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, Sporobolomyces are polyphyletic. With the implementation of the "One Fungus = One Name" nomenclatural principle these polyphyletic genera were revised. Nine genera, namely Banna, 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 Spiculoglobes is proposed to accommodate the order Spiculoglobales. The new families Bucklezyzmaceae with Bucklezyzma gen. nov. and Rhodosporomyces with Rhodosporomyces gen. nov., Microsporomyces with Microsporomyces gen. nov., Ruiniaceae with Ruiniaceae gen. nov., Symmetrosporaceae with Symmetrosporaceae gen. nov., Colacogloeaceae and Sakaguchiacetidae are proposed. The new genera Banna, Bucklezyzma, Bollowyza, Hamamota, Hasegawazyma, Jianyunia, Rhodosporidoides, Obwinklerzyma, Phenolfila, Pseudobensingtonia, Pseudohyphozyma, Sampaizyma, Sloofzia, Speranza, Symmetrozyza, Tanagha, and Yunzhangaia are proposed to accommodate species segregated from the genera Bensingtonia, Rhodosporidium, Rhodotorula, Sporobolomyces and Sporobolomyces. Cystobasidiosis is emended and reintroduced to include three Sporobolomyces species of the saccicola 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.
INTRODUCTION

The subphylum Pucciniomycotina (Phylum Basidiomycota, Kingdom Fungi) presently includes eight classes, and four of these, namely the Agaricomycetes, Cystobasidiomycetes, Microbotryomycetes and Mixomycetes, 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, Scorzzetti 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, Scorzzetti et al. 2002, Boekhout et al. 2011, Hamamoto et al. 2011, Sampaio et al. 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, Scorzzetti et al. 2002, Boekhout et al. 2011, Sampaio et al. 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, Scorzzetti 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), RP5 (the largest subunit of DNA polymerase II), RP52 (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 CYT1 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 enforced for species previously analysed using seven DNA loci. Only bi-partitions 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 bootstrapping 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 2008). A chronogram was calculated from the ML-based tree using the penalised likelihood method (Sanderson 2002) as implemented in the chronoplot 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 Pucciniamycetes 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 Mixiomyctes (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      |
| Agaricostilbomycetes  | Genus| 0.22827| 0         | 0      |
| ingoldi 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      |
| Kondoia clade*        | Genus| 0.28874| 0         | 0      |
| Bensingtonia*         | Genus| 0.24787| 0         | 0      |
| ruber clade           | Genus| 0.29828| 0         | 0      |
| subbrenneus clade     | Genus| 0.39731| 0.09225   | 0      |
| Cystobasidiomycetes   | Class| 0.51968| 0         | 0      |
| Erythrosidaceae clade*| Genus| 0.16907| 0         | 0      |
| Kieszocla 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      |
| magnusporus clade     | Genus| 0.33920| 0.03414   | 0      |
| Cystobasidium (minuta) clade* | Genus| 0.18036| 0         | 0      |
| Microbotryomycetes    | Class| 0.72324| 0.08419   | 0      |
| Sporidobolus clade    | Genus| 0.34525| 0.04020   | 0      |
| Rhodosporidium clade  | Genus| 0.40759| 0.10253   | 0      |
| mixed Rhodosporidium/ | Genus| 0.16275| 0         | 0      |
| Sporidobolus clade    | Genus| 0.16275| 0         | 0      |
| Kriegeria*            | Genus| 0.21892| 0         | 0      |
| glacialis clade       | Genus| 0.16560| 0         | 0      |
| buffoni clade         | Genus| 0.10602| 0         | 0      |
| yarrowi 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      |
| soncki 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., deviation even outside the upper or lower 95 % confidence band of the upper or lower threshold, respectively. *: 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.

Consequently, B. sakaguchi is placed into a new genus (see Taxonomy), which is presently treated as ‘incertae sedis’ in the Agaricostilbales.

Nine clades were identified at the family level within Cystobasidiomycetes by the nested analyses of GMYC (Table 2). The presently accepted families Cystobasidiaceae, Erythrosidaceae and Naohideaceae belong to Cystobasidiales, Erythrosidiales and Naohideales, respectively. The genus Occultifur is separated from Cystobasidiaceae as a family in the GMYC analyses, but we presently keep to this genus in the Cystobasidiaceae due to the low number of taxa in this genus. The Cyreneilla and Rhodorutula lactosa lineages were suggested as two new families in the Erythrosidales by the GMYC nested analyses, however, these two lineages represent single species each, and, therefore, we temporarily placed them as ‘incertae sedis’ in the Erythrosidiales. The aurantica 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 magnusporus 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 Leucosporidaceae 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 Rhodorutula hylophilota, 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 inostophilus were identified as one family that was supported by the phylogenetic analysis of seven genes with strong support values (Wang et al. 2015a); the buffooni, tsugae and yarrowi 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 et al. 2015a),
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      | Kondo                          | supported  |
|                        |                 | Bensingtonia                   | supported  |
|                        | Sterigmatomyces | (Agaricostilbum clade)         | supported  |
|                        | Pseudobensingtonia | (indoldi clade)          | supported  |
|                        | Chionosphaeraceae |                               | supported  |
|                        |                 | Chionosphaera                  |           |
|                        |                 | Kurtzmanomyces                 |           |
|                        |                 | Mycogloea nipponica            |           |
|                        |                 | Ballistosporomyces (sasicola clade) |           |
|                        |                 | Cystobasidiopsis (lactophilus clade) |           |
|                        | Ruineniaceae    | Ruinenia (ruber clade)         | new family |
|                        |                 | Jianyunia (Bensingtonia sakaguchii) | new family |
|                        | Spiculogloeomycetes |                 | not supported |
|                        | Spiculogloeales | Spiculogloeaceae              | supported  |
|                        |                 | Phyllozyma (subbrunneus clade) |           |
|                        | Cystobasidiomycetes | Cystobasidiaceae       | not supported |
|                        | Cystobasiales   | Occultifur                     |           |
|                        |                 | Cystobasidiomycetaceae        |           |
|                        | Erythrobasiales | Erythrobasidiaceae            | supported  |
|                        |                 | Erythrobasidium               |           |
|                        |                 | Bannoa                         |           |
|                        |                 | Hasegawazyma (Rhodotorula lactosa) | new family |
|                        |                 | Cyrenella                      | new family |
|                        | Naohideales     | Naohideaceae                   | supported  |
|                        |                 | Naohidea                       |           |
|                        | incertae sedis in the Cystobasidiomycetes |           |
|                        | Buckleyzymaceae | Buckleyzyma (aurantiaca clade) | not supported |
|                        | Symmetosporaceae |                               | not supported |
|                        | Sakaguchiaceae  | Sakaguchia                     | new family |
|                        | Microsporomycetaceae |                         | new family |
|                        |                 | Microsporomyces (magnisporus clade) | not supported |
|                        | Microbotryomycetes |                            | not supported |
|                        | Sporidiobolales |                                |           |

(continued on next page)
| Class/Order                      | family            | Genus                                   | GMYC                  |
|----------------------------------|-------------------|-----------------------------------------|-----------------------|
| *Sporidiobolaceae*               |                   | *Rhodotorula* (Rhodosporidium clade)    | not supported         |
|                                  |                   | *Rhodosporidiobolus* (mixed Rhodosporidium/Sporidiobolus clade) | new family           |
|                                  |                   | *Sporobolomyces* (Sporidiobolus clade)  | new family           |
| *Kriegeriales*                   |                   | *Kriegeria*                             | not supported         |
|                                  |                   | *Meredithblackwellia*                   |                       |
|                                  |                   | *Phenolferia* (glacialis clade)         |                       |
|                                  |                   | *Yamadamyces* (Rhodotorula rosulata)    |                       |
|                                  | *Camptobasidiaceae*| *Glaciozyma*                            | not supported         |
| *Leucosporidiales*               |                   | *Leucosporidium*                        | supported             |
| *Microbotryales*                 |                   | *Microbotryum*                          | supported             |
|                                  | *Ustilentylomataceae*| *Ustilentyloma*                      | supported             |
| *Heterogastridiales*             | *Heterogastridiae*| *Heterogastridium*                      | supported             |
| incertae sedis in the *Microbotryomycetes* |                   | *Chrysozymaceae*                        | new family           |
|                                  |                   | *Chrysozyma* (griseoflavus clade)       |                       |
|                                  |                   | *Bannozyma* (yamatoana clade)           |                       |
|                                  |                   | *Hamamotoa* (singularis clade)          |                       |
|                                  | *Colacogloeaceae* | *Colacogloea*                           | new family           |
| Genera incertae sedis in the *Microbotryomycetes* |                   | *Pseudohyphozyma* (buffonii clade)      | new family           |
|                                  |                   | *Slooffia* (tsugae clade)               | new family           |
|                                  |                   | *Oberwinklerozyma* (yarrowii clade)     | new family           |
|                                  |                   | *Sampaiozyma* (vanillica clade)         | new family           |
|                                  |                   | *Yunzhangia* (sonckii clade)            | new family           |
|                                  |                   | *Curvibasidium*                         | new family           |
|                                  |                   | *Pseudoleucosporidium* (Leucosporidium fasciculatum) | new family |
|                                  |                   | *Udeniozyma* (Rhodotorula ferulica)     | new family           |
|                                  |                   | *Reniforma*                             | new family           |
|                                  |                   | *Trigonosporomycetes* (Rhodotorula hylophila) | new family         |
|                                  |                   | *Vonarxula* (Rhodotorula javanica)      | new family           |
|                                  |                   | *Spencerozyma* (Rhodotorula crocea)     | new family           |

**Note:** NA means “not analysed”. In the overall GMYC analysis, Naohideales is a separate class from Cystobasidiomycetes; Spiculoglomycetes 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 1000 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 Ustilentylopha) 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 hordeae (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 fitetarium, 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, Cystobasiidiopsis 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. Rueniaceae 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 Kondochaeeae were accepted in this order by Bauer et al. (2006). Here we propose Rueniaceae 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, asetate 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           | 9      |         |     |
| Bensingtonia                            | 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 (ingoldi clade)      | v       | v         | v       | +         | -       | v          | v                    |               | v           |            |           | v          | v           | 9      |         |     |
| **Chironosphaeraceae**                  |         |           |         |           |         |            |                      |               |             |            |           |            |             |        |         |     |
| Ballistosporomycetes (sasciola clade)   | +       | v         | v       | v         | v       | v          | v                    |               | v           |            |           | v          | v           | 10     |         |     |
| Cystobasidiopsis (lactophilus clade)    | +       | v         | v       | v         | v       | v          | v                    |               | v           |            |           | v          | v           | 10     |         |     |
| Kurtzmanomyces                          | v       | v         | v       | v         | v       | v          | v                    |               | v           |            |           | v          | v           | 10     |         |     |
| Chironosphaera                          | -       | -         | v       | v         | -       | v          | v                    |               | -           |            |           | v          | v           | 10     |         |     |
| Jianyunia (Bensingtonia sakaguchii)     | -       | -         | +       | +         | v       | v          | v                    |               | v           |            |           | v          | v           | 9      |         |     |
| Ruhenia (rubner clade)                  | +       | +         | v       | v         | v       | v          | v                    |               | v           |            |           | v          | v           | 10     |         |     |
| **Spiculogloeales**                     |         |           |         |           |         |            |                      |               |             |            |           |            |             |        |         |     |
| Phyllozyma (subbrunneus clade)          | v       | v         | v       | v         | -       | -          | v                    |               | v           |            |           | v          | v           | 10     |         |     |
| **Cystobasidiomycetes**                 |         |           |         |           |         |            |                      |               |             |            |           |            |             |        |         |     |
| Cystobasidiales                         |         |           |         |           |         |            |                      |               |             |            |           |            |             |        |         |     |
| Cystobasidiomycetes (minuta clade)      | v       | v         | v       | v         | v       | v          | v                    |               | v           |            |           | v          | v           | 9,10   |         |     |
| Occultifur externus                     | +       | -         | +       | +         | +       | -          | v                    |               | v           |            |           | v          | v           | 9,10   |         |     |
| **Erythrobasidiales**                   |         |           |         |           |         |            |                      |               |             |            |           |            |             |        |         |     |
| Erythrobasidium                         | +       | -         | -       | +         | +       | +          | v                    |               | v           |            |           | v          | v           | 10(H2) |         |     |
| Bannoa                                  | +       | +         | v       | +         | +       | +          | v                    |               | v           |            |           | v          | v           | 10(H2) |         |     |
| Hasegawazyma (Rhodotorula lactosa)      | +       | +         | +       | +         | +       | -          | v                    |               | v           |            |           | v          | v           | 9      |         |     |
| Cyrenella elegans                       | +       | +         | -       | +         | +       | +          | v                    |               | v           |            |           | v          | v           | 9      |         |     |
| Microsporomycetes (magnisporus clade)   | 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)
| 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           | 10      |         |     |
| Sakaguchia                                | v       | v         | −       | +         | v       | v          | v                   | v             | v           | v          | v         | v          | v           | 10      |         |     |
| Naohideales                               |         |           |         |           |         |            |                     |               |             |            |           |            |             |         |         |     |
| Naohidea sebacea                          | −       | −         | −       | −         | −       | −          | −                   | −             | +           | −           | +         | −          | −           | n       |         |     |
| Mixiomyctetes                             | −       | −         | −       | −         | −       | +          | v                   | −             | −           | −          | −         | −          | −           | 10      |         |     |
| Microbotryomyctetes                       |         |           |         |           |         |            |                     |               |             |            |           |            |             |         |         |     |
| Sporidiobolales                           |         |           |         |           |         |            |                     |               |             |            |           |            |             |         |         |     |
| Rhodotorula (Rhodosporidium clade)       | +       | v         | −       | +         | v       | v          | v                   | v             | +           | −           | v         | v          | v           | 9,10    |         |     |
| Rhodosporidobilus (mixed Rhodosporidium/Sporidiobolus clade) | v       | v         | −       | +         | v       | v          | v                   | v             | v           | v          | −         | +          | +           | 9,10    |         |     |
| Sporobolomyces (Sporidiobolus clade)     | +       | v         | −       | v         | v       | v          | v                   | v             | v           | v          | v         | v          | v           | 10      |         |     |
| Leucosporidiales                          | v       | v         | −       | v         | v       | v          | v                   | v             | v           | +          | −         | v          | v           | 9,10    |         |     |
| Kriegeriales                              |         |           |         |           |         |            |                     |               |             |            |           |            |             |         |         |     |
| Kriegeriaceae                             |         |           |         |           |         |            |                     |               |             |            |           |            |             |         |         |     |
| Phenoliferia (glacialis clade)            | +       | +         | −       | −         | −       | +          | +                   | −             | −           | −          | +         | −          | n           |         |         |     |
| Meredithblackwellia eburnea               | +       | −         | −       | +         | +       | +          | −                   | w             | +           | +          | −         | −          | n           |         |         |     |
| Yamadamycyes (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       | −          | −                   | −             | −           | +          | −         | −          | −           | 9       |         |     |
| Hamamotoa (singulares clade)              | −       | −         | +       | −         | −       | −          | v                   | v             | +           | −          | −         | −          | n           |         |         |     |
| Fellozyma (Sporobolomyces inositophilus)  | +       | −         | −       | +         | +       | −          | −                   | −             | +           | +          | +         | +          | +           | 10      |         |     |
| Colacogloea                               | v       | v         | −       | v         | v       | v          | −                   | v             | v           | v          | v         | v          | v           | 9       |         |     |
| Udeniozyma (Rhodotorula ferulica)         | +       | −         | +       | +         | +       | −          | −                   | +             | +          | −         | v         | +          | +           | 10      |         |     |
| Pseudohyphozyma (buffonii clade)          | −       | −         | −       | v         | v       | v          | −                   | v             | v           | +          | −         | v          | v           | 10      |         |     |
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. = Agaricostilbium 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 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, gen. nov. MycoBank MB813078.

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 % inferred 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 %).
Rhodotorula phylloplana
AF190004

Microbotryomycetes (96/94)
Ballistosporomyces (100/100)
Sporobolomyces sp. AY313055
Cystobasiomycetis (99/100)
Bensingtonia sakaguchi AF363646

Bensingtonia sp. EU678947
Ruinenia (99/100)
Sterigmatomyces (100/100)
Pseudobensingtonia (100/100)

Phylozyma (100/100)
Mixia osmundae DQ831009

Fig. 5. Phylogenetic relationships of yeasts and related taxa from the Cystobasiomycetes 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% inferred 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% inferred 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 Agaricomycotina (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 Kondoaeeae (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. Basispecies: *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. Basispecies: *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. Basispecies: *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. Basispecies: *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 coppinsi* 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.
This genus is emended to include species of Cystobasidiosis and anamorphic species of the lactophilus clade (Wang et al. 2015a), which occurred as a well supported clade related to the genus Ballistosporomycetes 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. Ballistocnidial present or not, ellipsoidal, amygdaliform or falcate. Major CoQ system Q-9. Butyrous. Budding cells present or not. Ballistoconidia present or not. 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 single, uniperforate. Major CoQ system Q-9.

Species accepted:
1) Cystobasidiosis 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) Cystobasidiosis lofpatheri (Nakase, Tszuzuki, F.L. Lee, Jindam. & M. Takash.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813084. Basionym: Sporobolomyces lofpatheri Nakase et al., J. Gen. Appl. Microbiol. 51: 282. 2005.
3) Cystobasidiosis nirenberigae R. Bauer et al., Mycol. Res. 113: 962. 2009.

Note: The emended genera Cystobasidiosis and Ballistosporomycetes can be distinguished by colony morphology and some physiological characteristics (Table 3, Fig. 3A). The species of Cystobasidiosis form white colonies and assimilate D-arabinose, glycerol and D-lactate, whereas the species of Ballistosporomycetes 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: Kondoia Y. Yamada et al.

This family was proposed to accommodate the genus Kondoia that has ballistosporic phragmobasidia, as well as members of the genus Bensingtonia (Bauer et al. 2006). Genera accepted: Bensingtonia Ingold, Kondoia 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. 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).

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

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

This genus is emended to include species of the genera Kondoia and Bensingtonia hitherto classified in the Kondoia 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 Kondoia clade will be transferred into the genus Kondoia 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) Kondoia aeria Á. Fonseca, J.P. Samp. & Fell, Antonie van Leeuwenhoek 77: 295.
2) Kondoia 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 MB813087.

Basionym: Sporobolomyces miscanthus Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 33: 133, 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 MB813088.

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 phyllada (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 MB813089.

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

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

7) **Kondoa subrosea** (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 *rubra* 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. Hyphe and pseudohyphae present or not. Ballistocinoida 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 *diospyro*) 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. & Nakase, 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. *rubra* 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).
**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. Ballistoconidia present, ellipsoidal, fusiform or sickle-shaped. Major CoQ system Q-10.**

**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 MB813101.

**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.

**Species**:

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: 159. 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.

**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.

**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*).

**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 *Mixiomyctes* 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*).
Phylogeny of Cystobasidiomycetes

5) Phyllozyma novozaelandica (Hamam. & Nakase) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813322.

Basionym: Phyllozyma novazealandica Hamam. & Nakase, Antonie van Leeuwenhoek 67: 156. 1995.

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

Type order: Cystobasidiales R. Bauer et al.

Note: S. productus and S. corallinus were not included in our previous phylogenetic study (Wang et al. 2015b). These two species were placed in the subbrunneus lineage closely related to S. subbrunneus and S. dimenae 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.

Type genus: Cystobasidium Lagerh. emend. A.M. Yurkov et al., Occultifur Oberw.

Cystobasidium (Lagerh.) emend. A.M. Yurkov et al., Antonie van Leeuwenhoek 107: 179. 2015.

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 calyptrigena (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 hypogymnicola Diederich & Ahl, Bibliothca Lichenol. 61: 21. 1996.
5) Cystobasidium laryngis (Reiersö) 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 palidum (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, Bibliothca 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 corticorum* 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. corticorum*, *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-treelidioid 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 *Hasegawaazyza* (Fig. 1). Thus, this order includes the family *Erythrobasidiaeae* and the genera *Cyrenella* and *Hasegawaazyza*, which are treated as 'incertae sedis' in the *Erythrobasidiales*.

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

Type genus: *Erythrobasidium* Hamam. et al.

The name *Erythrobasidiaeae* 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. Pseudothypae absent. Ballistoconidia present or not, ovoid and ellipsoidal. Major CoQ system Q-10(H2).

Species accepted:
1) *Bannoa bischofiae* (Hamam., Than & 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., Than & 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., Than & 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. Pseudothypae absent. Ballistoconidia present or not, ovoid and ellipsoidal. 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 Erythrobasiellales**

*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 *Erythrobasiellales* (*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 *Bannonia*, *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, *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 *Erythrobasiellales* 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.
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, *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 amygdailiform. 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.

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

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

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

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

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

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

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

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

**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.

**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.

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

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, *gen. nov.* MycoBank MB813127.

**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 *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 amygdailiform. 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. 176
Species accepted:

1) *Microsporomyces bloemfonteiniensis* (Pohl, M.S. Smit & Albertyn) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB814789.
   **Basionym:** *Rhodotorula bloemfonteiniensis* 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:** *Rhodotorula magnispora* 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 dacyroidea* (Fell et al.) Y. Yamada et al.

This genus is emended to include *Sakaguchia dacyroidea* 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 & Scorzaetti) 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 dacyroidea* (Fell et al.) Y. Yamada et al., Biosc. Biotechn. Biochem. 58: 102. 1994.

3) *Sakaguchia lamellibrachiae* (Nagah., Hamam., Nakase & Hirokoshi) 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 melii* (Libkind, van Broock & J.P. Sampa.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813148.
   **Basionym:** *Rhodotorula melii* 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 *Chrysosyzymaceae* fam., nov. to accommodate the *griseoflavus*, *yamatoana*, *singularis* and *Sporobolomyces inosithophilus* clades, and *Cologloeaceae* 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 Campybotasidiaceae (Toome et al. 2013). The teleomorphic members of this order are characterised by the presence of ‘simple’ septal pores and subglobose 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 multigene 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 Yamadamycetes.

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

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

= Zymoxenogloea D.J. McLaughlin & Doubles, 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.

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.

*Yamadamycetes* 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**: Yamadamycetes rosulatus (Golubev & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

**Species accepted**:

1. *Yamadamycetes rosulatus* (Golubev & Scorzetti) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813578.
Basionym: Rhodotorula rosulata Golubev & Scorzetii, 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-a-ro-gluconate, -arabinose and -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 Marvanov & Suberk.

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

Genera accepted: Camptobasidium Marvanov & Suberk., 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 Microbotryomycetidae.

Camptobasidium Marvanov & Suberk., Mycologia 82: 209. 1990.

= Crucella Marvanov & Suberk., Mycologia 82: 212. 1990.

Type species: Camptobasidium hydrophilum Marvanov & Suberk.

Species accepted:
1) Camptobasidium hydrophilum Marvanov & Suberk., Mycologia 82: 209. 1990.

Notes: Camptobasidium hydrophilum is a slow-growing psychrophilic fungus without a yeast stage but with a tetraradate 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 (Marvanov & 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 martini 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 Leuco- sporidiella 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 Garcia 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 scotti 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 golubevi Gadanho et al., Mycol. Progr. 2: 57. 2003.
6) Leucosporidium scotti 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 García 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.
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, *Rhodosporidium* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Sporobolomyces* Klyuyver & 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, allantoid or amygdaliform. Major CoQ systems Q-9 or Q-10.

**Species accepted:**

1) *Rhodotorula alborubescens* (Dexr) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813323.

   Basionym: *Sporobolomyces alborubescens* Dexr, Anns 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 dairrenensis* (T. Haseg. & I. Banno) Fell, J.P. Samp. & Gadagho, FEBS 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* Marcella.

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 kraotchivilvae* (Hamam., Sugiy. & Komag.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813353.

   Basionym: *Rhodosporidium kraotchivilvae* 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 paludigena* Nagah. & Hamam., Int. J. Syst. Evol. Microbiol. 56: 297. 2006.

12) *Rhodotorula paludigenus* (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 genus *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 RNA gene dataset, in which it occurred as a well supported clade within *Sporidiobolaceae* (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 butyros. Budding cells present. Pseudohyphae or true hyphae present or not. Ballistocinidica formed or not, ellipsoidal. 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.

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**PHYLOGENETIC CLASSIFICATION OF YEASTS AND RELATED TAXA**
1949. Thus we propose to keep the genus name *Sporidiobolus*, Sp. johnsonii (Figs 1, 8). From this perspective the name *Sporobolomyces* has taxonomic priority over *Sporidiobolus* clade (Wang et al. 2015a). The diagnosis of the family *Colacogloeaceae* is based on the description of the genus *Colacogloea*. The nomenclature of the family is based on the description of the genus *Colacogloea*.

**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 banaenensis* 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. Fuji ex F.Y. Bai & Boekhout, Int. J. Syst. Evol. Microbiol. 52: 2313. 2002.
5. *Sporobolomyces longiusculus* (Libkind, van Broock & J.P. Sampa.) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov.* MycoBank MB813380.
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.
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* Kuyver & C.B. Niel, Centbl. Bakt. ParasitKde Abt. II 63: 19. 1924. *emend.* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.
13. *Sporobolomyces salmonicolor* F. Y. Bai & J.H. Zhao, Int. J. Syst. Evol. Microbiol. 53: 2092. 2003.
14. *Sporobolomyces salmoneus* F.Y. Bai & J.H. Zhao, Int. J. Syst. Evol. Microbiol. 53: 2092. 2003.
15. *Sporobolomyces salmonicolor* Derx, Annls mycol. 28: 17. 1930.

**Presentation 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* Oberwinkler & Bandoni.

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

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

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

**Presentation 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* Oberwinkler & Bandoni.

**Genus accepted:** *Colacogloea* Oberwinkler & 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.

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 forilorum* (Ruinen) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813163. Basionym: *Candida forilorum* Ruinen, Antonie van Leeuwenhoek 29: 436. 1963.

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.

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, *Hamamotaea* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *Fellozyma* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

*Chrysozyma* 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 *Chrysosporiales* (*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. 61: 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 griseoflava* 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 inositophilia* (Nakase & M. Suzuki) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

**Species accepted:**

1) **Fellozyma inositophilia** (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.) Rozejmans 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 α-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. Ramirez) 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) van Arx & Weijman.
≡ *Candida bogoriensis* Deinema var. lipolytica Ruinen.
≡ *Vanrijia bogoriensis* (Deinema) Moore.

2) *Pseudohyphozyma buffonii* (C. Ramirez) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, comb. nov. MycoBank MB813191.

Basionym: *Torulopsis buffonii* C. Ramirez, Microbiol. 10: 236. 1957.
≡ *Rhodotorula buffonii* (C. Ramirez) 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) Rodri. 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 *Sloffia* (i.e. 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 *Sloffia* (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.

*Sampaiozyma* 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.

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, *Int. J. Syst. Bacteriol.* 28: 205. 1962.
   ≡ *Sporobolomyces tsugae* (Phaff & do Carmo-Sousa) Nakase & M. Itoh.

**Notes**: Species of *Slooffia* can be distinguished from those of *Pseudozyma* (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 hylaphila* (*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 *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 hylaphilus* (van der Walt, van der Klift & D.B. Scott) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout.

Species accepted:
1) *Trigonosporomyces hylaphilus* (van der Walt, van der Klift & D.B. Scott) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, *comb. nov*. MycoBank MB813208.
   *Basionym*: *Candida hylaphila* van der Walt et al., *Antonie van Leeuwenhoek* 37: 449. 1971.
   ≡ *Rhodotorula hylaphila* (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 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) Rodri. & Weijman.
   ≡ Candida auriculariae (Nakase) Meyer & Yarrow.
2) **Yunzhangia sonckii** (Hoppsu-Havu, Tunella & Yarrow) Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, **comb. nov.** MycoBank MB813212.
   **Basionym**: Candida sonckii Hoppsu-Havu et al., Antonie van Leeuwenhoek 44: 436. 1978.
   ≡ Rhodotorula sonckii (Hoppsu-Havu et al.) Rodri. & 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 fungal taxonomy.

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 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: *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.

**Mixiomyces** 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 ‘uncertain 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 utilizing 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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