.

8) ***Rhodosporidiobolus odoratus*** (J.P. Samp., Á. Fonseca & Valério) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813377.

*Basionym*: *Sporobolomyces odoratus* J.P. Samp. *et al.*, FEMS Yeast Res. 2: 15. 2002.

9) ***Rhodosporidiobolus poonsookiae*** (M. Takash. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813379.

*Basionym*: *Sporobolomyces poonsookiae* M. Takash. & Nakase, Mycoscience 41: 365. 2000.

***Sporobolomyces*** Kluyver & C.B. Niel, Centbl. Bakt. ParasitKde Abt. II 63: 19. 1924. **emend.** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

= *Sporidiobolus* Nyland, Mycologia 41: 686. 1949.

*Type species*: *Sporobolomyces roseus* Kluyver & C.B. Niel

This genus is emended to include *Sporobolomyces* species and their sexual counterparts *Sporidiobolus*, which belong to the ***Sporobolomyces*** clade (Wang *et al.* 2015a) that occurred as a well supported clade within the *Sporidiobolaceae* (*Sporidiobolales*). The ***Sporidiobolus*** clade contains the type species of *Sporobolomyces, S. salmonicolor*, and the type species of *Sporidiobolus, Sp. johnsonii* (Figs 1, 8). From this perspective the name *Sporobolomyces* has taxonomic priority over *Sporidiobolus*, as the former was published in 1924 and the latter in 1949. Thus we propose to keep the genus name *Sporobolomyces* for this clade.

Sexual reproduction observed in some species. Clamp connections present. Teliospores are formed and germinate to produce transversely septate basidia. Colonies salmon-pink, red and butyrous. Budding cells present. Pseudohyphae or true hyphae present or not. Ballistoconidia formed, ellipsoidal, allantoid or amygdaliform. Major CoQ system Q-10.

*Species accepted*:

1) *Sporobolomyces bannaensis* F.Y. Bai & J.H. Zhao, Int. J. Syst. Evol. Microbiol. 53: 2092. 2003.
2) *Sporobolomyces beijingensis* F.Y. Bai & Q.M. Wang, FEMS Yeast Res. 4: 582. 2004.
3) *Sporobolomyces blumeae* M. Takash. & Nakase, Mycoscience 41: 366. 2000.
4) *Sporobolomyces carnicolor* Yamasaki & H. Fujii ex F.Y. Bai & Boekhout, Int. J. Syst. Evol. Microbiol. 52: 2313. 2002.
5) ***Sporobolomyces longiusculus*** (Libkind, van Broock & J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813380.

   *Basionym*: *Sporidiobolus longiusculus* Libkind *et al.*, Int. J. Syst. Evol. Microbiol. 55: 505. 2005.
6) *Sporobolomyces japonicus* Iizuka & Goto, J. Gen. Appl. Microbiol. 11: 333. 1965.
7) *Sporobolomyces jilinensis* F.Y. Bai & Q.M. Wang, FEMS Yeast Res. 4: 584. 2004.
8) ***Sporobolomyces johnsonii*** (Nyland) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813382.

   *Basionym*: *Sporidiobolus johnsonii* Nyland, Mycologia 41: 687. 1949.
9) *Sporobolomyces koalae* Satoh & Makimura, Int. J. Syst. Evol. Microbiol. 58: 2985. 2008.
10) *Sporobolomyces patagonicus* Libkind *et al.*, Int. J. Syst. Evol. Microbiol. 55: 506. 2005.
11) *Sporobolomyces phaffii* F.Y. Bai *et al.*, Int. J. Syst. Evol. Microbiol. 52: 2313. 2002.
12) *Sporobolomyces roseus* Kluyver & C.B. Niel, Centbl. Bakt. ParasitKde Abt. II 63: 19. 1924.
13) *Sporobolomyces ruberrimus* Yamasaki & H. Fujii ex Fell *et al.*, FEMS Yeast Res. 1: 267. 2002
14) *Sporobolomyces salmonicolor* (B. Fisch. & Brebeck) Kluyver & C.B. Niel, Centbl. Bakt. ParasitKde Abt. II 63: 19. 1924.
15) *Sporobolomyces salmoneus* Derx, Annls mycol. 28: 17. 1930.

## Taxa *incertae sedis* in the *Microbotryomycetes*

**Family *Colacogloeaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813158.

Member of the *Microbotryomycetes*. The diagnosis of the family *Colacogloeaceae* is based on the description of the genus *Colacogloea*. The nomenclature of the family is based on the genus *Colacogloea*.

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

*Genus accepted*: *Colacogloea* Oberw. & Bandoni.

***Colacogloea*** Oberwinkler & Bandoni, Can. J. Bot. 68: 2532. 1990. **emend.** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Type species*: *Colacogloea peniophorae* (Bourdot & Galzin) Oberwinkler & Bandoni.

This genus is emended to include species of *Colacogloea* and related *Rhodotorula* species in the ***Colacogloea*** clade (Wang *et al.* 2015a), which occurred as a well supported clade within *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction observed in some species. Teleomorphic taxa mycoparasitic, and the sexual state develops only in the host. Basidiocarps minute, pulvinate to effuse, and mucoid-gelatinous. Basidia auricularioid (i.e., transversely septate). Hyphae thin-walled, hyaline, with clamp connections, and grow intrahymenially in host fructifications. Septal pores 'simple'. Colacosomes (or lenticular body) occur at the interface between the parasite and the host (Sampaio *et al.* 2011). Colonies cream, mucoid or butyrous. Budding cells present. Ballistoconidia not formed. Major CoQ system Q-10.

*Species accepted*:

1) ***Colacogloea cycloclastica*** (Thanh, M.S. Smit, Moleleki & Fell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813159.
   *Basionym*: *Rhodotorula cycloclastica* Thanh *et al.*, FEMS Yeast Res. 4: 858. 2004.
2) ***Colacogloea diffluens*** (Ruinen) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813160.
   *Basionym*: *Candida diffluens* Ruinen, Antonie van Leeuwenhoek 29: 437. 1963.
   ≡ *Rhodotorula diffluens* (Ruinen) von Arx & Weijman
   ≡ *Vanrija diffluens* (Ruinen) R.T. Moore
3) ***Colacogloea eucalyptica*** (C.H. Pohl, M.S. Smit & Albertyn) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813161.
   *Basionym*: *Rhodotorula eucalyptica* C.H. Pohl *et al.*, Int. J. Syst. Evol. Microbiol. 61: 2326. 2011.
4) ***Colacogloea falcata*** (Nakase, M. Itoh & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813162.
   *Basionym*: *Sporobolomyces falcatus* Nakase *et al.*, Trans. Mycol. Soc. Japan 28: 296. 1987.
5) ***Colacogloea foliorum*** (Ruinen) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813163.
   *Basionym*: *Candida foliarum* Ruinen, Antonie van Leeuwenhoek 29: 436. 1963.
   ≡ *Rhodotorula foliorum* (Ruinen) Rodr. Mir. & Weijman
6) *Colacogloea peniophorae* (Bourdot & Galzin) Oberwinkler & Bandoni, Can. J. Bot. 68: 2532. 1990.
7) ***Colacogloea philyla*** (van der Walt, Klift & D.B. Scott) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813164.
   *Basionym*: *Torulopsis philyla* van der Walt *et al.*, Antonie van Leeuwenhoek 37: 464. 1971.
   ≡ *Rhodotorula philyla* (van der Walt *et al.*) Rodr. Mir. & Weijman
8) ***Colacogloea retinophila*** (Thanh, M.S. Smit, Moleleki & Fell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813166.
   *Basionym*: *Rhodotorula retinophila* Thanh *et al.*, FEMS Yeast Res. 4: 859. 2004.
9) ***Colacogloea terpenoidalis*** (Thanh, M.S. Smit, Moleleki & Fell) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813169.
   *Basionym*: *Rhodotorula terpenoidalis* Thanh *et al.*, FEMS Yeast Res. 4: 860. 2004.

*Note*: Additional sequences representing three potential new species of this genus were found in public databases (Fig. 6).

**Family *Chrysozymaceae*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **fam. nov.** MycoBank MB813171.

Member of the *Microbotryomycetes*. The diagnosis of the family *Chrysozymaceae* is based on the description of the genus *Chrysozyma*. The nomenclature of the family is based on the genus *Chrysozyma*.

*Type genus*: *Chrysozyma* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Genera accepted*: *Bannozyma* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Chrysozyma* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Hamamotoa* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Fellozyma* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

***Bannozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813173.

*Etymology*: The genus is named in honour of I. Banno for his contributions to yeast taxonomy.

This genus corresponds to the **yamatoana** clade (Wang *et al.* 2015a). Member of *Chrysozymaceae* (*Microbotryomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade within *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies pale yellow to greyish-yellow, butyrous. Budding cells present. Pseudohyphae and septate hyphae present or not. Ballistoconidia present or not, kidney-shaped, allantoid or elongate. Major CoQ system Q-9.

*Type species*: *Bannozyma yamatoana* (Nakase, M. Suzuki & M. Itoh) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Bannozyma arctica*** (Vishniac & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813176.
   *Basionym*: *Rhodotorula arctica* Vishniac & M. Takash., Int. J. Syst. Evol. Microbiol. 60: 1215. 2010.
2) ***Bannozyma yamatoana*** (Nakase, M. Suzuki & M. Itoh) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813179.
   *Basionym*: *Sporobolomyces yamatoanus* Nakase *et al.*, J. Gen. Appl. Microbiol. 33: 446. 1987.
   ≡ *Bensingtonia yamatoana* (Nakase *et al.*) Nakase & Boekhout.

***Chrysozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813180.

*Etymology*: The genus is named because the type species produces yellowish colonies.

This genus agrees with the **griseoflavus** clade (Wang *et al.* 2015a). Member of *Chrysozymaceae* (*Microbotryomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade closely related to the **yamatoana** clade within *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies greyish-white to yellowish-cream, butyrous. Budding cells present. Hyphae and pseudohyphae not observed. Ballistoconidia present, ellipsoidal, allantoid or lunate. Major CoQ system Q-10.

*Type species*: *Chrysozyma griseoflava* (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Chrysozyma fushanensis*** (Nakase, F.L. Lee & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813181.
   *Basionym*: *Sporobolomyces fushanensis* Nakase *et al.*, J. Gen. Appl. Microbiol. 51: 43. 2005.
2) ***Chrysozyma griseoflava*** (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813183.
   *Basionym*: *Sporobolomyces griseoflavus* Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 33: 168. 1987.

*Note*: Species of *Chrysozyma* and *Bannozyma* can be distinguished from each other by the presence of Q-10 and Q-9, respectively.

***Fellozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813184.

*Etymology*: The genus is named in honour of Jack.W. Fell for his contributions to yeast taxonomy.

This genus agrees with the *Sporobolomyces inositophilus* lineage (Wang *et al.* 2015a). Member of the *Chrysozymaceae* (*Microbotryomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a single-species lineage within the *Microbotryomycetes* (Figs 1, 6). *S. inositophilus* is related to the **singularis** clade in the MP analysis of the combined seven genes-based dataset. This, however, was not supported in the ML and Bayesian analyses (Wang *et al.* 2015a).

Sexual reproduction not known. Colonies greyish-cream, butyrous. Budding cells present. Hyphae and pseudohyphae not observed. Ballistoconidia present, amygdaliform to falcate. Major CoQ system Q-10.

*Type species*: *Fellozyma inositophila* (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

*Species accepted*:

1) ***Fellozyma inositophila*** (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813185.
   *Basionym*: *Sporobolomyces inositophilus* Nakase & M. Suzuki, Antonie van Leeuwenhoek 53: 246. 1987.

*Note*: Additional sequence representing a potential new species of this genus was found in public databases (Fig. 6).

***Hamamotoa*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813186.

*Etymology*: The genus is named in honour of Dr. Makiko Hamamoto for her contributions to yeast taxonomy.

This genus agrees with the **singularis** clade (Wang *et al.* 2015a). Member of *Chrysozymaceae* (*Microbotryomycetes*). The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade closely related to the **griseoflavus** and **yamatoana** clades within *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies cream-coloured to pale yellowish-brown, mucoid. Budding cells present. Hyphae and pseudohyphae not present. Ballistoconidia present or not, ellipsoidal or kidney-shaped. Major CoQ system Q-10.

*Type species*: *Hamamotoa singularis* (Phaff & do Carmo-Sousa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Hamamotoa lignophila*** (Dill, C. Ramírez & González) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813187.
   *Basionym*: *Candida lignophila* Dill *et al.*, Antonie van Leeuwenhoek 50: 220. 1984.
   ≡ *Rhodotorula lignophila* (Dill *et al.*) Roeijmans *et al.*
2) ***Hamamotoa singularis*** (Phaff & do Carmo-Sousa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813188.
   *Basionym*: *Sporobolomyces singularis* Phaff & do Carmo-Sousa, Antonie van Leeuwenhoek 28: 205. 1962.
   ≡ *Bullera singularis* (Phaff & do Carmo-Sousa) Rodr. Mir.

*Note*: Species of *Hamamotoa* (i.e. the **singularis** clade) assimilate lactose and DL-lactate, but not melezitose and form highly mucoid colonies (Fig. 3D). The species of *Chrysozyma* (i.e. the **griseoflavus** clade) and *Bannozyma* (i.e. the **yamatoana** clade) are not able to grow on the former two carbon sources and have colonies with a butyrous texture (Fig. 3D).

***Pseudohyphozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813189.

*Etymology*: The name of the genus refers to the presence of pseudohyphae in all known species of this clade.

This genus agrees with the **buffonii** clade (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade within the *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies cream-coloured and butyrous. Budding cells present. Pseudohyphae of branched chains of ovoid to cylindrical cells. Ballistoconidia not produced. Major CoQ system Q-10.

*Type species*: *Pseudohyphozyma buffonii* (C. Ramírez) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Pseudohyphozyma bogoriensis*** (Deinema) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813190.
   *Basionym*: *Candida bogoriensis* Deinema, J. Econ. Biol. 61: 40. 1961.
   ≡ *Rhodotorula bogoriensis* (Deinema) von Arx & Weijman.
   ≡ *Candida bogoriensis* Deinema var. *lipolytica* Ruinen.
   ≡ *Vanrija bogoriensis* (Deinema) Moore.
2) ***Pseudohyphozyma buffonii*** (C. Ramírez) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813191.
   *Basionym*: *Torulopsis buffonii* C. Ramírez, Microbiol. 10: 236. 1957.
   ≡ *Rhodotorula buffonii* (C. Ramírez) Roeijmans.
3) ***Pseudohyphozyma pustula*** (Buhagiar) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813192.
   *Basionym*: *Torulopsis pustula* Buhagiar, J. Gen. Microbiol. 86: 3. 1975.
   ≡ *Rhodotorula pustula* (Buhagiar) Rodr. Mir. & Weijman.

*Note*: Species of the genus *Pseudohyphozyma* (i.e. the **buffonii** clade) have a butyrous colony texture on slants with potato dextrose agar (PDA) and differ from members of the genus *Slooffia* (the **tsugae** clade), which are usually mucoid on PDA (Fig. 3D).

***Pseudoleucosporidium*** V. de Garcia *et al.*, FEMS Yeast Res. 15: 11. 2015.

*Type species*: *Pseudoleucosporidium fasciculatum* (Babeva & Lisichk.) V. de Garcia *et al.*

*Species accepted*:

1) *Pseudoleucosporidium fasciculatum* (Babeva & Lisichk.) V. de Garcia *et al.*, FEMS Yeast Res. 15: 13. 2015.

*Note*: Our analyses suggest a close relationship between the genera *Pseudoleucosporidium* and *Curvibasidium*, as revealed by the multi-gene analyses (Wang *et al.* 2015a) and the analysis of the enlarged LSU rRNA gene dataset (Fig. 7).

***Oberwinklerozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813193.

*Etymology*: The genus is named in honour of Franz. Oberwinkler for his contributions to the taxonomy of *Basidiomycota*.

This genus agrees with the **yarrowii** clade (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade within the *Microbotryomycetes* (Figs 1, 6). The **yarrowii**, **buffonii** and **tsugae** clades clustered together with low support in the ML analysis, but were not supported by the MP and BI analyses (Wang *et al.* 2015a).

Sexual reproduction not known. Colonies cream-coloured. Budding cells present. Pseudohyphae present. Ballistoconidia not produced. Major CoQ system Q-9.

*Type species*: *Oberwinklerozyma yarrowii* (Á. Fonseca & van Uden) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Oberwinklerozyma silvestris*** (Golubev & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813194.
   *Basionym*: *Rhodotorula silvestris* Golubev & Scorzetti, Int. J. Syst. Evol. Microbiol. 60: 2501. 2010.
2) ***Oberwinklerozyma straminea*** (Golubev & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813195.
   *Basionym*: *Rhodotorula straminea* Golubev & Scorzetti, Int. J. Syst. Evol. Microbiol. 60: 2501. 2010.
3) ***Oberwinklerozyma yarrowii*** (Á. Fonseca & van Uden) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813196.
   *Basionym*: *Cryptococcus yarrowii* Á. Fonseca & van Uden, Antonie van Leeuwenhoek 59: 177. 1991.
   ≡ *Rhodotorula yarrowii* (Á. Fonseca & van Uden) Boekhout *et al.*

*Note*: Species of the genus *Oberwinklerozyma* (i.e. the **yarrowii** clade) have major coenzyme Q system Q-9 and are able to assimilate raffinose and myo-inositol, whereas members of the genera *Pseudohyphozyma* (i.e. the **buffonii** clade) and *Slooffia* (i.e. the **tsugae** clade) have coenzyme Q-10 and do not use these two carbon sources (Table 3).

***Sampaiozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813197.

*Etymology*: The genus is named in honour of J.P. Sampaio for his contributions to yeast taxonomy.

This genus agrees with the **vanillica** clade (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade within *Microbotryomycetes* (Figs 1, 7).

Sexual reproduction not known. Colonies cream or yellowish. Budding cells present. Pseudohyphae and true hyphae absent. Ballistoconidia not produced. Major CoQ system Q-10.

*Type species*: *Sampaiozyma ingeniosa* (Di Menna) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Sampaiozyma ingeniosa*** (Di Menna) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813198.
   *Basionym*: *Torulopsis ingeniosa* Di Menna, J. Gen. Microbiol. 19: 581. 1958.
   ≡ *Rhodotorula ingeniosa* (Di Menna) von Arx & Weijman.
   ≡ *Candida ingeniosa* (Di Menna) Meyer & Yarrow.
   ≡ *Vanrija ingeniosa* (Di Menna) Moore.
2) ***Sampaiozyma vanillica*** (J.P. Samp.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813199.
   *Basionym*: *Rhodotorula vanillica* J.P. Samp., Syst. Appl. Microbiol. 17: 616. 1994.

***Spencerozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813200.

*Etymology*: The genus is named in honour of I. Spencer-Martins for her contributions to yeast taxonomy and physiology.

This genus agrees with the ***Rhodotorula crocea*** lineage (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a single-species lineage within the *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies yellowish-cream, butyrous. Budding cells present. Pseudohyphae and true hyphae absent. Ballistoconidia not produced. Major CoQ system Q-10.

*Type species*: *Spencerozyma crocea* (Shifrine & Phaff) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Spencerozyma crocea*** (Shifrine & Phaff) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813201.
   *Basionym*: *Rhodotorula crocea* Shifrine & Phaff, Mycologia 48: 50. 1956.

***Slooffia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813202.

*Etymology*: The genus is named in honour of W.C. Slooff for her contributions to yeast taxonomy.

This genus corresponds to the **tsugae** clade (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade within *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies cream-coloured and mucoid. Budding cells present. Hyphae and pseudohyphae not formed. Ballistoconidia present or not, ellipsoidal. Major CoQ system Q-10

*Type species*: *Slooffia tsugae* (Phaff & do Carmo-Sousa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

*Species accepted*:

1) ***Slooffia cresolica*** (Middelhoven & Spaaij) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813203.
   *Basionym*: *Rhodotorula cresolica* Middelhoven & Spaaij, Int. J. Syst. Bacteriol. 47: 324. 1997.
2) ***Slooffia pilati*** (F.H. Jacob, Faure-Raynaud & Berton) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813204.
   *Basionym*: *Torulopsis pilati* F.H. Jacob *et al.*, Mycopathologia 69: 83. 1979.
   ≡ *Rhodotorula pilati* (F.H. Jacob *et al.*) Barnett *et al.*
3) ***Slooffia tsugae*** (Phaff & do Carmo-Sousa) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813206.
   *Basionym*: *Bullera tsugae* Phaff & do Carmo-Sousa, Antonie van Leeuwenhoek 28: 205. 1962.
   ≡ *Sporobolomyces tsugae* (Phaff & do Carmo-Sousa) Nakase & M. Itoh.

*Notes*: Species of *Slooffia* can be distinguished from those of *Pseudohyphozyma* (the **buffonii** clade) by their colony texture (see above, Fig. 3D). Additional sequences representing two potential new species of this genus were found in public databases (Fig. 6).

***Trigonosporomyces*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813207.

*Etymology*: The genus is named based on the morphology of the type species that forms triangular cells on pseudohyphae.

This genus agrees with the ***Rhodotorula hylophila*** (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a single-species lineage within the *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies cream-coloured. Budding cells present. Pseudohyphae of long, slender cells, often triangular. Ballistoconidia not produced. Major CoQ system unknown.

*Type species*: *Trigonosporomyces hylophilus* (van der Walt, van der Klift & D.B. Scott) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Trigonosporomyces hylophilus*** (van der Walt, van der Klift & D.B. Scott) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813208.
   *Basionym*: *Candida hylophila* van der Walt *et al.*, Antonie van Leeuwenhoek 37: 449. 1971.
   ≡ *Rhodotorula hylophila* (van der Walt *et al.*) Rodr. Mir. & Weijman.

***Yunzhangia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813209.

*Etymology*: The genus is named in honour of Yun-Zhang Wang, former professor at the Institute of Microbiology, Chinese Academy of Sciences, for his contributions to the taxonomic study of *Pucciniales* in China.

This genus agrees with the **sonckii** clade (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a well supported clade diverged from the other clades within the *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies cream-coloured, mucoid or butyrous. Budding cells present. Pseudohyphae and true hyphae not observed. Ballistoconidia not produced. Major CoQ system unknown.

*Type species*: *Yunzhangia auriculariae* (Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Yunzhangia auriculariae*** (Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813210.
   *Basionym*: *Torulopsis auriculariae* Nakase, J. Gen. Appl. Microbiol. 17: 413. 1971.
   ≡ *Rhodotorula auriculariae* (Nakase) Rodr. Mir. & Weijman.
   ≡ *Candida auriculariae* (Nakase) Meyer & Yarrow.
2) ***Yunzhangia sonckii*** (Hopsu-Havu, Tunnela & Yarrow) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813212.
   *Basionym*: *Candida sonckii* Hopsu-Havu *et al.*, Antonie van Leeuwenhoek 44: 436. 1978.
   ≡ *Rhodotorula sonckii* (Hopsu-Havu *et al.*) Rodr. Mir. & Weijman.

***Udeniozyma*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813213.

*Etymology*: The genus is named in honour of N.J. van Uden for his contributions to the study and taxonomy of basidiomycetous yeasts.

This genus agrees with the *Rhodotorula ferulica* lineage (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as single-species lineage within the *Microbotryomycetes* (Figs 1, 6). *R. ferulica* seems to have affiliation to *Colacogloea*, but did not receive high bootstrap values and Bayesian posterior probability.

Sexual reproduction not known. Colonies cream-coloured, mucoid. Budding cells present. Hyphae and pseudohyphae present or not. Ballistoconidia not produced. Major CoQ system Q-10.

*Type species*: *Udeniozyma ferulica* (J.P. Samp. & van Uden) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Udeniozyma ferulica*** (J.P. Samp. & van Uden) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813214.
   *Basionym*: *Rhodotorula ferulica* J.P. Samp. & van Uden, Syst. Appl. Microbiol. 14: 146. 1991.

***Vonarxula*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **gen. nov.** MycoBank MB813216.

*Etymology*: The genus is named in honour of J.A. von Arx for his contributions to fungal taxonomy.

This genus agrees with the *Rhodotorula javanica* lineage (Wang *et al.* 2015a). Member of the *Microbotryomycetes*. The genus is mainly circumscribed by the phylogenetic analysis of seven genes and the analysis of the enlarged LSU rRNA gene dataset, in which it occurred as a single-species lineage within the *Microbotryomycetes* (Figs 1, 6).

Sexual reproduction not known. Colonies cream-coloured. Budding cells present. Pseudohyphae of branched chains of fusiform cells. Ballistoconidia not produced. Major CoQ system Q-9.

*Type species*: *Vonarxula javanica* (Ruinen) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Species accepted*:

1) ***Vonarxula javanica*** (Ruinen) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813218.
   *Basionym*: *Candida javanica* Ruinen, Antonie van Leeuwenhoek 29: 436. 1963.
   ≡ *Rhodotorula javanica* (Ruinen) von Arx & Weijman.

***Mixiomycetes*** R. Bauer *et al.*, Mycol. Progr. 5: 47. 2006.

*Type order*: *Mixiales* R. Bauer *et al.*

***Mixiales*** R. Bauer *et al.*, Mycol. Progr. 5: 47. 2006.

*Type family*: *Mixiaceae* C.L. Kramer.

This order is characterised by multinucleate hyphae and multiple spores produced simultaneously on sporogenous cells (Bauer *et al.* 2006).

***Mixiaceae*** C.L. Kramer, Stud. Mycol. 30: 159. 1987.

*Type genus*: *Mixia* C.L. Kramer.

This family was proposed to accommodate the *Taphrina*-like genus *Mixia* (Kramer 1987), which is an intracellular parasite of ferns belonging to the genus *Osmunda*.

*Genus accepted*: *Mixia* C.L. Kramer

***Mixia*** C.L. Kramer, Mycologia 50: 924. 1958.

*Type species*: *Mixia osmundae* (Nishida) C.L. Kramer.

*Species accepted*:

1) *Mixia osmundae* (Nishida) C.L. Kramer, Mycologia 50: 924. 1958.

## Suggestion for new species descriptions

In the future descriptions of new species in the genera *Rhodotorula*, *Sporobolomyces* and *Bensingtonia* should be restricted to the clades containing the respective type species (Figs 1, 4, 8). In the case of unclassified *Microbotryomycetes* or '*incertae sedis*', none of the aforementioned generic names should be used to describe new species, and new genera have to be introduced following a robust phylogenetic analysis utilising several independent DNA loci or whole-genome comparisons (e.g. Wang *et al.* 2015a). Our results show that using the LSU rRNA gene alone is not sufficient to resolve the high-level phylogenetic relationships in *Microbotryomycetes*.

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