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Taxogenomic reclassification of *Candida* and related genera in *Saccharomycotina*

Miao-Miao Liu[1#], Xue-Mei Zhao[1#], Jie Bai[1], Teun Boekhout[2], Andrey Yurkov [3], Gábor Péter[4], Konstanze Bensch[5], Fei Liu[1], Tian-Xiang Cui[1], Zi-Qian Liu[1], Yu-Jing Zhao[1], Yu-Xuan Zhang[1], Xiao-Hai Zhang[1], Jia-Hao Liu[1], Jia-Chen Wang[1], Hao-Ze Li[1], Feng-Yan Bai[6], Meredith Blackwell[7] and Qi-Ming Wang[1,8,9*]

[1]School of Life Sciences, Institute of Life Sciences and Green Development, Hebei University, Baoding 071002, Hebei, China; [2]The Yeasts Foundation, Amsterdam, the Netherlands; [3]Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures, Braunschweig, Germany; [4]National Collection of Agricultural and Industrial Microorganisms, Institute of Food Science and Technology, Hungarian University of Agriculture and Life Sciences, Somlói út 14-16, H-1118 Budapest, Hungary; [5]Westerdijk Institute of Fungal Biodiversity, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands; [6]State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China; [7]Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, and University of South Carolina, Columbia, SC 29208, USA; [8]Hebei Basic Science Center for Biotic Interaction, Hebei University, Baoding 071002, Hebei, China; [9]Engineering Research Center of Ecological Safety and Conservation in Beijing-Tianjin-Hebei (Xiong'an New Area) of MOE, Baoding, Hebei, China.

[#]These authors contributed equally to this work

***Corresponding authors:** wangqm@hbu.edu.cn (Q.-M. W.)

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Abstract

The genus *Candida* in the *Saccharomycotina* has long reflected the historical practice of yeast classification based on phenotypic characteristics, retaining remnants of dual nomenclature even after its abandonment in 2011. Following this shift, many *Candida* species were reclassified into existing or newly proposed genera; yet, *Candida* itself remained heterogeneous and phylogenetically divergent. This heterogeneity is also true for genera like *Ogataea*, *Starmerella*, and *Wickerhamomyces*. While this heterogeneity has been demonstrated in previous studies, including several recent proposals for new genera, the inclusion of reclassified *Candida* species in these genera will make them more phylogenetically diverse. Despite widespread recognition of the polyphyletic nature of *Candida*, confusion persists due to the continued use of this single generic name for species belonging to lineages distantly related to that of the generic type species, *Candida vulgaris*, a current synonym under *Candida tropicalis*. In this study, we aim to reduce the genetic heterogeneity of the genus *Candida* by (i) focusing on lineages distantly related to its nomenclature type and (ii) assessing the diversity and composition of genera into which former *Candida* species have been reassigned. Phylogenomic analyses were conducted to determine the positions of *Candida* species and several genomic metrics, including average amino acid identity (AAI), percentage of conserved proteins (POCP), and presence-absence patterns of orthologs (PAPO), in order to quantify genetic divergence in genera and clades, were calculated to assist the reclassification decisions as complementary approaches. In addition to phylogenomic analyses, comprehensive phylogenetic analyses using ITS and LSU D1/D2 rDNA sequence data were performed to include species that are not represented in the genome-scale analyses and to assist species recognition in future studies. This framework led to an updated classification of *Candida* species and related taxa, proposing 25 new genera to accommodate reclassified species and validating 4 genera, along with 175 new combinations and 87 newly recognized species.

Key words: 291 New taxa, Genome-based metrics, Phylogenomics, Yeasts

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Introduction

Similarly to many fungal groups, the present taxonomic classification of yeasts still bears the remnants of dual nomenclature and generic concepts that traditionally used a combination of physiological, biochemical and morphological characteristics. Before dual nomenclature was abandoned in 2011 (Hawksworth 2011), yeast genera were divided into two groups representing either sexual and asexual morphs that were referred to as teleomorphic and anamorphic genera, respectively. These two groups of genera were recognized because of differences in reproduction and were treated separately in the last two editions of the compendium *The Yeasts, a Taxonomic Study* (*TYTS*, Kurtzman & Fell 1998;

Kurtzman et al. 2011). Beyond this nomenclatural classification, it became clear that asexual and sexual species sometimes belong to the same phylogenetic clades in molecular phylogenetic analyses. With the development of molecular taxonomy and its use of DNA-based methods, the classification of yeasts experienced several events of splitting and lumping of genera (reviewed in Boekhout et al. 2021). Phylogenetic analyses using single-gene and later multigene approaches demonstrated that some traditionally delimited ascomycetous yeast genera, i.e., *Saccharomyces*, *Kluyveromyces*, *Pichia*, and *Candida*, were polyphyletic (Kurtzman & Robnett 1998, 2003). During the last two decades, Kurtzman and colleagues revised most of the teleomorphic ascomycetous yeasts and proposed various newly described genera based on multigene phylogenetic analyses (i.e., Kurtzman & Robnett 2003, 2007, 2010; Kurtzman et al. 2007, 2008; Kurtzman & Suzuki 2010). During this reclassification, the composition of several well-known genera changed following changes in generic concepts and methods for species delimitation. For example, most of the revised teleomorphic genera by Kurtzman (2003) in the *Saccharomycetaceae* can be recognized by phenotypic, phylogenetic and genomic features (Liu et al. 2024a).

The genus *Candida* is the largest anamorphic genus of yeasts and includes 314 species in the latest edition of the *TYTS* (Lachance et al. 2011). The genus *Candida* was introduced a century ago by C.M. Berkhout (1923) to include asexually reproducing yeasts that form hyphae that may disarticulate and form blastoconidia (or yeast cells) by budding from either hyphae or from other blastoconidia. *Candida vulgaris*, currently a taxonomic synonym of *C. tropicalis* (Lachance et al. 2011), was selected by Berkhout as the generic type. Many molecular phylogenetic studies demonstrated that the genus *Candida* is polyphyletic and consists of 11 to 15 clades spread over large parts of the subphylum *Saccharomycotina* (Kurtzman & Robnett 1998, 2003; Lachance et al. 2011; Daniel et al. 2014; Takashima & Sugita 2022). Daniel et al. (2014) indicated that the taxonomy of the genus *Candida,* as well as other yeast genera including asexually reproducing species, needs to be revised to make generic demarcations and membership consistent with their phylogenetic affinities. Following the 'One fungus = One name' principle and using results from many molecular phylogenetic sequence analyses, especially those based on multigene-based datasets, approximately half of the *Candida* species have already been placed into more than 36 existing genera and 14 newly proposed genera (e.g., Kurtzman 2016; Kurtzman et al. 2016; de Vega et al. 2017; Santos et al. 2018; Takashima & Sugita 2022; Liu et al. 2024b). Despite these efforts, the polyphyletic nature of the genus *Candida* has not been fully resolved, as the phylogenetic positions of many species remain unclear. This is particularly true for under-sampled lineages that occupy basal positions or those that are loosely placed in clades that received weak support (Daniel et al. 2014; Takashima & Sugita 2022). Although the recognition of new monotypic genera is criticized by some members of the yeast taxonomy community (e.g., Lachance 2018), monotypic genera (and higher ranks) are not rare in fungi with yeast states, e.g., see the genera *Aciculiconidium*, *Babjeviella*, *Cyrenella* and *Kriegeria* (Kurtzman 2011b; Sampaio 2011; Sampaio & Oberwinkler 2011; Smith 2011). Furthermore, Takashima & Sugita (2022) argued that the proposal of monotypic genera might be useful because it reduces the polyphyletic nature of the genera in which the species concerned have been classified before. Whether monotypic lineages are the result of conserved evolution or insufficient sampling is another valid point for discussion. In several instances, new species belonging to these initially monotypic genera have been described shortly after the genus was firstly established. For example, this was true for several originally monotypic genera described within the last decade, *Babjevia*, *Deakozyma*, *Nematodospora* and *Yueomyces* (Gouliamova et al. 2016; Ren et al. 2016; Zheng et al. 2017; Yamazaki et al. 2020; Yu et al. 2023). While it may still be difficult to decide on whether to introduce new monotypic yeast genera, genome-based statistics can help to objectivate decisions on generic demarcations in the absence of other criteria (Liu et al. 2024a, b). Particularly, the three genomic metrics, average amino acid identity (AAI), percentage of conserved proteins (POCP) and presence-absence patterns of orthologs (PAPO), have been tested for their utility in *Saccharomycetaceae* and *Metschnikowiaceae* using genera that were traditionally recognized based on their morphology (including sexual morphs) and physiological traits (Liu et al. 2024a, b). These studies showed that genera delimited using the approach combining sexual reproduction, physiology and multi-gene phylogenies in these two families exhibited a range of 80–92% POCP values and a range of 60–70% AAI values.

In the present study, we generated a robust genome-scale phylogeny, together with the LSU rDNA gene and combined ITS+LSU-based datasets in order to include all *Candida* species for which no genome data were available. We explored the heterogeneity of currently recognized yeast genera using the same genome metrics, i.e., AAI, POCP and PAPO, as used previously in the studies of Liu et al. (2024a, b), adopted some RED values calculated by Li et al. (2021), and evaluated phenotypic data to resolve the classification of the highly heterogeneous genus *Candida.* Here, we propose an updated taxonomy of *Candida* and related genera in the *Saccharomycotina*, including 175 new combinations, 87 new species, mainly validations of previously invalidly published names including 4 generic names, and 25 new genera.

Materials and methods

Genome assembly and annotation

The nuclear DNA of some yeast strains, i.e., *Candida* sp. XZY480-2, *Candida* sp. gmt3-3-4, *Candida* sp. XZY238F3 was extracted in this study using the method previously described by Wang & Bai (2008) (Table S1). Genomic libraries with 150 bp paired-end reads were constructed using the TruSeq Nano DNA library prep kit (Illumina) according to the manufacturer's instructions and sequenced on an Illumina HiSeq 2000 platform with the TruSeq SBS Kit (Illumina). Low-quality and adapter sequences were removed using Fastp v0.20.1 with default settings (Chen et al. 2018). The genome assembly was performed using SPAdes v3.15.0 (Bankevich et al. 2012) with parameters set to "--memory 800 -k 21,33,55,77,99 --careful --cov-cutoff auto". Gene prediction was carried out using GeneMark-ES (Ter-Hovhannisyan et al. 2008).

Genome quality assessment

We evaluated the quality of genome assemblies using the Benchmarking Universal Single-Copy Orthologs (BUSCO) v5.3.2 (Manni et al. 2021) and the Fungi odb10 database v4. The proportion of single-copy BUSCO genes in each genome indicates its completeness. To reduce missing data and exclude potentially low-quality genomes, we only included genomes with > 40% complete BUSCO genes.

Phylogenomic analysis and comparative genomics

To determine the evolutionary relationships of species classified in the genus *Candida* and related genera in *Saccharomycotina*, we analyzed single-copy orthologs from 906 genomes as listed in Table S1. Four genome datasets, namely, the *Dipodascomycetes*_dataset, the *Phaffomycetales*_dataset, the *Pichiales*_dataset and the *Serinales*_dataset, were used to construct phylogenomic trees. To preserve as much genomic information as possible, we selected 526 single-copy genes for the *Dipodascomycetes*_dataset, 652 for the *Phaffomycetales*_dataset, 545 for the *Pichiales*_dataset, and 583 for the *Serinales*_dataset, respectively, each of which has more than 95% of each genome dataset occupancy. For strains with a high duplicated BUSCOs rate, we first used the EMBOSS water alignment software (Madeira et al. 2019; Li et al. 2020) to perform intra-copy comparisons for each multicopy gene to select one copy from genes with an identity greater than 95%. This step was used to reduce the bias of our random selection. These orthologues were then aligned using MAFFT v7.475 with the G-INS-i option (Katoh & Standley 2013), concatenated using Perl scripts available at (https://github.com/Liufei0823/Single_Copy_Orthologue/), and a maximum likelihood (ML) gene tree was generated with IQ-TREE 2 (Minh et al. 2020), employing the MFP model and performing 1000 ultrafast bootstrap repeats (-m MFP -B 1000 -redo -mredo -nt AUTO). The alignments were deposited in TreeBASE (www.treebase.org, No. 31986).

Calculation of AAI value

We evaluated the amino acid identity (AAI) of species of *Candida* and related genera or clades utilizing the CompareM (available at https://github.com/dparks1134/CompareM) v0.1.2 software and applied the default settings as used before (Liu et al. 2024a, b).

Calculation of Presence-absence patterns of orthologs (PAPO)

Orthologous Groups (OGs) were determined by clustering all proteins with OrthoFinder v2.5.4 (Emms & Kelly 2019). The method by Takashima et al. (2019) was used to create presence-absence patterns of orthologs (PAPO). Based on the OrthoFinder results, OGs that were absent were labeled as 0, while those that were present were labeled as 1. Core proteins were defined as OGs that existed in a clade, pan proteins were OGs found in at least one strain of a clade, and unique proteins were OGs found in all strains of a clade but not in any other clades (Liu et al. 2024a, b).

Calculation of the percentage of conserved proteins (POCP) value

Following the method outlined by Qin et al. (2014), we determined the percentage of conserved proteins (POCP) between two strains. We utilized BLASTp (Tatusova & Madden 1999) to compare the proteins of both strains and identified conserved proteins based on criteria such as identity greater than 40%, aligned length of at least 50%, and an e-value of less than 1×10^{-5}. The POCP was then calculated as the ratio of conserved proteins in the two proteomes (Liu et al. 2024a, b).

The impact of horizontal transfer genes (HTGs) and reductive evolution on the AAI and POCP analyses

To evaluate the impact of HTGs on the AAI and POCP analyses, the suspected HTGs in the genus *Starmerella* were identified using a pipeline adapted from Nowell et al. (2018). The protein sequences were aligned against the UniRef90 database using DIAMOND (Buchfink et al. 2021) with an e-value threshold of $1e^{-5}$, retaining the top 500 hits per query. Alignment results were processed using the diamond_to_HGT_candidates.pl script, which employs a Lowest Common Ancestor (LCA) algorithm. Genes meeting both of the following criteria were designated as horizontal gene transfer (HGT) candidates: 1) HGT Index (hU) ≥ 50: computed as the difference in bitscores between the best outgroup match (e.g., bacteria or plants) and the best ingroup match (fungi); 2) consensus Hit Support (CHS) ≥ 95%: defined as the percentage of all supporting hits consistent with the outgroup classification [(Number of outgroup-supporting hits/total hits) × 100%]. The HGT candidates were removed from the protein sequence files using SeqKit v0.10.0 (Shen et al. 2024). The AAI and POCP values were then calculated using the filtered protein files. Scatter plots were then constructed using the ggplot2 package (Wickham 2016) in R (R Core Team 2025) to visually illustrate the distribution trends of AAI (or POCP) values before and after the removal of HGT candidates. The horizontal axis represented AAI (or POCP) values between any pairwise combination of species calculated based on all proteins (with HTGs retained), while the vertical axis represented AAI (or POCP) values for the corresponding species pairs calculated after removal of HGT candidates. A linear regression model was fitted to the two datasets using the ggpmisc package (Aphalo 2025) in R, and the slopes of the linear regression equations, as well as the coefficients of determination (R^2), were calculated. Wherein, the R^2 value ranges between 0 and 1, and is used to evaluate the goodness of fit of the linear regression model to the data: the closer R^2 is to 1, the better the model's fitting effect (Draper & Smith 1998). If the slope of the linear regression equation was close to 1 and the R^2 value was high, it indicated high consistency in AAI (or POCP) values for any pair of species before and after removal of HTGs, implying that HTGs had no significant interference on AAI (or POCP) analysis. Conversely, a slope noticeably deviating from 1 or a low R^2 value suggested that HTGs might affect the results of AAI (or POCP) analysis.

The BUSCO analysis showed that *Starmerella* had a higher rate of missing BUSCOs, ranging from 13.5% to 34.1% (Table S1), which indicates that *Starmerella* undergoes reductive evolution, which is in agreement with the results from Gonçalves et al. (2020, 2022) and Pontes et al. (2024). To evaluate the impact of reductive evolution on the AAI and POCP analysis, the orthologous groups (OGs) occurring in ≥

95% and ≥ 90% species of *Starmerella* were extracted using SeqKit v0.10.0, respectively, and assigned to two datasets, namely the *Starmerella*_95_dataset and *Starmerella*_90_dataset, which were used to calculate the AAI and POCP values. Two sets of data were then used to generate scatter plots using the ggplot2 package in R: 1) AAI values (serving as the horizontal axis) between any pairwise species calculated based on all proteins, and 2) AAI values (serving as the vertical axis) for the corresponding species pairs calculated based on *Starmerella*_90_dataset or *Starmerella*_95_dataset. Linear regression analyses were performed using the ggpmisc package in R to assess the similarity between these sets of data, determining whether reductive evolution affects AAI analysis. The same approach was applied to evaluate the impact of reductive evolution on POCP analysis using the ggpmisc and ggplot2 packages in R.

The impact of introgressions, hybridization and alloaneuploidy on the AAI and POCP analyses

To assess the impact of hybridization (or alloaneuploidy) on the AAI and POCP analyses, the *Dipodascus/Galactomyces/Geotrichum* lineage was used as an example in this study. Three distinct datasets with/without duplicated genes were constructed: 1) All_genome_dataset includes all proteins (genes) for each species of *Dipodascus/Galactomyces/Geotrichum* lineage; 2) Subgenome_1_dataset contains orthologous groups (OGs) without paralogous genes; 3) Subgenome_2_dataset is composed of OGs without paralogous genes and one copy of paralogous genes that was randomly selected from the paralog-containing OGs. All conserved proteins of species in the *Dipodascus/Galactomyces/Geotrichum* lineage were extracted with SeqKit v.0.10.0. The pairwise AAI and POCP values between species were then calculated based on these three datasets. Then, scatter plots were generated and linear regression analyses were performed to determine whether hybridization (or alloaneuploidy) affected the results of the AAI analysis. Wherein, the horizontal axis represented AAI values between any pairwise species calculated based on the All_genome_dataset, while the vertical axis represented AAI values for the corresponding species pairs calculated based on Subgenome_1_dataset or Subgenome_2_dataset. Following the same approach, the impact of hybridization (or alloaneuploidy) on POCP analysis was assessed.

Currently, phylogenetic evidence indicates that *Saccharomyces cerevisiae* DBVPG 6765 carries a large amount of introgressed material (D'Angiolo et al. 2020). *Saccharomyces pastorianus* has been identified as an interspecies hybrid between *S. cerevisiae* and *Saccharomyces eubayanus* (Monerawela & Bond 2018). Similarly, *Saccharomyces bayanus* has been identified as a hybrid derivative of *Saccharomyces uvarum* and *S. eubayanus* (Pérez-Través et al. 2014). *Saccharomyces cerevisiae* × *Saccharomyces kudriavzevii* strains have been isolated from beer fermentation environments (Peris et al. 2012). Therefore, we used *Saccharomyces* as an example to address the reliability of AAI and POCO analyses affected by introgressions and hybridization (or alloaneuploidy). Three genome datasets were generated: 1) *Saccharomyces*_9_dataset includes only nine natural species, namely *Saccharomyces arboricola*, *S. cerevisiae*, *Saccharomyces chiloensis*, *S. eubayanus*, *Saccharomyces jurei*, *S. kudriavzevii*, *Saccharomyces mikatae*, *Saccharomyces paradoxus* and *S. uvarum*; 2) *Saccharomyces*_10_dataset is composed of nine natural species and *S. cerevisiae* DBVPG 6765 with introgression; 3) *Saccharomyces*_12_dataset contains nine natural species and three hybrid species (or strains), namely *S. bayanus*, *S. pastorianus* and *S. cerevisiae* × *S. kudriavzevii*. The AAI and POCP analyses were conducted separately for each dataset.

Genome-wide analysis of multidrug resistance in the revised *Candida* species

To evaluate the antifungal resistance profiles of *Candida* species assigned to the newly created genera in this study, we retrieved known antifungal resistance-associated genes of *C. albicans* from NCBI, including: 1) the *ERG11* gene (with mutation sites F126L, Y132F, K143R, F145L, G448E, F449V, G450E, and G464S) associated with azole resistance; 2) the *ERG2* gene (with mutation site F105SfsX23) associated with polyene resistance; 3) the *FKS1* gene (with mutation sites S645P/Y/F and F641Y) associated with echinocandin resistance; 4) the *FUR1* gene (with mutation site F211I) associated with nucleoside analog resistance (Katiyar et al. 2006; Jensen et al. 2015; Wu & Ying 2016). The blastdb tool within the BLAST software was then used to construct a non-redundant (NR) database for these antifungal resistance-associated gene sequences. The software Blastp v2.11.0+ (Camacho et al. 2009) was used to perform sequence alignment between the protein sequence files of the studied strains and the previously constructed NR database, as well as the extraction of homologous antifungal resistance-associated gene sequences to obtain the corresponding gene sequences of *Candida* species in the newly created genera. Subsequently, we used Mafft v7.475 (Katoh & Standley 2013) to conduct sequence alignment on all the obtained homologous genes. The alignment results were analyzed to identify the similarities and differences in antifungal resistance-associated genes between resistant and susceptible strains.

Ribosomal DNA (rDNA) phylogenetic analysis

The DNA sequences of ITS (including 5.8S) and LSU D1/D2 domains of ribosomal DNA (rDNA) (Table S2) were acquired from NCBI and aligned using the MAFFT G-INS-i program (Katoh & Standley 2013). A Maximum Likelihood (ML) tree was constructed using RAxML v8.2.12 (Stamatakis 2014) with the GRT+I+G model. The reliability of the phylogenetic branches was determined through 1,000 bootstrap analyses (Felsenstein 1985).

Generic delineation

Takashima et al. (2019) proposed the PAPO analysis to delineate genera for basidiomycetous yeasts in the *Trichosporonales*. Recently, a range of 80–92% POCP values and a range of 60–70% AAI values were recommended as indicative values to delimitate genera in *Saccharomycetaceae* (Liu et al. 2024a), which were also used in the reclassification of *Candida* species in *Metschnikowiaceae* (Liu et al. 2024b). The RED approach has been applied to yeasts and fungal taxonomy (Li et al. 2021;

Groenewald et al. 2023). The RED ± 0.1 intervals have been calculated for different taxonomic levels, i.e., 0.29 ± 0.1 for phylum, 0.695 ± 0.1 for class, 0.79 ± 0.1 for order, 0.889 ± 0.1 for family, 0.96 ± 0.1 for genus. Notably, all clades are assigned in this study based on the combined analyses of the AAI, POCP, PAPO approaches, and the RED index was used if RED values were available.

Results and discussion

Genome-scale and rDNA phylogenetic analyses

Candida vulgaris, the type species of the genus *Candida,* and currently interpreted as a synonym under *C. tropicalis* (Lachance et al. 2011), is phylogenetically placed in the class *Pichiomycetes*, order *Serinales*, family *Debaryomycetaceae* (Groenewald et al. 2023). Although the heterogenic and polyphyletic features of the genus *Candida* have been reduced by several molecular phylogenetic studies and recent taxonomic reclassifications (e.g., Kurtzman 2016; Kurtzman et al. 2016; de Vega et al. 2017; Santos et al. 2018; Takashima & Sugita 2022; Avesani et al. 2024, Liu et al. 2024b), this genus still includes 189 species scattered across *Saccharomycotina* (Table S2) with 10, 148 and 31 species belonging to *Dipodascomycetes*, *Pichiomycetes* and *Saccharomycetes*, respectively. To provide a well-supported placement of these species in relation to already described genera, 157 genomes of *Candida* species and 749 genomes of the related species in the *Dipodascomycetes*, *Pichiomycetes* and *Saccharomycetes* were used to generate phylogenomic trees (Figs. 1, 6, 9, 12, 14–15, 17 and Figs. S1–S4) and run three genome-based metrics analyses, i.e., AAI, POCP and PAPO analyses (Table 1). Although most *Candida* species have been included in the genome-scale analyses, for about 35 *Candida* species no genome sequences are available yet. To obtain a reliable placement of these latter yeast species, a phylogenetic analysis of nucleotide sequences representing LSU rDNA (D1/D2 domains) and ITS was carried out using all described *Candida* species published before December 2024, as well as some yet undescribed taxa (Figs. 2–5, 7–8, 10–11, 13, 16, 18 and Figs. S5–S13). In the next sections, we provide a comprehensive analysis of the phylogenomics data and genome statistics of 906 strains, and the phylogenetic trees based on rDNA data of 840 yeast species.

Candida species in the *Dipodascomycetes*

Ten *Candida* species were placed in the *Dipodascomycetes* (Fig. 1, Table S1 and S2). These species are phylogenetically distant from the core of the genus *Candida*, they belong to a different class, namely *Dipodascomycetes* rather than *Pichiomycetes*. Thus, there is no objective reason to classify these yeasts in the genus *Candida*. Our phylogenomic analysis showed that eight *Candida* species were located in the *Trichomonascaceae* (*Dipodascales*), where the other *Candida* species were placed as *incertae sedis* in the *Dipodascomycetes* (Fig. 1, Table S1 and S2).

Candida species and related genera *Deakozyma* and *Limtongella* (*Trichomonascaceae*, *Dipodascales*, *Dipodascomycetes*)

Our analyses showed that *Candida bentonensis*, *Candida incommunis* and *Deakozyma indianensis* were placed within the *Deakozyma* lineage (Fig. 1). Recently, the new genus *Limtongella* was proposed by Sakpuntoon et al. (2020) for *Limtongella siamensis*, which was found to be closely related to *D. indianensis* and *C. incommunis*. However, unfortunately, *C. bentonensis* was not included in the multigene phylogenetic analysis made by Sakpuntoon et al. (2020). Our phylogenetic analysis showed that *D. indianensis* and *Deakozyma yunnanensis* (Zheng et al. 2017) formed a well-supported clade in the ITS+D1/D2 tree (Fig. 2). The genus *Limtongella* and *C. incommunis* clustered together with 91% bootstrap support, while *C. bentonensis* formed a separate and long branch, clearly distinct from both *Deakozyma* and *Limtongella* (Fig. 2). These findings suggest that *C. incommunis* belongs to the genus *Limtongella*, whereas *C. bentonensis* represents another genus. To accommodate *C. bentonensis*, we propose the erection of a new genus, named *Grinbergsozyma gen. nov.* (Fig. 2, Table S2). The D1/D2 LSU rDNA phylogenetic analysis revealed that the newly identified *C. bentonensis* lineage (*Grinbergsozyma gen. nov.*) contains at least three potential new species isolated from various substrates, including the flux of *Quercus rubra* in Canada, the flux of *Quercus oleoides* in Costa Rica, as well as soil and rotting wood in Brazil (Fig. S5, Table S2), all of which differ from *C. bentonensis* by 2.16–15% in the D1/D2 domains. Additionally, the genus *Limtongella* includes three potential new species labelled in GenBank as *Candida* cf. *incommunis* UWO(PS)01-669.2 (GenBank AF530616) isolated from the flux of *Hymenaea courbaril* in Costa Rica, *Candida* sp. YWW5-1 (GenBank LC387304) isolated from mangrove forests in Thailand, and *Candida* sp. DMKU-FW29-11 (GenBank OL679539) obtained from food waste in Thailand (Fig. S5, Table S2).

Candida species and related genera *Diddensiella* and *Sugiyamaella* (*Trichomonascaceae*, *Dipodascales*, *Dipodascomycetes*)

Sylvester et al. (2015) described *Candida sungouii* and concluded that this species did not belong to any known genus, but indicated its affinity to the genera *Diddensiella* and *Sugiyamaella* in *Trichomonascaceae*. The same authors also indicated close relationships of *C. sungouii* with two potential new species labelled as *Candida* sp. BG02-5-30-009A-1 (GenBank AY520421) and *Candida* sp. BG02-7-18-018A-2-2 (GenBank AY520408), both isolated from basidiocarp-feeding beetles (Suh et al. 2005). Our ITS+D1/D2 LSU phylogenetic analysis showed that *C. sungouii* clustered with *Diddensiella* and *Spencermartinsiella* with low bootstrap support (Fig. 3). *Candida* sp. BG02-7-18-018A-2-2 (GenBank AY520408) isolated from the gut of a tenebrionid beetle in the USA showed a 4.3% D1/D2 sequence difference from the sequence of *C. sungouii*, thus suggesting that strain BG02-7-18-018A-2-2 likely represents a new member, closely related to *C. sungouii*, of this putative new genus (Fig. S6). Hence, we propose a new genus, *Westerdijkia gen. nov.*, to accommodate *C. sungouii* and *Candida* sp. BG02-7-18-018A-2-2 (Fig. 3, Fig. S6, Table S2).

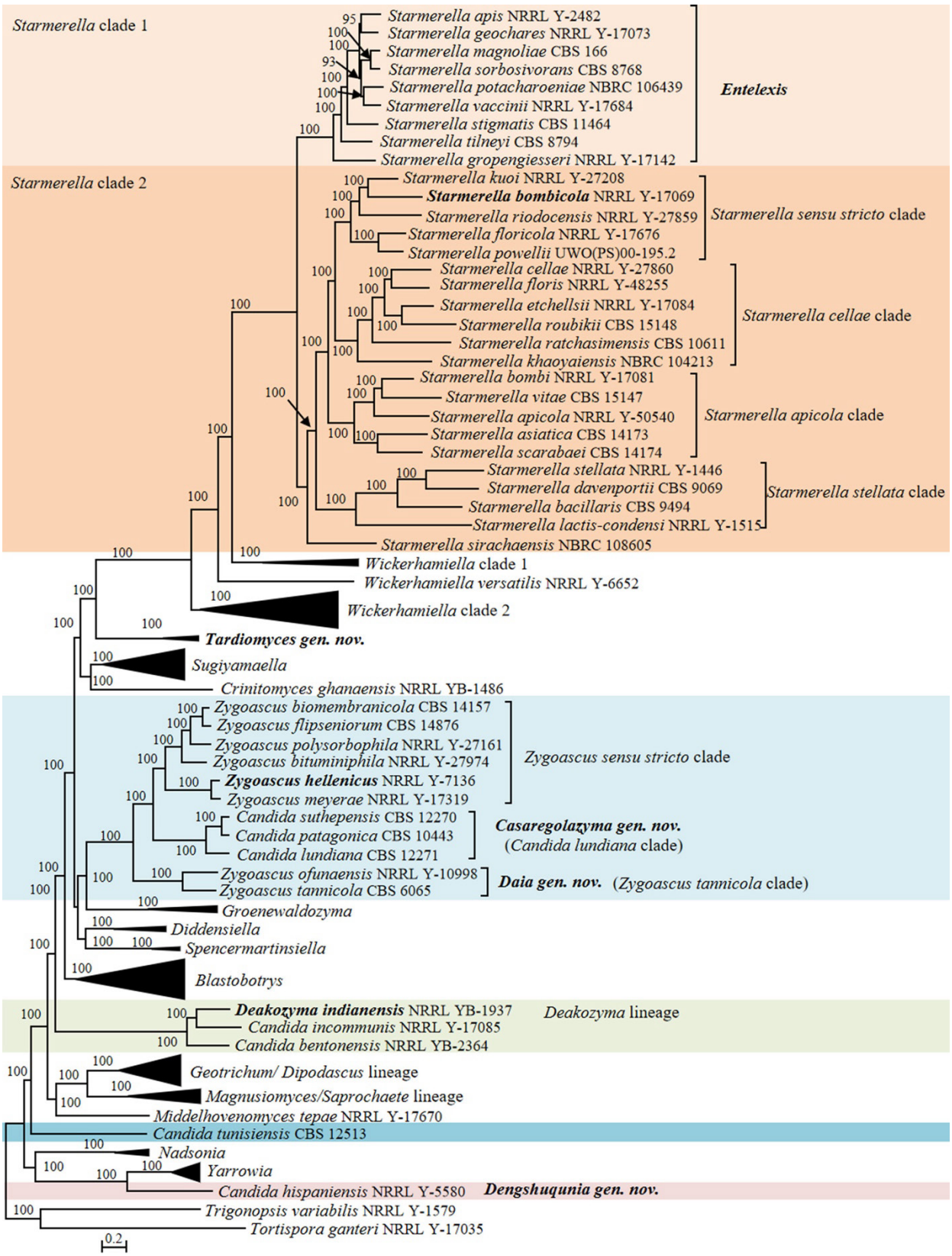

Fig. 1. Phylogenomic tree inferred using 526 single-copy orthologue proteins showing the phylogenetic relationships between *Candida* and related taxa in *Dipodascomycetes*. Bootstrap percentages of maximum likelihood analysis from 1,000 bootstrap replicates are shown on the major branches. *Trigonopsis variabilis* and *Tortispora ganteri* were used as outgroups. Bar = 0.2 substitutions per nucleotide position.

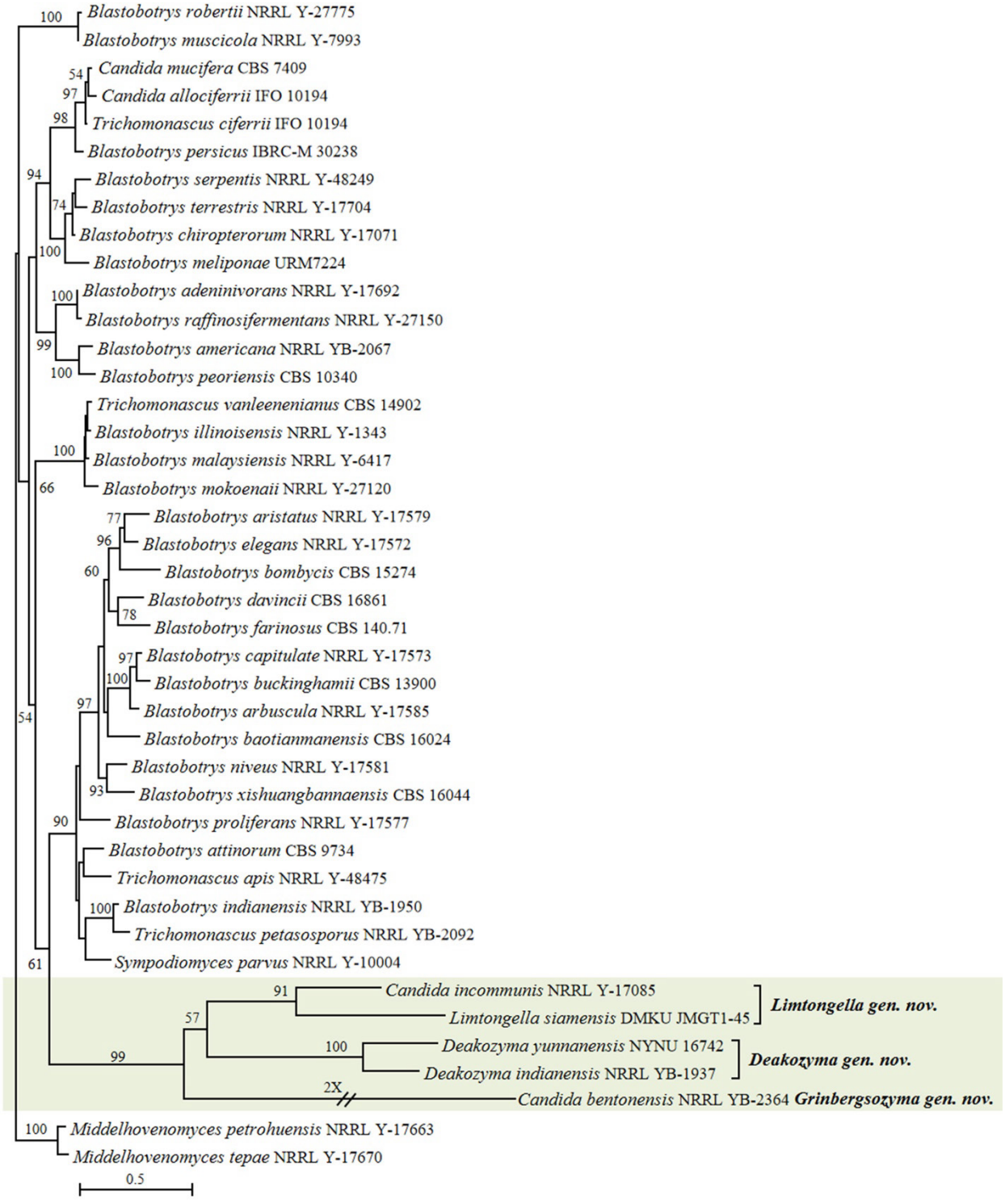

Fig. 2. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida bentonensis*, *Candida incommunis*, *Deakozyma* and *Limtongella*. Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Middelhovenomyces petrohuensis* and *Middelhovenomyces tepae* were used as outgroups. Bar = 0.5 substitutions per nucleotide position.

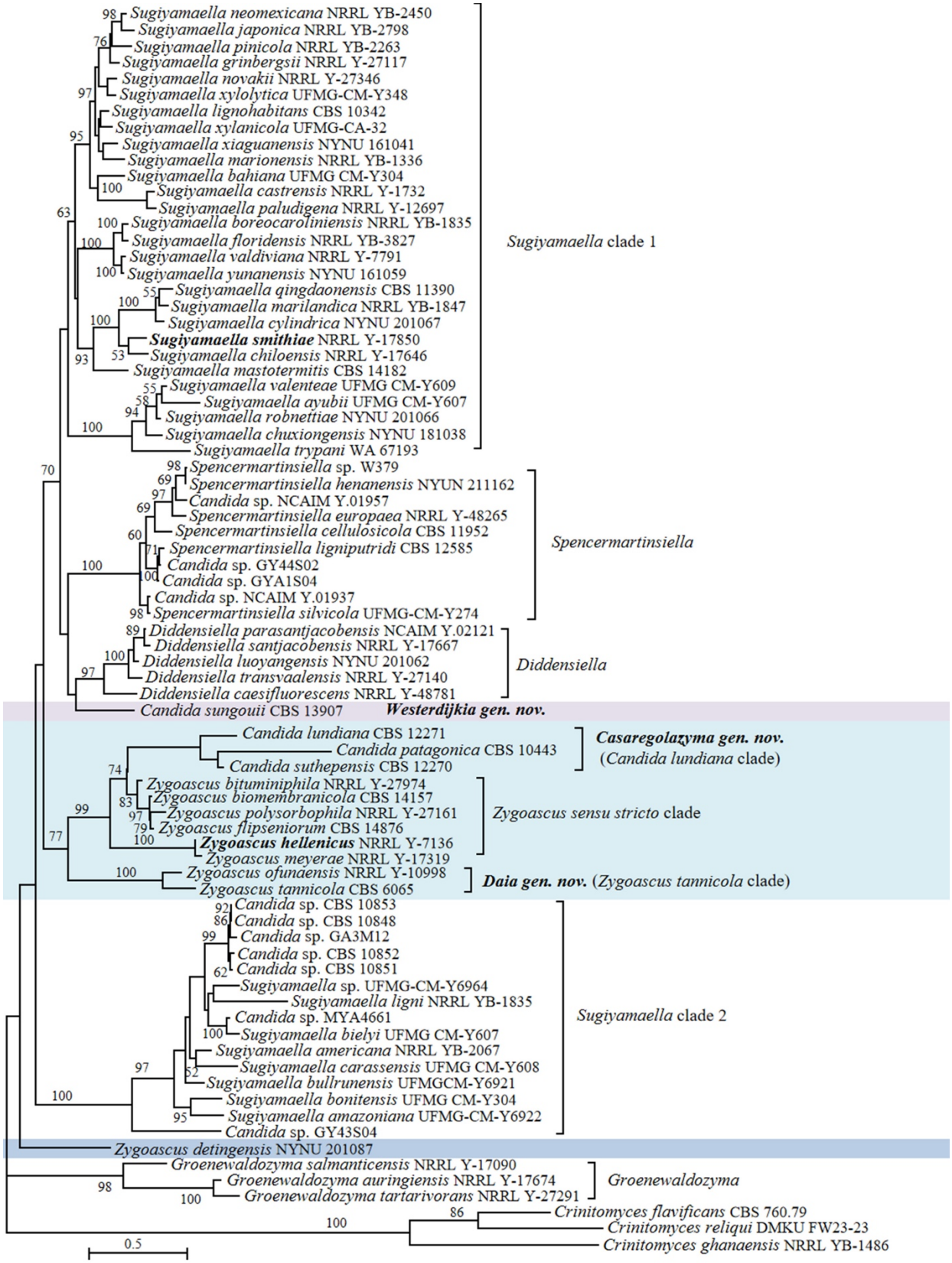

Fig. 3. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida* species and related genera in the *Trichomonascaceae*. Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Crinitomyces* species were used as outgroups. Bar = 0.5 substitutions per nucleotide position.

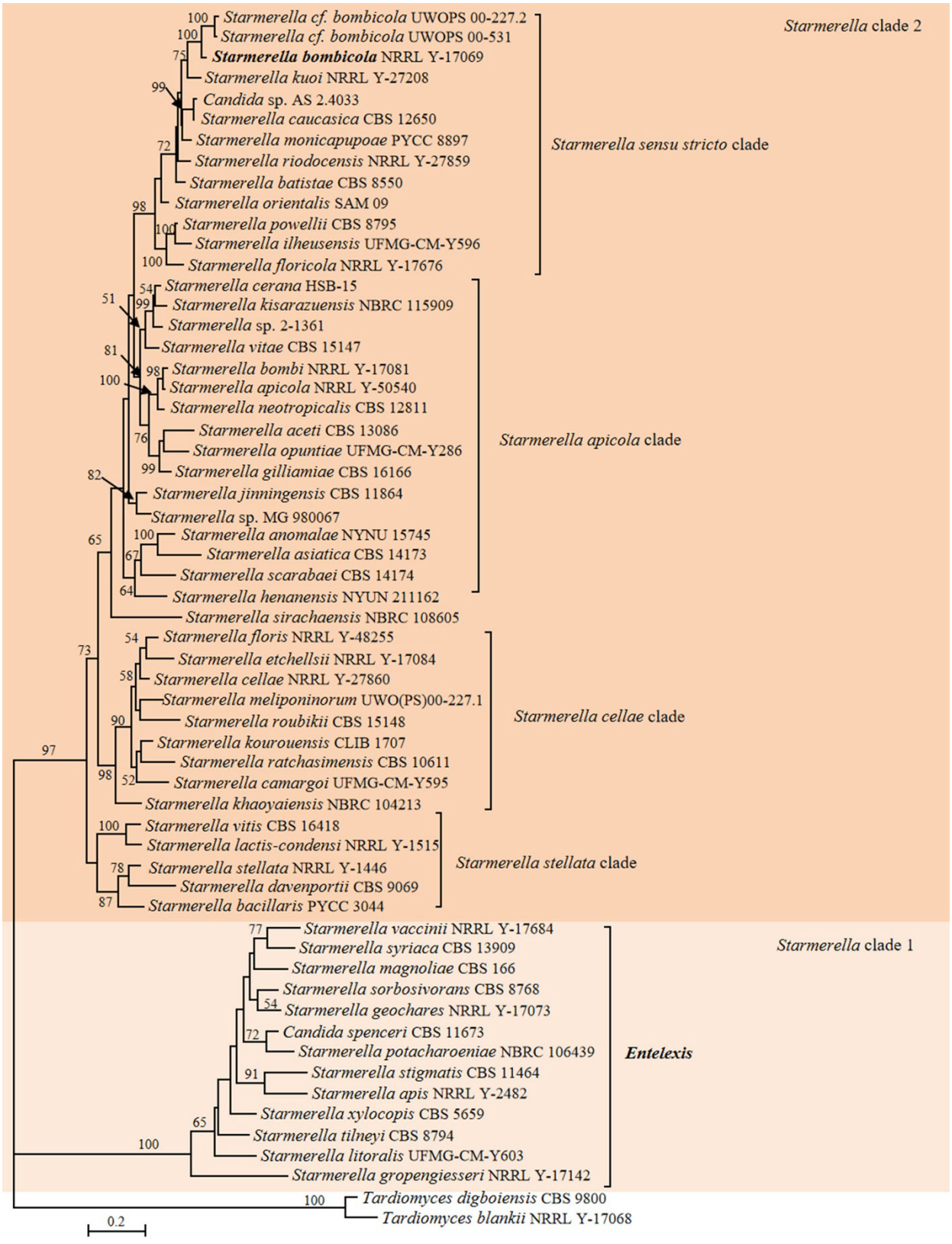

Fig. 4. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida spenceri* and *Starmerella*. Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Tardiomyces digboiensis* and *Tardiomyces blankii* were used as outgroups. Bar = 0.2 substitutions per nucleotide position.

Candida species and related genus *Starmerella* (*Trichomonascaceae*, *Dipodascales*, *Dipodascomycetes*)

Candida spenceri is phylogenetically related to the genus *Starmerella* (Daniel et al. 2014). *Starmerella* was introduced by Rosa & Lachance (1998) with a single species, namely *Starmerella bombicola*. Later, a second species, *Starmerella meliponinorum,* was described by Teixeira et al. (2003). Based on a rDNA phylogenetic analysis, Lachance et al. (2011) demonstrated that various *Candida* species were phylogenetically related to the *Starmerella* lineage and these formed two separate groups. Daniel et al. (2014) argued that there was insufficient support to justify splitting the genus *Starmerella* into two different genera at that time. Subsequently, Santos et al. (2018) transferred 25 related *Candida* species into *Starmerella* based on a D1/D2 LSU rDNA sequence analysis. More recently, Sipiczki & Baghela (2025) proposed a new species *Starmerella aleppica* in the *sensu stricto* subclade (referred to as *Starmerella* clade 2 in this study) and argued that the *sensu lato* subclade (referred to as *Starmerella* clade 1 in this study) and the *Starmerella sensu stricto* subclade may represent two genera. This hypothesis was based on the ITS+D1/D2 LSU rDNA sequence analysis, as well as taxon-specific markers or signatures (InDel markers) in the D1/D2 and ITS regions (Sipiczki & Baghela 2025).

In agreement with the above studies and a recent phylogenomic study (Opulente et al. 2024), our phylogenomic analysis revealed a well-supported bifurcation within *Starmerella*. Specifically, the *Starmerella* clade 1 (previously referred to as the *Candida magnoliae* subclade by Daniel et al.) diverges from the other species within the genus (Fig. 1).

The genus *Starmerella* appears to be heterogeneous based on our analyses using genomic metrics. *Starmerella* exhibited a lower than expected range of both, AAI values (55.13–88.10%) and POCP values (49.07–93.24%) (Table 1). The RED value estimated for *Starmerella* by Li et al. (2021) was 0.91, suggesting that this genus may represent a family-level taxon (family RED interval 0.889 ± 0.1). Considering the taxonomic heterogeneity suggested above, we calculated the genome metrics of *Starmerella* clade 1. According to our results (AAI: 71.55–88.10%; POCP: 80.33–93.54%; PAPO: 19), the values fell within the range observed for genera in *Saccharomycetaceae* (Liu et al. 2024a), suggesting that this clade would represent a taxonomic unit at the genus level with genomic heterogeneity within the expected range. However, genomic indices of the *Starmerella* clade 2 (AAI: 55.13–76.61%; POCP: 49.07–91.12%; PAPO: 0) indicated this clade remained too genetically heterogeneous when compared to the *Starmerella* clade 1. Our phylogenomic analysis identified four distinct clades within *Starmerella* clade 2 (Fig. 1). Genomic metrics were applied to assess the genetic heterogeneity within these smaller clades: *Starmerella sensu stricto* clade (AAI: 65.96–76.61%; POCP: 78.62–91.12%; PAPO: 3), the *Starmerella apicola* clade (AAI: 62.44–69.07%; POCP: 77.02–85.86%; PAPO: 4), the *Starmerella cellae* clade (61.78–70.71%; POCP: 60.03–85.26%; PAPO: 1), the *Starmerella stellata* clade (AAI: 58.08–68.13%; POCP: 60.00–78.43%; PAPO: 2), and the single-species lineage *Starmerella sirachaensis* (Fig. 1).

The genus *Entelexis* was proposed to accommodate the perfect state of *Torulopsis magnoliae* by van der Walt & Johannsen (1973). Yarrow & Meyer (1978) amended the genus *Candida* to include non-hyphal species and transferred *Torulopsis* species into *Candida*, consequently, *T. magnoliae* was assigned to *Candida* as a new combination. Later, Santos et al. (2018) transferred *C. magnoliae* (as known as *T. magnoliae*) to the genus *Starmerella.* The type of *Entelexis magnoliae* CBS 2798 (AY521568) differed from the type of *C. magnoliae* (also known as *T. magnoliae* and *Starmerella magnoliae*) CBS 166 (NG_060814) by 31 nucleotides in the D1/D2 domains of LSU rDNA, which indicated that *E. magnoliae* and *C. magnoliae* belong to different species. Our D1/D2 sequence analysis showed that both *E. magnoliae* and *C. magnoliae* were located in the *Starmerella* clade 1 (Fig. S7). Considering the results of phylogenomic analyses (Fig. 1 in this study, Opulente et al. 2024) and the arguments provided by Sipiczki & Baghela (2025), we propose the reclassification of *Candida spenceri* and the species within the *Starmerella* clade 1 (Fig. 4) into *Entelexis.* Moreover, a new name will be proposed in the Taxonomy section for *C. magnoliae* to avoid the synonymy of those two species. Although our genome-based metric analyses showed that *Starmerella* clade 2 is heterogeneous (Table 1), its reclassification will be addressed in the future after consultation with relevant yeast taxonomy experts.

Table 1 List of the AAI, POCP and PAPO values of genera (clades) and lineages used in this study

Taxa	AAI (%)	POCP (%)	PAPO
Dipodascomycetes			
Crinitomyces	N/A	N/A	446
Diddensiella	65.80–74.65	83.30–90.99	38
Groenewaldozyma	62.14–74.45	73.70–90.00	111
Nadsonia	67.44–91.67	81.87–93.64	197
Spencermartinsiella	74.34–74.34	89.58–89.58	109
Starmerella	55.13–88.10	49.07–93.24	2
Starmerella clade 1	71.55–88.10	80.33–93.24	19
Starmerella clade 2	55.13–76.61	49.07–91.12	0
Starmerella sensu stricto clade	65.96–76.61	78.62–91.12	3

Taxa	AAI (%)	POCP (%)	PAPO
Starmerella apicola clade	62.44–69.07	77.02–85.86	4
Starmerella cellae clade	61.78–70.71	60.03–85.26	1
Starmerella stellata clade	58.08–68.13	60.00–78.43	2
Starmerella sensu stricto clade+*Starmerella cellae* clade	60.16–76.61	60.03–91.12	0
Starmerella apicola clade+*Starmerella sensu stricto* clade+*Starmerella cellae* clade	58.62–76.61	60.03–91.12	1
Starmerella sirachaensis single–species lineage	N/A	N/A	122
Sugiyamaella	61.27–89.30	65.88–97.11	1
Tardiomyces	70.92–84.63	88.82–95.14	134
Zygoascus lineage	59.76–88.95	71.75–98.27	6
Zygoascus sensu stricto clade	67.17–88.95	87.31–98.27	21
Candida lundiana clade	77.81–89.01	88.85–95.34	74
Zygoascus tannicola clade	70.14–70.14	90.94–90.94	67
Zygoascus sensu stricto clade+*Candida lundiana* clade	61.98–89.01	74.47–98.27	9
Candida tunisiensis single–species lineage	N/A	N/A	382
Yarrowia	74.08–93.66	83.66–95.78	165
Yarrowia+Candida hispaniensis	60.80–93.66	68.29–95.78	196
Candida hispaniensis single–species lineage	N/A	N/A	262
Pichiomycetes			
Pichiales			
Ambrosiozyma	60.29–100.0	62.38-99.93	9
Citeromyces	71.28–85.77	87.41–91.71	134
Brettanomyces	61.89–96.77	72.69–94.27	5
Candida insectalens clade	62.99–62.99	82.72–82.72	9
Komagataella	85.54–97.90	94.43–98.89	141
Kregervanrija	88.94–89.70	95.45–96.48	79
Ogataea	56.34–99.54	55.36–97.74	0
Ogataea clade 1	58.82–99.54	61.91–97.74	0
Ogataea sensu stricto subclade	64.30–99.54	76.83–97.74	2
Ogataea pilisensis subclade	61.27–90.18	75.32–97.46	0
Ogataea saltuana subclade	66.24–85.70	86.12–97.29	1
Ogataea wickerhamii subclade	65.49–86.36	87.03–94.58	5
Ogataea saltuana subclade+*Ogataea sensu stricto* subclade	61.77–99.54	71.15–97.74	0
Ogataea saltuana subclade+*Ogataea wickerhamii* subclade+*Ogataea sensu stricto* subclade	59.79–99.54	67.84–97.74	2
Ogataea clade 2	58.46–90.74	68.35–97.84	6
Ogataea naganishii subclade	58.98–58.98	70.68–70.68	0
Ogataea ramenticola subclade	66.21–90.74	82.94–97.84	32
Candida methanosorbosa subclade	63.02–63.02	78.80–78.80	0
Ogataea naganishii subclade+*Candida methanosorbosa* subclade	58.98–63.02	70.68–78.80	0
Ogataea ramenticola subclade+*Ogataea naganishii* subclade	58.46–90.74	68.35–97.84	0
Ogataea methylovora single–species lineage	N/A	N/A	100
Candida boidinii single–species lineage	N/A	N/A	284
Pichia	61.31–94.88	62.33–97.35	0

Taxa	AAI (%)	POCP (%)	PAPO
Saturnispora	61.90–97.97	77.35–98.62	14
Serinales			
Cephaloascaceae			
Cephaloascus	66.77–66.77	84.06–84.06	110
Cephaloascus+*Candida chilensis*	60.62–66.77	74.92–84.06	61
Debaryomycetaceae			
Aciculoconidium	N/A	N/A	380
Debaryomyces	58.87–91.79	73.93–97.16	0
Candida/*Lodderomyces* lineage	60.91–99.45	65.88–98.28	1
Candida sensu stricto clade	69.03–99.45	75.64–98.28	7
Candida corydali clade	67.27–81.01	81.71–93.33	3
Lodderomyces clade	64.25–83.42	73.73–96.02	4
Lodderomyces clade+*Candida corydali* clade	60.91–83.42	68.47–96.02	0
Nematodospora	76.99–76.99	94.83–94.83	5
Candida aurita clade	67.97–93.93	79.72–98.15	11
Candida railenensis clade	63.07–99.43	81.11–97.82	4
Candida aurita clade+*Candida railenensis* clade	61.51–99.43	74.04–98.15	2
Candida aurita clade+*Candida railenensis* clade+*Kurtzmaniella*	58.77–99.43	67.61–98.15	3
Candida blackwelliae clade	70.58–90.56	89.31–96.41	8
Candida glaebosa clade	65.65–86.35	82.55–96.03	23
Candida nonsorbophila clade	73.43–73.43	90.52–90.52	19
Candida tibetensis clade	74.16–74.16	94.09–94.09	10
Candida alai single–species lineage	N/A	N/A	132
Candida anutae single–species lineage	N/A	N/A	153
Candida argentea single–species lineage	N/A	N/A	180
Candida ascalaphidarum single–species lineage	N/A	N/A	68
Candida glucosophila single–species lineage	N/A	N/A	124
Candida multigemmis single–species lineage	N/A	N/A	95
Candida sake single–species lineage	N/A	N/A	84
Diutina	63.98–96.29	70.47–93.52	69
Candida glaebosa clade+*Diutina*	56.87–100.0	58.58–99.90	2
Kodamaea	60.35–91.83	60.41–95.76	0
Kurtzmaniella	64.66–85.58	84.41–96.46	16
Meyerozyma	67.31–94.33	90.39–98.21	18
Millerozyma	62.43–90.68	85.42–98.78	6
Priceomyces	63.86–84.38	85.48–96.33	4
Scheffersomyces	57.69–98.69	64.12–98.73	0
Spathaspora	62.35–90.50	70.35–93.21	0
Spathaspora sensu stricto clade	77.82–81.60	85.56–93.20	32
Hemisphaericaspora clade	71.91–90.50	77.12–93.21	11
Spathaspora sensu stricto clade+*Hemisphaericaspora* clade	65.17–90.50	71.32–93.21	2
Spathaspora sensu stricto clade+*Hemisphaericaspora* clade+*Candida alai*	64.79–90.50	71.32–93.21	1
Spathaspora sensu stricto clade+*Candida alai*	65.10–81.60	75.10–93.20	4

Taxa	AAI (%)	POCP (%)	PAPO
Suhomyces	66.35–96.44	86.82–98.34	0
Suhomyces+*Candida tibetensis* clade	63.89–96.44	84.33–98.34	1
Schwanniomyces	57.79–95.46	68.69–96.20	0
Teunomyces	74.25–96.37	92.42–98.43	12
Wickerhamia fluorescens single–species lineage	N/A	N/A	329
Yamadazyma	59.65–90.55	73.35–97.21	0
Yamadazyma olivae clade	62.06–97.75	77.72–98.83	0
Yamadazyma epiphylla clade	69.16–69.16	89.77–89.77	5
Yamadazyma triangularis clade	69.45–69.45	87.92–87.92	14
incertae sedis* in *Serinales			
Babjeviella	N/A	N/A	231
Limtongozyma	81.76–81.76	93.60–93.60	299
Candida chilensis single–species lineage	N/A	N/A	196
Saccharomycetes			
Phaffomycetales			
Barnettozyma	64.52–86.96	81.56–95.37	0
Barnettozyma sensu stricto clade	70.01–86.96	88.56–95.37	15
Barnettozyma wickerhamii clade	69.91–95.36	88.46–96.27	0
Barnettozyma wickerhamii clade+*Barnettozyma salicaria*	68.17–95.36	87.09–96.27	3
Barnettozyma siamensis clade	79.96–79.96	91.36–91.36	17
Barnettozyma siamensis clade+*Barnettozyma botsteinii*	72.73–79.96	87.80–91.36	0
Barnettozyma salicaria single–species lineage	N/A	N/A	46
Millerago	89.67–89.67	92.25–92.25	30
Millerago+*Candida ficus*	74.47–89.67	85.02–92.25	5
Phaffomyces	80.33–89.98	92.21–94.30	0
Phaffomyces clade	80.33–94.80	91.59–96.74	20
Cyberlindnera	61.78–93.06	69.12–96.40	0
Cyberlindnera sensu stricto clade	67.15–90.85	76.63–94.72	2
Williopsis clade	63.63–99.97	78.24–99.67	4
Candida freyschussii single–species lineage	N/A	N/A	70
Starmera	61.57–92.68	67.37–97.98	4
Starmera sensu stricto clade	67.88–92.68	81.76–97.98	30
Starmera dryadoides clade	65.26–83.33	81.67–89.88	16
Wickerhamomyces	56.06–100.0	44.43–99.82	0
Wickerhamomyces sensu stricto clade	67.21–100.0	83.51–99.82	4
Hansenula clade	68.07–84.27	80.37–94.72	11
Wickerhamomyces bovis clade	65.53–98.19	82.92–96.62	2
Wickerhamomyces pijperi clade	71.66–81.75	63.80–92.13	87
Wickerhamomyces mucosus single–species lineage	N/A	N/A	525
Wickerhamomyces mucosus+*Wickerhamomyces pijperi* lineage	62.78–81.75	54.89–92.13	29
Wickerhamomyces hampshirensis clade	71.33–71.33	89.78–89.78	27
Wickerhamomyces chambardii clade	67.51–90.85	79.62–91.90	91
Wickerhamomyces silvicola single–species lineage	N/A	N/A	126

Taxa	AAI (%)	POCP (%)	PAPO
Wickerhamomyces kurtzmanii single–species lineage	N/A	N/A	280

Note: N/A referring to data not available

Candida species and related genus *Zygoascus* (*Trichomonascaceae*, *Dipodascales*, *Dipodascomycetes*)

Three species, *Candida lundiana*, *Candida patagonica* and *Candida suthepensis*, formed a well-supported clade, referred to as the *Candida lundiana* clade, which is nested within the genus *Zygoascus* (Fig. 1). This placement agrees with a previous study (Opulente et al. 2024). The genus *Zygoascus* was originally proposed by Smith (1986) for only the yeast species *Zygoascus hellenicus*, characterized by septate hyphae and hemispherical to galeate ascospores (referred to as the *Zygoascus sensu stricto* clade). Later, Kurtzman & Robnett (2007) transferred *Pichia ofunaensis* and *Pichia tannicola* into *Zygoascus* based on a multigene sequence analysis, recognizing their close relatedness to other *Zygoascus* species. However, unlike species comprising *Zygoascus sensu stricto* clade, *Z. ofunaensis* and *Z. tannicola* do not produce septate hyphae. Similarly, members of the *Candida lundiana* clade can be distinguished from *Zygoascus sensu stricto* by some physiological characteristics, such as the lack of fermentation and septate hyphae by the former. Given these distinctions, we explored the possibility of separating the *Candida lundiana* clade from the *Zygoascus sensu stricto* clade. The RED analysis conducted by Li et al. (2021) revealed substantial heterogeneity within *Zygoascus* and suggested that this genus is under-classified, potentially representing an order-level taxon. This conclusion was particularly based on the RED value (0.813) of this genus, which falls in the range of the order-level RED interval (viz., 0.79 ± 0.1). Our genome-based metric analyses showed that *Zygoascus* exhibited lower AAI (59.76–88.95%) and POCP (71.75–98.27%) values (Table 1) compared to several genera in Saccharomycetaceae studied by Liu et al. (2024a). Next to it, we calculated genomic metrics of the combined *Zygoascus sensu stricto* clade+*Candida lundiana* clade. Our genomic metrics showed that the POCP value of the two clades combined was 74.47–98.27% (Table 1), indicating that even this combined group remains too heterogeneous compared to values expected for genera based on the previous experience from *Saccharomycetaceae* and *Metschnikowiaceae* (Liu et al. 2024a, b).

Considering the evolving concept of the genus *Zygoascus*, the phenotypically distinguished characteristics between the *Candida lundiana* clade, the *Zygoascus sensu stricto* clade and the *Zygoascus tannicola* clade (Table S3) and the genome-based metric analyses, we suggest to resolve this taxonomic complexity and reduce the heterogeneity within the genus. We propose two new genera: *Casaregolazyma gen. nov.* to accommodate species in the *Candida lundiana* clade and *Daia gen. nov.* for members of the *Zygoascus tannicola* clade.

One newly published *Zygoascus* species, namely *Zygoascus detingensis*, was not included in the phylogenomic analysis because of the unavailability of its genome. Phylogenetically, this species is positioned distantly from the other *Zygoascus* members in our ITS+D1/D2 LSU tree (Fig. 3). Chai et al. (2022) showed that *Z. detingensis* occurred in a long basal to other *Zygoascus* species based on the combined ITS and D1/D2 LSU sequences analysis. However, our phylogenetic analysis demonstrated that *Z. detingensis* does not belong to any of the described clades within the *Dipodascomycetes* and represents a candidate monotypic genus, which can be formally proposed after more related new species are described in the future.

Candida species and related genera *Nadsonia* and *Yarrowia* (*incertae sedis*, *Dipodascomycetes*)

Phylogenetic analyses conducted in this study, along with previous research data (Shen et al. 2018; Opulente et al. 2024), have identified two distinct *Candida* lineages, namely *Candida hispaniensis* and *Candida tunisiensis* single-species lineages, within this class. The *Candida hispaniensis* lineage formed a long sister branch to the genera *Yarrowia* and *Nadsonia* in the phylogenomic tree (Fig. 1). While it is evident that this *Candida* species requires reclassification, its phylogenetic placement raises the possibility of assigning it to the genus *Yarrowia*. To assess the validity of this classification, we first evaluated its genome content and size. *C. hispaniensis* has about 11 Mb genome size and 41.69% GC content, whereas *Yarrowia* species have double the genome size (about 20 Mb) and 43.46–50.89% GC content compared to *C. hispaniensis* (Table S3). Our genome-based metric analysis showed that the POCP value of *Yarrowia* is 83.66–95.78% that fell in the range of the generic values (80–92%) suggested by Liu et al. (2024a), whereas the POCP value (68.29–95.78%) of *Yarrowia*+*C. hispaniensis* is lower than the recommended generic values, which suggests that it is better to place *Yarrowia* and *C. hispaniensis* in different genera, rather than to combine them in one genus. The *Candida tunisiensis* lineage is placed in the phylogenomic analysis as a sister group to the other known genera within *Dipodascomycetes*, but without a well-supported association with any specific genus (Fig. 1). In our opinion, the above analyses showed that *C. hispaniensis* and *C. tunisiensis* do not belong to any known genera in *Dipodascomycetes* and should be classified in two new genera instead of merging them with already existing genera. Therefore, *Dengshuqunia gen. nov.* is proposed for *C. hispaniensis* lineage. Although only one species is included in the *Dengshuqunia* so far, our ITS+D1/D2 LSU and D1/D2 LSU analyses showed that four potential new species belong to *Dengshuqunia* (Fig. 5 and Fig. S8), including organisms labelled as *Yarrowia* sp. VR546, *Yarrowia* sp. VR547, *Yarrowia* sp. VR571 and *Yarrowia* sp. VR572, which were all isolated from soils in Brazil (Table S2). The *Candida tunisiensis* lineage will remain a candidate genus until more closely related species are discovered in the future.

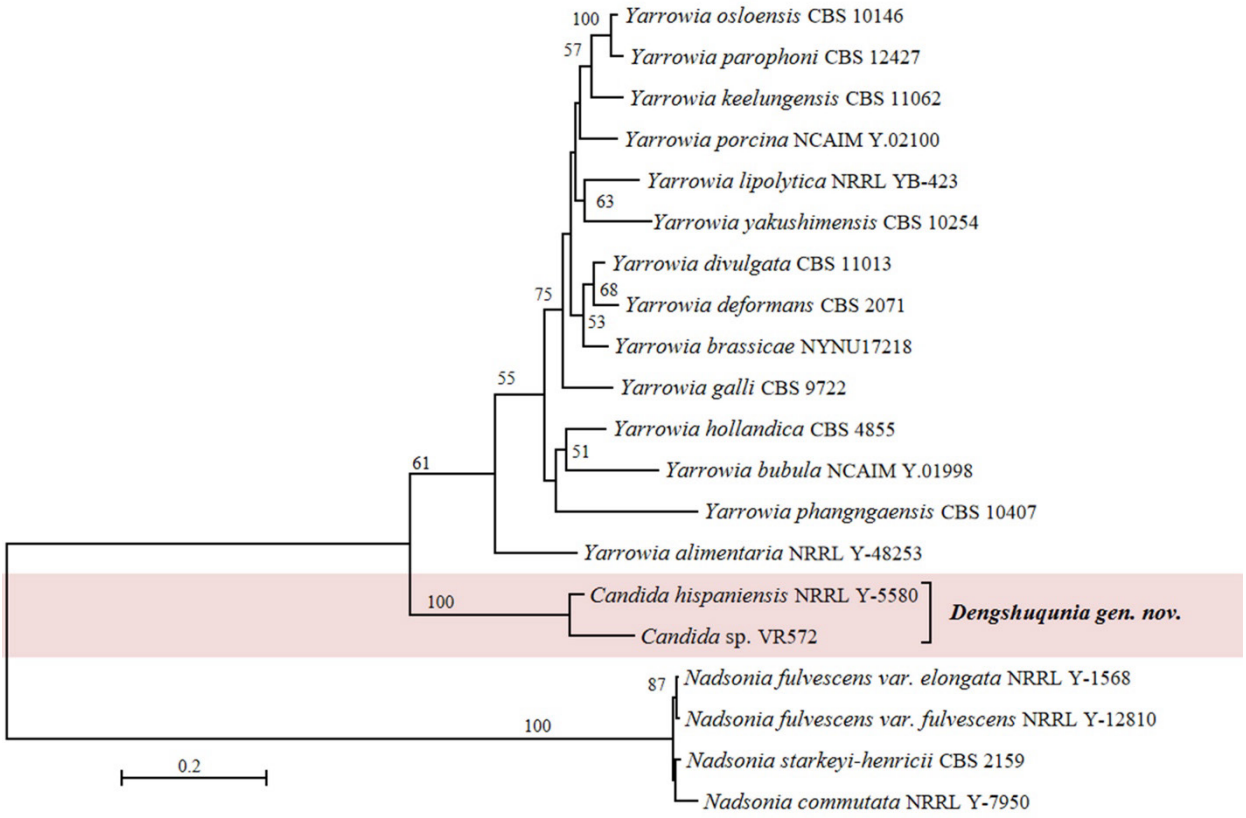

Fig. 5. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida hispaniensis*, *Yarrowia* and undescribed strains. Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Nadsonia* species were used as outgroups. Bar = 0.2 substitutions per nucleotide position.

Candida species in the *Pichiomycetes*

One hundred forty-eight *Candida* species occur in the orders *Pichiales* and *Serinales* of *Pichiomycetes* (Table S2). The core of the genus *Candida* is also located in *Pichiomycetes*, namely in the order *Serinales*, family *Debaryomycetaceae*. Despite previous attempts to reclassify *Candida*, numerous species still require reclassification, the vast majority of which are placed in *Pichiomycetes*.

Candida species and related genera *Allodekkera*, *Ambrosiozyma*, *Brettanomyces* and *Pichia* (*Pichiaceae*, *Pichiales*, *Pichiomycetes*)

Candida insectalens and *Candida silvatica* formed a clade labelled as *Candida insectalens* clade, which was placed close to the genera *Brettanomyces* and *Allodekkera* (Fig. 6). *Candida sorboxylosa* was related to *Pichia terricola* in the phylogenomic tree (Fig. 6). The position of the three species was different in the ITS+D1/D2 LSU analysis. Specifically, *C. insectalens* and *C. sorboxylosa* formed two distinct branches with an affinity to the genus *Komagataella*, whereas *C. silvatica* was found to be phylogenetically more closely related to *Brettanomyces,* but with low bootstrap support for this placement (Fig. 7). The LSU rDNA analysis showed that these three *Candida* species were located in distinct branches (Fig. S9). *C. silvatica* and two sequences, strain *Candida* sp. JCM 16747 (GenBank AB552927) and environmental sequence Fungal sp. QmPIPB-1-59 (GenBank AB291684), isolated from galleries of *Platypus quercivorus,* the oak ambrosia beetle, in Japan, formed a *C. silvatica* clade without bootstrap support. *C. sorboxylosa* formed a very long branch near the *C. silvatica* clade. *C. insectalens* and Fungal sp. QmPIEG-2-8 (GenBank AB291677) isolated from the gallery of *P. quercivorus* in Japan formed a long branch with low bootstrap support (Fig. S9). The phylogenetic position of these yeasts remained unresolved in previous studies that utilized solely rDNA sequences in their phylogenetic analyses. Kurtzman & Robnett (1998) placed *C. sorboxylosa* as a sister species to *C. silvatica*, indicating its affinity with *Dekkera* species. They also positioned *C. insectalens* and *C. incommunis* together based on a D1/D2 LSU sequence analysis. In contrast, Sugita & Nakase (1999) demonstrated that *C. insectalens* was located in a basal position next to the *Starmerella* clade based on a phylogenetic analysis using SSU rDNA sequences. Suzuki & Nakase (2002) indicated that *C. sorboxylosa* formed a long branch near *Saturnispora* species and *Pichia membranifaciens*. More recently, Lachance et al. (2011) showed that *C. insectalens* occurred on a long branch next to *C. sorboxylosa* using a phylogenetic analysis of D1/D2 LSU rDNA data. In the multi-locus analysis based on the combined rDNA and *TEF1* sequence, *C. sorboxylosa* was more closely related to *Komagataella* (Kurtzman et al. 2008). Considering that the phylogenomic analysis is usually more reliable than the rDNA and multigene-

based phylogenetic analyses, we assign *C. sorboxylosa* to the genus *Pichia* and propose a new genus *Xiuguozyma gen. nov.* to accommodate *C. insectalens* and *C. silvatica*.

Candida boidinii was located at a branch positioned basal to *Allodekkera*, *Ambrosiozyma*, *Brettanomyces*, *Kregervanrija*, *Martiniozyma*, *Ogataea*, *Pichia*, and *Saturnispora* (Fig. 6), which suggests that this single-species lineage represents a genus. This species has been resolved as a basal single-species lineage to *Ogataea* in a previous study (Kurtzman & Robnett 2010). Therefore, *Ramirezia gen. nov.* is proposed to accommodate *C. boidinii*. In the search for potential members of the novel genus, more than 92 ITS sequences of *C. boidinii*, such as CBS 6056 (GenBank KY101981), and four nucleotide sequences (GenBank EF060568, EF060866, EF060905 and EF060925) were retrieved from public databases, showing 97–100% sequence similarity with the type strain of *C. boidinii*. Sequences with lower similarity values may correspond to species different from *C. boidinii*. Our ITS phylogenetic analysis showed that at least two groups, namely group 1 and group 2, represent two potential new species closely related to *C. boidinii* (Fig. S10).

Candida awuaii was located within the genus *Pichia* (Fig. 7) and is therefore transferred to *Pichia*. Similarly, *Candida wuzhishanensis* was positioned within the genus *Ambrosiozyma*, showing a close relationship to *Ambrosiozyma pseudovanderkliftii* with 99% and 100% sequence similarity in the ITS and D1/D2 LSU regions, respectively. This high similarity strongly suggests that *C. wuzhishanensis* is a synonym of *A. pseudovanderkliftii* (Fig. 8).

Candida species and related genus *Ogataea* (*Pichiaceae*, *Pichiales*, *Pichiomycetes*)

Our phylogenetic analyses showed that 20 *Candida* species were placed in the genus *Ogataea* in *Pichiales* (Figs. 6, 8, Table S2). The genus *Ogataea* is mainly comprised of methanol-assimilating yeasts. Since the erection of the genus to accommodate hat-shaped ascospore-forming, nitrate-assimilating *Pichia* species (Yamada et al. 1994a), the circumscription and size of the genus varied with more species being transferred to *Ogataea* or newly discovered in nature. Kurtzman & Robnett (2010) demonstrated a distant relatedness between *Ogataea* and *Pichia*, and transferred eight species to *Ogataea* and the newly erected genus *Peterozyma*. The authors employed a multi-locus phylogeny to resolve subclades of *Ogataea* and distinguish them from *Ambrosiozyma*. Previous studies that used rDNA sequences only, failed to resolve *Ogataea* and *Ambrosiozyma*, but Glushakova et al. (2010) used a combined rDNA phylogeny and advanced maximum-likelihood-based statistics, confirming the observations by Kurtzman & Robnett (2010) regarding the monophyly of *Ogataea* and the clade represented by *Pichia methanolica*, *Pichia trehalophila*, and *Williopsis salicorniae*. Later, Kurtzman (2011a) argued that the clade represented by *Ogataea naganishii* may be separated from *Ogataea* as a sister genus when a more robust dataset becomes available. One of the molecular features of yeasts comprising this phylogenetic group that complicates the phylogenetic analyses and species demarcation is the low variability of rDNA sequences. Therefore, whole-genome sequencing seems a good opportunity to reassess the boundaries of the genus and the relatedness of the species presently accommodated in *Ogataea*. More recently, a large phylogenomic analysis revealed complex relationships between *Ogataea* and *Ambrosiozyma*, suggesting that *Ogataea* is polyphyletic (Shen et al. 2018). The clade that is comprised by *Candida succiphila*, *O. naganishii*, *Ogataea ramenticola*, and *Ogataea methylivora* occupied a basal position to the core of *Ogataea* and *Ambrosiozyma*. The same phylogenetic relationship has been observed in the subsequent study conducted by Opulente et al. (2024), who additionally identified *Candida methanosorbosa*, *Candida nanaspora*, *Candida nitratophila*, and *Candida suzuki* as the members of that basal clade. The phylogenomic analysis performed in our study confirmed the previous observations regarding the polyphyly of the genus *Ogataea* that was split into two large clades labelled here as *Ogataea* clade 1 and *Ogataea* clade 2 (Fig. 6).

Further examination of the genus *Ogataea* as currently accepted, using the genome-based metric analyses, demonstrated that the genus is heterogeneous (Table 1). Specifically, the ranges of AAI values (56.34–99.54%) and POCP values (55.36–97.74%) were substantially lower than that of the genera recognized in the *Saccharomycetaceae* (Liu et al. 2024a). The RED value calculated by Li et al. (2021) was 0.829, which suggests that this genus is likely under-classified and may represent a family-level or order-level taxon. The PAPO value is 0 and no common gene (viz., unique gene) has been found across the clade, indicating that this genus is too heterogeneous and likely under-classified.

Based on the above arguments, we propose to split the genus *Ogataea* and propose a new genus *Wenyingozyma gen. nov.* to accommodate the *Ogataea* clade 2 that contains six *Candida* species. A total of fourteen *Candida* species located in the *Ogataea* clade 1 are transferred to the genus *Ogataea* (Fig. 6 and Table S2). To test for the degree of genomic heterogeneity for this proposed reclassification, we determined indices values for that *Ogataea* clade 1 (AAI: 58.82–99.54%; POCP: 61.91–97.74%; PAPO: 0) and *Ogataea* clade 2 (AAI: 58.46–90.74%; POCP: 68.35–97.84%; PAPO: 6). Both clades are characterized by higher genetic diversity compared to the genera accepted in *Saccharomycetaceae* (Liu et al. 2024a) and *Pichiales* (Table 1), e.g., *Citeromyces*, *Komagataella* and *Kregervanrija*. Our phylogenetic analysis identified four subclades in the *Ogataea* clade 1, namely the *Ogataea sensu stricto* subclade, the *Ogataea pilisensis* subclade, the *Ogataea saltuana* subclade, and the *Ogataea wickerhamii* subclade (Fig. 6). The four subclades were characterized by the following genomic metrices, the *Ogataea sensu stricto* subclade (AAI: 64.30–99.54%; POCP: 76.83–97.74%; PAPO: 2) including two *Candida* species; the *Ogataea pilisensis* subclade (AAI: 61.27–90.18%; POCP: 75.32–97.46%; PAPO: 0) including eight *Candida* species; the *Ogataea saltuana* subclade (AAI: 66.24–85.70%; POCP: 86.12–97.29%; PAPO: 1) including three *Candida* species; and the *Ogataea wickerhamii* subclade (AAI: 65.49–86.36%; POCP: 87.03–94.58%; PAPO: 5) including one *Candida* species, namely *Candida maris*. In the *Ogataea* clade 2, several well-supported subclades were detected in the phylogenomic analysis (Fig. 6), namely the *Ogataea naganishii* subclade (AAI: 58.98%; POCP: 70.68%; PAPO: 0) including two *Candida* species, the *Candida methanosorbosa* subclade (AAI: 63.02%; POCP: 78.80%; PAPO: 0) including one *Candida* species, the *Ogataea ramenticola* subclade (AAI: 66.21–90.74%; POCP: 82.94–97.84%; PAPO: 32) including three described *Candida* species, and one single-species

lineage represented by *Ogataea methylovora.* The multigene analysis, including LSU rDNA, SSU rDNA, *TEF1* and mitochondrial SSU rDNA genes, positioned *C. methanosorbosa* distantly related from *C. succiphila* and *O. naganishii* (Kurtzman & Robnett 2010). The above genome metric analyses showed that the *Ogataea* clade 1 and the *Ogataea* clade 2 are likely too heterogeneous and should be considered separate genera. However, more robust analyses and careful evaluation by community experts are needed to confirm their taxonomic conclusions in the future.

Candida species and related genera *Hemisphaericaspora*, *Lodderomyces*, *Nematodospora* and *Spathaspora* (*Debaryomycetaceae*, *Serinales*, *Pichiomycetes*)

The order *Serinales* currently includes families *Cephaloascaceae*, *Debaryomycetaceae* and *Metschnikowiaceae*. The family *Debaryomycetaceae* contains more than 109 *Candida* species, including the type species*, C. vulgaris*, which is now considered a synonym of *C. tropicalis* (Lachance et al. 2011). The phylogenetic lineage bearing the type species is often referred to as the *Candida*/*Lodderomyces* lineage (or clade), which currently contains 42 *Candida* species, including most clinically important ones (Figs. 9–10 and Table S2). Our phylogenomic analysis revealed four clades in the lineage, namely the *Candida sensu stricto* clade (AAI: 69.03–99.45%; POCP: 75.64–98.28%; PAPO: 7), the *Candida corydali* clade (AAI: 67.27–81.01%; POCP: 81.71–93.33%; PAPO: 3), the *Lodderomyces* clade (AAI: 64.25–83.42%; POCP: 73.73–96.02%; PAPO: 4), and the *Nematodospora* clade (AAI: 76.99%; POCP: 94.83%; PAPO: 5) (Fig. 9, Table 1). For a long time, the lineage included only one known sexual species, *Lodderomyces elongisporus*. The genus was proposed by van der Walt (1966), who reclassified the species *Saccharomyces elongisporus,* placing it in a lineage closely related to *Candida parapsilosis*. The genus *Nematodospora* was later established in the *Candida*/*Lodderomyces* lineage to accommodate a distinct yeast species characterized by a unique ascospore morphology, distinguishing it from *Lodderomyces* (Gouliamova et al. 2016). Although the genus *Nematodospora* was placed close to *Lodderomyces*, both currently known species exhibit an ascospore morphology distinct from that of *Lodderomyces* (Gouliamova et al. 2016; Ren et al. 2016). In the phylogenomic analysis, the *Lodderomyces* and the *Candida corydali* clades clustered together closely to *Nematodospora,* whereas the *Candida sensu stricto* clade was positioned as a sister group to *Nematodospora*, the *Candida corydali* clade, and the *Lodderomyces* clade (Fig. 9). This topology is consistent with previous phylogenomic analyses (Shen et al. 2018; Opulente et al. 2024). As the result, the phylogenomic analysis reveals four clades, which are harbouring nomenclature types of three genera, namely *Candida*, *Lodderomyces* and *Nematodospora*. This *Candida corydali* clade puts it in the position of a sister taxon to the *Candida sensu stricto* clade and also makes the genus polyphyletic.

The phylogenetic lineage *Candida*/*Lodderomyces* showed a rather low range of POCP values (65.88–98.28%), indicating its greater genetic heterogeneity compared to most genera in *Saccharomycetacea* (Liu et al. 2024a). Consequently, we further examined the genetic metrics in the *Candida*/*Lodderomyces* lineage to explore available options for a meaningful and statistically supported reclassification. Based on the phylogenomic tree, one potential option is to create a large clade that would comprise the *Candida corydali* and the *Lodderomyces* clades. However, the POCP (68.47–96.02%) and PAPO (0, without unique genes) values of the combined *Candida corydali* clade+*Lodderomyces* clade (Table 1) suggest that it is preferable to recognize those two clades as distinct genera, rather than combine them into a single genetically heterogeneous genus. At the moment, the *Candida corydali* clade contains 10 *Candida* species, six of which were isolated from insects (Nguyen et al. 2007; Lachance et al. 2011; Liu et al. 2016), while the remaining three species were isolated from leaves of *Pterocarpus indicus*, flowers of *Verbascum*, and a mushroom (Nakase et al. 2009; Limtong et al. 2012; Sipiczki 2013). Considering the origin of species in the *Candida corydali* clade, we propose the new genus *Insectozyma gen. nov.* to accommodate these yeasts and transfer 10 *Candida* species to this genus. Additionally, eight *Candida* species, including the clinically-relevant *C. parapsilosis* and two *Lodderomyces* species, clustered in the *Lodderomyces* clade (Fig. 9, Table S2). Consequently, we transfer them into the *Lodderomyces* genus. The genus *Nematodospora*, comprising two species, forms an isolated clade in *Candida*/*Lodderomyces* lineage. The *Candida sensu stricto* clade, which includes 22 species, including the clinically relevant species *C. albicans*, *C. dubliniensis*, and *C. tropicalis*, forms a well-supported clade in the phylogenomic tree. Furthermore, the analysis revealed a clade comprising *Candida parablackwelliae*, *Candida blackwelliae* and *Spathaspora boniae* (i.e., the *Candida blackwelliae* clade), which is positioned basally to the *Candida*/*Lodderomyces* lineage (Fig. 9).

At the time of description, phylogenetic and phylogenomic analyses placed *Spathaspora boniae* outside the *Spathaspora* clade in a basal position to the *Candida*/*Lodderomyces* lineage (Morais et al. 2017). The same authors concluded that the genus *Spathaspora* as currently defined is paraphyletic, but nonetheless opted to describe the new species as *Spathaspora boniae* in that genus. This *Candida blackwelliae* clade is well-defined based on the phylogenomic analysis and genome-based metric analyses with AAI, POCP and PAPO values of 70.58–90.56%, 89.31–96.41% and 8, respectively. Both, phylogenetic position of the clade and the range of genomic metrics suggest this is a good candidate genus. Hence, the new genus *Zhuliangozyma gen. nov.* is proposed for this clade.

Candida alai was located in a long branch close to the *Spathaspora sensu stricto* clade (Fig. 9). *Candida alai* differs from species of the *Spathaspora sensu stricto* clade by the lack of assimilation of erythritol and N-acetyl-D-glucosamine (Table S3). The above physiological and phylogenetic analyses indicated that *C. alai* do not belong either to the genus *Candida*, nor to *Spathaspora*. Therefore, the new genus *Intestinozyma gen. nov.* was proposed to accommodate *C. alai*. The sequence of a yeast labelled as *Candida* sp. B53C (GenBank MW165503), isolated from an insect gut in Brazil, differs by 11 nt ITS sequence differences from the sequence of *C. alai* (Fig. S11). This placement suggests that *Candida* sp. B53C may represent another new member of the genus *Intestinozyma*, which is currently only represented by *C. alai.*

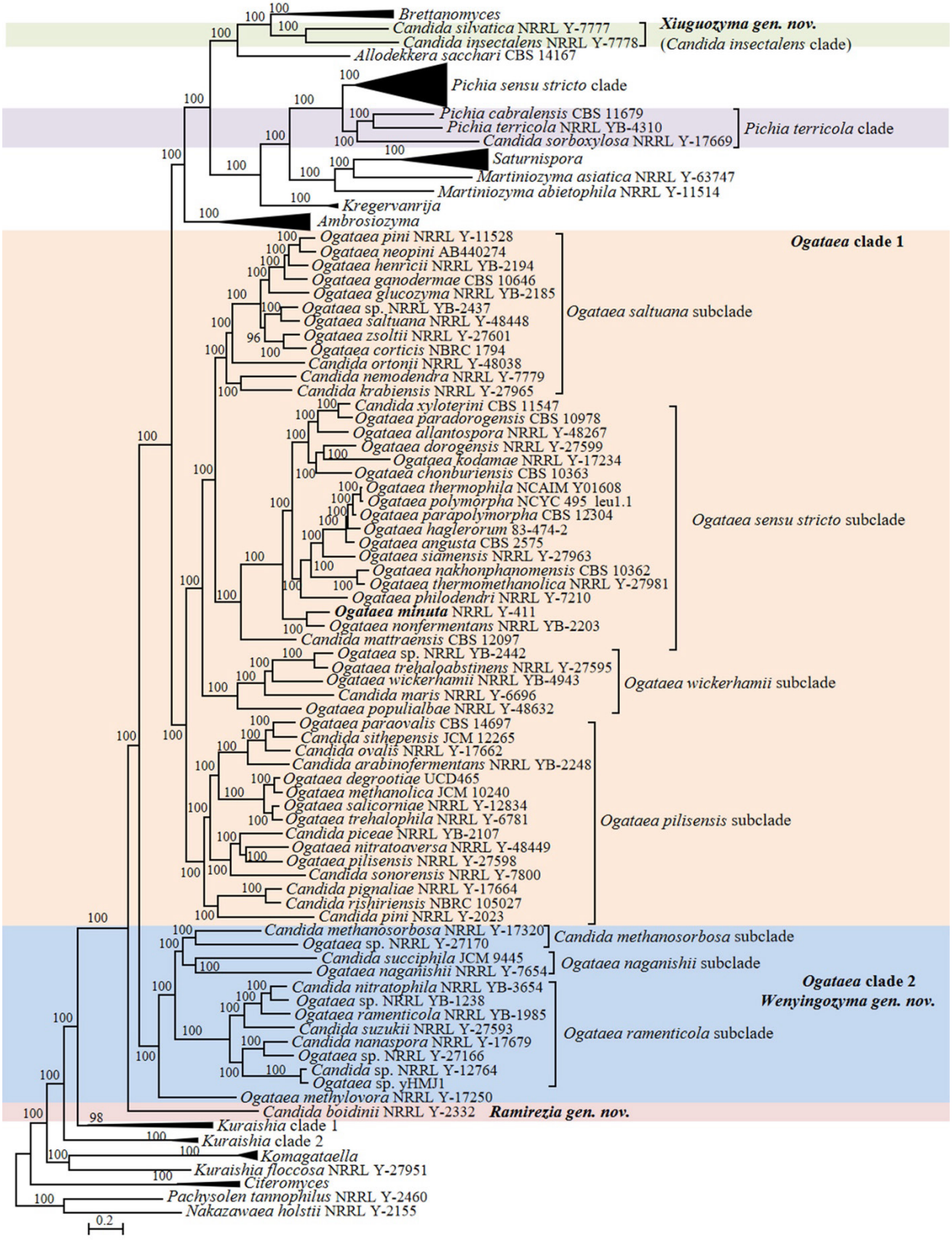

Fig. 6. Phylogenomic tree inferred using 545 single-copy orthologue proteins showing the phylogenetic relationship between *Candida* species and related taxa in *Pichiales* (*Pichiomycetes*). Bootstrap percentages of maximum likelihood analysis from 1,000 bootstrap replicates are shown on the major branches. *Nakazawaea holstii* and *Pachysolen tannophilus* were used as outgroups. Bar = 0.2 substitutions per nucleotide position.

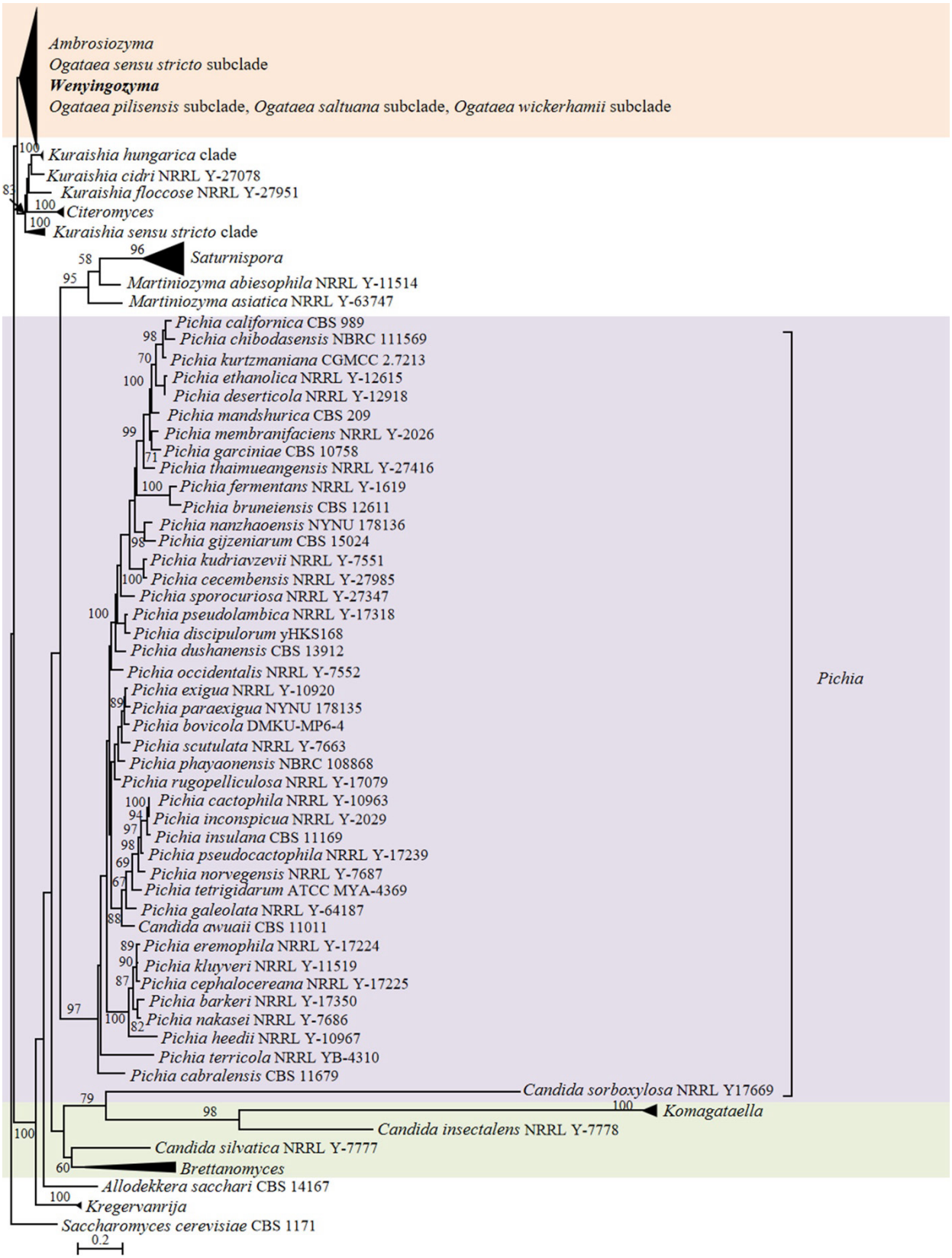

Fig. 7. A phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida* species and related taxa in *Pichiales* (*Pichiomycetes*). Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Saccharomyces cerevisiae* was used as the outgroup. Bar = 0.2 substitutions per nucleotide position.

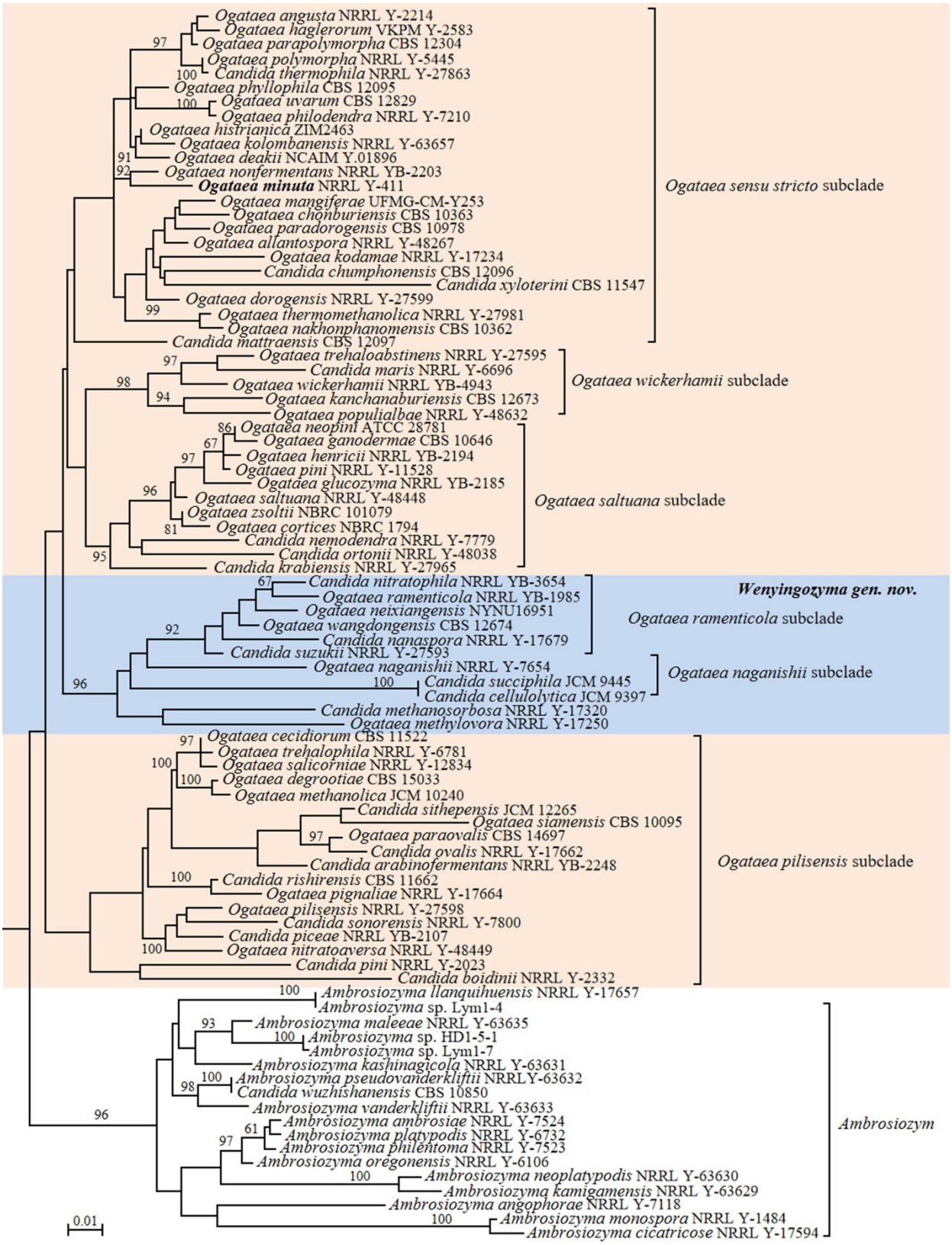

Fig. 8. A phylogenetic sub-tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida* species and related taxa in *Ogataea* (*Pichiales*, *Pichiomycetes*). Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. Bar = 0.01 substitutions per nucleotide position.

In agreement with previous observations (Opulente et al. 2024), *Candida lyxosophila*, *Candida subhashii* and *Candida xylanilytica*, and three *Spathaspora* species were located in the *Hemisphaericaspora* clade (Figs. 9–11). Consequently, we suggest transferring those species into the genus *Hemisphaericaspora*.

Candida species and related genus *Diutina* (*Debaryomycetaceae*, *Serinales*, *Pichiomycetes*)

The *Candida glaebosa* clade includes seven *Candida* species that are closely related to the genus *Diutina* (Fig. 9). Members of the clade share the following features with a lower GC content (31.16–41.24%), whereas the genus *Diutina* has a higher GC content (41.23–53.05%) (Table S3). The genome metrics analyses showed that the *Candida glaebosa* clade (AAI: 65.65–86.35%; POCP: 82.55–96.03%; PAPO: 23) is a good candidate genus in terms of its genomic heterogeneity, as demonstrated by its AAI and POCP values that are within the ranges of those previously observed for *Saccharomycetaceae* and *Metschnikowiaceae* (Liu et al. 2024a, b). Therefore, *Suzukiozyma gen. nov.* is proposed to accommodate members of the *Candida glaebosa* clade

Candida species and related genera *Suhomyces*, *Teunomyces* and *Wickerhamia* (*Debaryomycetaceae*, *Serinales*, *Pichiomycetes*)

Candida caryicola and *Candida tibetensis* formed the *Candida tibetensis* clade, which is positioned basal to the genus *Suhomyces* (Fig. 9). Our genome-based metric analyses showed that the AAI and POCP values of *Suhomyces*+*Candida tibetensis* clade were 63.89–96.44% and 84.33–98.34%, respectively, which fell in the range of generic AAI and POCP values previously reported for *Saccharomycetaceae* by Liu et al. (2024a) and supported of the transfer of *C. caryicola* and *C. tibetensis* to *Suhomyces*. New combinations for these two species are provided in the Taxonomy section.

Candida sake was placed in a long branch closely related to *Teunomyces* (Fig. 9). The species *C. sake* has a 14 Mb genome size with GC 38.76%, whereas *Teunomyces* has a low genome size (10–13Mb) and higher GC content (41.03–46.16%) (Table S3). The above analyses show *C. sake* do not belong either to the genus *Candida*, nor to any presently known genera. Therefore, the most pragmatic solution is to accommodate *C. sake* in the genus *Fermentozyma gen. nov.* Crous et al. (2017) showed that *Candida vespimorsuum* was closely related to *C. sake* with which it formed a well-supported clade, suggesting that they might belong to the same genus. Our ITS+D1/D2 LSU rDNA phylogenetic analysis supports the observation that *C. vespimorsuum* and *C. sake* belong to the same new genus *Fermentozyma* (Fig. 10). Another potential new species in that genus is represented by the strain *Candida* sp. KBP Y-6292 (GenBank OP941477), isolated from ants in Vietnam, is placed in *Fermentozyma* with good statistical support (Fig. 10).

Candida anutae and *Candida argentea* formed two distinct long branches closely related to *Wickerhamia fluorescens* (Fig. 9). In the absence of other closely related species, *C. anutae* and *C. argentea* were retained as *Candida pro tempore* at present. Because of their distant placement from the core of the genus *Candida*, they will be reclassified into new genera after more closely related taxa are found.

Candida species and related genera *Cephaloascus* and *Kurtzmaniella* (*Debaryomycetaceae*, *Serinales*, *Pichiomycetes*)

The phylogenomic analysis revealed that *Candida chilensis* was placed in a long branch closely related to the genus *Cephaloascus* (Fig. 12). Given this distant placement from the type clade of *Candida* and other hitherto described genera, we propose *Nothofagozyma gen. nov.* to accommodate *C. chilensis*. Our D1/D2 LSU rDNA phylogenetic analysis showed that strain *Candida* cf. *chilensis* CBS 11766 (GenBank FN824503) isolated from soil in Germany (Yurkov et al. 2012), is closely related to, but distinct from *C. chilensis*, and appears to represent a new species of *Nothofagozyma*, currently only represented by *C. chilensis* (Fig. S9). The rDNA blast against the NCBI nucleotide database showed that CBS 11766 differed from *C. chilensis* by 10 nucleotides (1.8%) in the D1/D2 LSU sequences.

According to our phylogenomic analyses, six *Candida* species and three *Candida* species were placed in the *Candida railenensis* clade and the *Candida aurita* clade, respectively. Both clades were found to be related to the genus *Kurtzmaniella* (Fig. 12). Lachance et al. (2011) and Daniel et al. (2014) suggested that *Candida anglica*, *Candida boleticola*, *Candida fragi*, *Candida oleophila*, *C. railenensis*, *Candida santamariae*, *Candida schatavii* and *Candida zeylanoides* were members of the *Kurtzmaniella* clade. Lopes et al. (2019) transferred *C. fragi*, *C. quercitrusa* and *C. natalensis* to the genus *Kurtzmaniella*, and argued that reclassification of *C. anglica*, *C. boleticola*, *C. oleophila*, *C. railenensis*, *C. santamariae*, *C. schatavii* and *C. zeylanoides* into *Kurtzmaniella* needed more robust data, because *C. schatavii* was found to be highly divergent from *Kurtzmaniella* and placed on a long branch to the clade (Shen et al. 2018). In order to evaluate the relative heterogeneity of the *Kurtzmaniella* clade, genomic metrics were calculated. The AAI and POCP values of the large clade, *Kurtzmaniella*+the *Candida railenensis* clade+*Candida aurita* clade, are 58.77–99.43% and 67.61–98.15%, respectively, which are lower than the values observed in well-defined genera in *Saccharomycetaceae* and *Metschnikowiaceae* (Liu et al. 2024a, b) and in other genera in *Debaryomycetaceae* (Table 1). Considering a larger genus size and heterogeneity compared to other genera in the family, we prefer not to merge the *Candida railenensis* clade and the *Candida aurita* clade with *Kurtzmaniella*, but keep them as separate genera. This option is supported by our phylogenomic and rDNA phylogenetic analyses that showed that the *Candida railenensis* clade (AAI: 63.07–99.43%; POCP: 81.11–97.82%; PAPO: 4) and the *Candida aurita* clade (AAI: 67.97–93.93 %; POCP: 79.72–98.15 %; PAPO: 11) are distinct from *Kurtzmaniella* (Figs. 12–13). We explored the option of accommodating these *Candida* species in a single larger genus. The members of the two *Candida* clades are solely asexual morphs, but differ from each other by growth on 0.1% cycloheximide (Table S3). The POCP value of the *Candida railenensis* clade+*Candida aurita* clade was 74.04–98.15%, which is lower than the values observed in well-defined and generally accepted genera in *Saccharomycetaceae* (Liu et al. 2024a), thus suggesting that the *Candida aurita* clade and the *Candida railenensis* clade are better to accommodate in two

genera. Therefore, *Chernovozyma gen. nov.* and *Dujonia gen. nov.* are proposed for the *Candida aurita* clade and the *Candida railenensis* clade, respectively. The single-species lineage *C. anglica* was closely related to *Kurtzmaniella* in our phylogenomic analysis (Fig. 12), but this species was placed on a basal branch related to the *Candida railenensis* clade and the *Candida aurita* clade (Opulente et al. 2024). Therefore, *C. anglica* is assigned as *Candida pro tempore* at present, which has to be resolved in the future.

Candida species and related genera *Debaryomyces*, *Millerozyma* and *Schwanniomyces* (*Debaryomycetaceae*, *Serinales*, *Pichiomycetes*)

Candida glucosophila formed a long branch related to *Debaryomyces singareniensis* and *Schwanniomyces etchellsii* (Fig. 12). *Candida multigemmis* was located at a long branch without any genera as close relatives (Fig. 12). As the above two *Candida* species were characterized as separated long branches or clades, they do not seem to belong to any known genera or assigned clades in the *Serinales*. Therefore, it is pragmatic to accommodate them in new genera. The name *Glucitozyma gen. nov.* is proposed for *C. multigemmis.* A search for sequences of potential new species in GenBank resulted in *Candida* sp. CPD-35-1 (GenBank MZ701688), which is different from *C. multigemmis* by 14 nt (2%) in the ITS region and represents a potential new member of *Glucitozyma gen. nov.* (Fig. S12). In contrast, single species-lineage *C. glucosophila* will be assigned as *Candida pro tempore* due to the current lack of close relatives.

Candida thasaenensis, *Scheffersomyces gosingicus* and *Scheffersomyces spartinae* formed a clade in the phylogenomic tree (i.e., the *Scheffersomyces gosingicus* clade), which is more closely related to *Priceomyces* and *Schwanniomyces* than to the *Scheffersomyces sensu stricto* clade (Fig. 10). An observation that is consistent with the analysis by Opulente et al. (2024). Our ITS+LSU rDNA analysis showed that *C. thasaenensis*, clustered with *S. gosingicus* and *S. spartinae* with 100% bootstrap support, forming a clade closely that is related to the *Candida glaebosa* clade, and yet distinct from the other *Scheffersomyces* species (Fig. 11). The above rDNA-based and phylogenomic analyses suggested that the *Scheffersomyces gosingicus* clade should be accommodated in a distinct genus for which we propose the name *Lizanozyma gen. nov.* Consequently, *C. thasaenensis*, *S. gosingicus* and *S. spartinae* will be transferred to this newly created genus in the Taxonomy section below.

Four more *Candida* species were located in known genera in the *Serinales*. Specifically, *Candida broadrunensis*, *Candida pseudofarinosa*, *Candida psychrophila* and *Candida rongomai-pounamu* were placed in the genera *Scheffersomyces*, *Millerozyma* and *Debaryomyces*, respectively (Figs. 12–13).

Candida species and related genus *Yamadazyma* (*Debaryomycetaceae*, *Serinales*, *Pichiomycetes*)

Twenty-eight *Candida* species were distributed across the genus *Yamadazyma* in the phylogenomic analysis (Figs. 12–13, Table S2). The RED value (0.814) of *Yamadazyma* calculated by Li et al. (2021) suggested that the genus *Yamadazyma* is likely under-classified and may represent an order-level taxon. We further assessed the heterogeneity of this genus using the genome-based metrics. Our analyses confirmed that the genus *Yamadazyma* is heterogeneous, as indicated by the lower than expected ranges of metrics (AAI: 59.65–90.55%; POCP: 73.35–97.21%; PAPO: 0). The phylogenomic analysis revealed four distinct clades, namely the *Yamadazyma sensu stricto* clade, the *Yamadazyma epiphylla* clade, the *Yamadazyma olivae* clade, and the *Yamadazyma triangularis* clade. Our analyses suggest that the four clades may correspond to genus-level taxa, as suggested by the ranges of genomic metrics such as *Yamadazyma olivae* clade (AAI: 62.06–97.75%; POCP: 77.72–98.83%; PAPO: 0), the *Yamadazyma epiphylla* clade (AAI: 69.16%; POCP: 89.77%; PAPO: 5), and the *Yamadazyma triangularis* clade (AAI: 69.45%; POCP: 87.92%; PAPO: 14). The delimitation and composition of the genus *Yamadazyma*, including potential competing names in the genus, will be carefully discussed in the community of yeast taxonomists before undertaking a large-scale reclassification.

Eight *Candida* species were located in the *Yamadazyma sensu stricto* clade and should therefore be transferred to the genus *Yamadazyma*. Recently, Avesani et al. (2024) described two new *Yamadazyma* species and transferred 11 *Candida* species into *Yamadazyma*. These two new species and 11 new combinations are all placed in the *Yamadazyma sensu stricto* clade, which is supported by this study. However, five new combinations proposed by Avesani et al. (2024) in the *Yamadazyma sensu stricto* clade were invalid (https://www.indexfungorum.org/). Therefore, we will validate these five species in the genus *Yamadazyma* in the Taxonomy section. Eighteen *Candida* species were placed in the *Yamadazyma olivae* clade (Fig. 13). Among them, more recently, 15 species have been transferred to *Yamadazyma* (Qiu et al. 2025), but three ones are still in the genus *Candida*. Considering the consistency with the above study, we will transfer those three species into *Yamadazyma* in the Taxonomy section.

Candida ascalaphidarum, *Candida nonsorbophila* and *Candida sinolaborantium* were found to be closely related to *Yamadazyma* (Fig. 12). *Candida ascalaphidarum* was located in a separate branch, whereas *C. nonsorbophila* and *C. sinolaborantium* formed a well-supported *Candida nonsorbophila* clade, which indicated that those two lineages may represent two new genera. Here, we just propose *Keqinozyma gen. nov.* for *Candida nonsorbophila* clade, but assigned *C. ascalaphidarum* as *Candida pro tempore* due to the current lack of close relatives. Considering species for which no genome data is available, *Candida heliconiae* and *Candida temnochilae* are closely related to *Candida nonsorbophila* clade in an ITS+D1/D2 LSU rDNA phylogenetic analysis (Fig. 13) and will be recombined in the genus *Keqinozyma* (see Taxonomy below).

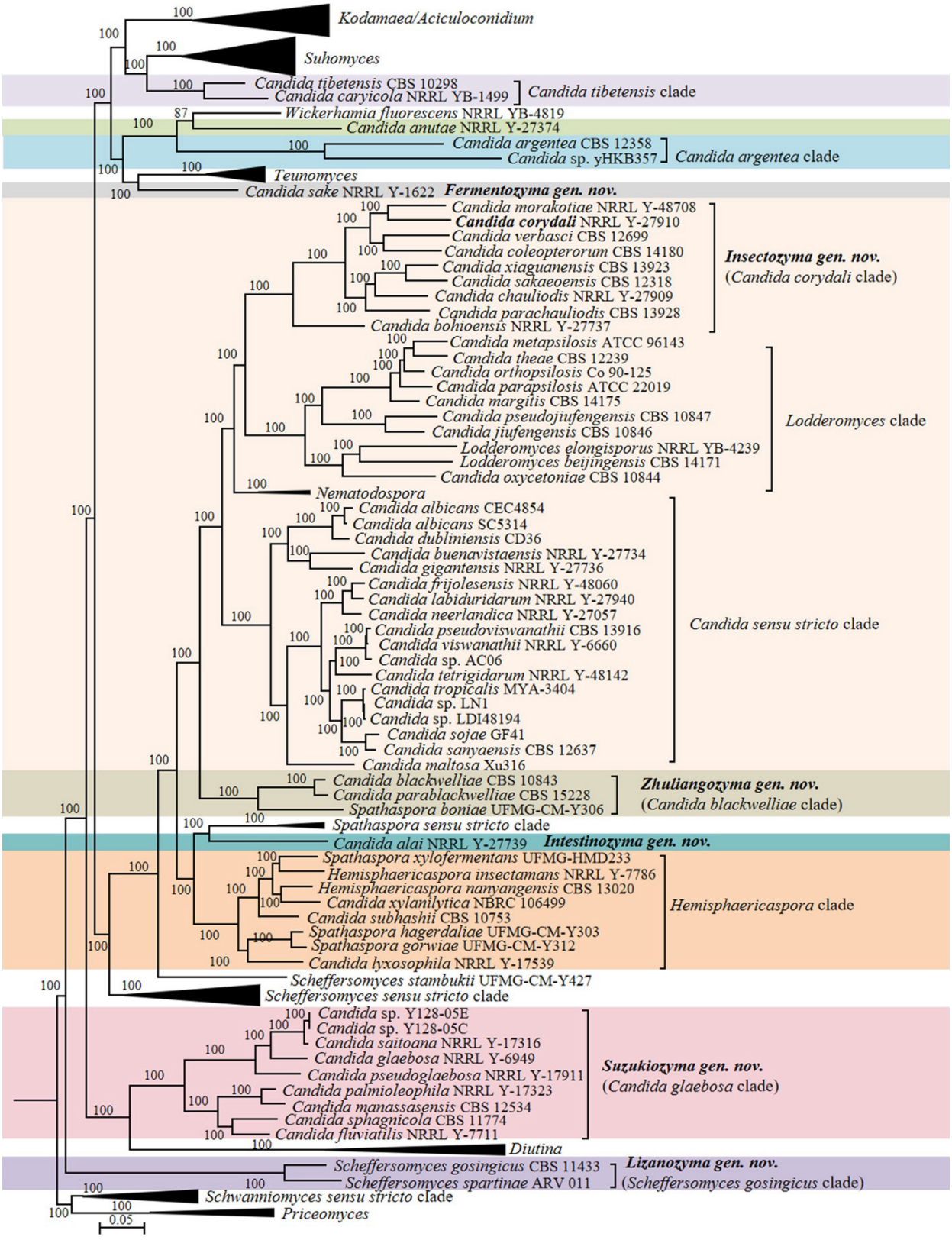

Fig. 9. A phylogenomic sub-tree inferred using 584 single-copy orthologue proteins showing the phylogenetic relationship between *Candida* species and related taxa in *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). Bootstrap percentages of maximum likelihood analysis from 1,000 bootstrap replicates are shown on the major branches. *Nakazawaea holstii* and *Pachysolen tannophilus* were used as outgroups. Bar = 0.05 substitutions per nucleotide position.

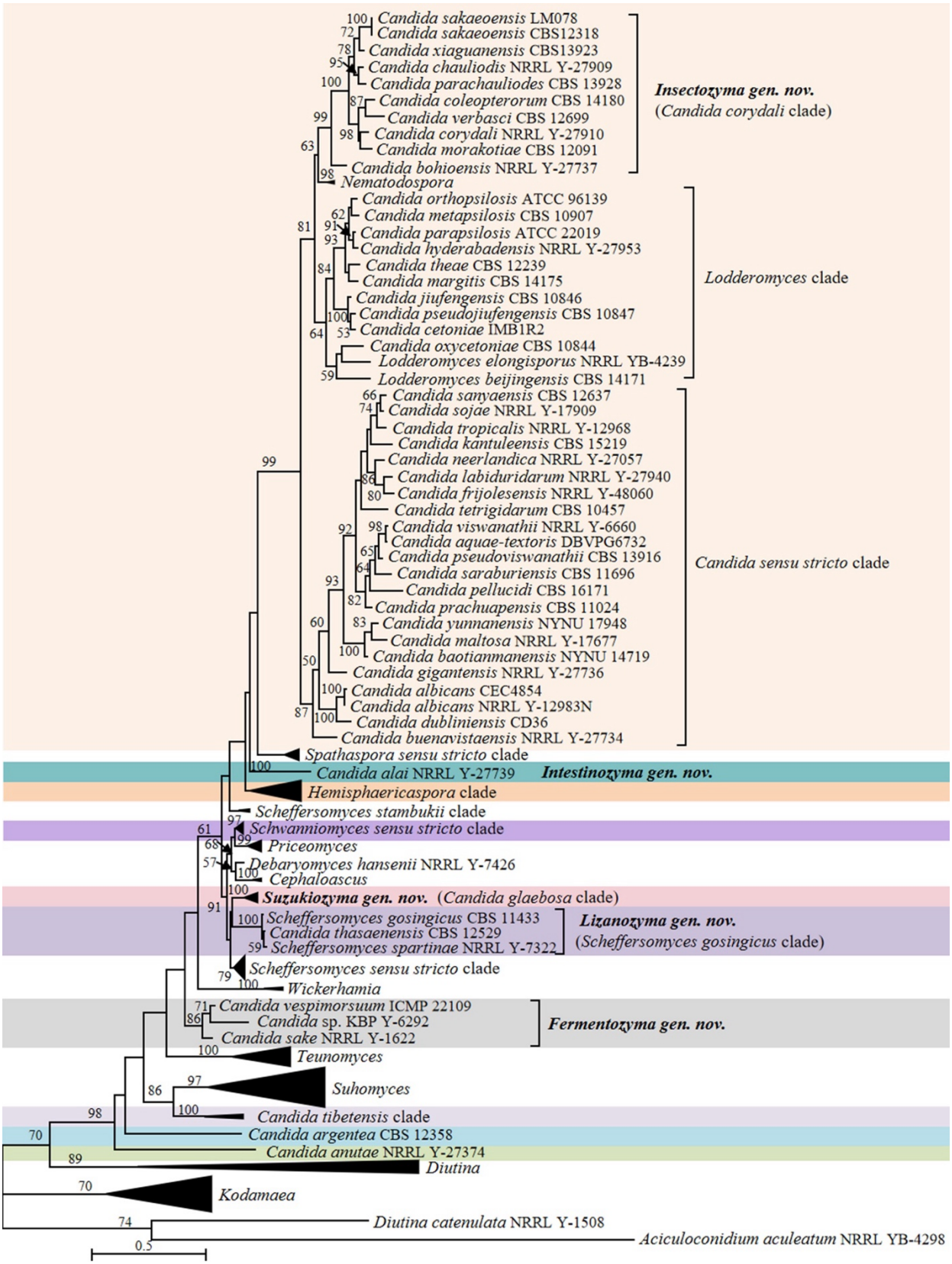

Fig. 10. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida* species and related taxa in *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Aciculoconidium aculeatum* and *Diutina catenulata* were used as outgroups. Bar = 0.5 substitutions per nucleotide position.

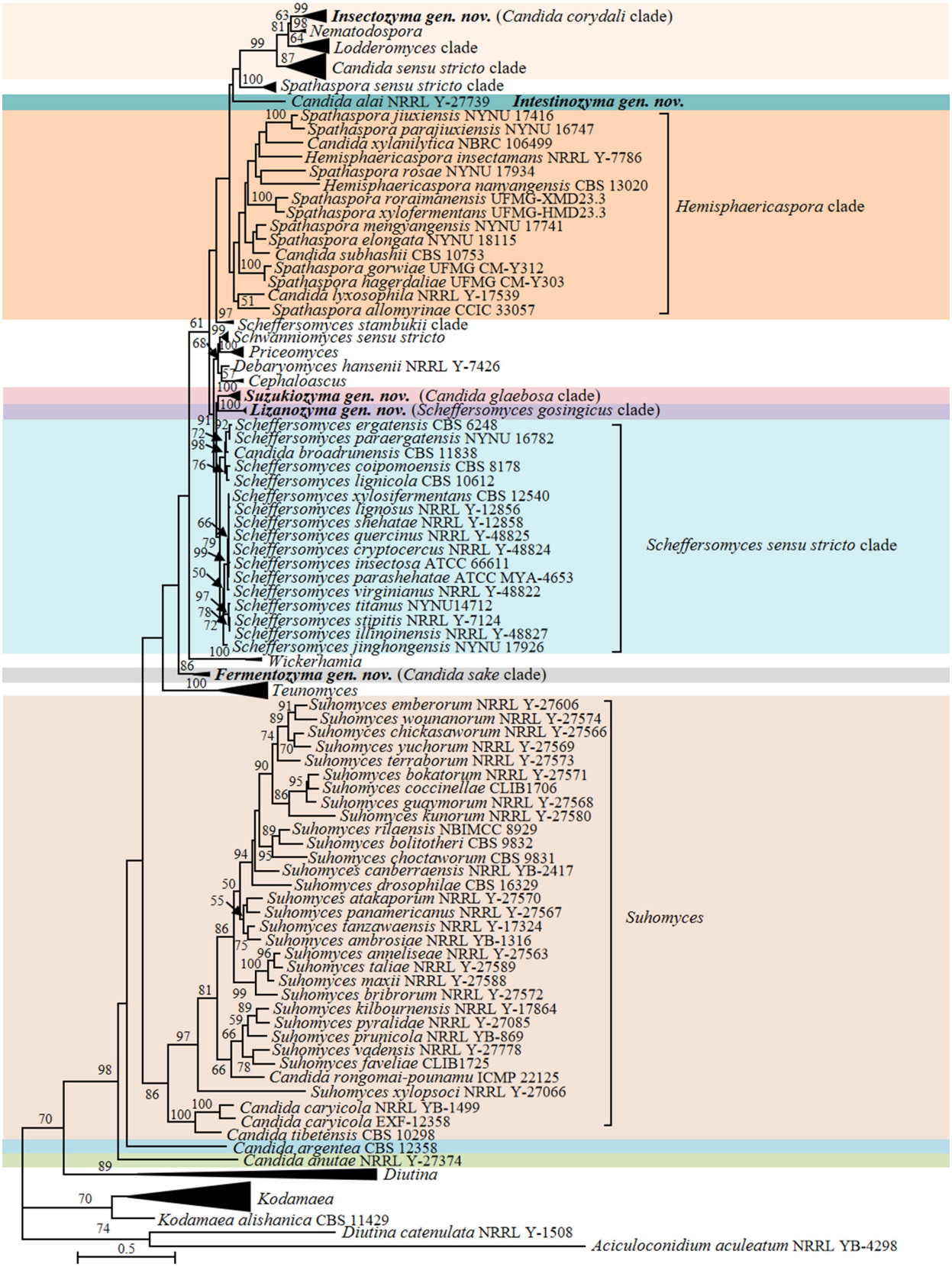

Fig. 11. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida* species and *Hemisphaericaspora*, *Scheffersomyces* and *Suhomyces* in *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Aciculoconidium aculeatum* and *Diutina catenulata* were used as outgroups. Bar = 0.5 substitutions per nucleotide position.

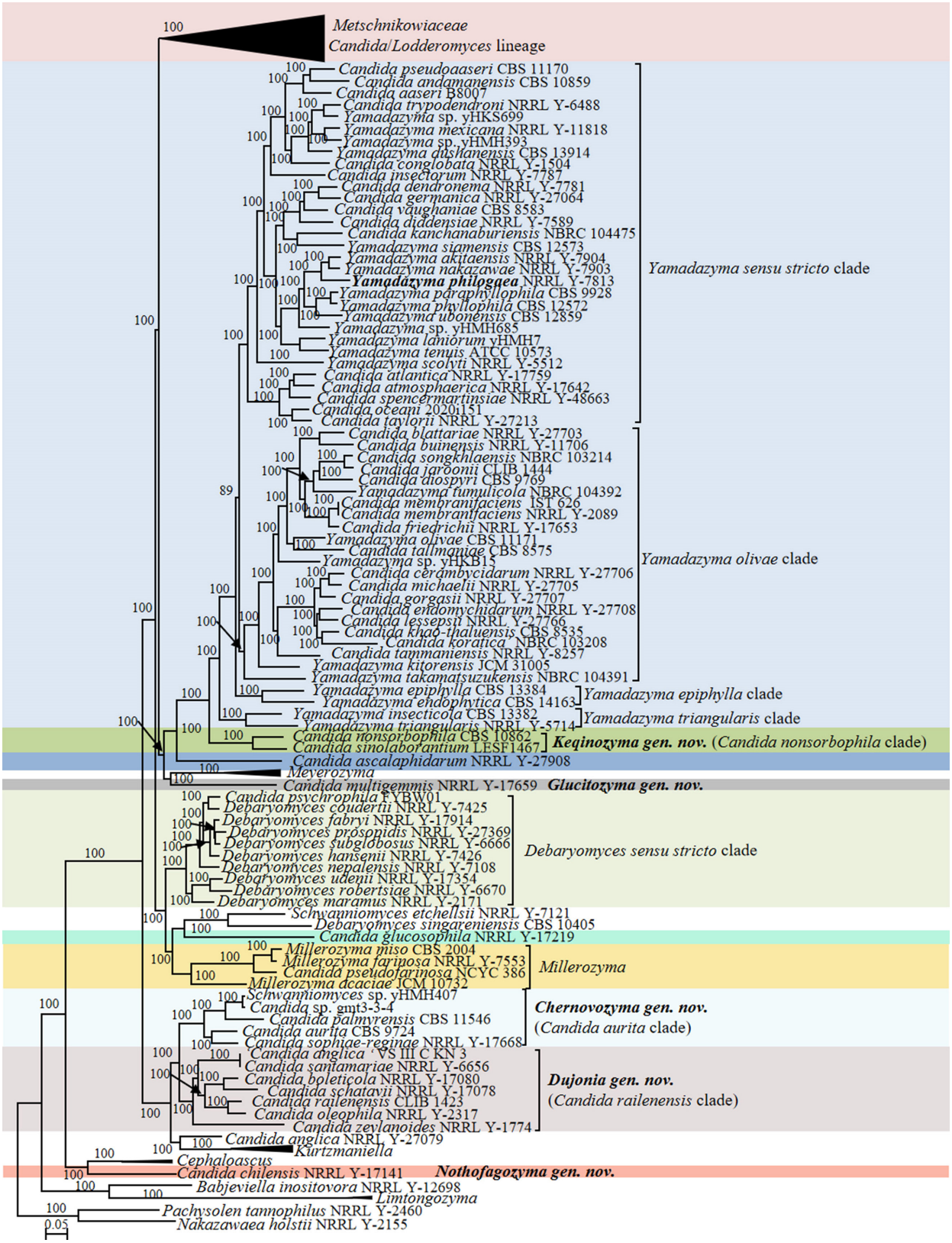

Fig. 12. A phylogenomic tree inferred using 584 single-copy orthologue proteins showing the phylogenetic relationship between *Candida* species and related taxa in *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). Bootstrap percentages of maximum likelihood analysis from 1,000 bootstrap replicates are shown on the major branches. *Nakazawaea holstii* and *Pachysolen tannophilus* were used as outgroups. Bar = 0.05 substitutions per nucleotide position.

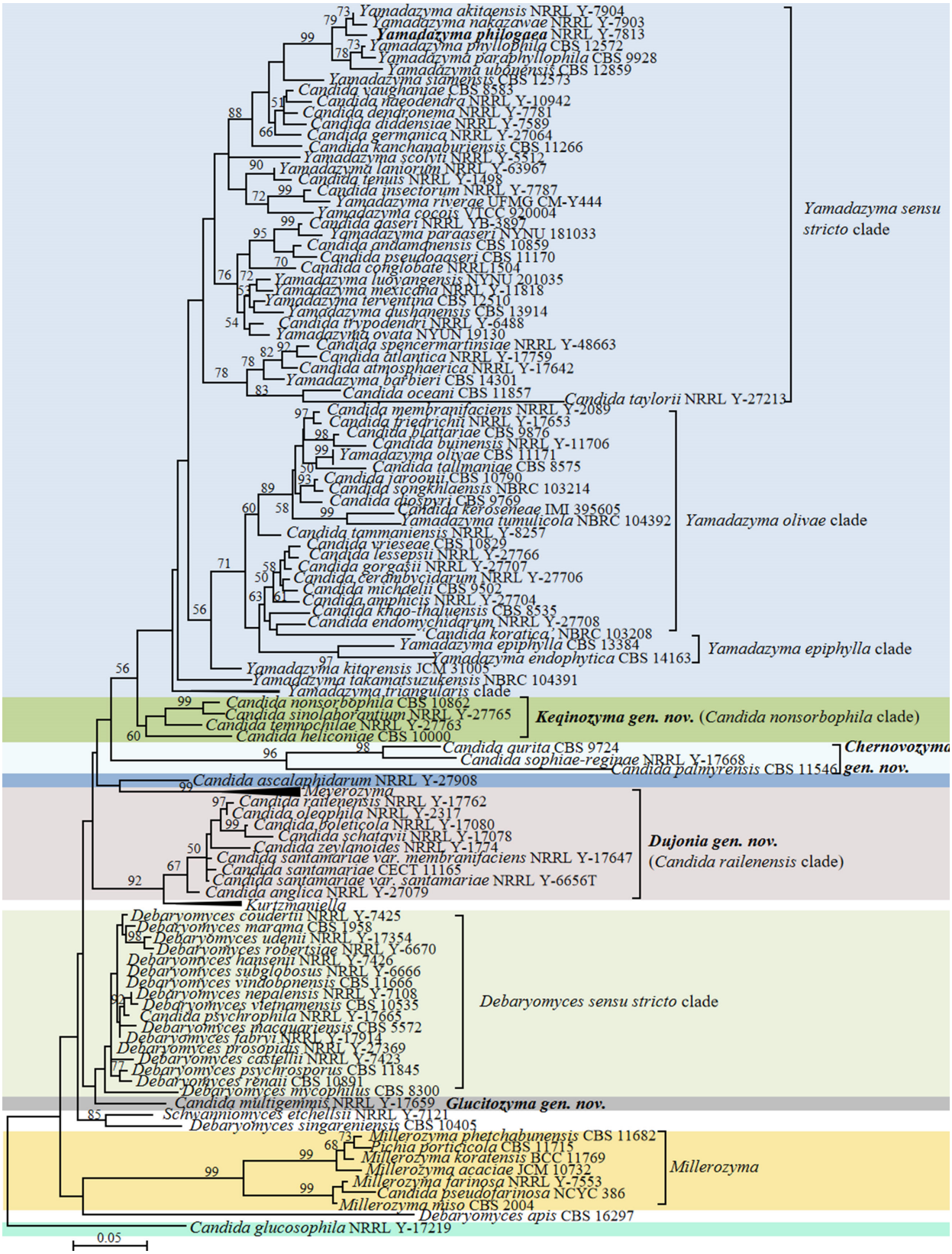

Fig. 13. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida* species and *Debaryomyces*, *Kurtzmaniella*, *Millerozyma* and *Yamadazyma* in *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Candida glucosophila* was used as the outgroup. Bar = 0.05 substitutions per nucleotide position.

Candida species and related genus *Metschnikowia* (*Metschnikowiaceae*, *Serinales*, *Pichiomycetes*)

The re-classification of *Candida* species and related genera in the family *Metschnikowiaceae* has been done recently by Liu et al. (2024b) and resulted in 13 new genera to accommodate species that are distantly related to the core *Candida*-clade in *Debaryomycetaceae*. However, for pragmatic reasons, the circumscription of the large genus *Metschnikowia* was maintained in that study and will be reconsidered in a future study. This decision particularly concerns the classification of *Candida wancherniae* in the *M. agaves* clade, *Candida hawaiiana* in the *M. arizonensis* clade, *Candida golubevii* and *Candida magnifica* in the *M. bicuspidata* clade, *Candida hainanensis* in the *M. caudata* clade and the single-species *Candida danieliae* in the *Metschnikowia* lineage (Fig. 14, Fig. S1 in Liu et al. 2024b). These species will be kept *pro tempore* in *Candida*. The position of *Candida citri* and *Candida xylosifermentans* was also not resolved by Liu et al. (2024b) and we refrain also here from any taxonomic changes until more closely related species are described.

Candida species in the *Saccharomycetes*

In the phylogenomic analysis, a total of 31 *Candida* species in the *Phaffomycetales* (*Saccharomycetes*) have been placed close to the genera *Barnettozyma*, *Cyberlindnera*, *Phaffomyces*, *Starmera* and *Wickerhamomyces* (Fig. 15). The results of the analysis revealed several taxonomic conflicts and showed that several large genera in the order *Phaffomycetales* are polyphyletic. The genera *Barnettozyma*, *Millerago*, and *Phaffomyces* formed a well-supported clade, in which *Millerago* was nested inside a polyphyletic genus *Barnettozyma* (Fig. 15). *Phaffomyces* formed a well-supported clade, but members of the genus *Barnettozyma* were placed in three different clades. Two *Candida* species, i.e., *Candida coquimbonensis* and *Candida orba*, clustered within the genus *Phaffomyces*, suggesting they should be transferred to this genus.

Candida species and related genera *Barnettozyma*, *Millerago* and *Phaffomyces* (*Phaffomycetaceae*, *Phaffomycetales*, *Saccharomycetes*)

The *Barnettozyma sensu stricto* clade includes the type of the genus, *Barnettozyma populi*, and the type of the former genus *Zygowilliopsis* (Kudryavtsev 1960), *Zygowilliopsis californica* (current name *Barnettozyma californica*), which is also the type species of the genus *Zygohansenula*. *Candida sanyiensis* clustered in the *Barnettozyma sensu stricto* clade, suggesting this species should be transferred to this clade. Whether the names *Barnettozyma*, *Zygohansenula* or *Zygowilliopsis* will be selected for this clade will be decided after discussions with the yeast taxonomic community. Consequently, *C. sanyiensis* is kept as *pro tempore* in the genus *Candida* at present. Other species were placed in three subclades that formed a well-supported clade with *Phaffomyces*. The subclades included (i) *Barnettozyma siamensis*, *Barnettozyma botsteinii*, and *Candida montana*; (ii) *Millerago* and *Candida ficus*; (iii) *Barnettozyma pratensis*, *Barnettozyma salicaria*, *Barnettozyma wickerhamii*, *Candida norvegiva* and *Candida qinlingensis*. The phylogenetic analyses convincingly demonstrated the taxonomic conflict between *Barnettozyma*, *Millerago*, and *Phaffomyces*, and additionally showed that the genus *Barnettozyma* in its present circumscription is not monophyletic. When restricted to its core, the composition of *Barnettozyma* (= *Zygowilliopsis* = *Zygohansenula*) must be revised, addressing the classification of the above subclades. This is also supported by the genomic metrics for the *Barnettozyma* clade showing AAI values of 64.52–86.96% and POCP values of 81.56–95.37%, both falling within the range of the generic boundaries as observed by Liu et al. (2024a). However, the absence of unique genes (PAPO: 0) suggests that *Barnettozyma* might be phylogenetically heterogeneous. Here, we refrain from further taxonomic decisions on the matter and prefer to discuss this with the broader yeast taxonomy community.

Candida ficus and the genus *Millerago* clustered together in the phylogenomic tree (Fig. 15). Recently, García-Acero et al. (2024) proposed the new genus *Millerago* to accommodate *Candida galis* and the newly described species *Millerago phaffii* based on the ITS+LSU rDNA sequences and phylogenomic analyses. García-Acero et al. (2024) did not place *C. ficus* in the genus *Millerago* because this species formed a long branch near *Millerago* in the D1/D2 LSU rDNA-based tree and suggested leaving *C. ficus* in its current taxonomic position and resolving this in the future. A recent phylogenomic analysis demonstrated that *C. ficus* and *C. galis* form a well-supported clade, with genetic distances visually comparable to those in neighboring clades (Opulente et al. 2024). To determine whether these two species could be grouped into a single clade, we estimated genomic metrics for this lineage (Table 1). The metrics for *Millerago*+*Candida ficus* showed the following ranges: AAI (74.47–89.67%), POCP (85.02–92.25%) and PAPO (5), suggesting that they fall within the values for genera previously observed in *Saccharomycetaceae* (Liu et al. 2024a). These results support a close relationship between *C. ficus* and the genus *Millerago* and further highlight the superior resolution of phylogenomic trees compared to LSU rDNA-based trees. Therefore, we suggest to merge *C. ficus* to the genus *Millerago*.

Candida montana and *B. siamensis* formed a well-supported clade in our phylogenomic analysis (Fig. 15) that was distantly positioned to the *Barnettozyma sensu stricto* clade, suggesting that the two clades might represent distinct genera. This observation agrees with previous phylogenomic analyses (Shen et al. 2018; Opulente et al. 2024). *Barnettozyma botsteinii* was not included in earlier studies. This species occupied a basal position to the clade formed by *C. montana* and *B. siamensis* (Fig. 15). Similarly to *B. siamensis*, this species requires to be reclassified due to its distant position from the *Barnettozyma sensu stricto* clade. We explored the genetic heterogeneity in *Barnettozyma siamensis* clade+*B. botsteinii* and observed AAI values of 72.73–79.96% and POPC values of 87.80–91.36%, falling within the range of the generic values previously observed in *Saccharomycetaceae* by Liu et al. (2024a). Therefore, we suggest to recombine these species into a new genus, for which the name *Gotozyma gen. nov.* (see Taxonomy).

Candida norvegica, *C. qinlingensis*, *B. pratensis,* and *B. wickerhamii* were placed in the *Barnettozyma wickerhamii* clade (Fig. 16). This clade included *B. pratensis,* and *B. wickerhamii*, *B. salicaria*, *C. qinlingensis*, and *C. norvegica*

and was previously resolved in a recent phylogenomic analysis by Opulente et al. (2024), where it received strong (100%) support. Before Kurtzman et al. (2008) reclassified yeast species with saturn-shaped spores based on multi-gene phylogeny and introduced the genus *Barnettozyma*, the genus *Komagataea* was described by Yamada et al. (1994b) based on an LSU and SSU rDNA phylogenetic analysis with *Komagataea pratensis* (basionym: *Williopsis pratensis* Babeva & Reshetova) as the type species. Although Kurtzman et al. (2008) considered the genus *Komagataea* congeneric to *Barnettozyma*, several earlier observations suggested that these clades may represent distinct genera. For example, Naumova et al. (2004) observed that species of *Komagataea* and the *Williopsis sensu stricto* complex have different karyotypes. We propose to reinstate the genus *Komagataea* to accommodate *B. pratensis*, *B. salicaria*, *B. wickerhamii*, *C. norvegica* and *C. qinlingensis* because of the distant relationships between the *B. wickerhamii* and *Barnettozyma sensu stricto* clades, as well as the topology of the phylogenomic tree that showed that the *Barnettozyma sensu stricto* clade branched first within the clade that included the *Phaffomyces*, *Gotozyma*, *Millerago*, and *Komagataea* clades. Our LSU rDNA-based analysis revealed another potential new species in *Komagataea* (Fig. S13), namely the sequence labelled as *B. salicaria* isolate 0H4 (KM103057) and *B. salicaria* isolate 0H7 (KM103057), from surface water in South Africa that differed from the type strain CBS 5456 of *B. salicaria* by 7–39 nt (1.3–6.5%) in the D1/D2 domain of LSU rDNA.

Candida species and related genus *Cyberlindnera* (*Phaffomycetaceae*, *Phaffomycetales*, *Saccharomycetes*)

In the reclassification of the genus *Pichia*, Kurtzman et al. (2008) introduced the genus *Lindnera* for a monophyletic lineage typified by *Lindnera americana* (basionym: *Hansenula bimundalis* var. *americana*). However, since the name *Lindnera* was a homonym of a plant genus, Minter (2009) renamed and reclassified it into *Cyberlindnera*. In our phylogenomic analysis, *Cyberlindnera* has been resolved as a monophyletic lineage consisting of two large clades: *Cyberlindnera sensu stricto* and *Williopsis* (Fig. 17), this topology agreeing with results from earlier phylogenomic studies by Shen et al. (2018) and Opulente et al. (2024). We examined the genetic heterogeneity within this lineage using the genomic metrics. The entire *Cyberlindnera* lineage was characterized by slightly higher heterogeneity (AAI: 61.78–93.06%; POCP: 69.12–96.40%; PAPO: 0) compared to that of genera in the *Saccharomycetaceae* (Liu et al. 2024a). The two clades showed values in the following ranges: *Cyberlindnera sensu stricto* (AAI: 67.15–90.85%, POCP: 76.63–94.72%, PAPO: 2) and *Williopsis* clade (AAI: 63.63–99.97%, POCP: 78.24–99.67%, PAPO: 4) (Table 1). The lower RED score (0.867) calculated for the genus *Cyberlindnera* by Li et al. (2021) suggests that this lineage is likely under-classified and may correspond to the family- or order-level taxon.

Candida takata and *Candida vartiovaarae* occurred in the *Williopsis* clade (Fig. 17) that contains *Williopsis saturnus* (presently *Cyberlindnera saturnus*), the type species of the genus *Williopsis* and some other *Cyberlindnera* species. Like the genus *Hansenula* described below, the genus name *Williopsis* will be reintroduced instead of creating a new genus to accommodate the *Williopsis* clade. As a result, *C. takata* and *C. vartiovaarae* will be transferred into the genus *Williopsis*.

Candida adriatica, *Candida easanensis*, *Candida hungchunana*, *Candida maesa*, *Candida pattaniensis*, *Candida stauntonica* and *Candida taoyuanica* belong to the *Cyberlindnera sensu stricto* clade, which also contains the type species of *Cyberlindnera*, *Cyberlindnera americana* (Fig. 17). As discussed below, most of the sexual species in the clade were previously classified in the genera *Hansenula* and *Pichia*. The *Cyberlindnera sensu stricto* clade also contains *Cyberlindnera rhodanensis*, the type species of the genus *Petasospora* (Boidin & Abadie 1954). Although Kurtman et al. (2008) has considered *Saccharomyces rhodanensis* Ramírez & Boidin (1953), the basionym of *Cyberlindnera rhodanensis*, in their reclassification, neither these authors nor Minter (2009) acknowledged the name *Petasospora* as a potentially competing name for the clade. However, *Petasospora* is a validly published name and predates *Cyberlindnera*, thereby holding taxonomic priority. Therefore, those seven *Candida* species, along with 17 *Cyberlindnera* species, will be transferred to the reinstated and emended genus *Petasospora* as new combinations.

In our phylogenomic analysis, *Candida freyschussii* was placed on a long branch closely related to *Cyberlindnera* (Figs. 15 and 17), which is in agreement with the observations by Opulente et al. (2024). Additionally, in the LSU rDNA-based sequence analysis, this species clustered with the sequence labelled as *Candida* sp. NIAH-01 (GenBank AB703242) from a clinical bovine mastitic milk sample in Japan (Fig. S13). *Candida* sp. NIAH-01 differs from *C. freyschussii* by 38 nucleotides (6%) in the D1/D2 LSU sequence dataset, which indicates that this strain likely represents another species closely related to *C. freyschussii*. Considering its distant relationship to *Cyberlindnera* and the clade containing the type of the genus *Candida*, *Buckleya gen. nov.* is proposed to accommodate *C. freyschussii* and *Candida* sp. NIAH-01.

Candida species and related genus *Starmera* (*Phaffomycetaceae*, *Phaffomycetales*, *Saccharomycetes*)

The genus *Starmera* received good support in the phylogenomics analysis that revealed two clades in the genus, namely the *Starmera sensu stricto* clade and the *Starmera dryadoides* clade (Fig. 17). The same topology and composition were observed in a recent phylogenomic analysis by Opulente et al. (2024). The genus *Starmera* was proposed by Yamada et al. (1998) based on LSU and SSU rDNA sequence analysis to accommodate *Pichia amethionina* and its variety *Pichia amethionina* var. *pachycereana. Pichia amethionina* exhibited several unique morphological and physiological characteristics, which correlated with its phylogenetic divergence from other *Pichia* species. Somewhat later, *Pichia caribaea* was transferred to *Starmera* (Yamada et al. 1999). The genus was further expanded by Kurtzman et al. (2008) to include *Pichia dryadoides* and *Pichia quercuum*, based on their multi-gene phylogenetic analysis of the genus *Pichia*. Two species, *Candida berthetii* and *Candida dendrica*, clustered with *S. dryadoides* and *Starmera quercuum* in the *Starmera dryadoides* clade (Fig. 17).

Our genome-based analyses showed that the genus

Starmera is genetically heterogeneous, as shown by the genomic metrics AAI (61.57–92.68%), POCP (67.37–97.98%), and PAPO (4) (Table 1). Particularly, the POCP values of *Starmera* are lower than those observed in genera of the *Saccharomycetaceae* (Liu et al. 2024a) and some members of the *Metschnikowiaceae* (Liu et al. 2024b). Additionally, the lower RED score (0.823) for *Starmera* calculated by Li et al. (2021) suggests that this lineage is likely under-classified and may correspond to a family- or order-level taxon. Genomic metrics calculated for the two *Starmera* clades (Table 1) indicate a higher consistency of their respective ranges: *Starmera sensu stricto* clade (AAI: 67.88–92.68% and POCP: 81.76–97.98%), and *Starmera dryadoides* clade (AAI: 65.26–83.33% and POCP: 81.67–89.88%).

Kurtzman (2011c) showed that *S. dryadoides* and *S. quercuum* do not require an exogenous source of L-methionine or L-cysteine, whereas the species of *Starmera sensu stricto* clade depend on these two amino acids. This metabolic distinction suggests that *S. dryadoides* and *S. quercuum* may represent a new sister genus to *Starmera*. Thus, we propose the establishment of a new genus, *Liangdongia gen. nov.*, for the *Starmera dryadoides* clade. In agreement with their phylogenetic position in this clade, *C. berthetii* and *C. dendrica* will be transferred to *Liangdongia.* Additionally, *Candida laemsonensis* was placed in the *Starmera dryadoides* clade in our ITS+LSU rDNA-based analysis (Fig. 16), indicating that this species should also be reassigned to *Liangdongia*.

Candida species and related genus *Wickerhamomyces* (*Wickerhamomycetaceae*, *Phaffomycetales*, *Saccharomycetes*)

Our study, along with the previous phylogenomic analysis by Opulente et al. (2024), resolved the genus *Wickerhamomyces* is polyphyletic. Similar to *Barnettozyma*, the genus *Wickerhamomyces* comprises multiple clades that do not form a monophyletic group, with some clades occurring interspersed among other genera (Figs. 15–18, Table S2). Two major clades, i.e., the *Wickerhamomyces sensu stricto* and the *Wickerhamomyces bovis* clades, have been resolved in the phylogenomic analysis. *Wickerhamomyces silvicola* occupied a basal position to the two clades, as well as to the *Phaffomyces-Millerago-Barnettozyma* lineage (Fig. 15). Other clades containing *Wickerhamomyces* species were placed closer to the *Cyberlindnera*, *Starmera,* and *Williopsis* clade. Consequently, the genus *Wickerhamomyces* showed genetic heterogeneity in the analysis of genomic metrics (AAI: 56.06–100.00%; POCP: 44.43–99.82%; PAPO: 0). The genus *Wickerhamomyces* contained six clades and three single-species lineages that might represent genera based on the phylogenomic analysis and the genome-based indexes (Figs. 15 and 17, Table 1). *Candida jianshihensis*, *Candida quercuum* and *Candida ulmi* were located in the *Wickerhamomyces sensu stricto* clade (Figs. 15–16), and will therefore be transferred to *Wickerhamomyces* as new combinations in the Taxonomy section. The single-species lineage *Wickerhamomyces silvicola* is placed as *pro tempore* at present, although it occupied a basal position to the two clades, as well as to the *Phaffomyces-Millerago-Barnettozyma* lineage (Fig. 15).

Candida dajiaensis, *Candida odintsovae*, *Candida peoriensis* and *Candida yuanshanica* belonged to the *Wickerhamomyces bovis* clade (Fig. 16), which is phylogenetically located near the lineage of *Barnettozyma-Millerago-Phaffomyces*. The clade received good support in both the present phylogenetic analysis and the study by Opulente et al (2024). The clade is characterized by moderate genomic heterogeneity, as indicated by its genomic metrics (AAI: 65.53–98.19%, POCP 82.92–96.62% and PAPO: 2), which are comparable with those observed within genera of *Saccharomycetaceae* (Liu et al. 2024a). Species in the clade have been previously described in the genera *Candida* and *Pichia*. The oldest species, *Wickerhamomyces* (*Pichia*) *bovis*, was also assigned to the genus *Zymopichia* by Novák & Zsolt (1961). However, since the authors did not designate a type species for the genus, this name is nomenclaturally invalid and unavailable for reinstatement. A new generic name, *Taiozyma gen.nov.*, will be proposed for members of this clade in the Taxonomy section.

Candida solani is located in the *Wickerhamomyces pijperi* clade, which is close to the single-species lineage *Wickerhamomyces mucosus* (Fig. 17). The clade has also been resolved in the study by Opulente et al. (2024) and was phylogenetically placed closely to the *Cyberlindnera-Williopsis* lineage. The genetic heterogeneity examined within the clade (AAI 71.66–81.75%, POCP 63.80–92.13%, PAPO: 87) is comparable to that observed in the accepted genera of *Saccharomycetaceae* (Liu et al. 2024a). Although the POCP values appear to be somewhat lower, the number of 87 shared orthologs was high (Table 1). The species *Wickerhamomyces mucosus* was originally described as *Pichia mucosa* by Wickerham & Kurtzman (1971). Later, Muller & Kock (1986) reassigned this species to the newly established genus *Waltiozyma*. However, Kurtzman et al. (2008) transferred this species once again, moving it from *Waltiozyma* to *Wickerhamomyces* based on a multigene analysis. Based on our analyses, we propose to reinstate the genus *Waltiozyma* for the *Wickerhamomyces mucosus*+ *Wickerhamomyces pijperi* lineage*.* Another clade, closely positioned to the *Cyberlindnera-Williopsis* lineage and comprising *Wickerhamomyces hampshirensis* and *Wickerhamomyces strasburgensis*, will be reclassified due to its distant relationship with the *Wickerhamomyces sensu stricto* clade. While *Wickerhamomyces hampshirensis* has been originally described in the genus *Pichia*, *Wickerhamomyces strasburgensis* has been previously classified in the genera *Saccharomyces* (basionym: *Saccharomyces strasburgensis*), *Petasospora* and *Zymopichia*. Because the generic name *Zymopichia* is invalid, and *Saccharomyces* and *Petasospora* phylogenetically belong to different phylogenetic lineages, we propose to accommodate these two species in a new genus *Xingzhongia gen. nov.* (see Taxonomy section below).

Candida namnaoensis and *Candida ponderosae* are positioned within the *Wickerhamomyces chambardii* clade, which is phylogenetically related to the genus *Starmera* (Fig. 17). This observation is in agreement with the analysis by Opulente et al. (2024). Because this clade is distant from the type lineage of *Wickerhamomyces*, we propose to accommodate these yeasts in a new genus, *Ruyongia gen. nov.* Another species, *Wickerhamomyces kurtzmanii*, occupied a basal position in *Wickerhamomycetaceae*, which seems to represent a new genus. But we place it as *Wickerhamomyces pro tempore* at present, which will be resolved in the future.

Candida silvicultrix, *Wickerhamomyces anomalus* (syn.

Hansenula anomala, the type species of the genus *Hansenula*) and four other *Wickerhamomyces* species occurred in the *Hansenula* clade (Fig. 17). This clade is positioned closer to the *Cyberlindnera-Williopsis* lineage and the genus *Starmera*, as indicated in the phylogenomic tree (Fig. 17) and the recent study by Opulente et al. (2024). The genus *Hansenula* was distinguished from *Pichia* based on phenotypic characteristics, particularly in the assimilation of nitrate – *Hansenula* species assimilating nitrate, whereas *Pichia* species not utilizing this compound (Stelling-Dekker 1931; Kurtzman 1984a, b; Bhunjun et al. 2024). Kurtzman (1984c) argued that nitrate assimilation could not serve as a genus defining character, as DNA-DNA reassociation values among phenotypically similar species of *Pichia* and *Hansenula* species indicated a close taxonomic relationship. Consequently, *Hansenula* was synonymized under *Pichia*, leading to an expanded concept of the genus *Pichia* that included 91 species (Kurtzman 1998). Subsequent phylogenetic analyses based on rDNA and multigene sequences revealed that this broadened concept of *Pichia* was highly polyphyletic (Billon-Grand 1989; Liu & Kurtzman 1991; Yamada et al. 1994a, b, 1995a, b, 1998; Kurtzman & Robnett 1998; Kurtzman 2006; Kurtzman et al. 2008). As a result, several genera were split from *Pichia* (as adopted by Kurtzman 1998), including *Barnettozyma*, *Cyberlindnera* (originally *Lindnera*), *Kregervanrija*, *Kodamaea*, *Komagataella*, *Kuraishia*, *Nakazawaea*, *Phaffomyces*, *Ogataea*, *Saturnispora*, *Starmera*, *Yamadazyma,* and *Wickerhamomyces* (Bhunjun et al. 2024). *Pichia anomala* (formerly classified as *Hansenula anomala*) was reassigned to the genus *Wickerhamomyces* based on a multigene sequence analysis (Kurtzman et al. 2008).

Our phylogenomic analysis showed that *H. anomala* (currently named *Wickerhamomyces anomalus*) and *Pichia myanmarensis*, *C. silvicultrix*, and 10 other *Wickerhamomyces* species formed a well-supported *Hansenula* clade. This clade exhibited moderate genetic heterogeneity (AAI: 68.07–84.27%; POCP: 80.37–94.72%; PAPO: 11), with genomic metrics in the range of those reported for genera in *Saccharomycetaceae* (Liu et al. 2024a). This clade appeared distinct from the other *Wickerhamomyces* species, as well as from *Barnettozyma, Cyberlindnera* and *Phaffomyces* (Figs. 17–18), suggesting that the *Hansenula* clade does not belong to the genus *Wickerhamomyces*.

Kurtzman et al. (2008) and Kurtzman (2011c) argued against the reintroduction of *Hansenula* and discussed the reclassification of *Pichia anomala*. While considering the relatedness of *P. anomala* to *C. silvicultrix*, *Pichia ciferrii*, *Pichia subpelliculosa*, *Pichia sydowiorum* and *Pichia lynferdii* (i.e., the *Hansenula* clade in Fig. 17), Kurtzman (2011c) suggested that these species belonged to the large *Wickerhamomyces* clade, as indicated by the multi-gene phylogenetic analysis performed by Kurtzman et al. (2008). The taxonomic history of *Saccharomyces anomalus* (the original name of *P. anomala*) is complex, having undergone transitions through *Willia* (homonym of a moss) and *Hansenula*. The situation was further complicated by an older heterotypic synonym, *Saccharomyces sphaericus*, later synonymized with *H. anomala*, though no type material was preserved. The lack of type material for reliable authentication rendered these names impractical, even if not always formally invalid. As Kurtzman (2011c) indicated, the oldest valid name associated with available type material for a heterotypic synonym of *H. anomala* was *Endoblastoderma pulverulentum*. Although a neotype was proposed for *H. anomala*, two different strains were independently selected around the same time by Lodder & Kreger-van Rij and Wickerham, respectively. However, no formal proposal was made to conserve *Hansenula* using a neotype of either *S. sphaericus* or *S. anomalus*, or by adopting *E. pulverulentum* as a conserved name (Kurtzman 2011c). Consequently, Daniel et al. (2012) proposed conserving the name *Wickerhamomyces* against *Hansenula* and rejecting the questionable name *Saccharomyces sphaericus* Sacc. 1877. They designated strain NRRL Y-366 as an epitype to the newly designated lectotype of *S. anomalus*. Furthermore, these authors indicated that the concerns expressed by Kurtzman (2011c) about the lack of type material did not render the names *S. sphaericus* and *S. anomalus* invalid. As a result, the name *Hansenula* was validly published, thus holding priority over *Wickerhamomyces* (Daniel et al. 2012). Additionally, the latter authors suggested that *Endoblastoderma* was a synonym of *Saccharomyces*, rather than *Hansenula*.

The conservation of *Wickerhamomyces* over *Hansenula* was preferred because *Hansenula* was highly polyphyletic, whereas *Wickerhamomyces* was adopted for a monophyletic group at that time (Daniel et al. 2012). If future taxonomic revisions will indicate that the types of *Wickerhamomyces* and *Hansenula* belong to different genera, both names are available from a nomenclatural point of view. Malimas et al. (2023) reintroduced *Hansenula* and assigned nine species to this genus based on pair-wise sequence similarities of the LSU rDNA. However, *C. silvicultrix*, *Wickerhamomyces queroliae*, *Wickerhamomyces spegazzinii* and *Wickerhamomyces sylviae,* belonging to the *Hansenula* clade (Figs. 17–18), were not assigned to *Hansenula* by Malimas et al. (2023). Therefore, those four species will be transferred to *Hansenula* in the Taxonomy section below.

The impact of reductive evolution, HTGs, hybridization (or alloaneuploidy) and introgressions on the values of genomic metrics

Genomic metrics, such as AAI and POCP, have been used as valuable approaches to delineate genera for bacteria (Qin et al. 2014; Kuzmanović et al. 2022; Montecillo 2023). Recently, those two approaches were recommended to delimit yeast genera (Liu et al. 2024a, b). However, some evolutionary factors, such as reductive evolution, hybridization, horizontal transfer genes (HTGs), introgressions, and alloaneuploidy, may affect the values of AAI and POCP. To address those issues, we used the *Dipodascus/Galactomyces/Geotrichum* lineage, *Saccharomyces* and *Starmerella* as examples to evaluate those impacts.

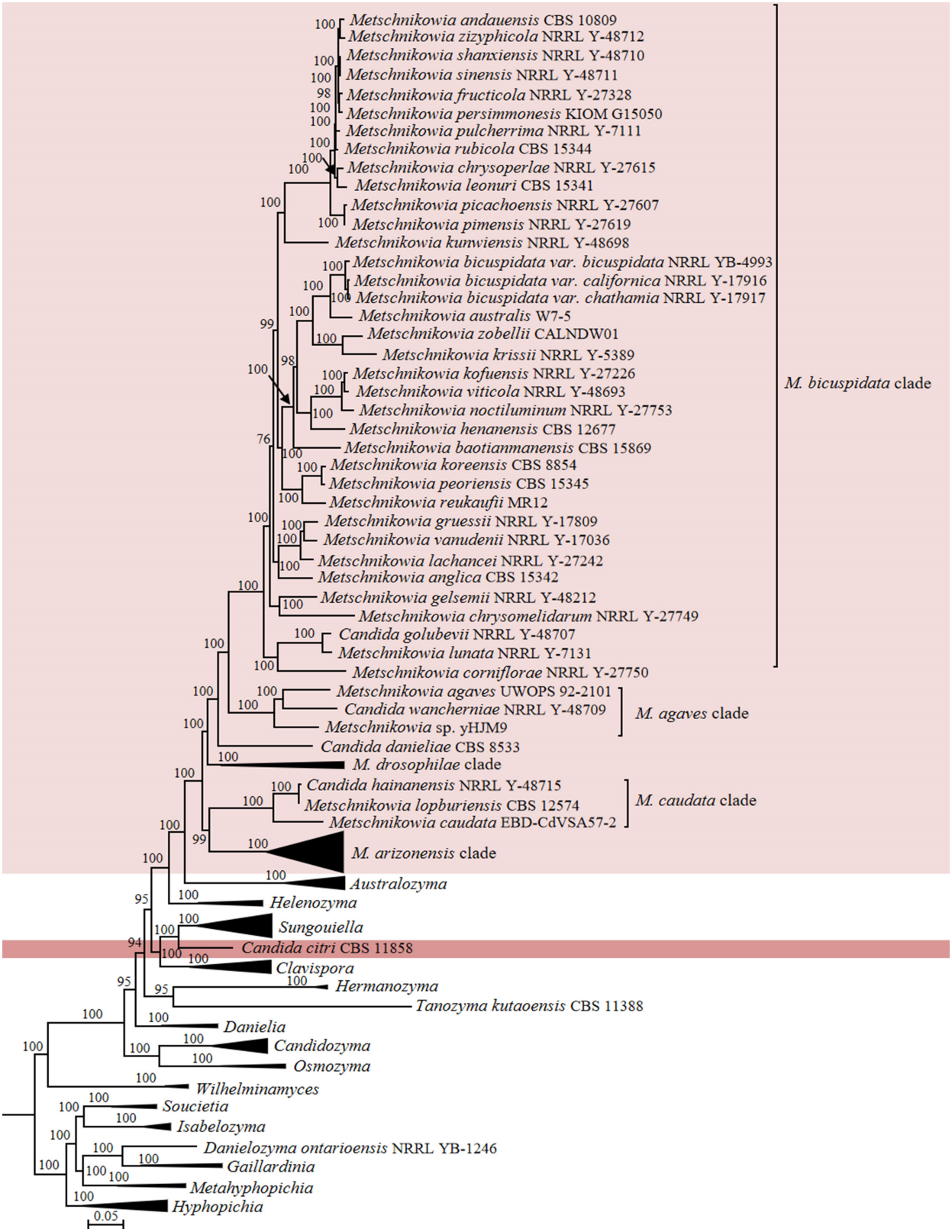

Fig. 14. A phylogenomic sub-tree inferred using 584 single-copy orthologue proteins showing the phylogenetic relationship between *Candida* species and related taxa in *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). Bootstrap percentages of maximum likelihood analysis from 1,000 bootstrap replicates are shown on the major branches. *Nakazawaea holstii* and *Pachysolen tannophilus* were used as outgroups. Bar = 0.05 substitutions per nucleotide position.

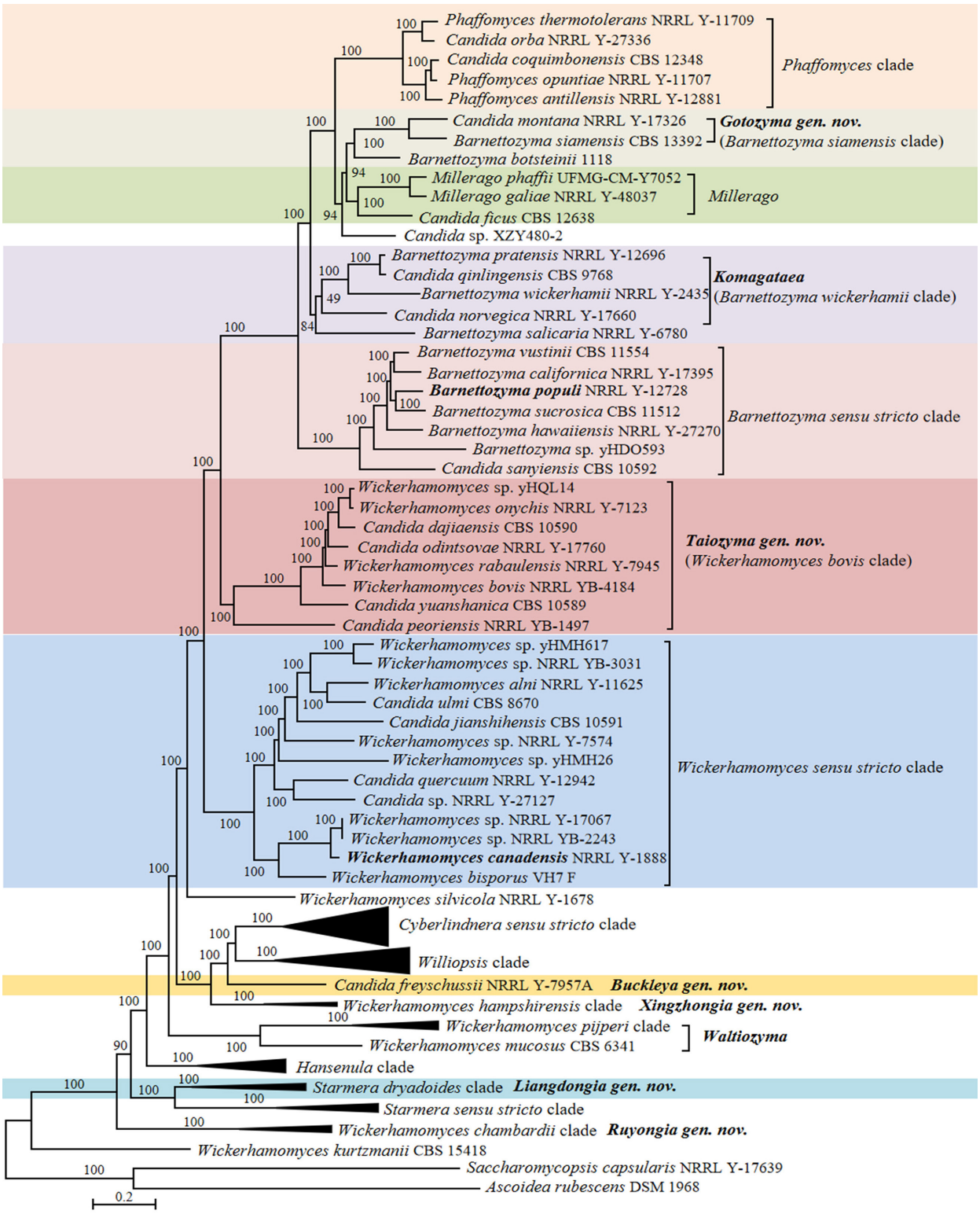

Fig. 15. Phylogenomic tree inferred using 652 single-copy orthologue proteins showing the phylogenetic relationship between *Candida* species and *Barnettozyma*, *Millerago*, *Phaffomyces* and *Wickerhamomyces* in *Phaffomycetales* (*Saccharomycetes*). Bootstrap percentages of maximum likelihood analysis from 1,000 bootstrap replicates are shown on the major branches. *Ascoidea rubescens* and *Saccharomycopsis capsularis* were used as outgroups. Bar = 0.2 substitutions per nucleotide position.

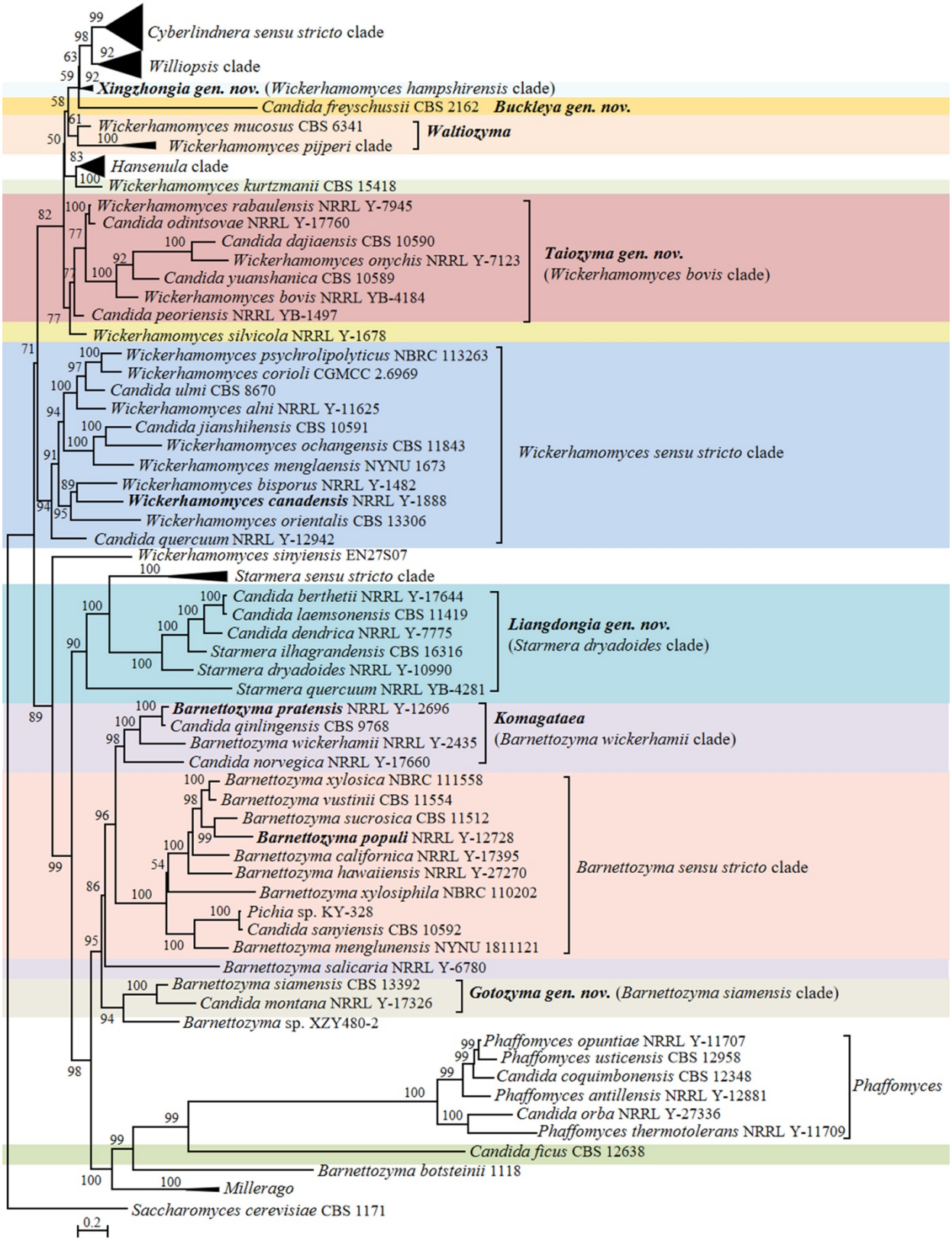

Fig. 16. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida* species and related taxa in *Phaffomycetales* (*Saccharomycetes*). Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Saccharomyces cerevisiae* was used as the outgroup. Bar = 0.2 substitutions per nucleotide position.

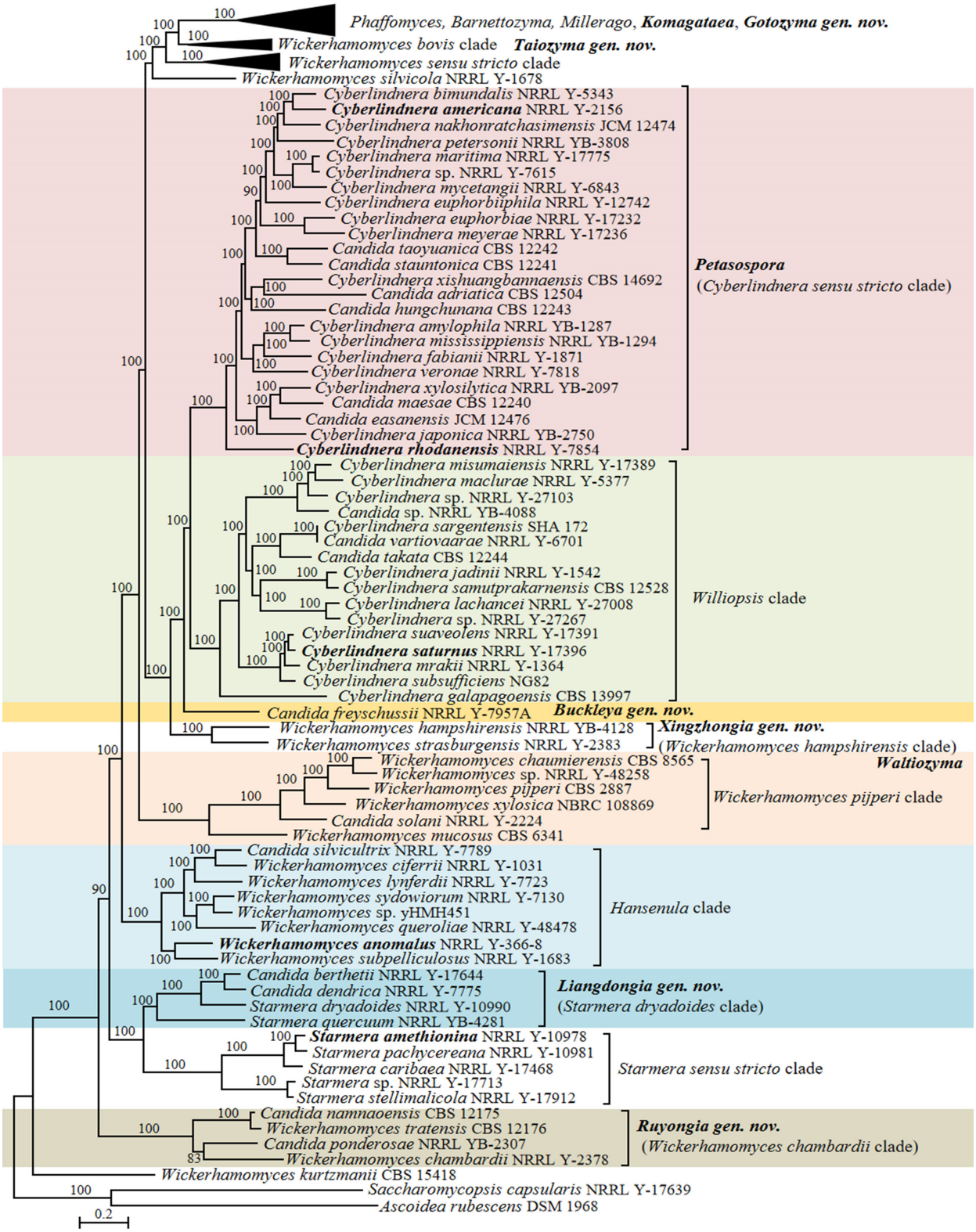

Fig. 17. Phylogenomic tree inferred using 652 single-copy orthologue proteins showing the phylogenetic relationship between *Candida* species and the genera *Cyberlindnera* and *Wickerhamomyces* in *Phaffomycetales* (*Saccharomycetes*). Bootstrap percentages of maximum likelihood analysis from 1,000 bootstrap replicates are shown on the major branches. *Ascoidea rubescens* and *Saccharomycopsis capsularis* were used as outgroups. Bar = 0.2 substitutions per nucleotide position.

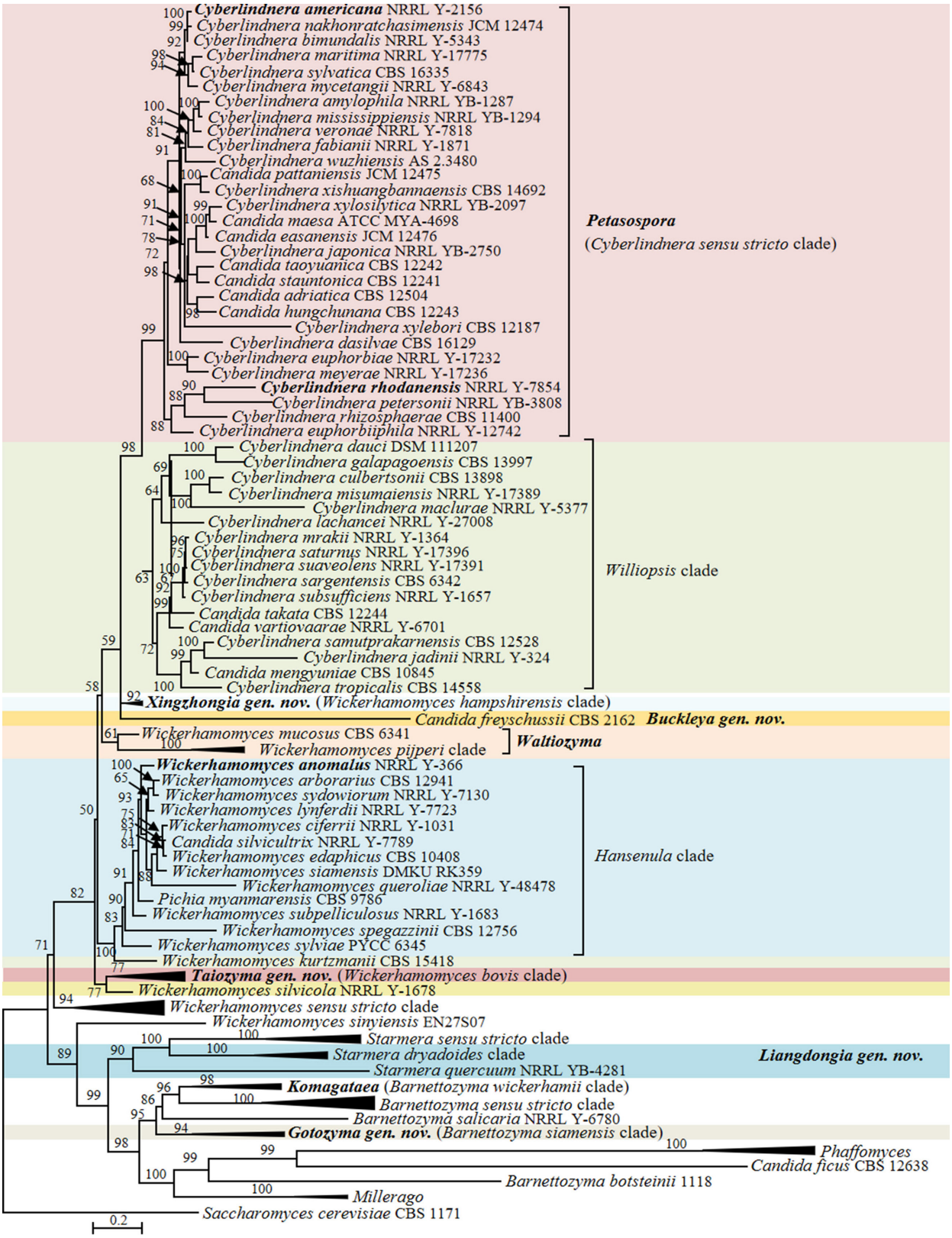

Fig. 18. Phylogenetic tree inferred using the combined ITS and D1/D2 LSU rDNA showing the phylogenetic relationship between *Candida* species and related taxa in *Wickerhamomycetaceae* (*Phaffomycetales*, *Saccharomycetes*). Bootstrap percentages of ML analysis over 50% from 1,000 bootstrap replicates are shown on the major branches. *Saccharomyces cerevisiae* was used as the outgroup. Bar = 0.2 substitutions per nucleotide position.

Most species of *Dipodascus/Galactomyces/Geotrichum* lineage seem to be hybrid (or alloaneuploidy) due to having a higher rate of duplicated BUSCOs (Table S1). Therefore, this lineage was selected to evaluate the impact of hybridization (or alloaneuploidy) on AAI and POCP values. We calculated pairwise AAI and POCP values using the three datasets described in the method section and conducted linear regression analysis. Our results demonstrated that the AAI and POCP values of All_genome_dataset (with paralog-OGs, containing hybrid) and that of Subgenome_1_dataset and Subgenome_2_dataset (without paralog-OGs, omitting hybrid) are remarkably consistent (Table 2). Furthermore, extremely high consistency was observed in the AAI values of the same pairwise species with and without paralog-OGs. When evaluating the impact of hybridization (or alloaneuploidy) on AAI analysis using Subgenome_1_dataset and Subgenome_2_dataset (Fig. 19), the slopes of the linear regression equations were both close to 1 (1.08 or 1), indicating that hybridization (or alloaneuploidy) had no significant impact on the overall level of AAI values within the lineage. And high R^2 values (0.98 or 1) further confirmed that the linear relationship between the two sets of AAI values was stable with no systematic bias caused by the removal of paralog-OGs. When evaluating the impact of hybridization (or alloaneuploidy) on the POCP analysis (Fig. 20), the POCP values of the same pairwise species combinations also showed high consistency across different datasets. Although local variations in hybridization levels or gene duplication levels resulting from alloaneuploidy among different species led to slight deviations of some points in the scatter plots, the regression equations based on the two subgenome datasets still maintained high slopes (1.03 or 0.912), and the R^2 values (0.92 or 0.97) were also at a high level. The above analyses indicate that the effect of hybridization (or allopolyploidy) seems not to cause a major impact on AAI and POCP values.

Table 2 The results of AAI and POCP values of *Dipodascus/Galactomyces/Geotrichum* lineage analyzed based on different genome (or subgenome) datasets

Datasets	AAI values (%)	POCP values (%)
All_genome_dataset	61.01–91.09	60.12–94.63
Subgenome_1_dataset	59.58–90.80	57.10–92.60
Subgenome_2_dataset	60.53–89.71	62.91–93.10

Note: All_genome_dataset includes all proteins (genes) for each species of *Dipodascus/Galactomyces/Geotrichum* lineage; Subgenome_1_dataset contains orthologous groups (OGs) without paralogous genes; Subgenome_2_dataset is composed of OGs without paralogous genes and one copy of paralogous genes that was randomly selected from the paralog-containing OGs.

Table 3 The AAI and POCP values calculated based on different datasets with/without HTGs and reductive evolution

Taxa	1	2	3	4	5	6	7	8
Starmerella	56.87–89.06%	56.92–89.11%	57.76–90.67%	58.36–91.08%	49.07–93.24%	49.47–93.24%	60.46–97.89%	62.05–97.90%
Starmerella clade 1	72.77–89.06%	72.85–89.11%	74.55–90.67%	75.21–91.08%	80.33–93.24%	80.38–93.24%	87.08–97.89%	88.59–97.90%
Starmerella clade 2	56.87–77.34%	56.92–77.40%	57.76–79.36%	58.36–80.05%	49.07–91.12%	49.47–90.89%	60.46–96.58%	62.05–96.98%
Starmerella apicola clade	63.11–70.44%	63.17–70.49%	64.45–71.72%	65.13–72.36%	77.02–85.86%	77.11–85.83%	87.44–93.86%	88.48–94.63%
Starmerella cellae clade	62.67–74.03%	62.67–74.11%	63.83–75.26%	64.48–75.76%	60.03–85.26%	59.80–85.48%	73.52–91.79%	75.25–92.51%
Starmerella sensu stricto clade	66.62–77.34%	66.70–77.40%	68.41–79.36%	69.19–80.05%	78.62–91.12%	78.63–90.89%	87.41–96.58%	88.21–96.98%
Starmerella stellata clade	58.45–69.19%	58.50–69.24%	59.45–70.62%	59.97–71.18%	60.00–78.43%	60.52–78.57%	69.78–87.14%	71.41–87.99%

Note: 1, The AAI values calculated based on all proteins (genes) for each species of the clade (genus); 2, The AAI values of the clade (genus) calculated after removal of HTGs; 3, The AAI values of the clade (genus) calculated based on *Starmerella*_90_dataset that contains orthologous groups (OGs) occurring in ≥ 90% species of *Starmerella*; 4, The AAI values of the clade (genus) calculated based on *Starmerella*_95_dataset that contains orthologous groups (OGs) occurring in ≥ 95% species of *Starmerella*; 5, The POCP values calculated based on all proteins (genes) for each species of the clade (genus); 6, The POCP values of the clade (genus) calculated after removal of HTGs; 7, The POCP values of the clade (genus) calculated based on *Starmerella*_90_dataset that contains orthologous groups (OGs) occurring in ≥ 90% species of *Starmerella*; 8, The POCP values of the clade (genus) calculated based on *Starmerella*_95_dataset that contains orthologous groups (OGs) occurring in ≥ 95% species of *Starmerella*.

Starmerella species acquired many HTGs from bacteria or other fungi (Gonçalves et al. 2020, 2022; Pontes et al. 2024). To assess the bias introduced by HTGs on AAI and POCP analyses, we omitted the HTGs from the genome datasets of *Starmerella*, then we calculated the AAI and POCP values and compared them with the results obtained from the whole genome dataset. After removal of the HTGs, the AAI values of *Starmerella* (i.e., 56.92–89.11%) exhibited minor changes

compared to that calculated from the all-genome datasets with HTGs (i.e., 56.87–89.06%). The POCP values of *Starmerella* calculated after removal of HTGs (i.e., 49.47–93.24%) had a slight difference from that calculated based on whole genome datasets (i.e., 49.07–93.24%) (Table 3). Linear regression analysis further confirmed that extremely high consistency was observed in AAI and POCP values of the same pairwise species within this genus before and after removal of HTGs, respectively (Fig. 21). The slopes of the regression equations based on AAI and POCP values were 1 and 0.987, respectively, indicating that the presence or absence of HTGs had no significant impact on the overall levels of these two indicators. High coefficients of determination (R^2 values: 0.98 for AAI; 1 for POCP) further confirmed that the linear relationships of the two sets of AAI and POCP values were stable, and the same pairwise species showed high consistency for the same indicator. Based on these results, it can be inferred that the presence or removal of HTGs had no significant interference with the AAI and POCP analyses.

To evaluate the impact of the reductive evolution on AAI and POCP calculations, two subgenome datasets were created in the method section. Our results demonstrated that the AAI values calculated based on *Starmerella*_90_dataset and *Starmerella*_95_dataset are similar to that calculated based on the whole genome dataset. However, the POCP values calculated based on those two subgenome datasets increased compared to the whole genome dataset without the removal of reductive OGs (Table 3). Linear regression analysis further showed that when evaluating the impact of reductive evolution on AAI analysis (Fig. 22), the slopes of the regression equations and coefficients of determination (R^2) based on the two subgenome datasets were high, indicating that the AAI values calculated based on different subgenome datasets are similar to that calculated based on the whole genome dataset. So reductive evolution may have no significant effect on AAI analysis. In contrast, when evaluating its impact on POCP analysis (Fig. 23), the slopes (0.78 or 0.736) of the linear regression equations deviated significantly from 1, but the R^2 values (0.96) were high, suggesting that the POCP values calculated based on different subgenome datasets had evident differences from that calculated based on the whole genome dataset. Based on the linear regression equations, it can be inferred that reductive evolution may cause an evident increase in POCP results. Thus, it can be concluded that reductive evolution may have a significant impact on POCP analysis (leading to elevated results) but may have no effect on the outcome of the AAI analysis. It is noted that the POCP values of *Starmerella* calculated based on *Starmerella*_90_dataset and *Starmerella*_95_dataset (Table 3) are still much lower than the generic values recommended by Liu et al. (2024a), which indicates that the genus *Starmerella* is still genetically heterogeneous even when omitting the impact of reductive evolution. The higher POCP values of *Starmerella*_90_dataset and *Starmerella*_95_dataset may be caused by the reductive denominator during the POCP analysis.

The genus *Saccharomyces* includes at least two hybrid species, namely *S. bayanus* and *S. pastorianus*, and some hybrid strains, e.g., *S. cerevisiae* × *S. kudriavzevii*. D'Angiolo et al. (2020) demonstrated that the *S. cerevisiae* Alpechin lineage, e.g., strain DBVPG6765, carries abundant *S. paradoxus* introgressions. We used *Saccharomyces* with three datasets described in the method as an example to address introgressions and hybridization (or alloaneuploidy) impacts on the reliability of AAI and POCP analyses. The obtained AAI values of *Saccharomyces*_9_dataset, *Saccharomyces*_10_dataset and *Saccharomyces*_12_dataset were 82.30–97.09%, 82.30–99.39% and 80.66–98.13%, respectively (Table 4). The POCP values of the *Saccharomyces*_9_dataset, *Saccharomyces*_10_dataset and *Saccharomyces*_12_dataset were 95.95–98.42%, 95.95–98.97% and 94.38–98.42%, respectively (Table 4). The above analysis results indicate that the hybridization (or alloaneuploidy) does not have an impact on the AAI and POCP values, which is in agreement with the results from the analysis of *Dipodascus/Galactomyces/Geotrichum* lineage described above. The results from the *Saccharomyces* analysis also indicate that introgression does not cause any bias for the reliability of AAI and POCO analyses (Table 4), but this issue should be studied further using a more robust data analysis.

Genomic insights into multidrug resistance in revised *Candida* species assigned to the new genera

Fifty-five *Candida* species were assigned to 22 newly created genera in this study. Only three *Candida* species, namely, *C. palmioleophila*, *C. sake* and *C. zeylanoides*, are clinical-related yeasts (https://www.atlasclinicalfungi.org/), while the other *Candida* species do not seem to be identified in clinical settings based on the data analysis collected from the latest edition of the *TYTS*, The Yeasts Trust Database (https://theyeasts.org/), the medical database, Atlas of Clinical Fungi (https://www.atlasclinicalfungi.org/), and related references searched from PubMed (https://pubmed.ncbi.nlm.nih.gov/). To evaluate the antifungal resistance profiles of species assigned to the newly created genera in this study based on the genome analysis, we retrieved known antifungal resistance-associated genes of *C. albicans* from NCBI, including: 1) the *ERG11* gene (with mutation sites F126L, Y132F, K143R, F145L, G448E, F449V, G450E, and G464S) associated with azole resistance; 2) the *ERG2* gene (with mutation site F105SfsX23) associated with polyene resistance; 3) the *FKS1* gene (with mutation sites S645P/Y/F and F641Y) associated with echinocandin resistance; 4) the *FUR1* gene (with mutation site F211I) associated with nucleoside analog resistance. Using these genes as reference sequences, we employed the BLASTP software to extract the corresponding genes from the protein sequences of the target species. Subsequently, multiple sequence alignment was performed on the obtained homologous genes to identify differences and similarities in antifungal resistance-associated genes between resistant and susceptible strains. The results (Table S4) showed that no mutations were detected at the sites of the *ERG2*, *FUR1* and *ERG11* genes across all revised *Candida* species assigned to the newly created genera in this study. In the analysis of echinocandin resistance, three *Candida* species that have been reclassified into novel genera in this study, namely *C. sake* NRRL Y-1622 (S645A), *C. multigemmis* NRRL Y-17659 (S645A) and *C. tibetensis* CBS 10298 (S645A), have a mutation in the S645 locus (Table S4). Only one type of amino acid substitution (A) was observed, but no mutations were detected in the F641 locus. This suggests that there may be a certain locus preference in the echinocandin resistance-associated mutations of these reclassified species. In

contrast, the remaining *Candida* species that have been reclassified into novel genera exhibited no mutations at the antifungal resistance-associated gene mutation loci related to various antifungal drugs.

Table 4 The results of AAI and POCP values of *Saccharomyces* analyzed based on different genome datasets

Datasets	AAI values (%)	POCP values (%)
*Saccharomyces*_9_dataset	82.30–97.09	95.95–98.42
*Saccharomyces*_10_dataset	82.30–99.39	95.95–98.97
*Saccharomyces*_12_dataset	80.66–98.13	94.38–98.42

Note: *Saccharomyces*_9_dataset includes only nine natural species; *Saccharomyces*_10_dataset is composed of nine natural species and *S. cerevisiae* DBVPG6765; *Saccharomyces*_12_dataset contains nine natural species and three hybrid species (or strains).

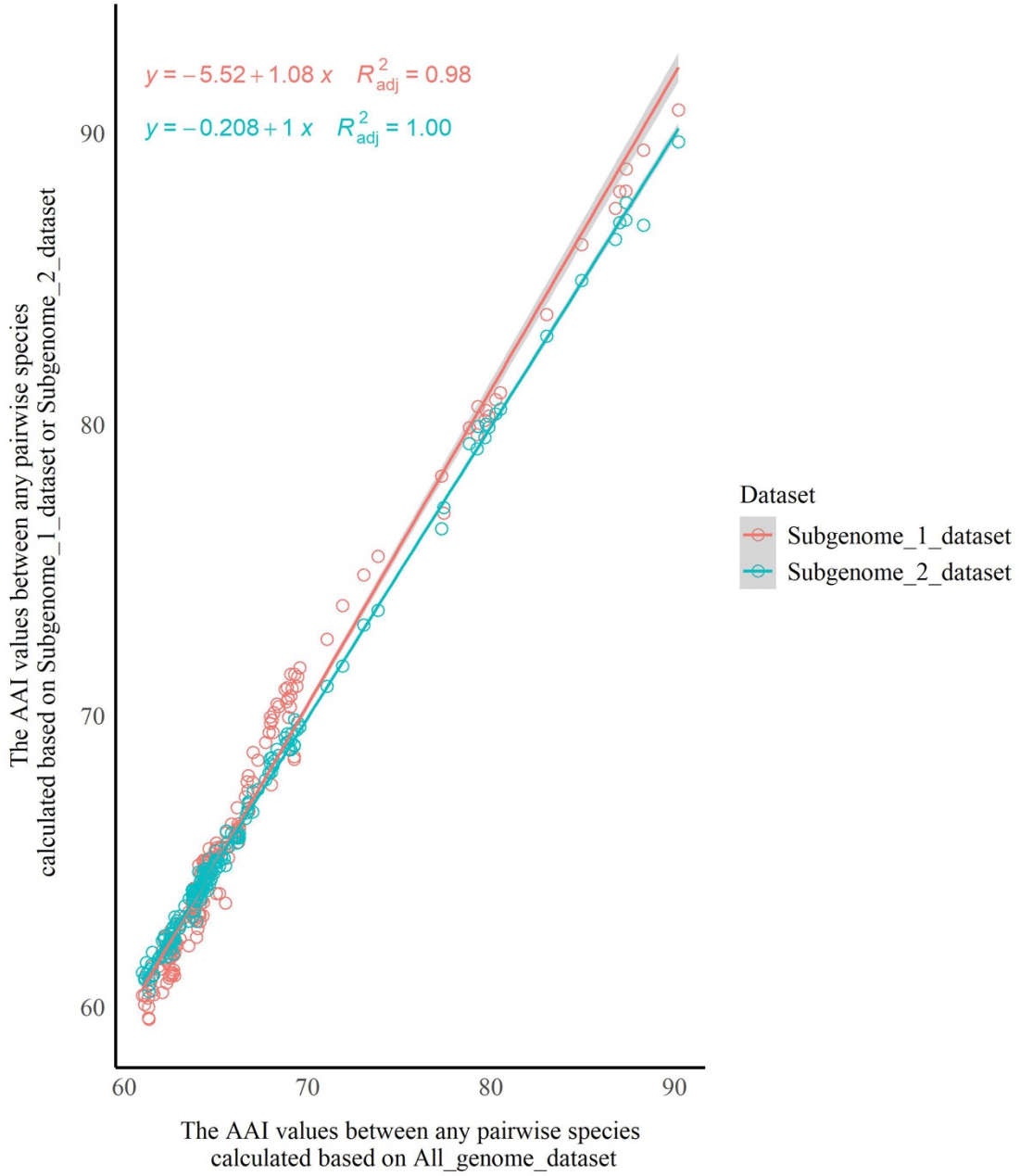

Fig. 19. Linear regression analysis to evaluate the impact of hybridization (or alloaneuploidy) on AAI analysis. The horizontal axis represented AAI values between any pairwise species calculated based on the All_genome_dataset, and the vertical axis represented AAI values for the corresponding species pairs calculated based on Subgenome_1_dataset or Subgenome_2_dataset. If the slope of the linear regression equation was close to 1 and the R^2 value was high, it indicated hybridization (or alloaneuploidy) had no significant interference on AAI analysis. Conversely, a slope noticeably deviating from 1 or a low R^2value suggested that hybridization (or alloaneuploidy) might affect the results of AAI analysis.

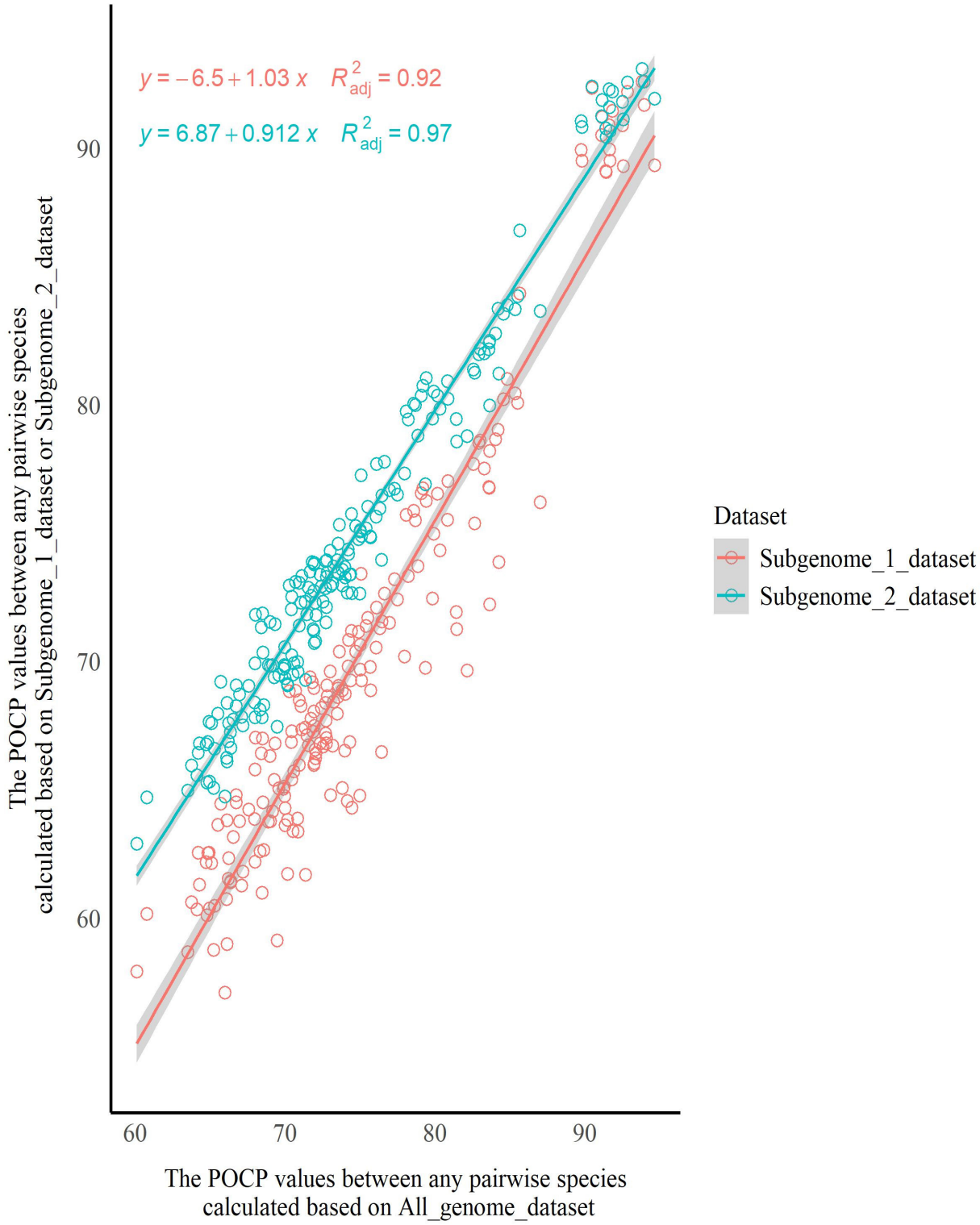

Fig. 20. Linear regression analysis to evaluate the impact of hybridization (or alloaneuploidy) on POCP analysis. The horizontal axis represented POCP values between any pairwise species calculated based on the All_genome_dataset, and the vertical axis represented POCP values for the corresponding species pairs calculated based on Subgenome_1_dataset or Subgenome_2_dataset.

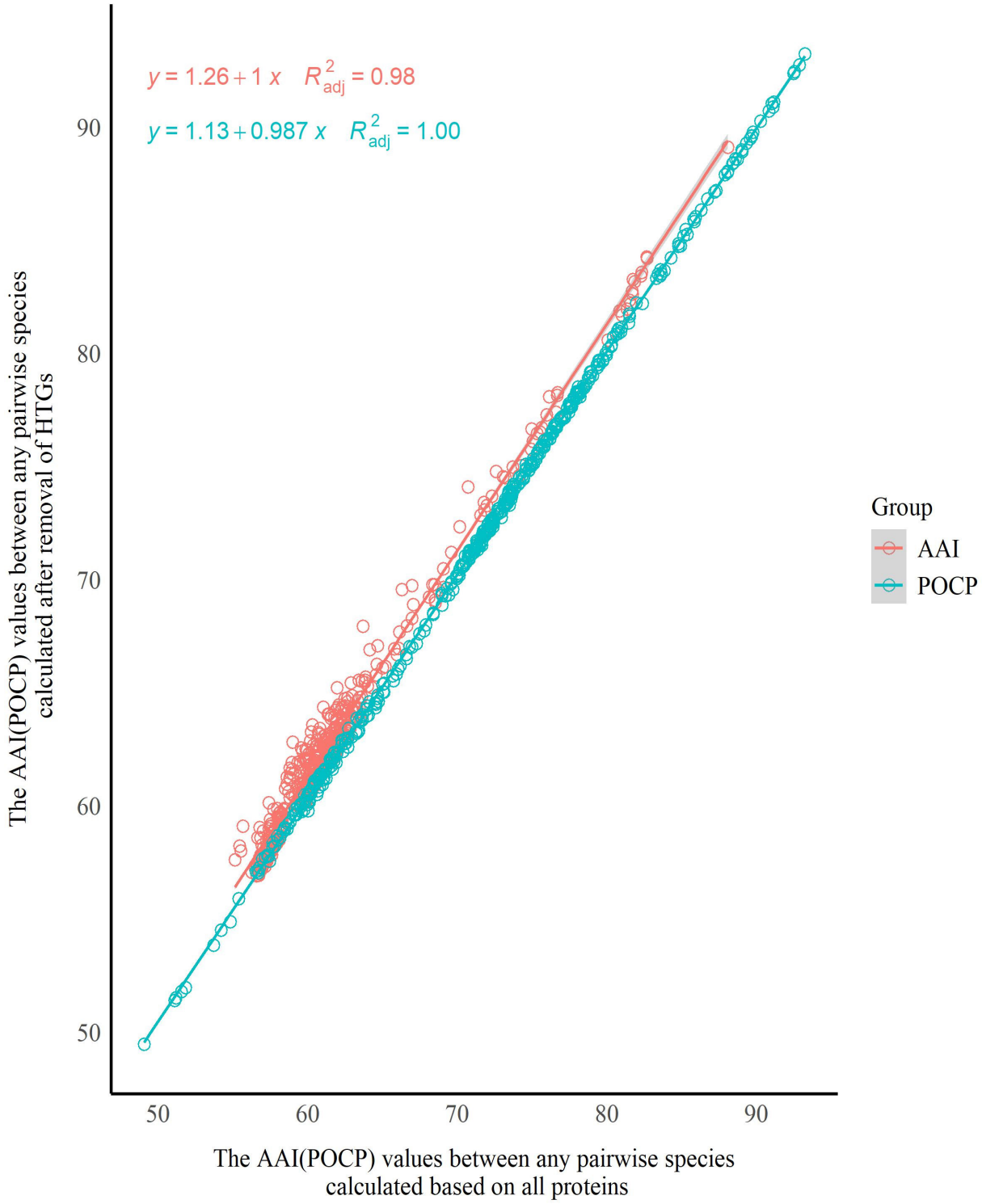

Fig. 21. Linear regression analysis to evaluate the impact of HTGs on AAI and POCP analyses. The horizontal axis represented AAI (or POCP) values between any pairwise species calculated based on all proteins (with HTGs retained), and the vertical axis represented AAI (or POCP) values for the corresponding species pairs calculated after removal of HGT candidates.

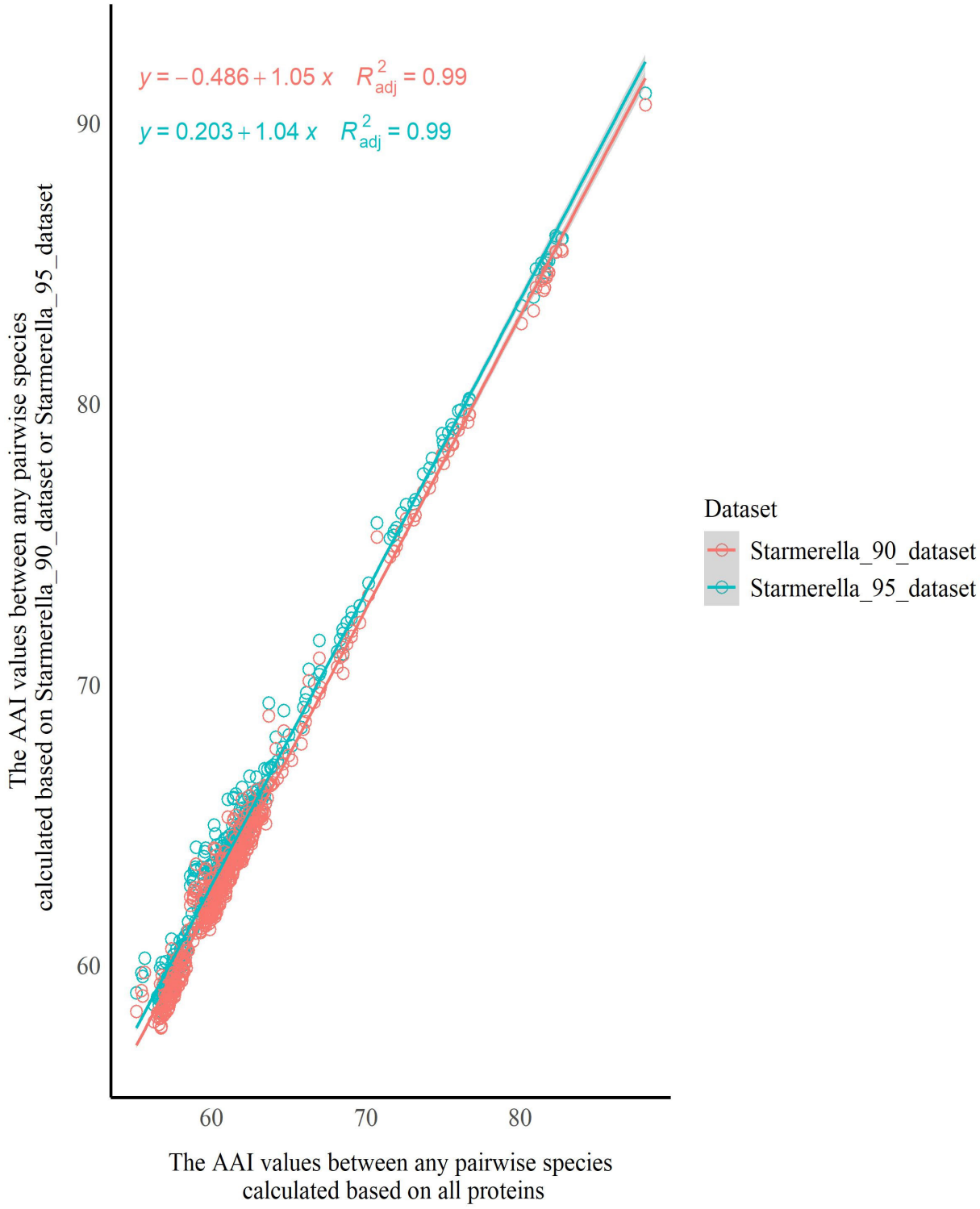

Fig. 22. Linear regression analysis to evaluate the impact of reductive evolution on AAI analysis. The horizontal axis represented AAI values between any pairwise species calculated based on all proteins, and the vertical axis represented AAI values for the corresponding species pairs calculated based on *Starmerella*_90_dataset or *Starmerella*_95_dataset.

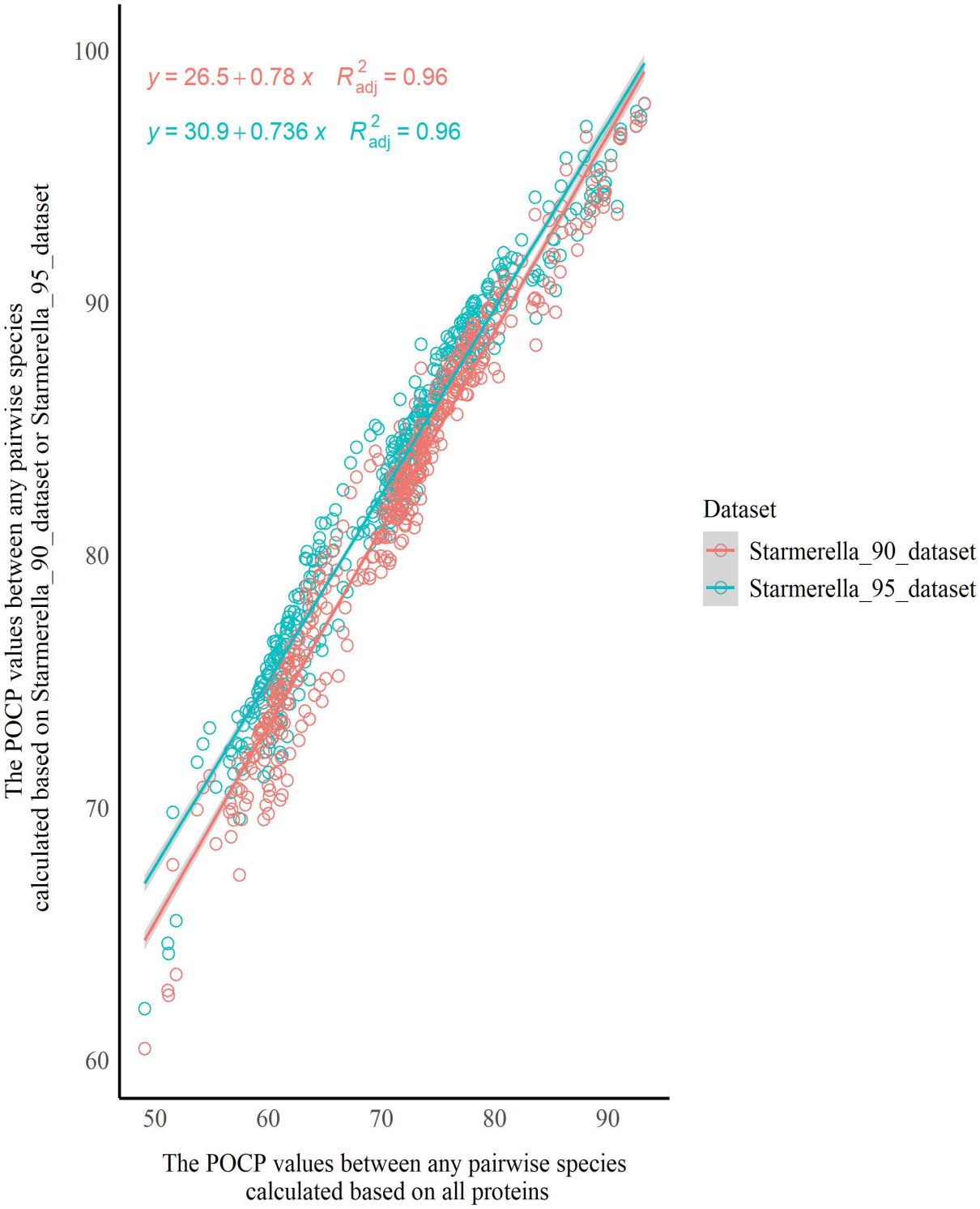

Fig. 23. Linear regression analysis to evaluate the impact of reductive evolution on POCP analysis. The horizontal axis represented POCP values between any pairwise species calculated based on all proteins, and the vertical axis represented POCP values for the corresponding species pairs calculated based on *Starmerella*_90_dataset or *Starmerella*_95_dataset.

The above results indicate that: 1) these non-clinical *Candida* species may be generally susceptible to polyene drugs; 2) the three clinically relevant species, namely *C. zeylanoides*, *C. palmioleophila* and *C. sake*, have 8–16 μg/mL fluconazole MIC values (Pereira et al. 2010; Jensen & Arendrup 2011; Kucukates et al. 2016), which indicate a level of resistance distinct from typical *C. albicans* and may have new resistance mechanisms differing from *C. albicans* or other core *Candida* species. Stavrou et al. (2019) and Schmalreck et al. (2014) demonstrated that yeast phylogeny may be a guide to predict antifungal susceptibility profiles (ASPs), thereby improving treatment strategies, the impact of clinical diagnostics, and epidemiological tracking of yeast infections. Therefore, the different ASPs of *C. zeylanoides*, *C. palmioleophila* and *C. sake* and the core *Candida* species may be correlated with their different phylogenetic position.

Phenotypic features for yeast genus recognition

Yeast genera were traditionally recognized based on their phenotypic characteristics (Boekhout et al. 2021). However, molecular phylogenetic analyses have shown that most phenotypically defined genera are not monophyletic (Kurtzman 2011a; Boekhout et al. 2021). Can phenotypic features still be used to additionally characterize genera in both ascomycetous yeasts and basidiomycetous yeasts? In some cases, this is possible as, several genera can be recognized by their morphological or physiological characteristics. For example, the genus *Eremothecium* is characterized by its fusiform or acicular (needle-shaped) ascospores. The sister genera *Zygosaccharomyces* and *Zygotorulaspora* can be distinguished by physiology: all species of *Zygotorulaspora* can ferment raffinose, whereas all members of *Zygosaccharomyces* cannot. Other sister genera in the *Saccharomycetaceae* can be differentiated by phenotypic synapomorphies; some more distinctly than others (see Liu et al. 2024a). Most genera recognized through the phylogenomic analysis and the genomic metrics AAI, POCP and PAPO approaches in Liu et al. (2024b) can be recognized by phenotypic characters. For example, *Australozyma* vs *Helenozyma* vs *Hermanozyma*, *Candidozyma* vs *Osmozyma*, *Danielozyma* vs *Gaillardinia* vs *Metahyphopichia*, *Isabelozyma* vs *Soucietia*, and *Clavispora* vs *Sungouiella* exhibit notable phenotypic differences between them (for details see Liu et al. 2024b). In this study, we conducted a phenotypic comparison of sister genera identified, seeking morphological or physiological synapomorphies to support their generic circumscriptions. Among 25 newly described genera, 11 ones (44%) have distinct phenotypic features that differ from related genera (for details, see the Taxonomy section below). The new genera with phenotypic synapomorphies are *Cariosilvazyma*, *Casaregolazyma*, *Chernovozyma*, *Daia*, *Grinbergsozyma*, *Intestinozyma*, *Liangdongia*, *Lizanozyma*, *Nothofagozyma*, *Westerdijkia* and *Xiuguozyma*. Although the new genera *Gotozyma* and *Xingzhongia* can't be distinguished from their related taxa by phenotypic characteristics, they have distinct GC% content from their relatives (Table S3).

Are the monotypic genera realistic?

About 14 *Candida* species are placed at basal positions of specific clades in our phylogenomic analysis and are thus separated from known genera. This is in agreement with earlier rDNA-based sequence phylogenetic analyses (Daniel et al. 2014; Takashima & Sugita 2022). The phylogenomic and rDNA phylogenetic analyses suggest that those single-genome (single-species) lineages could be interpreted as new genera. However, the proposal of new monotypic genera has been disputed (Lachance 2018). In fact, monotypic genera are not rare for yeasts, e.g., the genera *Aciculiconidium*, *Babjeviella*, *Cyrenella* and *Kriegeria* (Kurtzman 2011b; Sampaio 2011; Sampaio & Oberwinkler 2011; Smith 2011). This issue is not only relevant for interpreting phylogenies of yeasts, but is also true for all fungi. Hyde et al. (2024) demonstrated that 39.5% of described fungal genera are monotypic and argued whether other species in these monotypic genera will be found during a worldwide survey. Bhunjun et al. (2022) demonstrated that, likely, new species will be found and described after monotypic genera are published. For various initially monotypic yeast genera, such as *Babjevia*, *Deakozyma*, *Nematodospora* and *Yueomyces,* new species have been described shortly after the genus was proposed (Gouliamova et al. 2016; Ren et al. 2016; Zheng et al. 2017; Yamazaki et al. 2020; Yu et al. 2023).

To assign single-species *Candida* lineages as new genera has two benefits: 1) the proposal of monotypic genera might be useful as it will reduce the polyphyletic nature of the genus *Candida* (Takashima & Sugita 2022); 2) the proposal of monotypic genera will accelerate new species descriptions and assignment to those monotypic genera. Many undescribed *Candida* species have been deposited in the GenBank database (https://www.ncbi.nlm.nih.gov/nucleotide/), and some of them are closely related to the single-species *Candida* lineages that we recognized in this work. For example, more than one potential new species is closely related to *C. alai*, *C. bentonensis*, *C. boidinii*, *C. chilensis*, *C. freyschussii*, *C. hispaniensis*, *C. multigemmis*, *C. sake* and *C. sungouii* (Fig. 5, Figs. S5–S13, and see in the phylogenetic analysis section). Those undescribed species (or potential new species) hamper the study of yeast diversity, taxonomy, and even our understanding of yeasts' evolution. Thus, those single-species *Candida* lineages containing potential new species need to be assigned to new genera and making it possible to formally describe those species new to science in the future. For the time being, we decided to consider single-species *Candida* lineages without known closely related undescribed species, such as *Candida anutae*, *Candida argente*, *C. ascalaphidarum*, *C. glucosophila* and *C. tunisiensi*, as lineages in *Candida pro tempore.*

Strengths and limitations of the genome-based phylogeny of *Candida*

Since the genus *Candida* was introduced (Berkhout 1923), the concept and taxonomy of this genus have been changed various times (Lachance et al. 2011). The molecular sequence, including the LSU rDNA and ITS, studies demonstrated that the genus *Candida,* initially defined based on the phenotypic characteristics, is highly polyphyletic, and species can be found in various families across *Saccharomycotina* (Kurtzman & Robnett 1998, 2003; Lachance et al. 2011; Daniel et al. 2014; Takashima & Sugita 2022). This genus name is, however, of high importance in the medical field due to some species, such as *C. albicans*, *C. dubliniensis*, *C. parapsilosis*

and *C. tropicalis*, which are frequently isolated from patients and can cause various infections, including candidemia (Kurtzman et al. 2011; Stavrou et al. 2019; Takashima & Sugita 2022). The current knowledge shows that most medically important *Candida* species occur in the *Serinales* (*Pichiomycetes*), whereas few of them, such as *Candida glabrata* (currently named *Nakaseomyces glabratus*), are classified in the *Saccharomycetales* (*Saccharomycetes*) (Takashima & Sugita 2022; Groenewald et al. 2023), which indicates that most *Candida* species in other orders and classes are not pathogenic, at least not yet.

In contrast, some *Candida* species are used in the biotechnological and fermentation industries, i.e., *Cyberlindnera jadinii* (asexual morph *Candida utilis*), are used for protein production, biosynthesis of (R)-phenylacetylcarbinol and other biotechnological products (Miura et al. 1998; Lee & Kim 2001; Villas-Bôas et al. 2002; Kurtzman 2011d); and *Candida apicola*, *Candida batistae*, *Candida kuoi*, *Candida riodocensis* and *Candida stellata* produce sophorolipids (Kurtzman et al. 2015). To reduce the heterogeneity of *Candida* from an evolutionary and taxonomic perspective and to distinguish it in the medical and biotechnological fields, it is necessary to reclassify the genus. More than half of the *Candida* species have been reassigned into existing and newly proposed genera (Takashima & Sugita 2022; Liu et al. 2024b), but the heterogeneous nature of the genus remains, and especially the phylogenetic positions of those *Candida* species that occur as deep internal branches in the LSU rDNA or multigene-based trees were not resolved (Lachance et al. 2011).

In this study, we mostly used the phylogenomic analysis and the complementary genome-based metrics, including the AAI, POCP and PAPO that have been used to discriminate genera in *Saccharomycetaceae* and *Metschnikowiaceae* (Liu et al. 2024a, b) and the RED approach that has been applied to evaluate the evolutionary divergences of different taxonomic ranks across fungi (Li et al. 2021; Groenewald et al. 2023), to reclassify the genus *Candida*. Our analyses assigned most *Candida* species into phylogenetically distinct known or newly created genera. The phylogenetic and taxonomic positions of species, which were unresolved based on LSU rDNA or multigene-based datasets, were resolved based on the phylogenomic analysis and the genome-based metric analyses in this study. For example, the phylogenetic position of *C. anutae*, *C. argentea*, *C. insectalens*, *C. silvatica*, and *C. sorboxylosa* varied in different phylogenetic studies due to the high divergent LSU rDNA sequence (Bab'eva et al. 2000; Holland et al. 2011), but our phylogenomic analysis showed that 1) *C. anutae* and *C. argentea* are closely related to *Wickerhamia fluorescens*; 2) *C. insectalens* and *C. silvatica* form a clade related to the genus *Brettanomyces*; 3) *C. sorboxylosa* is located in the genus *Pichia*, which are all in agreement with the results from Opulente et al. (2024).

Although most issues of *Candida* taxonomy have been resolved in this study, 15 *Candida* species were assigned as *Candida pro tempore*, especially those single-species lineages in the phylogenomic trees (Figs. 1, 6, 9, 12, 14–15, 17 and Figs. S1–S4). As we discussed above, those single-species *Candida* lineages will be resolved with more related species described. The other limitation of this reclassification is that seven newly created genera, i.e., *Buckleya*, *Keqinozyma*, *Ramirezia*, *Ruyongia*, *Taiozyma* and *Wenyingozyma*, are phylogenetically distinct from other genera, but they are described mostly based on phylogenomic and genome-based metric analyses without distinguishing phenotypic characteristics because species in those genera and their related genera are phenotypically divergent and do not have physiological or biochemical synapomorphic features (Table S3). This problem may be resolved based on the chromosome syntenic analysis or a special metabolic network analysis with complete genome (T2T assembled genome) datasets in the future.

The other limitation of this study is that the generic AAI and POCP values recommended by Liu et al. (2024a) were not suitable for some genera (or clades), such as the genus *Yamadazyma*, the *Ogataea* clade 1 and the *Ogataea* clade 2, which are characterized by high genetic diversity compared to the genera accepted in *Saccharomycetaceae* (Liu et al. 2024a) and *Pichiales* (Table 1), e.g. *Citeromyces*, *Komagataella* and *Kregervanrija*. Therefore, a fixed generic boundary of the genome-based metrics should be addressed for different families or higher ranks, as was done in prokaryotes by Riesco & Trujillo (2024), in the future. The combined approaches, phylogenomic analysis, phenotypic synapomorphic comparison and the genome-based metrics, are recommended to provide a conceptual or methodological framework for yeasts, and even for other fungal groups, taxonomic delineation.

Conclusions

We assigned 160 *Candida* species to 25 new genera, 6 reinstated genera and 15 known genera, including 4 validated genera, in this study. However, for pragmatic reasons, 15 *Candida* species are listed as *pro tempore* as we suggest to delay taxonomic conclusions until consensus is reached among yeast taxonomists regarding the classification of those lineages. Among those unresolved *Candida* species, *C. tunisiensis* occurs in the *Dipodascomycetes*; *C. argentea*, *C. anglica*, *C. anutae*, *C. ascalaphidarum* and *C. glucosophila* occur in the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*); *C. citri*, *C. danieliae*, *C. golubevii*, *C. hainanensis*, *C. hawaiiana*, *C. magnifica*, *C. wancherniae* and *C. xylosifermentans* locate in the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*); *C. sanyiensis* occurs in *Barnettozyma* (*Phaffomycetaceae*, *Phaffomycetales*, *Saccharomycetes*). Like Liu et al. (2024b), we refrain from making taxonomic conclusions on those lineages as the discovery of more related species is needed to classify them properly.

Taxonomy

In this section, we propose a new classification of 160 *Candida* species and related taxa in *Saccharomycotina* presented in Tables S1–S2, including the reinstatement of several genera, i.e., *Entelexis*, *Komagataea*, *Petasospora*, *Waltiozyma* and *Williopsis* based on the results of the studies discussed above. Furthermore, 91 invalid names of the taxa indicated in the Index Fungorum, Fungal Names and MycoBank are validated. The four invalid genera, namely *Deakozyma*, *Limtongella*, *Tardiomyces* and *Hemisphaericaspora*, are validated as new genera; the other 89 invalid species are treated as new species for validation. Note that we list only the most important synonyms for those species

with applied and clinical relevance. For the full list of synonyms, we refer to The Yeasts database (https://theyeasts.org) and *TYTS*, 5th edition (Kurtzman et al. 2011). All proposed new taxa are listed in Table 5. The genus-specific OGs (unique genes) used as diagnostic characters for the newly proposed, emended and reinstated genera are listed in Table 6.

Table 5 The new taxa proposed in this study

Taxa	Basionym or important synonyms
Dipodascomycetes	
Dipodascales	
Trichomonascaceae	
Casaregolazyma gen. nov.	
C. lundiana comb. nov.	*Candida lundiana*
C. patagonica sp. nov.	*Candida patagonica*
C. suthepensis comb. nov.	*Candida suthepensis*
Daia gen. nov.	
D. ofunaensis comb. nov.	*Hansenula ofunaensis*; *Zygoascus ofunaensis*
D. tannicola comb. nov.	*Pichia tannicola*; *Zygoascus tannicola*
Deakozyma gen. nov.	
D. indianensis sp. nov.	*Deakozyma indianensis*
D. yunnanensis sp. nov.	*Deakozyma yunnanensis*
Entelexis	
E. apis comb. nov.	*Candida apis*; *Starmerella apis*; *Torulopsis apis*
E. geochares comb. nov.	*Candida geochares*; *Starmerella geochares*; *Torulopsis geochares*
E. gropengiesseri comb. nov.	*Candida gropengiesseri*; *Starmerella gropengiesseri*; *Torula gropengiesseri*
E. litoralis comb. nov.	*Starmerella litoralis*
E. magnoliae	
E. paramagnoliae nom. nov.	*Candida magnoliae*; *Starmerella magnoliae*; *Torulopsis magnoliae*
E. potacharoeniae comb. nov.	*Candida potacharoeniae*; *Starmerella potacharoeniae*
E. sorbosivorans comb. nov.	*Candida sorbosivorans*; *Starmerella sorbosivorans*
E. spenceri comb. nov.	*Candida spenceri*
E. syriaca sp. nov.	*Starmerella syriaca*
E. tilneyi sp. nov.	*Candida tilneyi*; *Starmerella tilneyi*
E. vaccinii comb. nov.	*Candida vaccinii*; *Starmerella vaccinii*
E. xylocopis comb. nov.	*Starmerella xylocopis*
Grinbergsozyma gen. nov.	
G. bentonensis comb. nov.	*Candida bentonensis*
Limtongella gen. nov.	
L. siamensis sp. nov.	*Limtongella siamensis*
L. incommunis comb. nov.	*Candida incommunis*
Starmerella sensu stricto	
S. powellii sp. nov.	*Candida powellii*; *Starmerella powellii*
Tardiomyces gen. nov.	
T. blankii comb. nov.	*Candida blankie*; *Tardiomyces blankii*
T. depauwii sp. nov.	*Tardiomyces depauwii*
T. digboiensis comb. nov.	*Candida digboiensis*; *Tardiomyces digboiensis*
Westerdijkia gen. nov.	
W. sungouii sp. nov.	*Candida sungouii*

Taxa	Basionym or important synonyms
Incertae sedis* in *Dipodascomycetes	
Dengshuqunia gen. nov.	
D. hispaniensis comb. nov.	*Candida hispaniensis*
Yarrowia	
Y. brassicae sp. nov.	*Yarrowia brassicae*
Y. divulgata sp. nov.	*Yarrowia divulgata*
Y. keelungensis sp. nov.	*Yarrowia keelungensis*
Y. phangngaensis sp. nov.	*Candida phangngaensis*; *Yarrowia phangngaensis*
Pichiomycetes	
Pichiales	
Pichiaceae	
Ogataea	
O. arabinofermentans comb. nov.	*Candida arabinofermentans*
O. chonburiensis sp. nov.	*Ogataea chonburiensis*
O. chumphonensis sp. nov.	*Candida chumphonensis*
O. deakii sp. nov.	*Ogataea deakii*
O. ganodermae sp. nov.	*Ogataea ganodermae*
O. histrianica sp. nov.	*Ogataea histrianica*
O. kanchanaburiensis sp. nov.	*Ogataea kanchanaburiensis*
O. kolombanensis sp. nov.	*Ogataea kolombanensis*
O. krabiensis sp. nov.	*Candida krabiensis*
O. maris comb. nov.	*Candida maris*; *Torulopsis maris*
O. mattraensis sp. nov.	*Candida mattraensis*
O. nakhonphanomensis sp. nov.	*Ogataea nakhonphanomensis*
O. nemodendra comb. nov.	*Candida nemodendra*; *Torulopsis nemodendra*
O. ortonii sp. nov.	*Candida ortonii*
O. ovalis comb. nov.	*Candida ovalis*
O. piceae comb. nov.	*Candida piceae*
O. pinus comb. nov.	*Candida pinus*; *Torulopsis pinus*
O. phyllophila sp. nov.	*Ogataea phyllophila*
O. rishirensis comb. nov.	*Candida rishirensis*
O. siamensis sp. nov.	*Ogataea siamensis*; *Pichia siamensis*
O. sithepensis sp. nov.	*Candida sithepensis*
O. sonorensis comb. nov.	*Candida sonorensis*; *Torulopsis sonorensis*
O. thermomethanolica sp. nov.	*Ogataea thermomethanolica*; *Pichia thermomethanolica*
O. thermophila sp. nov.	*Candida thermophila*
O. xyloterini comb. nov.	*Candida xyloterini*
Pichia	
P. awuae sp. nov.	*Candida awuae*
P. bruneiensis sp. nov.	*Pichia bruneiensis*
P. chibodasensis sp. nov.	*Pichia chibodasensis*
P. dushanensis sp. nov.	*Pichia dushanensis*
P. insulana sp. nov.	*Pichia insulana*
P. phayaonensis sp. nov.	*Candida phayaonensis*; *Pichia phayaonensis*
P. sorboxylosa comb. nov.	*Candida sorboxylosa*
P. thaimueangensis sp. nov.	*Candida thaimueangensis*; *Pichia thaimueangensis*

Taxa	Basionym or important synonyms
Ramirezia gen. nov.	
R. boidinii comb. nov.	*Candida boidinii*
Wenyingozyma gen. nov.	
W. methanosorbosa comb. nov.	*Candida methanosorbosa*; *Torulopsis methanosorbosa*
W. methylovora comb. nov.	*Ogataea methylovora*; *Pichia methylovora*
W. naganishii comb. nov.	*Ogataea naganishii*; *Pichia naganishii*
W. nanaspora comb. nov.	*Candida nanaspora*
W. neixiangensis comb. nov.	*Ogataea neixiangensis*
W. nitratophila comb. nov.	*Candida nitratophila*; *Torulopsis nitratophila*
W. ramenticola comb. nov.	*Ogataea ramenticola*; *Pichia ramenticola*
W. succiphila comb. nov.	*Candida cellulolytica*; *Candida succiphila*
W. suzukii comb. nov.	*Candida suzukii*
W. wangdongensis sp. nov.	*Ogataea wangdongensis*
Xiuguozyma gen. nov.	
X. insectalens comb. nov.	*Candida insectalens*; *Torulopsis insectalens*
X. silvatica comb. nov.	*Candida silvatica*; *Torulopsis silvatica*
Serinales	
Debaryomycetaceae	
Candida emend.	
C. baotianmanensis sp. nov.	*Candida baotianmanensis*
C. pseudoviswanathii sp. nov.	*Candida pseudoviswanathii*
C. sanyaensis sp. nov.	*Candida sanyaensis*
C. saraburiensis sp. nov.	*Candida saraburiensis*
Chernovozyma gen. nov.	
C. aurita comb. nov.	*Candida aurita*
C. palmyrensis comb. nov.	*Candida palmyrensis*
C. sophiae-reginae comb. nov.	*Candida sophiae-reginae*
Debaryomyces	
D. psychrophila comb. nov.	*Candida psychrophila*; *Torulopsis psychrophila*
D. renaianus sp. nov.	*Debaryomyces renaii*
D. vindobonensis sp. nov.	*Debaryomyces vindobonensis*
Dujonia gen. nov.	
D. boleticola comb. nov.	*Candida boleticola*
D. oleophila comb. nov.	*Candida oleophila*
D. railenensis comb. nov.	*Candida railenensis*
D. santamariae comb. nov.	*Candida santamariae*
D. schatavii comb. nov.	*Candida schatavii*; *Torulopsis schatavii*
D. zeylanoides comb. nov.	*Candida zeylanoides*; *Monilia zeylanoides*
Fermentozyma gen. nov.	
F. sake comb. nov.	*Candida sake*; *Eutorulopsis sake*
F. vespimorsuum comb. nov.	*Candida vespimorsuum*
Glucitozyma gen. nov.	
G. multigemmis comb. nov.	*Candida multigemmis*; *Torulopsis multigemmis*
Hemisphaericaspora gen. nov.	
H. elongata comb. nov.	*Spathaspora elongata*
H. gorwiae comb. nov.	*Spathaspora gorwiae*
H. haegerdaliae comb. nov.	*Spathaspora haegerdaliae*

Taxa	Basionym or important synonyms
H. insectamans comb. nov.	*Candida insectamans*; *Hemisphaericaspora insectamans*
H. jiuxiensis comb. nov.	*Spathaspora jiuxiensis*
H. lyxosophila comb. nov.	*Candida lyxosophila*
H. mengyangensis comb. nov.	*Spathaspora mengyangensis*
H. nanyangensis sp. nov.	*Hemisphaericaspora nanyangensis*
H. parajiuxiensis comb. nov.	*Spathaspora parajiuxiensis*
H. roraimensis comb. nov.	*Spathaspora roraimensis*
H. rosae comb. nov.	*Spathaspora rosae*
H. subhashii comb. nov.	*Candida subhashii*
H. xylanilytica sp. nov.	*Candida xylanilytica*
H. xylofermentans comb. nov.	*Spathaspora xylofermentans*
Insectozyma gen. nov.	
I. bohioensis comb. nov.	*Candida bohioensis*
I. chauliodis comb. nov.	*Candida chauliodis*
I. coleopterorum comb. nov.	*Candida coleopterorum*
I. corydali comb. nov.	*Candida corydali*
I. morakotiae comb. nov.	*Candida morakotiae*
I. parachauliodis comb. nov.	*Candida parachauliodis*
I. prachuapensis sp. nov.	*Candida prachuapensis*
I. sakaeoensis sp. nov.	*Candida sakaeoensis*
I. verbasci sp. nov.	*Candida verbasci*
I. xiaguanensis comb. nov.	*Candida xiaguanensis*
Intestinozyma gen. nov.	*Candida verbasci*
I. alai comb. nov.	*Candida alai*
Keqinozyma gen. nov.	
K. heliconiae comb. nov.	*Candida heliconiae*
K. nonsorbophila comb. nov.	*Candida nonsorbophila*
K. sinolaborantium comb. nov.	*Candida sinolaborantium*
K. temnochilae comb. nov.	*Candida temnochilae*
Lizanozyma gen. nov.	
L. gosingicus sp. nov.	*Candida gosingica*; *Scheffersomyces gosingicus*
L. spartinae comb. nov.	*Pichia spartinae*; *Scheffersomyces spartinae*
L. thasaensis sp. nov.	*Candida thasaensis*
Lodderomyces	
L. cetoniae comb. nov.	*Candida cetoniae*
L. hyderabadensis comb. nov.	*Candida hyderabadensis*
L. jiufengensis comb. nov.	*Candida jiufengensis*
L. margitis comb. nov.	*Candida margitis*
L. metapsilosis comb. nov.	*Candida metapsilosis*
L. orthopsilosis comb. nov.	*Candida orthopsilosis*
L. oxycetoniae comb. nov.	*Candida oxycetoniae*
L. parapsilosis comb. nov.	*Candida parapsilosis*; *Monilia parapsilosis*
L. pseudojiufengensis comb. nov.	*Candida pseudojiufengensis*
L. theae sp. nov.	*Candida theae*
Millerozyma	
M. porticicola comb. nov.	*Pichia porticicola*
M. pseudofarinosa comb. nov.	*Candida pseudofarinosa*

Taxa	Basionym or important synonyms
Nothofagozyma gen. nov.	
N. chilensis *comb. nov.*	*Candida chilensis*
Scheffersomyces	
S. broadrunensis comb. nov.	*Candida broadrunensis*
S. lignicola sp. nov.	*Candida lignicola*; *Scheffersomyces lignicola*
Spathaspora sensu stricto	
S. brasiliensis sp. nov.	*Spathaspora brasiliensis*
S. suhii sp. nov.	*Spathaspora suhii*
Suhomyces	
S. caryicola comb. nov.	*Candida caryicola*
S. rongomai-pounamu comb. nov.	*Candida rongomai-pounamu*
S. tibetensis comb. nov.	*Candida tibetensis*
Suzukiozyma gen. nov.	
S. candida comb. nov.	*Candida saitoana*; *Torulopsis candida*
S. fluviatilis comb. nov.	*Candida fluviatilis*
S. glaebosa comb. nov.	*Candida glaebosa*
S. manassasensis comb. nov.	*Candida manassasensis*
S. palmioleophila comb. nov.	*Candida palmioleophila*
S. pseudoglaebosa comb. nov.	*Candida pseudoglaebosa*
S. sphagnicola comb. nov.	*Candida sphagnicola*
Yamadazyma	
Y. andamanensis sp. nov.	*Candida andamanensis*
Y. dushanensis sp. nov.	*Yamadazyma dushanensis*
Y. oceani sp. nov.	*Candida oceani*; *Yamadazyma oceani*
Y. paraphyllophila sp. nov.	*Yamadazyma paraphyllophila*
Y. phyllophila sp. nov.	*Yamadazyma phyllophila*
Y. jaroonii sp. nov.	*Candida jaroonii*
Y. siamensis sp. nov.	*Yamadazyma siamensis*
Y. songkhlaensis sp. nov.	*Candida songkhlaensis*
Y. ubonensis sp. nov.	*Yamadazyma ubonensis*
Y. vrieseae sp. nov.	*Candida vrieseae*
Zhuliangozyma gen. nov.	
Z. blackwelliae comb. nov.	*Candida blackwellae*
Z. boniae comb. nov.	*Spathaspora boniae*
Z. parablackwelliae comb. nov.	*Candida parablackwelliae*
Saccharomycetes	
Phaffomycetales	
Phaffomycetaceae	
Barnettozyma	
B. sucrosica sp. nov.	*Barnettozyma sucrosica*
B. xylosica sp. nov.	*Barnettozyma xylosica*
B. xylosiphila sp. nov.	*Barnettozyma xylosiphila*
Gotozyma gen. nov.	
G. botsteinii sp. nov.	*Barnettozyma botsteinii*
G. montana comb. nov.	*Candida montana*
G. siamensis comb. nov.	*Barnettozyma siamensis*
Komagataea	

Taxa	Basionym or important synonyms
K. norvegica comb. nov.	*Candida norvegica*; *Torulopsis norvegica*
K. qinlingensis comb. nov.	*Candida qinlingensis*
K. salicaria comb. nov.	*Barnettozyma salicaria*; *Pichia salicaria*
K. wickerhamii comb. nov.	*Barnettozyma wickerhamii*; *Endomycopsis wickerhamii*
Millerago	
M. ficus sp. nov.	*Candida ficus*
Phaffomyces	
P. coquimbonensis sp. nov.	*Candida coquimbonensis*
P. orba comb. nov.	*Candida orba*
Wickerhamomycetaceae	
Buckleya gen. nov.	
B. freyschussii comb. nov.	*Candida freyschussii*
Hansenula	
H. queroliae comb. nov.	*Wickerhamomyces queroliae*
H. silvicultrix comb. nov.	*Candida silvicultrix*
H. spegazzinii sp. nov.	*Wickerhamomyces spegazzinii*
H. sylviae sp. nov.	*Wickerhamomyces sylviae*
Liangdongia gen. nov.	
L. berthetii comb. nov.	*Candida berthetii*
L. dendrica comb. nov.	*Candida dendrica*; *Torulopsis dendrica*
L. dryadoides comb. nov.	*Hansenula dryadoides*; *Starmera dryadoides*
L. ilhagrandensis comb. nov.	*Starmera ilhagrandensis*
L. laemsonensis sp. nov.	*Candida laemsonensis*
L. nongkratonensis comb. nov.	*Pichia nongkratonensis*
L. prunicorticola comb. nov.	*Starmera prunicorticola*
L. quercuum comb. nov.	*Pichia quercuum*; *Starmera quercuum*
Petasospora	
P. adriatica comb. nov.	*Candida adriatica*
P. americana comb. nov.	*Cyberlindnera americana*; *Hansenula bimundalis* var. *americana*
P. amylophila comb. nov.	*Cyberlindnera amylophila*; *Pichia amylophila*
P. bimundalis comb. nov.	*Cyberlindnera bimundalis*; *Hansenula bimundalis*
P. dasilvae comb. nov.	*Cyberlindnera dasilvae*
P. easanensis sp. nov.	*Candida easanensis*
P. euphorbiae comb. nov.	*Cyberlindnera euphorbiae*; *Pichia euphorbiae*
P. euphorbiiphila comb. nov.	*Cyberlindnera euphorbiiphila*; *Hansenula euphorbiiphila*
P. fabianii comb. nov.	*Cyberlindnera fabianii*; *Hansenula fabianii*
P. hubeiensis comb. nov.	*Cyberlindnera hubeiensis*
P. hungchunana sp. nov.	*Candida hungchunana*
P. japonica comb. nov.	*Cyberlindnera japonica*; *Pichia japonica*
P. juglandicorticola comb. nov.	*Cyberlindnera juglandicorticola*
P. maesae sp. nov.	*Candida maesae*
P. maritima comb. nov.	*Candida maritima*; *Cyberlindnera maritima*; *Trichosporon maritimum*
P. meyerae comb. nov.	*Cyberlindnera meyerae*; *Pichia meyerae*
P. mississippiensis comb. nov.	*Cyberlindnera mississippiensis*; *Pichia mississippiensis*
P. mycetangii comb. nov.	*Candida mycetangii*; *Cyberlindnera mycetangii*
P. nakhonratchasimensis sp. nov.	*Candida nakhonratchasimensis*; *Cyberlindnera nakhonratchasimensis*
P. pattaniensis sp. nov.	*Candida pattaniensis*

Taxa	Basionym or important synonyms
P. petersonii comb. nov.	*Cyberlindnera petersonii*; *Hansenula petersonii*
P. rhizosphaerae comb. nov.	*Cyberlindnera rhizosphaerae*; *Lindnera rhizosphaerae*
P. shennongjiaensis	*Cyberlindnera shennongjiaensis*
P. stauntonica sp. nov.	*Candida stauntonica*
P. sylvatica comb. nov.	*Cyberlindnera sylvatica*
P. taoyuanica sp. nov.	*Candida taoyuanica*
P. veronae comb. nov.	*Cyberlindnera veronae*; *Pichia veronae*
P. wuzhiensis comb. nov.	*Cyberlindnera wuzhiensis*; *Lindnera wuzhiensis*
P. xishuangbannaensis comb. nov.	*Cyberlindnera xishuangbannaensis*
P. xylebori comb. nov.	*Cyberlindnera xylebori*
P. xylosilytica comb. nov.	*Cyberlindnera xylosilytica*
Ruyongia gen. nov.	
R. chambardii comb. nov.	*Saccharomyces chambardii*; *Wickerhamomyces chambardii*
R. mori comb. nov.	*Wickerhamomyces mori*
R. namnaoensis comb. nov.	*Candida namnaoensis*
R. patagonica comb. nov.	*Wickerhamomyces patagonicus*
R. ponderosae comb. nov.	*Candida ponderosae*
R. rarassimilans comb. nov.	*Pichia rarassimilans*
R. tratensis comb. nov.	*Wickerhamomyces tratensis*
Taiozyma gen. nov.	
T. bovis comb. nov.	*Pichia bovis*; *Wickerhamomyces bovis*
T. dajiaensis sp. nov.	*Candida dajiaensis*
T. odintsovae comb. nov.	*Candida odintsovae*
T. onychis comb. nov.	*Pichia onychis*; *Wickerhamomyces onychis*
T. peoriensis comb. nov.	*Candida peoriensis*
T. rabaulensis comb. nov.	*Pichia rabaulensis*; *Wickerhamomyces rabaulensis*
T. yuanshanica sp. nov.	*Candida yuanshanica*
Waltiozyma	
W. chaumierensis comb. nov.	*Wickerhamomyces chaumierensis*
W. pijperi comb. nov.	*Pichia pijperi*; *Wickerhamomyces pijperi*
W. solani comb. nov.	*Candida solani*
W. xylosica sp. nov.	*Wickerhamomyces xylosica*
Wickerhamomyces sensu stricto	
W. jianshihensis sp. nov.	*Candida jianshihensis*
W. quercuum comb. nov.	*Candida quercuum*
W. ulmi comb. nov.	*Candida ulmi*
Williopsis	
W. culbertsonii sp. nov.	*Cyberlindnera culbertsonii*
W. dauci comb. nov.	*Cyberlindnera dauci*
W. galapagoensis comb. nov.	*Cyberlindnera galapagoensis*
W. jadinii comb. nov.	*Candida utilis*; *Cyberlindnera jadinii*; *Saccharomyces jadinii*
W. lachancei comb. nov.	*Cyberlindnera lachancei*; *Pichia lachancei*
W. maclurae comb. nov.	*Cyberlindnera maclurae*; *Pichia maclurae*
W. mengyuniae comb. nov.	*Candida mengyuniae*
W. misumaiensis comb. nov.	*Cyberlindnera misumaiensis*; *Pichia misumaiensis*
W. samutprakarnensis sp. nov.	*Cyberlindnera samutprakarnensis*
W. sargentensis comb. nov.	*Cyberlindnera sargentensis*; *Pichia sargentensis*

Taxa	Basionym or important synonyms
W. takata sp. nov.	*Candida takata*
W. tropicalis comb. nov.	*Cyberlindnera tropicalis*
W. vartiovaarae comb. nov.	*Candida vartiovaarae*; *Cyberlindnera vartiovaarae*; *Torulopsis vartiovaarae*
Xingzhongia gen. nov.	
X. hampshirensis comb. nov.	*Pichia hampshirensis*; *Wickerhamomyces hampshirensis*
X. scolytoplatypi comb. nov.	*Wickerhamomyces scolytoplatypi*
X. strasburgensis comb. nov.	*Saccharomyces strasburgensis*; *Wickerhamomyces strasburgensis*

Table 6 List of the genus-specific OGs (unique genes) to use as diagnostic characters for the newly proposed, emended and reinstated genera

Taxa	OGs to use as diagnostic characters
Dipodascomycetes	
Casaregolazyma	OG0008493; OG0010589; OG0011717
Daia	OG0017790; OG0024243; OG0024231
Deakozyma	OG0020116; OG0020113; OG0020111
Dengshuqunia	OG0013204; OG0015719; OG0015720
Entelexis	OG0009064; OG0009065
Grinbergsozyma	OG0015427; OG0015488; OG0019665
Tardiomyces	OG0013179; OG0015603; OG0015572
Pichiomycetes	
Pichiales	
Ramirezia	OG0009746; OG0009748; OG0009751
Wenyingozyma	OG0006088; OG0006166; OG0006167
Xiuguozyma	OG0009801; OG0009803; OG0011903
Serinales	
Candida sensu stricto clade	OG0006359; OG0006430
Chernovozyma	OG0009945; OG0009948; OG0010921
Dujonia	OG0009139
Fermentozyma	OG0012707; OG0015120; OG0019183
Glucitozyma	OG0018541; OG0018542; OG0018545
Insectozyma	OG0008208; OG0008209; OG0008210
Intestinozyma	OG0014078; OG0014079; OG0017124
Keqinozyma	OG0018587; OG0018588; OG0018589
Lizanozyma	OG0013736; OG0016664; OG0022956
Nothofagozyma	OG0017645; OG0017647; OG0017651
Suzukiozyma	OG0007615; OG0007616; OG0007620
Zhuliangozyma	OG0009199; OG0009200; OG0012185
Saccharomycetes	
Phaffomycetales	
Buckleya	OG0010458; OG0010457; OG0008787
Hansenula	OG0006330; OG0006334; OG0006336
Komagataea	OG0007192; OG0007193; OG0007195
Lacusozyma	OG0009727; OG0012681; OG0012683
Liangdongia	OG0007703; OG0007712; OG0007714

Taxa	OGs to use as diagnostic characters
Petasospora	OG0005539; OG0005586
Ruyongia	OG0007319; OG0007880; OG0007918
Taiozyma	OG0006108; OG0006424
Waltiozyma	OG0007005; OG0007007; OG0007012
Williopsis	OG0005812; OG0005845; OG0005847
Xingzhongia	OG0012666; OG0012667; OG0012668

New taxa in *Trichomonascaceae* (*Dipodascales*, *Dipodascomycetes*)

Casaregolazyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB857878

Etymology: the genus is named in honor of S. Casaregola for his contribution to yeast taxonomy.

Type species: *Casaregolazyma lundiana* (Saks., M. Suzuki, Lumyong, Ohkuma & Chantaw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Candida lundiana* clade, which occur in a separate lineage from the *Zygoascus sensu stricto* clade and the *Zygoascus tannicola* clade (Fig. 1). Member of the *Trichomonascaceae* (*Dipodascales*, *Dipodascomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0008493 and OG0010589 (Table 6).

Sexual reproduction not known. Colonies are white, cream, convex, fimbriate. Budding is multilateral. Pseudohyhae are present, hyphae are present or absent. Fermentation is absent.

Note: *Casaregolazyma* spp. can be distinguished from those of the closely related genera *Daia* and *Zygoascus sensu stricto* by lack of fermentation (Table S3).

Species accepted:

Casaregolazyma lundiana (Saks., M. Suzuki, Lumyong, Ohkuma & Chantaw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857879

Holotype: CBS 12271, preserved in a metabolically inactive state in the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands. THAILAND, isolated from the raw honey of *Homotrigona fimbriata*, December 2006.

Basionym: *Candida lundiana* Saks., M. Suzuki, Lumyong, Ohkuma & Chantaw., Antonie van Leeuwenhoek 101: 636. 2012.

Casaregolazyma patagonica Sangorrín, C.A. Lopes, Belloch, Querol & A.C. Caball. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857880

For a description: see Sangorrínet al., Antonie van Leeuwenhoek 92: 80. 2007.

Holotype: CBS 10443, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. ARGENTINA (North Patagonian Region), isolated from walls of fermentation vats and oak barrels in wine cellars, 2005.

Synonym: *Candida patagonica* Sangorrín, C.A. Lopes, Belloch, Querol & A.C. Caball., Antonie van Leeuwenhoek 92: 80. 2007. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Casaregolazyma suthepensis (Saks., M. Suzuki, Lumyong, Ohkuma & Chantaw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857881

Holotype: CBS 12270, preserved in a metabolically inactive state in the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands. THAILAND, isolated from raw honey of the Asian cavity-nesting honeybee (*Apis cerana*), February 2009.

Basionym: *Candida suthepensis* Saks., M. Suzuki, Lumyong, Ohkuma & Chantaw., Antonie van Leeuwenhoek 101: 637. 2012.

Daia Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB857911

Etymology: the genus is named in honor of Dr. Yu-Chen Dai for his contributions to the taxonomy of *Basidiomycota*, especially of macrofungal taxonomy.

Type species: *Daia tannicola* (F.H. Jacob) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Zygoascus tannicola* clade, which occur in a separate lineage from the *Zygoascus sensu stricto* clade and the *Candida lundiana* clade (Fig. 1). Member of the *Trichomonascaceae* (*Dipodascales*, *Dipodascomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0017790 and OG0024231 (Table 6).

Asci are persistent and contain one to four subspherical or hat-shaped ascospores. Colonies are tannish-white, butyrous, glistening. Budding is multilateral. Pseudohyphae are present, but hyphae are observed.

Note: *Daia* spp. can be distinguished from those of the closely related genera *Casaregolazyma* and *Zygoascus sensu stricto* by assimilation of melibiose (Table S3). Unlike *Zygoascus sensu stricto*, *Daia* species do not produce septate hyphae.

Species accepted:

Daia ofunaensis (Makig. & Asai) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857912

Holotype: CBS 8129, preserved in a metabolically inactive state in the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands. JAPAN, Ofuna, isolated from soil.

Basionym: *Hansenula ofunaensis* Makig. & Asai, J.Gen. Appl. Microbiol. 22: 200. 1976.

Synonym: *Zygoascus ofunaensis* (Makig. & Asai) Kurtzman & Robnett, FEMS Yeast Res. 7: 147. 2007.

Daia tannicola (F.H. Jacob) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857914

Holotype: CBS 6065, preserved in a metabolically inactive state in the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands. FRANCE, isolated from vegetable tanning fluid.

Basionym: *Pichia tannicola* F.H. Jacob, Bull. Trimestriel Soc. Mycol. France 85: 111. 1969.

Synonym: *Zygoascus tannicola* (F.H. Jacob) Kurtzman & Robnett [as '*tannicolus*'], FEMS Yeast Res. 7: 147. 2007.

Deakozyma Kurtzman & Robnett ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB857882

For a description: see Kurtzman & Robnett, Antonie van Leeuwenhoek 105: 938. 2014.

Synonym: *Deakozyma* Kurtzman & Robnett, Antonie van Leeuwenhoek 105: 938. 2014. Nom. inval., Art. 40.1 (Melbourne), the type species is invalid as more than one collection in which the type is conserved was specified.

Type species: *Deakozyma indianensis* Kurtzman & Robnett ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

Species accepted:

Deakozyma indianensis Kurtzman & Robnett ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857883

For a description: see Kurtzman & Robnett, Antonie van Leeuwenhoek 105: 938. 2014.

Holotype: NRRL YB-1937, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. INDIANA, isolated from the eggs of an insect.

Synonym: *Deakozyma indianensis* Kurtzman & Robnett, Antonie van Leeuwenhoek 105: 938. 2014. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Deakozyma yunnanensis F.L. Hui, K.F. Liu & Xiao J. Liu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857884

For a description: see Zeng et al., Int. J. Syst. Evol. Microbiol. 67: 2438. 2017.

Holotype: CICC 33160, preserved in a metabolically inactive state at the China Centre of Industrial Culture Collection (CICC), Beijing, China. CHINA, Yunnan province, Xishuangbanna tropical rainforest, isolated from rotten wood, July 2016.

Synonym: *Deakozyma yunnanensis* F.L. Hui, K.F. Liu & Xiao J. Liu, Int. J. Syst. Evol. Microbiol. 67: 2438. 2017. Nom. inval., Art. 35.1 (Shenzhen), the genus name is invalid.

Reinstated genus

Entelexis van der Walt & Johannsen, Antonie van Leeuwenhoek 39: 646. 1973.

MycoBank: MB1824

Type species: *Entelexis magnoliae* van der Walt & Johannsen, Antonie van Leeuwenhoek 39(4): 646. 1973.

Species accepted:

Entelexis apis (Lavie ex Uden & Vidal-Leir.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857888

Holotype: CBS 2674, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. UNITED KINGDOM, isolated from the trachea of *Apis* sp. (bee).

Basionym: *Torulopsis apis* Lavie ex Uden & Vidal-Leir., Yeasts, a taxonomic study, 2nd Edn (Amsterdam): 1245. 1970.

Synonyms: *Candida apis* (Lavie ex Uden & Vidal-Leir.) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 611. 1978.

≡ *Starmerella apis* (Lavie ex Uden & Vidal-Leir.) C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1340. 2018.

Entelexis geochares (van der Walt, Johannsen & Yarrow) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857889

Holotype: CBS 6870, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from isolated from soil.

Basionym: *Torulopsis geochares* van der Walt, Johannsen & Yarrow, Antonie van Leeuwenhoek 44: 98. 1978.

Synonyms: *Candida geochares* (van der Walt, Johannsen & Yarrow) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 612. 1978.

≡ *Starmerella geochares* (van der Walt, Johannsen & Yarrow) C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1341. 2018.

Entelexis gropengiesseri (F.C. Harrison) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857890

Holotype: CBS 156, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. UNKNOWN, isolated from the cocoon of cockroach (*Periplaneta orientalis*).

Basionym: *Torula gropengiesseri* F.C. Harrison, Trans. Roy. Soc. Canada, Sect. 5, Biol. Sci. 22: 187. 1928.

Synonyms: *Candida gropengiesseri* (F.C. Harrison) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 612. 1978.

≡ *Starmerella gropengiesseri* (F.C. Harrison) C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1341. 2018.

Entelexis litoralis (A.R.O. Santos, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857891

Holotype: CBS 14104, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRAZIL, Bahia, a sand dune ecosystem of the municipality, isolated from the flower of *Ipomoea imperati*.

Basionym: *Starmerella litoralis* A.R.O. Santos, Lachance & C.A. Rosa, Int. J. Syst. Evol. Microbiol. 68: 1338. 2018.

Entelexis magnoliae van der Walt & Johannsen, Antonie van Leeuwenhoek 39(4): 646. 1973.

MycoBank: MB313623

Entelexis paramagnoliae (Lodder & Kreger-van Rij) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***nom. nov.***

MycoBank: MB857893

Holotype: CBS 166, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. NETHERLANDS, isolated from the flower of *Magnolia* sp.

Replaced synonym: *Torulopsis magnoliae* Lodder & Kreger-van Rij, Yeasts, a Taxonomic Study, [Edn 1] (Amsterdam): 671. 1952, non *Entelexis magnoliae* Van der Walt & Johannsen.

≡ *Candida magnoliae* (Lodder & Kreger-van Rij) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

≡ *Starmerella magnoliae* (Lodder & Kreger-van Rij) C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1341. 2018.

Entelexis potacharoeniae (Nakase, Jindam., Imanishi, Am-In, Ninomiya, H. Kawas. & Limtong) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858031

Holotype: BCC 25963, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Science and Technology Development Agency (NSTDA), Pathumthani, Thailand. THAILAND, Bangkok, Chatuchak, isolated from flower of pink allamanda (*Mandevilla* sp.), March 2003.

Basionym: *Candida potacharoeniae* Nakase, Jindam., Imanishi, Am-In, Ninomiya, H. Kawas. & Limtong, J. Gen. Appl. Microbiol. 56: 291. 2010.

Synonym: *Starmerella potacharoeniae* (Nakase, Jindam., Imanishi, Am-In, Ninomiya, H. Kawas. & Limtong) C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1341. 2018.

Entelexis sorbosivorans (S.A. James, C.J. Bond & I.N. Roberts) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857894

Holotype: NCYC 2938, preserved in a metabolically inactive state at the National Collection of Yeast Cultures, Norwich, UK. GREAT BRITAIN, isolated from the sorbitol-to-sorbose continuous fermentation cascade.

Basionym: *Candida sorbosivorans* S.A. James, C.J. Bond & I.N. Roberts, Int. J. Syst. Evol. Microbiol. 51: 1218. 2001.

Synonym: *Starmerella sorbosivorans* (S.A. James, C.J. Bond & I.N. Roberts) C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1342. 2018.

Entelexis spenceri (Nakase, Jindam., Imanishi, Am-In, Ninomiya, H. Kawas. & Limtong) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857895

Holotype: BCC 15278, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Science and Technology Development Agency (NSTDA), Pathumthani, Thailand. THAILAND, Kanchanaburi, Amphoe Tong Pha Phum, isolated from the flower of the humble-plant (*Mimosa pudica*), November 2003.

Basionym: *Candida spenceri* Nakase, Jindam., Imanishi, Am-In, Ninomiya, H. Kawas. & Limtong, J. Gen. Appl. Microbiol. 56: 293. 2010.

Entelexis syriaca Sipiczki ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857897

For a description: see Sipiczki, Antonie van Leeuwenhoek 107: 851. 2014.

Holotype: CBS 13909, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SYRIA, Aleppo, isolated from the flowers of *Malva* sp.

Synonym: *Starmerella syriaca* Sipiczki, Antonie van Leeuwenhoek 107: 851. 2014. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Entelexis tilneyi Lachance ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857908

For a description: see Lachance et al., Int. J. Syst. Evol. Microbiol. 51: 1205. 2001.

Holotype: CBS 8794, preserved in a metabolically inactive state at Westerdijk Institute, Utrecht, the Netherlands. Costa Rica, Guanacaste, isolated from a beetle (*Conotelus* sp.) of a flower of *Ipomoea carnea*.

Synonyms: *Candida tilneyi* Lachance, Int. J. Syst. Evol. Microbiol. 51: 1205. 2001. Nom. inval., Art. 40.3 (Melbourne).

≡ *Starmerella tilneyi* Lachance ex C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1342. 2018. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified; published as a combination, but 'basionym' (*Candida tilneyi*) is invalid.

Entelexis vaccinii (Tokuoka, Ishit., Goto & Komag.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857909

Holotype: CBS 7318, preserved in a metabolically inactive state at Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from the flower of blueberry (*Vaccinium* sp.).

Basionym: *Candida vaccinii* Tokuoka, Ishit., Goto & Komag., J. Gen. Appl. Microbiol. 33: 8. 1987.

Synonym: *Starmerella vaccinii* (Tokuoka, Ishit., Goto & Komag.) C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1342. 2018.

Entelexis xylocopis (Gouliam., Dimitrov, M. Groenew., M.T. Sm. & Boekhout) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857910

Holotype: CBS 5659, preserved in a metabolically inactive state at Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from the larval feed of an Afrotropical bee *Xylocopa caffra*.

Basionym: *Starmerella xylocopis* Gouliam., Dimitrov, M. Groenew., M.T. Sm. & Boekhout, Persoonia 46: 507. 2021.

Grinbergsozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB857885

Etymology: the genus is named in honor of J. Grinbergs for his contribution to the study of yeast biodiversity, especially of the Valdivian rain forests in Chile.

Type species: *Grinbergsozyma bentonensis* (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the single-species lineage *Candida bentonensis*, which is closely related to the genera *Deakozyma* and *Limtongella* (Figs. 1–2). Member of the

Trichomonascaceae (*Dipodascales*, *Dipodascomycetes*). The genus is mainly circumscribed by phylogenomic analysis (Fig. 1) and rDNA phylogenetic analysis (Fig. 2), and the presence of genus-specific protein families OG0015427, OG0015488 and OG0019665 (Table 6).

Sexual reproduction not known. Colonies are white, semi-glistening and butyrous. Budding is multilateral. Pseudohyphae are present with elongate blastoconidia, but true hyphae are not observed.

Note: *Grinbergsozyma bentonensis* differs from species of the closely related genera *Deakozyma* and *Limtongella* by growth on 10% NaCl+5% glucose medium (Table S3). Our D1/D2 LSU analysis showed that at least three potential new species belong to *Grinbergsozyma* (Fig. S5, Table S2).

Species accepted:

Grinbergsozyma bentonensis (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857886

Holotype: NRRL YB-2364, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Illinois, Benton, isolated from apple cider, October 1950.

Basionym: *Candida bentonensis* Kurtzman, Antonie van Leeuwenhoek 88: 125. 2005.

Limtongella Sakpunt., Angchuan, Boontham, Khunnamw., Boonmak & Srisuk ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858217

For a description: see Sakpuntoon et al., Microorganisms 8 (27): 11. 2019.

Synonym: *Limtongella* Sakpunt., Angchuan, Boontham, Khunnamw., Boonmak & Srisuk, Microorganisms 8 (27): 11. 2019. Nom. inval., Art. F.5.1 (Shenzhen), the identifier of a recognized repository was not cited.

Type species: *Limtongella siamensis* Sakpuntoon, Angchuan, Boontham, Khunnamw., Boonmak & Srisuk ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

Species accepted:

Limtongella incommunis (Y. Ohara, Nonom. & M. Yamaz.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858218

Holotype: CBS 5604, preserved in a metabolically inactive state in the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands. JAPAN, isolated from grape must.

Basionym: *Candida incommunis* Y. Ohara, Nonom. & M. Yamaz., J. Gen. Appl. Microbiol. 11: 274. 1965.

Limtongella siamensis Sakpunt., Angchuan, Boontham, Khunnamw., Boonmak & Srisuk ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858219

For a description: see Sakpuntoon et al., Microorganisms 8 (27): 11. 2019.

Holotype: NBRC 114140, preserved in a metabolically inactive state at NITE Biological Resource Center (NBRC), Tokyo, Japan. THAILAND, Kasetsart University, isolated from the grease trap.

Synonym: *Limtongella siamensis* Sakpunt., Angchuan, Boontham, Khunnamw., Boonmak & Srisuk, Microorganisms 8 (27): 11. 2019. Nom. inval., Art. 35.1 (Shenzhen), the genus name is invalid as an identifier of a recognized repository was not cited.

Validated taxa of *Starmerella*

Starmerella powellii Lachance ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857934

For a description: see Lachance et al., Int. J. Syst. Evol. Microbiol. 51: 1206. 2001.

Holotype: CBS 8795, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. COSTA RICA, isolated from the nitidulid beetle (*Conotelus* sp.).

Synonyms: *Candida powellii* Lachance, Int. J. Syst. Evol. Microbiol. 51 (3): 1206. 2001. Nom. inval., Art. 40.3 (Melbourne).

≡ *Starmerella powellii* Lachance ex C.A. Rosa & Lachance, Int. J. Syst. Evol. Microbiol. 68: 1342. 2018. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified; published as a combination, but 'basionym' (*Candida powellii*) is invalid.

Tardiomyces Spruijtenburg, Meis & T. de Groot ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB857918

For a description: see Spruijtenburg et al., Infection 52: 1808. 2024.

Synonym: *Tardiomyces* Spruijtenburg, Meis & T. de Groot, Infection 52: 1808. 2024. Nom. inval., Art. F.5.1 (Shenzhen), the identifier of a recognized repository was not cited.

Type species: *Tardiomyces depauwii* Spruijtenburg, Meis & T. de Groot ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

Species accepted:

Tardiomyces blankii (H.R. Buckley & Uden) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857915

Holotype: CBS 1898, preserved in a metabolically inactive state in the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands. CANADA, isolated from blood of a mink (*Putorius vison*).

Basionym: *Candida blankii* H.R. Buckley & Uden, Mycopathol. Mycol. Appl. 36: 259. 1968.

Synonym: *Tardiomyces blankii* (H.R. Buckley & Uden) Spruijtenburg, Meis & T. de Groot, Infection 52: 1809. 2024. Nom. inval., Arts 35.1, 41.5, F.5.1 (Shenzhen), the identifier of a recognized repository was not cited.

Tardiomyces depauwii Spruijtenburg, Meis & T. de Groot ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857921

For a description: see Spruijtenburg et al., Infection 52: 1808. 2024.

Holotype: CBS 18495, preserved in a metabolically inactive state in the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands. UNITED KINGDOM, isolated from human blood.

Synonym: *Tardiomyces depauwii* Spruijtenburg, Meis & T.

de Groot, Infection 52: 1808. 2024. Nom. inval., Art. 35.1, F.5.1 (Shenzhen), the genus name is invalid and the identifier of a recognized repository was not cited.

Tardiomyces digboiensis (G.S. Prasad, Mayilraj, Sood & Ban. Lal) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857923

Holotype: CBS 9800, preserved in a metabolically inactive state in the Westerdijk Fungal Biodiversity Institute (CBS), Utrecht, The Netherlands. INDIA, Assam, Digboi, isolated from acid tar sludge-contaminated soil from the Digboi oil refinery.

Basionym: *Candida digboiensis* G.S. Prasad, Mayilraj, Sood & Ban. Lal, Int. J. Syst. Evol. Microbiol. 55: 968. 2005.

Synonym: *Tardiomyces digboiensis* (G.S. Prasad, Mayilraj, Sood & Ban. Lal) Spruijtenburg, Meis & T. de Groot, Infection 52: 1809. 2024. Nom. inval., Arts 35.1, F.5.1 (Shenzhen), the genus name is invalid and the identifier of a recognized repository was not cited.

Westerdijkia Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB857927

Etymology: the genus is named in honor of Johanna Westerdijk for her contribution to plant pathology, fungal collections, and her role as a leading female scientist and the first female professor in the Netherlands.

Type species: *Westerdijkia sungouii* Q.M. Wang, B. James, K. Sylvester & Hittinger ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the single-species lineage *Candida sungouii*, which occurs in a separate branch from the genera *Diddensiella* and *Spencermartinsiella* (Fig. 3). Member of the *Trichomonascaceae* (*Dipodascales*, *Dipodascomycetes*). The genus is mainly circumscribed by rDNA phylogenetic analysis.

No sexual stages are observed. Colonies are cream, butyrous, smooth. Budding is multilateral. Hyphae and pseudohyphae are not observed.

Note: *Westerdijkia sungouii* can be distinguished from species of the closely related genera *Diddensiella* and *Spencermartinsiella* by the absence of assimilation of ethanol (Table S3). Our D1/D2 LSU analysis showed *Candida* sp. BG02-7-18-018A-2-2 (GenBank AY520408) represents a potential new species of *Westerdijkia* (Fig. S6, Table S2).

Species accepted:

Westerdijkia sungouii Q.M. Wang, B. James, K. Sylvester & Hittinger ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857929

For a description: see Sylvester et al., FEMS Yeast Res. 15: 10. 2015.

Holotype: CBS 13907, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, Wisconsin, isolated from white slime, September 2011.

Synonym: *Candida sungouii* Q.M. Wang, B. James, K. Sylvester & Hittinger, FEMS Yeast Res. 15: 10. 2015. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Incertae sedis in *Dipodascales* (*Dipodascomycetes*)

Dengshuqunia Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB857935

Etymology: the genus is named after Prof. Shu-Qun Deng for his contribution to plant pathogenic fungi.

Type species: *Dengshuqunia hispaniensis* (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the single-species lineage *Candida hispaniensis*, which is phylogenetically positioned in a separate long branch distinct from *Yarrowia* (Fig. 1). Member of the *Dipodascomycetes*. The genus is mainly circumscribed by phylogenomic analysis, and the presence of genus-specific protein families OG0013204, OG0015719 and OG0015720 (Table 6).

Sexual reproduction not known. Colonies are white, semi-glistening and butyrous. Pseudohyphae and true hyphae are not present. However, some tapered outgrowths bear blastoconidia. Fermentation is absent.

Note: *Dengshuqunia* can be distinguished from its closely related genus *Yarrowia* by its low genome size (about 11 Mb) and GC content (41.69%), whereas all species of *Yarrowia* have a genome size of about 20 Mb (17% higher than the genome size of *Dengshuqunia*) and higher GC contents (43.46–50.89%). Our ITS+D1/D2 LSU and D1/D2 LSU analyses showed that four potential new species belong to *Dengshuqunia* (Fig. 5 and Fig. S8, Table S2).

Species accepted:

Dengshuqunia hispaniensis (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857936

Holotype: NRRL Y-5580, preserved in a metabolically inactive state at the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. SPAIN, isolated from the larva of longhorn beetle (*Spondylis buprestoides*) in conifer forest, April 1960.

Basionym: Candida hispaniensis Kurtzman, Antonie van Leeuwenhoek 88: 128. 2005.

Validated taxa in *Yarrowia*

Yarrowia brassicae F.L. Hui & K.F. Liu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857939

For a description: see Liu et al., Int. J. Syst. Evol. Microbiol. 68: 2026. 2018.

Holotype: CICC 33263, preserved in a metabolically inactive state at the China Centre of Industrial Culture Collection (CICC), Beijing, China. CHINA, Henan province, Nanyang, isolated from traditional Chinese sauerkraut.

Synonym: *Yarrowia brassicae* F.L. Hui & K.F. Liu, Int. J. Syst. Evol. Microbiol. 68: 2026. 2018. Nom. inval., Art. 40.7 (Shenzhen), more than one collection in which the type is conserved was specified.

Yarrowia divulgata Nagy, Niss, Dlauchy, Arneborg, D.S. Nielsen & G. Péter ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857940

For a description: see Nagy et al., Int. J. Syst. Evol. Microbiol. 63: 4821. 2013.

Holotype: CBS 11013, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. DENMARK, isolated from a bacon processing plant.

Synonym: *Yarrowia divulgata* Nagy, Niss, Dlauchy, Arneborg, D.S. Nielsen & G. Péter, Int. J. Syst. Evol. Microbiol. 63: 4821. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yarrowia keelungensis Chin F. Chang & S.M. Liu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857941

For a description: see Chang et al., Antonie van Leeuwenhoek 104: 1121. 2013.

Holotype: BCRC 23110, preserved in a metabolically inactive state at the Bioresource Collection and Research Center, Food Industry Research and Development Institute, Hsinchu, Taiwan, China. CHINA, Taiwan province, isolated from the sea-surface microlayer, 2006.

Synonym: *Yarrowia keelungensis* Chin F. Chang & S.M. Liu, Antonie van Leeuwenhoek 104: 1121. 2013. Nom. inval., Art. 40.1, 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yarrowia phangngaensis Limtong, Yongman., H. Kawas. & T. Seki ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB857942

For a description: see Limtong et al., Int. J. Syst. Evol. Microbiol. 58: 517. 2008.

Holotype: BCC 21231, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Science and Technology Development Agency (NSTDA), Pathumthani, Thailand. THAILAND, Phang-Nga Province, Mu Ko Ra-Ko Prathong National Park, isolated from water in a mangrove forest.

Synonyms: *Candida phangngaensis* Limtong, Yongman., H. Kawas. & T. Seki [as '*phangngensis*'], Int. J. Syst. Evol. Microbiol. 58: 517. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Yarrowia phangngaensis* (Limtong, Yongman., H. Kawas. & T. Seki) Gouliam., R.A. Dimitrov, M.T. Sm. & M. Groenew., Persoonia 39: 289. 2017. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified; published as a combination but 'basionym' (*Candida phangngaensis*) invalid.

New taxa in *Pichiaceae* (*Pichiales*, *Pichiomycetes*)

New combinations and validated taxa in *Ogataea*

Ogataea arabinofermentans (Kurtzman & Dien) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858229

Holotype: NRRL YB-2248, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Alaska, isolated from insect frass from dead *Larix*.

Basionym: *Candida arabinofermentans* Kurtzman & Dien, Antonie van Leeuwenhoek 74: 241. 1998.

Ogataea chonburiensis Limtong, Srisuk, Yongman., Yurim. & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858010

For a description: see Limtong et al., Int. J. Syst. Evol. Microbiol. 58: 304. 2008.

Holotype: BCC 21227, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Chonburi province, isolated from the soil.

Synonym: *Ogataea chonburiensis* Limtong, Srisuk, Yongman., Yurim. & Nakase, Int. J. Syst. Evol. Microbiol. 58: 304. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea chumphonensis Limtong, Koowadj., Jindam. & Yongman. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858011

For a description: see Koowadjanakul et al., Antonie van Leeuwenhoek 100: 213. 2011.

Holotype: BCC 42667, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, isolated from the leaves of the tree.

Synonym: *Candida chumphonensis* Limtong, Koowadj., Jindam. & Yongman., Antonie van Leeuwenhoek 100: 213. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea deakii G. Péter, Dlauchy & Čadež ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858012

For a description: see Čadež et al., Int. J. Syst. Evol. Microbiol. 63: 3121. 2013.

Holotype: CBS 12735, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. HUNGARY, Pilis mountains, isolated brown rotten wood of beech (*Fagus sylvatica*), 2003.

Synonym: *Ogataea deakii* G. Péter, Dlauchy & Čadež, Int. J. Syst. Evol. Microbiol. 63: 3121. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea ganodermae F.Y. Bai & Z.H. Ji ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB862204

For a description: see Ji & Bai, Int. J. Syst. Evol. Microbiol. 58: 1504. 2008.

Holotype: CGMCC 2.3435, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Hunan province, Mangshan mountain, isolated from the a basidiocarp of *Ganoderma* sp., October 2006.

Synonym: *Ogataea ganodermae* F.Y. Bai & Z.H. Ji, Int. J. Syst. Evol. Microbiol. 58: 1504. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea histrianica Čadež & G. Péter ex Q.M. Wang,

Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858013

For a description: see Čadež et al., Int. J. Syst. Evol. Microbiol. 63: 3120. 2013.

Holotype: CBS 12779, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SLOVENI, Ankaran, isolated from olive oil sediment of mixed varieties, 2011.

Synonym: *Ogataea histrianica* Čadež & G. Péter, Int. J. Syst. Evol. Microbiol. 63: 3120. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea kanchanaburiensis Limtong, Kaewwich. & M. Groenew. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB862206

For a description: see Limtong et al., Antonie van Leeuwenhoek 103(3): 554. 2012.

Holotype: BCC 47626, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Kanchanaburi province, Mueang District, Wang Dong sub district, isolated from the leaves of the mango tree (*Mangifera indica*).

Synonym: *Ogataea kanchanaburiensis* Limtong, Kaewwich. & M. Groenew., Antonie van Leeuwenhoek 103(3): 554. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea kolombanensis Čadež & G. Péter ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858014.

For a description: see Čadež et al., Int. J. Syst. Evol. Microbiol. 63: 3119. 2013.

Holotype: CBS 12778, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SLOVENI, Koper, isolated from olive oil sediment of the 'Istrska Belica' variety, 2009.

Synonym: *Ogataea kolombanensis* Čadež & G. Péter, Int. J. Syst. Evol. Microbiol. 63: 3119. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea krabiensis Limtong, Srisuk, Yongman., H. Kawas., Yurim., Nakase & N. Kato ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858230

For a description: see Limtong et al., J. Gen. Appl. Microbiol. 50: 123. 2004.

Holotype: TISTR 5820, preserved in a metabolically inactive state at TISTR Culture Collection Bangkok MIRCEN, Thailand Institute of Science and Technological Research, Bangkok 10900, Thailand. THAILAND, Krabi province, isolated from soil, 2000.

Synonym: *Candida krabiensis* Limtong, Srisuk, Yongman., H. Kawas., Yurim., Nakase & N. Kato, J. Gen. Appl. Microbiol. 50: 123. 2004. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea maris (Uden & Zobell) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858231

Holotype: CBS 5151, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. AUSTRALIA, Torres Strait, isolated from seawater.

Basionym: *Torulopsis maris* Uden & Zobell, Antonie van Leeuwenhoek 28: 281. 1962.

Synonym: *Candida maris* (Uden & Zobell) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Ogataea mattraensis Limtong, Koowadj., Jindam. & Yongman. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858015

For a description: see Koowadjanakul et al., Antonie van Leeuwenhoek 100: 214. 2011.

Holotype: BCC 42668, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, isolated from leaves of tree.

Synonym: *Candida mattraensis* Limtong, Koowadj., Jindam. & Yongman. [as '*mattranensis*'], Antonie van Leeuwenhoek 100: 214. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea nakhonphanomensis Limtong, Srisuk, Yongman., Yurim. & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858016

For a description: see Limtong et al., Int. J. Syst. Evol. Microbiol. 58: 305. 2008.

Holotype: BCC 21228, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Nakhon-Phanom province, isolated from a tree exudate.

Synonym: *Ogataea nakhonphanomensis* Limtong, Srisuk, Yongman., Yurim. & Nakase, Int. J. Syst. Evol. Microbiol. 58: 305. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea nemodendra (van der Walt, Klift & D.B. Scott) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858232

Holotype: CBS 6280, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from tunnels of *Xyleborus aemulus* in *Rapanea melanophloeos*.

Basionym: *Torulopsis nemodendra* van der Walt, Klift & D.B. Scott, Antonie van Leeuwenhoek 37: 468. 1971.

Synonym: *Candida nemodendra* (van der Walt, Klift & D.B. Scott) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Ogataea ortonii Lachance ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858233

For a description: see Lachance et al., FEMS Yeast Res. 1: 90. 2001.

Holotype: CBS 8843, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. COSTA RICA, isolated from the flux of old fustic tree (*Maclura tinctoria*).

Synonym: *Candida ortonii* Lachance, FEMS Yeast Res. 1: 90. 2001. Nom. inval., Art. 40.7 (Melbourne), more than one

collection in which the type is conserved was specified.

Ogataea ovalis (Kumam. & M. Yamam.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858234

Holotype: CBS 7298, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from soil.

Basionym: *Candida ovalis* Kumam. & M. Yamam., Trans. Mycol. Soc. Japan 27: 391. 1987.

Ogataea phyllophila Koowadj., Jindam., Yongman. & Limtong ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858017

For a description: see Koowadjanakul et al., Antonie van Leeuwenhoek 100: 211. 2011.

Holotype: BCC 42666, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Chumphon province, Chumphon Islands National Park, isolated from the leaves of a tree, May 2009.

Synonym: *Ogataea phyllophila* Koowadj., Jindam., Yongman. & Limtong, Antonie van Leeuwenhoek 100: 211. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea piceae (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858235

Holotype: CBS 8701, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, Alaska, isolated from insect frass in Sitka spruce (*Picea sitchensis*).

Basionym: *Candida piceae* Kurtzman, Can. J. Microbiol. 46: 54. 2000.

Ogataea pinus (Lodder & Kreger-van Rij) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858237

Holotype: CBS 970, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SWEDEN, isolated from the water-logged heart of a pine tree.

Basionym: *Torulopsis pinus* Lodder & Kreger-van Rij, Yeasts, a taxonomic study, [Edn 1] (Amsterdam): 671. 1952.

Synonyms: *Candida pinus* (Lodder & Kreger-van Rij) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

≡ *Paratorulopsis pinus* (Lodder & Kreger-van Rij) E.K. Novák & Zsolt, Acta Bot. Acad. Sci. Hung. 7: 141. 1961.

Ogataea rishiriensis (Nakase, Imanishi, Ninomiya & M. Takash.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858238

Holotype: NBRC 105027, preserved in a metabolically inactive state at NITE Biological Resource Center (NBRC), Tokyo, Japan. JAPAN, Hokkaido, isolated from the soil in a pine forest.

Basionym: *Candida rishiriensis* Nakase, Imanishi, Ninomiya & M. Takash. [as '*rishirensis*'], J. Gen. Appl. Microbiol. 56: 171. 2010.

Ogataea siamensis Limtong, Srisuk, Yongman., H. Kawas., Yurim., Nakase & N. Kato ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858018

For a description: see Limtong et al., J. Gen. Appl. Microbiol. 50: 121. 2004.

Holotype: JCM 12264, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. THAILAND, Kanchanaburi province, isolated from the flower of *Ervatamia coronaria*, 2001.

Synonyms: *Pichia siamensis* Limtong, Srisuk, Yongman., H. Kawas., Yurim., Nakase & N. Kato, J. Gen. Appl. Microbiol. 50: 121. 2004. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Ogataea siamensis* Limtong, Srisuk, Yongman., H. Kawas., Yurim., Nakase & N. Kato ex Limtong, Srisuk, Yongman., Yurim. & Nakase, Int. J. Syst. Evol. Microbiol. 58: 306. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea sithepensis Limtong, Srisuk, Yongman., H. Kawas., Yurim., Nakase & N. Kato ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858239

For a description: see Limtong et al., J. Gen. Appl. Microbiol. 50: 125. 2004.

Holotype: JCM 12265, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. THAILAND, Petchabun province, Sithep Historical Park, isolated from soil, 2000.

Synonym: *Candida sithepensis* Limtong, Srisuk, Yongman., H. Kawas., Yurim., Nakase & N. Kato, J. Gen. Appl. Microbiol. 50: 125. 2004. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea sonorensis (M.W. Mill., Phaff, M. Miranda, Heed & Starmer) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858240

Holotype: CBS 6792, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. MEXICO, isolated from the tissue of the organ-pipe cactus (*Lemaireocereus thurberi*).

Basionym: *Torulopsis sonorensis* M.W. Mill., Phaff, M. Miranda, Heed & Starmer, Int. J. Syst. Bacteriol. 26: 88. 1976.

Synonym: *Candida sonorensis* (M.W. Mill., Phaff, M. Miranda, Heed & Starmer) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Ogataea thermomethanolica Limtong, Srisuk, Yongman., Yurim., Nakase & N. Kato ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858019

For a description: see Limtong et al., Int. J. Syst. Evol. Microbiol. 55: 2226. 2005.

Holotype: BCC 16875, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Pathalung province, isolated from soil.

Synonyms: *Pichia thermomethanolica* Limtong, Srisuk, Yongman., Yurim., Nakase & N. Kato, Int. J. Syst. Evol. Microbiol. 55: 2226. 2005. Nom. inval., Art. 40.7 (Melbourne),

more than one collection in which the type is conserved was specified.

≡ *Ogataea thermomethanolica* Limtong, Srisuk, Yongman., Yurim., Nakase & N. Kato ex Limtong, Srisuk, Yongman., Yurim. & Nakase, Int. J. Syst. Evol. Microbiol. 58: 306. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea thermophila K.S. Shin, Y.K. Shin, J.H. Yoon & Y.H. Park ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858020

For a description: see Shin et al., Int. J. Syst. Evol. Microbiol. 51: 2168. 2001.

Holotype: JCM 10994, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. SOUTH KOREA, isolated from china clay.

Synonyms: *Candida thermophila* K.S. Shin, Y.K. Shin, J.H. Yoon & Y.H. Park, Int. J. Syst. Evol. Microbiol. 51: 2168. 2001. Nom. inval., Art. 40.7(Melbourne), more than one collection in which the type is conserved was specified.

≡ *Ogataea thermophila* G. Péter, Tornai-Leh., K.S. Shin & Dlauchy, FEMS Yeast Res. 7: 495. 2007. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Ogataea xyloterini (S.O. Suh & J.J. Zhou) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858021

Holotype: ATCC 62898, preserved in a metabolically inactive state at the American Type Culture Collection (ATCC), Manassas, USA. USA, Wisconsin, Palmyra, isolated from *Xyloterinus politus*.

Basionym: *Candida xyloterini* S.O. Suh & J.J. Zhou, Int. J. Syst. Evol. Microbiol. 60: 1704. 2010.

New combination and validated taxa in *Pichia*

Pichia awuae D.S. Nielsen, M. Jakobsen & Jespersen ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858022

For a description: see Nielsen et al., Int. J. Syst. Evol. Microbiol. 60: 1464. 2010.

Holotype: CBS 11011, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. GHANA, isolated from fermenting cocoa beans.

Synonym: *Candida awuae* D.S. Nielsen, M. Jakobsen & Jespersen [as '*awuaii*'], Int. J. Syst. Evol. Microbiol. 60: 1464. 2010. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Pichia bruneiensis Sipiczki ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858023

For a description: see Sipiczki, Int. J. Syst. Evol. Microbiol. 62: 3103. 2012.

Holotype: CBS 12611, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRUNEI, Borneo, isolated from the flowers of *Hibiscus.*

Synonym: *Pichia bruneiensis* Sipiczki, Int. J. Syst. Evol. Microbiol. 62: 3103. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Pichia chibodasensis R. Kobay., A. Kanti & H. Kawas. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858024

For a description: see Kobayashi et al., Int. J. Syst. Evol. Microbiol. 67: 1025. 2017.

Holotype: NBRC 111569, preserved in a metabolically inactive state at the Biological Resource Center, NITE (NBRC), Tokyo, Japan. INDONESIA, West Java, Chibodas Botanic Garden, isolated from soil and decayed wood, December 2014.

Synonym: *Pichia chibodasensis* R. Kobay., A. Kanti & H. Kawas., Int. J. Syst. Evol. Microbiol. 67: 1025. 2017. Nom. inval., Art. 40.7 (Shenzhen), more than one collection in which the type is conserved was specified.

Pichia dushanensis F.L. Hui, Y.C. Ren, S.T. Liu & Ying Li ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858025

For a description: see Ren et al., Int. J. Syst. Evol. Microbiol. 65: 2877. 2015.

Holotype: CBS 13912, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Dushan Forest Park in Nanyang, isolated from the gut of insect larvae.

Synonym: *Pichia dushanensis* F.L. Hui, Y.C. Ren, S.T. Liu & Ying Li, Int. J. Syst. Evol. Microbiol. 65: 2877. 2015. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Pichia insulana Ganter, Cardinali & Boundy-Mills ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858028

For a description: see Ganter et al., Int. J. Syst. Evol. Microbiol. 60: 1003. 2010.

Holotype: CBS 11169, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CURAÇAO, isolated from a rot pocket in a *Cereus repandus*.

Synonym: *Pichia insulana* Ganter, Cardinali & Boundy-Mills, Int. J. Syst. Evol. Microbiol. 60: 1003. 2010. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Pichia phayaonensis Limtong, Nitiyon, Kaewwich., Jindam., Am-In & Yongman. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858029

For a description: see Limtong et al., Int. J. Syst. Evol. Microbiol. 62: 2789. 2012.

Holotype: BCC 47634, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Phayao province, isolated from soil, December 2008.

Synonyms: *Candida phayaonensis* Limtong, Nitiyon, Kaewwich., Jindam., Am-In & Yongman., Int. J. Syst. Evol. Microbiol. 62: 2789. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Pichia phayaonensis* Limtong, Nitiyon, Kaewwich.,

Jindam., Am-In & Yongman. ex H.Y. Zhu, L.C. Guo & F.Y. Bai, Int. J. Syst. Evol. Microbiol. 74: 006306, 7. 2024. Nom. inval., Art. 40.1 (Shenzhen), published as a combination but 'basionym' (*Candida phayaonensis*) invalid.

Pichia sorboxylosa (Nakase) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858241

Holotype: CBS 6378, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from pineapple (*Ananas comosus*).

Basionym: *Candida sorboxylosa* Nakase, J. Gen. Appl. Microbiol. 17: 392. 1971.

Pichia thaimueangensis Limtong, Yongman., H. Kawas. & T. Seki ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858030

For a description: see Limtong et al., Int. J. Syst. Evol. Microbiol. 57: 651. 2007.

Holotype: BCC 21229, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Phang-Nga province, Kho Lumpee-Haad Thaimueang National Park, isolated from water in a mangrove forest.

Synonyms: *Candida thaimueangensis* Limtong, Yongman., H. Kawas. & T. Seki, Int. J. Syst. Evol. Microbiol. 57: 651. 2007. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Pichia thaimueangensis* Limtong, Yongman., H. Kawas. & T. Seki ex H.Y. Zhu, L.C. Guo & F.Y. Bai, Int. J. Syst. Evol. Microbiol. 74: 006306, 7. 2024. Nom. inval., Art. 40.1 (Shenzhen), published as a combination, but 'basionym' (*Candida thaimueangensis*) is invalid.

Ramirezia Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858227

Etymology: the genus is named in honor of C. Ramírez, who described the type species of this genus.

Type species: *Ramirezia boidinii* (C. Ramírez) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the single-species lineage *Candida boidinii*, which is in a separate long branch from the other genera in *Pichiales* (Fig. 6). Member of the *Pichiaceae* (*Pichiales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, and the presence of genus-specific protein families OG0009746, OG0009748 and OG0009751 (Table 6).

Sexual reproduction not known. Colonies are white to cream, butyrous. Budding is multilateral. Pseudohyphae with blastoconidia are present. Septate hyphae may be present. Coenzyme Q-7 is formed.

Note: Our ITS analysis showed that two potential new species belong to *Ramirezia* (Fig. S10, Table S2).

Species accepted:

Ramirezia boidinii (C. Ramírez) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858228

Holotype: CBS 2428, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SPAIN, isolated from tanning fluid.

Basionym: *Candida boidinii* C. Ramírez [as '*boidini*'], Microbiol. Esp. 6: 251. 1953.

Wenyingozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB857943

Etymology: the genus is named in honor of Wen-Ying Zhuang for her contributions to the taxonomy of *Ascomycota*, especially of *Pezizomycetes*.

Type species: *Wenyingozyma ramenticola* (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for species in the *Ogataea* clade 2 (i.e., the *Ogataea naganishii* subclade, the *Candida methanosorbosa* subclade, the *Ogataea ramenticola* subclade and the single-species *Ogataea methylovora*) which is in a separate clade from the *Ogataea* clade 1 (Fig. 6). Member of the *Pichiaceae* (*Pichiales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0006088, OG0006166 and OG0006167 (Table 6).

Both teleomorphic and anamorphic species occur. Asci originate from conjugation between a cell and its bud or between independent cells, and produce one to four hat-shaped ascospores. Colonies are cream to white, butyrous. Budding is multilateral. Neither pseudohyphae nor true hyphae are formed. Where known, coenzyme Q-7 is formed.

Species accepted:

Wenyingozyma methanosorbosa (S. Abe & Yokote) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858220

Holotype: CBS 7029, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from soil.

Basionym: *Torulopsis methanosorbosa* S. Abe & Yokote, J. Ferment. Technol. 52: 203. 1974.

Synonym: *Candida methanosorbosa* (S. Abe & Yokote) J.A. Barnett, R.W. Payne & Yarrow, Yeasts: Characteristics and Identification (Cambridge): 732. 1983.

Wenyingozyma methylovora (Kumam. & Seriu) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858221

Holotype: CBS 7300, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from a rotted tree.

Basionym: *Pichia methylovora* Kumam. & Seriu, Trans. Mycol. Soc. Japan 27: 394. 1987.

Synonym: *Ogataea methylovora* (Kumam. & Seriu) Kurtzman & Robnett [as '*methylivora*'], FEMS Yeast Res. 10: 357. 2010.

Wenyingozyma naganishii (K. Kodama) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858222

Holotype: CBS 6429, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from exudate from a camellia (*Camellia japonica*).

Basionym: *Pichia naganishii* K. Kodama, J. Ferment. Technol. 52: 9. 1974.

Synonym: *Ogataea naganishii* (K. Kodama) Kurtzman & Robnett, FEMS Yeast Res. 10: 357. 2010.

Wenyingozyma nanaspora (Saëz & Rodr. Mir.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857944

Holotype: CBS 7200, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. FRANCE, isolated from hair of capuchin monkey (*Cebus apella*).

Basionym: *Candida nanaspora* Saëz & Rodr. Mir., Bull. Trimestriel Soc. Mycol. France 104: 214. 1988.

Wenyingozyma neixiangensis (F.L. Hui & Jun Zheng) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857945

Holotype: CICC 33166, preserved in a metabolically inactive state at the China Centre of Industrial Culture Collection (CICC), Beijing, China. CHINA, Henan province, Baotianman Nature Reserve, isolated from rotting wood, September 2016.

Basionym: *Ogataea neixiangensis* F.L. Hui & Jun Zheng, Int. J. Syst. Evol. Microbiol. 67: 3041. 2017.

Wenyingozyma nitratophila (Shifrine & Phaff) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857946

Holotype: CBS 2027, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, California, isolated from bark beetle (*Dendroctonus monticolae*).

Basionym: *Torulopsis nitratophila* Shifrine & Phaff, Mycologia 48: 48. 1956.

Synonym: *Candida nitratophila* (Shifrine & Phaff) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Wenyingozyma ramenticola (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB857947

Holotype: NRRL YB-1985, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Florida, Wilma, isolated from frass in a tunnel of a beetle from *Pinus palustris*.

Basionym: *Pichia ramenticola* Kurtzman, Canad. J. Microbiol. 46: 51. 2000.

Synonym: *Ogataea ramenticola* (Kurtzman) Kurtzman & Robnett, FEMS Yeast Res. 10: 357. 2010.

Wenyingozyma succiphila (J.D. Lee & Komag.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858223

Holotype: CBS 8003, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from sap of a peach tree (*Amygdalus persica*).

Basionym: *Candida succiphila* J.D. Lee & Komag., Int. J. Syst. Bacteriol. 30: 518. 1980.

Synonym: *Candida cellulolytica* Nakase, M. Suzuki, M. Takash. & Hamam., J. Gen. Appl. Microbiol. 40: 521. 1994.

Note: *C. succiphila* and *C. cellulolytica* have the same LSU D1/D2 sequences and near 100% genome sequence similarity; therefore, *C. cellulolytica* is assigned as a synonym of *C. succiphila*.

Wenyingozyma suzukii (G. Péter, Tornai-Leh., Fülöp & Dlauchy) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858008

Holotype: CBS 9253, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, isolated from the bark of an unidentified tree.

Basionym: *Candida suzukii* G. Péter, Tornai-Leh., Fülöp & Dlauchy, Antonie van Leeuwenhoek 84: 149. 2003.

Wenyingozyma wangdongensis Limtong, Kaewwich. & M. Groenew. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858009

For a description: see Limtong et al., Antonie van Leeuwenhoek 103: 555. 2012.

Holotype: BCC 42667, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Kanchanaburi province, isolated from leaves of wine grape (*Vitis vinifera*), July 2009.

Synonym: *Ogataea wangdongensis* Limtong, Kaewwich. & M. Groenew., Antonie van Leeuwenhoek 103: 555. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Xiuguozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858224

Etymology: the genus is named in honor of Xiu-Guo Zhang for his contribution to fungal taxonomy, especially of *Hyphomycetes*.

Type species: *Xiuguozyma insectalens* (D.B. Scott, van der Walt & Klift) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species of the *Candida insectalens* clade, which is in a separate clade from *Allodekkera* and *Brettanomyces* in the phylogenomic tree (Fig. 6). Member of *Pichiaceae* (*Pichiales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, and the presence of genus-specific protein families OG0009801, OG0009803 and OG001190 (Table 6).

Sexual reproduction not known. Colonies are white to cream, butyrous, smooth, convex. Budding is multilateral. Fermentation is absent. Coenzyme Q-9 is formed.

Note: *Xiuguozyma* species can be distinguished from species of the closely related genus *Brettanomyces* by the lack of growth with 0.01% cycloheximide (Table S3). Ecologically, the new genus *Xiuguozyma* appears to be related to insects.

Species accepted:

Xiuguozyma insectalens (D.B. Scott, van der Walt & Klift) Q.M. Wang, Boekhout, A.M. Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858225

Holotype: CBS 6036, preserved in a metabolically inactive

state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from tunnels of *Crossotarsus extrernedentatus* in *Ficus sycomorus*.

Basionym: *Torulopsis insectalens* D.B. Scott, van der Walt & Klift, Antonie van Leeuwenhoek 37: 467. 1971.

Synonym: *Candida insectalens* (D.B. Scott, van der Walt & Klift) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Xiuguozyma silvatica (van der Walt, Klift & D.B. Scott) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858226

Holotype: CBS 6277, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from tunnels of *Crossotarsus extrernedentatus* in *Ficus sycomorus.*

Basionym: *Torulopsis silvatica* van der Walt, Klift & D.B. Scott, Antonie van Leeuwenhoek 37: 465. 1971.

Synonym: *Candida silvatica* (van der Walt, Klift & D.B. Scott) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

New taxa, reinstated and emended genera in *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*)

Candida Berkhout, ***nom. cons., emend.*** Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai

Type species: *Candida vulgaris* Berkhout.

This genus is emended to accommodate the species in the *Candida sensu stricto* clade including *Candida albicans, Candida dubliniensis* and *Candida tropicalis* (Fig. 9). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The emended genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0006430 and OG0006359 (Table 6).

Both teleomorphic and anamorphic species occur in this genus. Asci are unconjugated asci with one or two ellipsoidal to elongate ascospores. Colonies are white to cream, smooth and butyrous. Budding is multilateral. Pseudohyphae and septate hyphae are present or not. Where known, coenzyme Q-9 is formed.

Species accepted:

Candida albicans (C.P. Robin) Berkhout, Schimmelgesl. Monilia: 44. 1923.

MycoBank: MB256187

Synonyms: *Oidium albicans* C.P. Robin, Hist. Nat. Veg. Paras.: 488. 1853.

≡ *Dematium albicans* (C.P. Robin) E. Laurent, Bull. Soc. Belge Microscop. 16: 14. 1889.

≡ *Monilia albicans* (C.P. Robin) Zopf, Pilze: 478. 1890. Nom. illeg., Art. 53.1, non *Monilia albicans* Pers. 1822.

≡ *Myceloblastanon albicans* (C.P. Robin) M. Ota, Jap. J. Derm. Urol. 27: 170. 1927.

≡ *Mycotorula albicans* (C.P. Robin) Langeron & Talice, Ann. Parasitol. Humaine Comp. 10: 44. 1932.

≡ *Parasaccharomyces albicans* (C.P. Robin) Mello & L.G. Fern., Arq. Hig. Patol. Exot. 6: 207-316. 1918.

≡ *Procandida albicans* (C.P. Robin) E.K. Novák & Zsolt, Acta Bot. Acad. Sci. Hung. 7: 133. 1961. Nom. inval., Art. 41.5 (Melbourne).

≡ *Saccharomyces albicans* (C.P. Robin) Reess, Sitzungsber. Phys.-Med. Soc. Erlangen 9: 195. 1877.

≡ *Syringospora albicans* (C.P. Robin) C.W. Dodge, Medic. Mycol.: 274. 1935.

Candida aquae-textoris Vallini, Frassinetti & Scorzetti [as '*aquaetextoris*'], Int. J. Syst. Bacteriol. 47: 336. 1997.

MycoBank: MB436997

Candida baotianmanensis Y.C. Ren, L.L. Xu, Lin Zhang & F.L. Hui ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858036

For a description: see Ren et al., Int. J. Syst. Evol. Microbiol. 65: 3583. 2015.

Holotype: CBS 13915, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Baotianman Mountain in Nanyang, isolated from the gut of *Nitidula carnaria*.

Synonym: *Candida baotianmanensis* Y.C. Ren, L.L. Xu, Lin Zhang & F.L. Hui, Int. J. Syst. Evol. Microbiol. 65: 3583. 2015. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Candida buenavistaensis S.O. Suh, N.H. Nguyen & M. Blackw., FEMS Yeast Res. 8: 96. 2008.

MycoBank: MB505577

Candida dubliniensis D.J. Sullivan, Western., K.A. Haynes, Dés.E. Benn. & D.C. Coleman [as '*dublinionensis*'], Microbiology (Reading) 141: 1519. 1995.

MycoBank: MB254786

Candida frijolesensis S.O. Suh, N.H. Nguyen & M. Blackw., FEMS Yeast Res. 8: 96. 2008.

MycoBank: MB505950

Candida gigantensis S.O. Suh, N.H. Nguyen & M. Blackw., FEMS Yeast Res. 8: 92. 2008.

MycoBank: MB505574

Candida kantuleensis Nitiyon, Khunnamw., Lertwatt. & Limtong, Int. J. Syst. Evol. Microbiol. 68: 2316. 2018.

MycoBank: MB824179

Candida labiduridarum S.O. Suh, N.H. Nguyen & M. Blackw., FEMS Yeast Res. 8: 97. 2008.

MycoBank: MB505578

Candida maltosa Komag., Nakase & Katsuya, J. Gen. Appl. Microbiol., 10: 327. 1964.

MycoBank: MB327445

Candida neerlandica Kurtzman, Robnett & Yarrow, Antonie van Leeuwenhoek 80: 81. 2001.

MycoBank: MB456708

Candida pellucidi Glushakova, Tomashevskaya & Kachalkin [as '*pellucida*'], Persoonia 44: 369. 2020.

MycoBank: MB836057

Candida pseudoviswanathii Y.C. Ren, L.L. Xu, Lin Zhang & F.L. Hui ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858037

For a description: see Ren et al., Int. J. Syst. Evol. Microbiol. 65: 3584. 2015.

Holotype: CBS 13916, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Nanyang, isolated from the gut of a beetle larva (*Dorcus curvidens*).

Synonym: *Candida pseudoviswanathii* Y.C. Ren, L.L. Xu, Lin Zhang & F.L. Hui, Int. J. Syst. Evol. Microbiol. 65: 3584. 2015. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Candida sanyaensis F.L. Hui, Q.H. Niu, T. Ke & Ying X. Li ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858038

For a description: see Hui et al., Antonie van Leeuwenhoek 103: 50. 2013.

Holotype: CBS 12637, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Hainan province, Sanya, isolated from soil.

Synonym: *Candida sanyaensis* F.L. Hui, Q.H. Niu, T. Ke & Ying X. Li, Antonie van Leeuwenhoek 103: 50. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Candida saraburiensis Nitiyon, Boonmak, Am-In, Jindam., H. Kawas., Yongman. & Limtong ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858039

For a description: see Nitiyon et al., Int. J. Syst. Evol. Microbiol. 61: 465. 2011.

Holotype: CBS 11696, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Saraburi province, isolated from decaying corncobs.

Synonym: *Candida saraburiensis* Nitiyon, Boonmak, Am-In, Jindam., H. Kawas., Yongman. & Limtong, Int. J. Syst. Evol. Microbiol. 61: 465. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Candida sojae Nakase, M. Suzuki, M. Takash., Yozo Miyak., Kagaya, Fukaz. & Komag., J. Gen. Appl. Microbiol. 40: 163. 1994.

MycoBank: MB363475

Candida tetrigidarum S.O. Suh, N.H. Nguyen & M. Blackw., FEMS Yeast Res. 8: 97. 2008.

MycoBank: MB505573

Candida tropicalis (Castell.) Berkhout, Schimmelgesl. Monilia: 44. 1923.

MycoBank: MB280770

Synonyms: *Oidium tropicale* Castell., Philipp. J. Sci., B, Med. Sci. 5: 202. 1910.

≡ *Candida vulgaris* Berkhout, Schimmelgesl. Monilia: 42. 1923 (TYPE of the genus *Candida*).

Candida viswanathii R.S. Sandhu & H.S. Randhawa, Mycopath. Mycol. Appl. 18: 179. 1962.

MycoBank: MB294056

Synonym: *Candida viswanathii* T.S. Viswan. & H.S. Randhawa, Sci. Cult. 25: 86. 1959. Nom. inval., Art. 39.1 (Melbourne).

Candida yunnanensis F.L. Hui & L.N. Huang, Int. J. Syst. Evol. Microbiol. 69: 2778. 2019.

MycoBank: MB830819

Chernovozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***gen. nov.***

MycoBank: MB858242

Etymology: the genus is named in honor of I. Yu. Chernov for his contribution to yeast taxonomy and ecology.

Type species: *Chernovozyma aurita* (A.V. Polyak. & Chernov) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the *Candida aurita* clade, which occurs as a separate lineage closely related to *Kurtzmaniella* and the *Candida railenensis* clade in *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*) (Fig. 12). The genus is mainly circumscribed by the phylogenomic and rDNA phylogenetic analyses, and the presence of genus-specific protein families OG0009945, OG0009948 and OG0010921 (Table 6).

Sexual reproduction not known. Colonies are white, cream, butyrous. Budding is multilateral. Pseudohyphae is produced, but hyphae are not present.

Note: *Chernovozyma* spp. are different from those of the closely related genus *Dujonia* by the lack of growth on 0.1% cycloheximide (Table S3).

Species accepted:

Chernovozyma aurita (A.V. Polyak. & Chernov) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858243

Holotype: CBS 9724, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SIBERIA, isolated from the soil of a peat bog.

Basionym: *Candida aurita* A.V. Polyak. & Chernov, Microbiology, Moscow 71: 332. 2002.

Chernovozyma palmyrensis (S.O. Suh & J.J. Zhou) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858244

Holotype: ATCC 62899, preserved in a metabolically inactive state at the American Type Culture Collection (ATCC), Manassas, USA. USA, Wisconsin, Palmyra, isolated from *Xyloterinus politus*.

Basionym: *Candida palmyrensis* S.O. Suh & J.J. Zhou, Int. J. Syst. Evol. Microbiol. 60: 1706. 2010.

Chernovozyma sophiae-reginae (C. Ramírez & A.E. González) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858245

Holotype: CBS 8175, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHILE, isolated from rotten wood of Chilean laurel (*Laurelia sempervirens*).

Basionym: *Candida sophiae-reginae* C. Ramírez & A.E. González, Mycopathologia 88: 93. 1984.

New combinations and validated taxa in *Debaryomyces*

Debaryomyces psychrophilus (Goto, Sugiy. & Iizuka) Q.M.

Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858088

Holotype: CBS 5956, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. ANTARCTICA, isolated from the dung of *Spheniscidae*.

Basionym: *Torulopsis psychrophila* Goto, Sugiy. & Iizuka, Mycologia 61: 761. 1969.

Synonym: *Candida psychrophila* (Goto, Sugiy. & Iizuka) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Debaryomyces renaianus C.F. Lee & Y.R. Liu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858089

For a description: see Lee et al., Bot. Studies (Taipei) 50: 326. 2009.

Holotype: CBS 10891, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Nantou, Renai, isolated from forest soil.

Synonym: *Debaryomyces renaii* C.F. Lee & Y.R. Liu, Bot. Studies (Taipei) 50: 326. 2009. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Debaryomyces vindobonensis Lopandić, Rents. & Prillinger ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858090

For a description: see Lopandić et al., J. Gen. Appl. Microbiol. 59: 54. 2013.

Holotype: CBS 11666, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. AUSTRIA, Vienna, isolated from the wastewater treatment plant.

Synonym: *Debaryomyces vindobonensis* Lopandić, Rents. & Prillinger, J. Gen. Appl. Microbiol. 59: 54. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Dujonia Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***gen. nov.***

MycoBank: MB848190

Etymology: the genus is named in honor of Dr. Bernard Dujon for his contribution to comparative genomics and genetics of ascomycetous yeasts, and his leading role in the French Genolevures consortium.

Type species: *Dujonia schatavii* (Kock.-Krat. & Ondrush.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the *Candida railenensis* clade, which occurs as a separate lineage closely related to the genus *Kurtzmaniella* and the *Candida aurita* clade in *Debaryomycetaceae* (Figs. 12–13). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomics analysis, and the presence of genus-specific protein family OG0009139 (Table 6).

Sexual reproduction not known. Colonies are white, creamy, butyrous. Budding is multilateral. Hyphae are present or not. Pseudohyphae are produced.

Species accepted:

Dujonia boleticola (Nakase) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848192

Holotype: CBS 6420, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from the fruiting body of an earthstar mushroom (*Astraeus hygrometricus*).

Basionym: *Candida boleticola* Nakase, J. Gen. Appl. Microbiol. 17: 473. 1971.

Dujonia oleophila (Montrocher) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848193

Holotype: CBS 2219, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. ITALY, isolated from olives (*Olea europea*).

Basionym: *Candida oleophila* Montrocher, Rev. Mycol. (Paris) 32: 73. 1967.

Dujonia railenensis (C. Ramírez & A.E. González) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848194

Holotype: CBS 8164, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHILE, isolated from the rotten trunk of southern beech (*Nothofagus dombeyii*).

Basionym: *Candida railenensis* C. Ramírez & A.E. González, Mycopathologia 88: 55. 1984.

Dujonia santamariae (Montrocher) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848195

Holotype: CBS 4515, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SPAIN, isolated from the sugar solution.

Basionym: *Candida santamariae* Montrocher, Rev. Mycol. (Paris) 32: 77. 1967.

Dujonia schatavii (Kock.-Krat. & Ondrush.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848196

Holotype: CBS 6452, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CZECHOSLOVAKIA, isolated from the basidiocarp of a polypore (*Fomitopsis pinicola*).

Basionym: *Torulopsis schatavii* Kock.-Krat. & Ondrush., Biológia (Bratislava) 26: 483. 1971.

Synonym: *Candida schatavii* (Kock.-Krat. & Ondrush.) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Dujonia zeylanoides (Castell.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848197

Holotype: CBS 619, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SRI LANKA, isolated from blastomycotic macroglossia.

Basionym: *Monilia zeylanoides* Castell., J. Trop. Med. Hyg. 23: 17. 1920.

Synonym: *Candida zeylanoides* (Castell.) Langeron & Guerra, Ann. Parasitol. Humaine Comp. 16: 501. 1938.

Fermentozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***gen. nov.***

MycoBank: MB848183

Etymology: the genus is named after the fermentation ability of the type species.

Type species: *Fermentozyma sake* (Saito & M. Ota) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the lineage with *Candida sake*, which occurs in a separate branch from *Teunomyces* (Fig. 9). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis (Fig. 9) and rDNA-based phylogenetic analysis (Fig. 10), and the presence of genus-specific protein families OG0012707, OG0015120 and OG0019183 (Table 6).

Sexual reproduction not known. Colonies white or cream, soft. Budding is multilateral. Pseudohyphae present or not.

Note: *Fermentozyma* can be distinguished from its closely related genus *Teunomyces* by genome size and GC content (Table S3). *Fermentozyma* has a 14 Mb genome size with GC 38.76%, whereas *Teunomyces* has a low genome size (10–13Mb) and higher GC content (41.03–46.16%). Our ITS+D1/D2 LSU analysis showed that *Candida* sp. KBP Y-6292 (GenBank OP941477) may represent the third species of *Fermentozyma* (Fig. 10, Table S2).

Species accepted:

Fermentozyma sake (Saito & M. Ota) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848184

Holotype: CBS 159, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from sake-moto.

Basionym: *Eutorulopsis sake* Saito & M. Ota, J. Brew. 12: 166. 1934.

Synonym: *Candida sake* (Saito & M. Ota) Uden & H.R. Buckley ex S.A. Mey. & Ahearn, Mycotaxon 17: 298. 1983.

Fermentozyma vespimorsuum (Padamsee, B.S. Weir, M.E. Petterson & P.K. Buchanan) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848185

Holotype: PDD 105304. NEW ZEALAND, isolated from the surface of the cup fungus.

Basionym: *Candida vespimorsuum* Padamsee, B.S. Weir, M.E. Petterson & P.K. Buchanan, Persoonia 38: 349. 2017.

Glucitozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858042

Etymology: the genus is named based on the utilization of D-glucitol of species in this lineage.

Type species: *Glucitozyma multigemmis* (Buhagiar) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the single-species lineage *Candida multigemmis*, which occurs in a separate long branch from the other taxa in the *Serinales* (e.g., *Metschwnikowiaceae* and *Debaryomycetaceae*) (Fig. 12). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, and the presence of genus-specific protein families OG0018541, OG0018542 and OG0018545 (Table 6).

Sexual reproduction not known. Colonies are white, smooth, creamy, semi-glossy. Pseudohyphae and hyphae are absent. Coenzyme Q-9 is formed.

Note: *Glucitozyma* differs from its closely related genus *Meyerozyma* by lower 32.6% GC content, whereas the genus *Meyerozyma* has a higher 42.5–50% GC content (Table S3). The ITS blast analysis demonstrated that *Candida* sp. CPD-35-1 (GenBank MZ701688) differs from *C. multigemmis* by 14 nt (2%) in the ITS region, which indicates that *Candida* sp. CPD-35-1 represents a potential new member of *Glucitozyma* (Fig. S12).

Species accepted:

Glucitozyma multigemmis (Buhagiar) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858043

Holotype: CBS 6524, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. UK, isolated from raspberry (*Rubus idaeus*).

Basionym: *Torulopsis multigemmis* Buhagiar, J. Gen. Microbiol. 86: 7. 1975.

Synonym: Candida multigemmis (Buhagiar) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Hemisphaericaspora F.L. Hui, Y.C. Ren, Liang Chen, Ying Li, Lin Zhang & Q.H. Niu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858044

For a description: see Hui et al., PLoS ONE 9: e103737, 7. 2014.

Synonym: *Hemisphaericaspora* F.L. Hui, Y.C. Ren, Liang Chen, Ying Li, Lin Zhang & Q.H. Niu, PLoS ONE 9: e103737, 7. 2014. Nom. inval., Art. 40.1 (Melbourne). The name of the type species of *Hemisphaericaspora* is invalid, therefore, the genus name *Hemisphaericaspora* is also invalid without a type.

Type species: *Hemisphaericaspora nanyangensis* F.L. Hui, Y.C. Ren, Liang Chen, Ying Li, Lin Zhang & Q.H. Niu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

Species accepted:

Hemisphaericaspora elongata (C.Y. Chai & F.L. Hui) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858046

Holotype: NYNU 18115, preserved in a metabolically inactive state at Nanyang University, Henan province, China. CHINA, Yunnan province, Jinghong, Mengyang town, isolated from rotting wood from a tropical rainforest, August 2018.

Basionym: *Spathaspora elongata* C.Y. Chai & F.L. Hui, MycoKeys 75: 36. 2020.

Hemisphaericaspora gorwiae (M.R. Lopes, C.G. Morais, R.M. Cadete, C. Fonseca, Kominek, Hittinger, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858047

Holotype: UFMG-CM-Y312, preserved in a metabolically inactive state at the Collection of Microorganisms and Cells of Federal University of Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil. BRAZIL, isolated from rotting wood.

Basionym: *Spathaspora gorwae* M.R. Lopes, C.G. Morais, R.M. Cadete, C. Fonseca, Kominek, Hittinger, Lachance & C.A. Rosa [as '*gorwiae*'], FEMS Yeast Res. 16: fow044, 10. 2016.

Hemisphaericaspora haegerdaliae (M.R. Lopes, C.G. Morais, R.M. Cadete, C. Fonseca, Kominek, Hittinger, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858048

Holotype: UFMG-CM-Y303, preserved in a metabolically inactive state at the the Collection of Microorganisms and Cells of Federal University of Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil. BRAZIL, isolated from rotting wood.

Basionym: *Spathaspora haegerdaliae* M.R. Lopes, C.G. Morais, R.M. Cadete, C. Fonseca, Kominek, Hittinger, Lachance & C.A. Rosa [as '*hagerdaliae*'], FEMS Yeast Res. 16: fow044, 10. 2016.

Hemisphaericaspora insectamans (D.B. Scott, van der Walt & Klift) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858049

Holotype: CBS 6033, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from frass of beetle larvae in gum Arabic tree (*Acacia nilotica*).

Basionym: *Candida insectamans* D.B. Scott, van der Walt & Klift, Mycopathol. Mycol. Appl. 47: 226. 1972.

Synonym: *Hemisphaericaspora insectamans* (D.B. Scott, van der Walt & Klift) F.L. Hui, Y.C. Ren, Liang Chen, Ying Li, Lin Zhang & Q.H. Niu, PLoS ONE 9: e103737, 8. 2014. Nom. inval., Art. 35.1, the genus name is invalid (Melbourne).

Hemisphaericaspora jiuxiensis (C.Y. Chai & F.L. Hui) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858050

Holotype: NYNU 17416, preserved in a metabolically inactive state at Nanyang University, Henan province, China. CHINA, Yunnan province, Honghe prefecture, Luxi county, Jiuxi Mountain Forest Park, isolated from rotting wood, July 2017.

Basionym: *Spathaspora jiuxiensis* C.Y. Chai & F.L. Hui, MycoKeys 75: 40. 2020.

Hemisphaericaspora lyxosophila (van der Walt, N.P. Ferreira & Steyn) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858051

Holotype: CBS 8194, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from the surface of the woodland soil.

Basionym: *Candida lyxosophila* van der Walt, N.P. Ferreira & Steyn, Antonie van Leeuwenhoek 53: 93. 1987.

Hemisphaericaspora mengyangensis (C.Y. Chai & F.L. Hui) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858052

Holotype: NYNU 17741, preserved in a metabolically inactive state at Nanyang University, Henan province, China. CHINA, Yunnan province, Jinghong, Mengyang town, isolated from rotting wood from a tropical rainforest, July 2017.

Basionym: *Spathaspora mengyangensis* C.Y. Chai & F.L. Hui, MycoKeys 75: 38. 2020.

Hemisphaericaspora nanyangensis F.L. Hui, Y.C. Ren, Liang Chen, Ying Li, Lin Zhang & Q.H. Niu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858053

For a description: see Hui et al., PLoS ONE 9: e103737, 7. 2014.

Holotype: CBS 13020, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Nanyang, Baotianman Nature Reserve, isolated from the frass of beetle larvae, July 2013.

Synonym: *Hemisphaericaspora nanyangensis* F.L. Hui, Y.C. Ren, Liang Chen, Ying Li, Lin Zhang & Q.H. Niu, PLoS ONE 9: e103737, 7. 2014. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Hemisphaericaspora parajiuxiensis (C.Y. Chai & F.L. Hui) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858054

Holotype: NYNU 16747, preserved in a metabolically inactive state at Nanyang University, Henan province, China. CHINA, Yunnan province, Honghe prefecture, Luxi county, Jiuxi Mountain Forest Park, isolated from rotting wood, July 2016.

Basionym: *Spathaspora parajiuxiensis* C.Y. Chai & F.L. Hui, MycoKeys 75: 41. 2020.

Hemisphaericaspora roraimensis (R.M. Cadete, Zilli, M.J.S. Vital, F.C.O. Gomes, Stambuk, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858216

Holotype: UFMG-XMD 23.2. BRAZIL, Roraima, isolated from rotting wood in the Amazonian forest ecosystem.

Basionym: *Spathaspora roraimensis* R.M. Cadete, Zilli, M.J.S. Vital, F.C.O. Gomes, Stambuk, Lachance & C.A. Rosa [as '*roraimanensis*'], Antonie van Leeuwenhoek 103: 428. 2013.

Hemisphaericaspora rosae (C.Y. Chai & F.L. Hui) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858055

Holotype: NYNU 17934, preserved in a metabolically inactive state at Nanyang University, Henan province, China. CHINA, Yunnan province, Jinghong, Mengyang town, isolated from rotting wood in a tropical rainforest, July 2017.

Basionym: *Spathaspora rosae* C.Y. Chai & F.L. Hui, MycoKeys 75: 43. 2020.

Hemisphaericaspora subhashii (M. Groenew., Sigler & S.E. Richardson) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858056

Holotype: CBS 10753, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CANADA, Ontario, isolated from the peritoneal dialysis fluid of man.

Basionym: *Candida subhashii* M. Groenew., Sigler & S.E. Richardson, Med. Mycol. 47: 308. 2009.

Hemisphaericaspora xylanilytica Boonmak, Limtong, Jindam., Am-in, Yongman., Nakase & H. Kawas. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858057

For a description: see Boonmak et al., Int. J. Syst. Evol. Microbiol. 61: 1231. 2011.

Holotype: CBS 11761, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Nakhon Ratchasima, National Corn and Sorghum Research Center, isolated from decayed corn cobs.

Synonym: *Candida xylanilytica* Boonmak, Limtong, Jindam., Am-in, Yongman., Nakase & H. Kawas., Int. J. Syst. Evol. Microbiol. 61: 1231. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Hemisphaericaspora xylofermentans (R.M. Cadete, F.C.O. Gomes, Stambuk, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858058

Holotype: UFMG-HMD23.3. BRAZIL, Roraima, isolated from rotting wood in the Amazonian forest ecosystem.

Basionym: *Spathaspora xylofermentans* R.M. Cadete, F.C.O. Gomes, Stambuk, Lachance & C.A. Rosa, Antonie van Leeuwenhoek 103: 430. 2013.

Insectozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858064

Etymology: the genus name is based on the ecological origin of most species that were isolated from insects.

Type species: *Insectozyma corydali* (N.H. Nguyen, S.O. Suh & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species of the *Candida corydali* clade, which occur in a separate clade from the *Candida sensu stricto* clade, the *Lodderomyces* clade, *Nematodospora*, *Scheffersomyces*, the *Candida blackwelliae* clade, the *Hemisphaericaspora* clade, and the single-species lineage *Scheffersomyces stambukii* (Fig. 9). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0008208, OG0008209 and OG0008210 (Table 6).

Sexual reproduction not known. Colonies are white to cream, pinkish, smooth and butyrous. Budding is multilateral. Pseudohyphae and septate hyphae are present or not. Where known, coenzyme Q-9 is formed.

Species accepted:

Insectozyma bohioensis (S.O. Suh, N.H. Nguyen & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858065

Holotype: CBS 9897, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. PANAMA, Barro Colorado Island, isolated from the gut of an unidentified click beetle.

Basionym: *Candida bohioensis* S.O. Suh, N.H. Nguyen & M. Blackw. [as '*bohiensis*'], FEMS Yeast Res. 8: 94. 2008.

Insectozyma chauliodis (N.H. Nguyen, S.O. Suh & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858066

Holotype: NRRL Y-27909, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Louisiana, Livingston Parish, isolated from the surface of a male fishfly (*Chauliodes pectinicornis*).

Basionym: Candida chauliodis N.H. Nguyen, S.O. Suh & M. Blackw. [as '*chauliodes*'], Mycologia 99: 847. 2008 [2007].

Insectozyma coleopterorum (F.L. Hui & X.J. Liu) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858067

Holotype: CBS 14180, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Baotianman mountain, isolated from *Anomala heydeni.*

Basionym: *Candida coleopterorum* F.L. Hui & X.J. Liu, Int. J. Syst. Evol. Microbiol. 66: 4888. 2016.

Insectozyma corydali (N.H. Nguyen, S.O. Suh & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858068

Holotype: NRRL Y-27910, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Louisiana, Livingston Parish, isolated from the surface of a female *Corydalus cornutus*.

Basionym: *Candida corydali* N.H. Nguyen, S.O. Suh & M. Blackw., Mycologia 99: 849. 2008.

Insectozyma morakotiae (Nakase, Jindam., Ninomiya, Imanishi & H. Kawas.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858069

Holotype: BCC 7718, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Nakhonratchasima province, Khao-Yai National Park, isolated fruit body of an unidentified mushroom, November 2000.

Basionym: *Candida morakotiae* Nakase, Jindam., Ninomiya, Imanishi & H. Kawas., J. Gen. Appl. Microbiol. 55: 98. 2009.

Insectozyma parachauliodis (F.L. Hui & X.J. Liu) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858070

Holotype: CBS 13928, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Baotianman mountain, isolated from beetle larva, September 2014.

Basionym: *Candida parachauliodis* F.L. Hui & X.J. Liu [as '*parachauliodes*'], Int. J. Syst. Evol. Microbiol. 66: 4888. 2016.

Insectozyma prachuapensis Boonmak, Nitiyon, Am-in, Jindam., H. Kawas., Yongman. & Limtong ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858071

For a description: see Nitiyon et al., Int. J. Syst. Evol. Microbiol. 61: 466. 2011.

Holotype: CBS 11024, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Prachuap Khiri Khan province, isolated from water collected from a mangrove forest.

Synonym: *Candida prachuapensis* Boonmak, Nitiyon, Am-in, Jindam., H. Kawas., Yongman. & Limtong, Int. J. Syst. Evol. Microbiol. 61: 466. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Insectozyma sakaeoensis Limtong, Koowadj., Jindam., Yongman. & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858072

For a description: see Limtong et al., Antonie van Leeuwenhoek 102: 227. 2012.

Holotype: CBS 12318, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Sa Kaeo province, isolated from the phylloplane of Burma pad tree (*Pterocarpus indicus*).

Synonym: *Candida sakaeoensis* Limtong, Koowadj., Jindam., Yongman. & Nakase, Antonie van Leeuwenhoek 102: 227. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Insectozyma verbasci Sipiczki ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858073

For a description: see Sipiczki, Antonie van Leeuwenhoek 103: 573. 2012 [2013].

Holotype: CBS 12699, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. GEORGIA, Tbilisi, isolated from the flowers of *Verbascum*.

Synonym: *Candida verbasci* Sipiczki, Antonie van Leeuwenhoek 103: 573. 2012 [2013]. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Insectozyma xiaguanensis (F.L. Hui & X.J. Liu) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858074

Holotype: CBS 13923, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Baotianman mountain, isolated from *Anomala corpulenta*, August 2014.

Basionym: *Candida xiaguanensis* F.L. Hui & X.J. Liu, Int. J. Syst. Evol. Microbiol. 66: 4887. 2016.

Intestinozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858059

Etymology: the genus is named based on the ecological origin of the species that was isolated from the gut of a beetle.

Type species: *Intestinozyma alai* (S.O. Suh, N.H. Nguyen & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the single-species lineage *Candida alai*, which occurs in a separate long branch from the *Spathaspora sensu stricto* clade and the *Hemisphaericaspora* clade (Fig. 9). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, and the presence of genus-specific protein families OG0014078, OG0014079 and OG0017124 (Table 6).

Sexual reproduction not known. Colonies are cream, smooth, butyrous, shiny. Budding is multilateral. Pseudohyphae and true hyphae are not present.

Note: *Intestinozyma alai* differs from species of the closely related genus *Spathaspora* by lack of assimilation of erythritol and N-acetyl-D-glucosamine (Table S3). Ecologically, this new genus appears to be associated with the gut of insects. Our ITS analysis showed that *Candida* sp. B53C (GenBank MW165503) may represent another new member of the genus *Intestinozyma* (Fig. S11, Table S2).

Species accepted:

Intestinozyma alai (S.O. Suh, N.H. Nguyen & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858062

Holotype: NRRL Y-27739, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Louisiana, Livingston Parish, isolated from the gut of the blind click beetle (*Alaus myops*).

Basionym: *Candida alai* S.O. Suh, N.H. Nguyen & M. Blackw., FEMS Yeast Res. 8: 95. 2008.

Keqinozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858075

Etymology: the genus is named in honor of Dr. Ke-Qin Zhang for his contribution to the studies of biocontrol fungi against root-knot nematode.

Type species: *Keqinozyma sinolaborantium* (S.O. Suh, N.H. Nguyen & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Candida nonsorbophila* clade, which occur in a separate clade from the *Yamadazyma sensu stricto* clade, the *Yamadazyma epiphylla* clade, the *Yamadazyma olivae* clade, and the *Yamadazyma triangularis* clade (Figs. 12–13). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis (Fig. 12) and rDNA phylogenetic analysis (Fig. 13), and the presence of genus-specific protein families OG0018587, OG0018588 and OG0018589 (Table 6).

Sexual reproduction not known. Colonies are white to cream, smooth and butyrous. Budding is multilateral. Pseudohyphae are present, but hyphae are not observed. Where known, coenzyme Q-9 is formed.

Note: Ecologically, this new genus seems to be associated with the insects or the plant-water interface.

Species accepted:

Keqinozyma heliconiae (Ruivo, Pagnocca, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858076

Holotype: CBS 10000, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRAZIL, São Paulo, isolated from water accumulated in the flower bracts of *Heliconia velloziana.*

Basionym: *Candida heliconiae* Ruivo, Pagnocca, Lachance & C.A. Rosa, Int. J. Syst. Evol. Microbiol. 56: 1148. 2006.

Keqinozyma nonsorbophila (Nakase, Jindam., Am-in,

Ninomiya, H. Kawas. & Limtong) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858077

Holotype: BCC 25963, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), Pathumthani, Thailand. THAILAND, Ranong Province, Laem Son National Park, isolated from water in mangrove forest, May 2006.

Basionym: *Candida nonsorbophila* Nakase, Jindam., Amin, Ninomiya, H. Kawas. & Limtong, FEMS Yeast Res. 9: 665. 2009.

Keqinozyma sinolaborantium (S.O. Suh, N.H. Nguyen & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858078

Holotype: NRRL Y-27765, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. PANAMA, Barro Colorado Island, isolated from the gut of *Amphix*.

Basionym: *Candida sinolaborantium* S.O. Suh, N.H. Nguyen & M. Blackw., Mycol. Res. 109: 1053. 2005.

Keqinozyma temnochilae (S.O. Suh, N.H. Nguyen & M. Blackw.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858079

Holotype: NRRL Y-27763, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. PANAMA, Barro Colorado Island, isolated from the gut of *Temnochila.*

Basionym: *Candida temnochilae* S.O. Suh, N.H. Nguyen & M. Blackw., Mycol. Res. 109: 1052. 2005.

Lizanozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858032

Etymology: the genus is named in honor of the late artist Lizan Freijsen for her contribution to fungi-inspired textile art. She contributed to bridge the gap between science and art. Her master piece 'The Fungal Wall' is on display in the museum Micropia in Amsterdam and a new work is expected for 'Het Groote Museum', also in Amsterdam. In addition, she has been a great inspirator for young artists.

Type species: *Lizanozyma spartinae* (Ahearn, Yarrow & Meyers) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Scheffersomyces gosingicus* clade, which occur in a separate clade from *Priceomyces*, *Schwanniomyces* and other genera in *Serinales* (Figs. 9–10). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0013736 and OG0022956 (Table 6).

Both teleomorphic and anamorphic species occur in this genus. Asci are unconjugated or conjugated from the pairing of complementary mating types. Asci produce one, but usually two, hat-shaped ascospores. Colonies are white to tannish-white, smooth, butyrous, glistening. Budding is multilateral. Pseudohyphae are formed, but true hyphae do not develop. D-xylose is not assimilated. Where known, coenzyme Q-9 is formed.

Note: *Lizanozyma* spp. are distinct from those of the closely related genus *Priceomyces* by the lack of assimilation of galactose and the ability to ferment glucose. *Lizanozyma* spp. differs from *Schwanniomyces* spp. by the lack of xylose assimilation (Table S3).

Species accepted:

Lizanozyma gosingica C.F. Lee ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858033

For a description: see Chang et al., Int. J. Syst. Evol. Microbiol. 61: 692. 2011.

Holotype: CBS 11433, preserved in a metabolically inactive state at Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Nanto, isolated from soil.

Synonyms: *Candida gosingica* C.F. Lee, Int. J. Syst. Evol. Microbiol. 61: 692. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Scheffersomyces gosingicus* H. Urbina & M. Blackw., PLoS ONE 7: e39128, 7. 2012. Nom. inval., Art. 40.1 (Melbourne), published as a combination, but 'basionym' (*Candida gosingica*) is invalid and bibliographic error in the basionym reference.

Lizanozyma spartinae (Ahearn, Yarrow & Meyers) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858034

Holotype: NRRLY-7322, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Louisiana, Barataria Bay, isolated from oyster grass (*Spartina alterniflora*) marshes.

Basionym: *Pichia spartinae* Ahearn, Yarrow & Meyers, Antonie van Leeuwenhoek 36: 503. 1970.

Synonym: *Scheffersomyces spartinae* (Ahearn, Yarrow & Meyers) Kurtzman & M. Suzuki [as '*spartiniae*'], Mycoscience 51: 9. 2010.

Lizanozyma thasaensis Poomtien, Jindam., Limtong, Pinphan. & Thaniy. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858035

For a description: see Poomtien et al., Antonie van Leeuwenhoek 103: 236. 2012 [2013].

Holotype: CBS 12529, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Chumporn province, Thasae, a soil sediment pond of a palm oil biodiesel production plant, May 2009.

Synonym: *Candida thasaensis* Poomtien, Jindam., Limtong, Pinphan. & Thaniy. [as '*thasaenensis*'], Antonie van Leeuwenhoek 103: 236. 2012 [2013]. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

New combinations and validated taxa of *Lodderomyces*

Lodderomyces cetoniae (Gouliam., R.A. Dimitrov, M.T. Sm., M. Groenew. & Boekhout) Q.M. Wang, Boekhout, Yurkov, G.

Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858091

Holotype: IMB1R2, preserved in a metabolically inactive state at the yeast collection of the Institute of Microbiology, Sofia, Bulgaria. BULGARIA, East Rhodopes, isolated from the beetles *Cetonia aurata*.

Synonym: *Candida cetoniae* Gouliam., R.A. Dimitrov, M.T. Sm., M. Groenew. & Boekhout, Fungal Biol. 120: 188. 2016.

Lodderomyces hyderabadensis (R.Sreen. Rao, Bhadra, N.N. Kumar & Shivaji) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858092

Holotype: CBS 10444, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. INDIA, AP, Hyderabad, isolated from wine grapes.

Basionym: *Candida hyderabadensis* R.Sreen. Rao, Bhadra, N.N. Kumar & Shivaji, FEMS Yeast Res. 7: 491. 2007.

Lodderomyces jiufengensis (F.Y. Bai & Z.H. Ji) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858093

Holotype: CGMCC 2.3688, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Beijing, Jiufeng mountain, isolated from the gut of *Oxycetonia jucunda*, July 2007.

Basionym: *Candida jiufengensis* F.Y. Bai & Z.H. Ji, Antonie van Leeuwenhoek 95: 30. 2009.

Lodderomyces margitis (F.L. Hui & X.J. Liu) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858097

Holotype: CBS 14175, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Baotianman mountain, isolated from *Margites fulvidus*, August 2015.

Basionym: *Candida margitis* F.L. Hui & X.J. Liu, Int. J. Syst. Evol. Microbiol. 66: 4887. 2016.

Lodderomyces metapsilosis (Tavanti, A. Davidson, Gow, M. Maiden & Odds) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858098

Holotype: ATCC 96144, preserved in a metabolically inactive state at the American Type Culture Collection (ATCC), Manassas, USA. USA, Washington, isolated from the hand of *Homo sapiens*.

Basionym: *Candida metapsilosis* Tavanti, A. Davidson, Gow, M. Maiden & Odds, J. Clin. Microbiol. 43: 290. 2005.

Lodderomyces orthopsilosis (Tavanti, A. Davidson, Gow, M. Maiden & Odds) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858099

Holotype: ATCC 96139, preserved in a metabolically inactive state at the American Type Culture Collection (ATCC), Manassas, USA. USA, Texas, isolated from the tip of the catheter.

Basionym: *Candida orthopsilosis* Tavanti, A. Davidson, Gow, M. Maiden & Odds, J. Clin. Microbiol. 43: 290. 2005.

Lodderomyces oxycetoniae (F.Y. Bai & Z.H. Ji) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858100

Holotype: CGMCC 2.3656, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Beijing, Baiwangshan mountain, isolated from the gut of *Oxycetonia jucunda*, July 2007

Basionym: *Candida oxycetoniae* F.Y. Bai & Z.H. Ji, Antonie van Leeuwenhoek 95: 29. 2009.

Lodderomyces parapsilosis (Ashford) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858101

Holotype: CBS 604, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. PUERTO RICO, isolated from sprue.

Basionym: *Monilia parapsilosis* Ashford, Amer. J. Trop. Med. 8: 518. 1928.

Synonyms: *Candida parapsilosis* (Ashford) Langeron & Talice, Ann. Parasitol. Humaine Comp. 10: 54. 1932.

≡ *Mycocandida parapsilosis* (Ashford) C.W. Dodge, Medic. Mycol.: 294. 1935.

≡ *Mycotorula parapsilosis* (Ashford) Cif. & Redaelli, Atti Ist. Bot. Lab. Crittog. Univ. Pavia, sér. 5 3: 47. 1943.

Lodderomyces pseudojiufengensis (F.Y. Bai & Z.H. Ji) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858102

Holotype: CGMCC 2.3693, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Beijing, Jiufeng mountain, isolated from the gut of *Oxycetonia jucunda*, July 2007.

Basionym: *Candida pseudojiufengensis* F.Y. Bai & Z.H. Ji, Antonie van Leeuwenhoek 95: 30. 2009.

Lodderomyces theae C.F. Lee ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858103

For a description: see Chang et al., Int. J. Food Microbiol. 153: 13. 2012.

Holotype: CBS 12239, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, isolated from tea drink.

Synonym: *Candida theae* C.F. Lee, Int. J. Food Microbiol. 153: 13. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

New combinations of *Millerozyma*

Millerozyma porticicola (Ninomiya, Mikata, Nakagiri, Nakase & H. Kawas.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858104

Holotype: NBRC 100302, preserved in a metabolically inactive state at Biological Resource Center, NITE (NBRC), Tokyo, Japan. JAPAN, Wakavama Pref., isolated from the gallery of *Indocryphalus pubipennis* infesting *Quercus acutissima*.

Basionym: *Pichia porticicola* Ninomiya, Mikata, Nakagiri, Nakase & H. Kawas., J. Gen. Appl. Microbiol. 56: 284. 2010.

Millerozyma pseudofarinosa (S. Mallet, S. Weiss, N. Jacques & Casarég.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858105

Holotype: NCYC 386, preserved in a metabolically inactive state at Biological Resource Center, NITE (NBRC), Tokyo, Japan. JAPAN, isolated from an unknown substrate.

Basionym: *Candida pseudofarinosa* S. Mallet, S. Weiss, N. Jacques & Casarég., PLoS ONE 7: e35842, 9. 2012.

Nothofagozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858080

Etymology: the genus is named based on the ecological origin of the species that were isolated from decomposed wood of *Nothofagus*.

Type species: *Nothofagozyma chilensis* (Grinb. & Yarrow) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the single-species lineage *Candida chilensis*, which is located in a separate branch closely related to *Cephaloascus* (Fig. 12). Member of the *Cephaloascaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, and the presence of genus-specific protein families OG0017645, OG0017647 and OG0017651 (Table 6).

Sexual reproduction is not known. Colonies are cream, shiny, smooth and butyrous. Budding is multilateral. Hyphae may be present. Coenzyme Q-9 is formed.

Note: *Nothofagozyma chilensis* assimilates sucrose, maltose, melezitose, methyl-α-D-glucoside, D-ribose, erythritol, hexadecane, nitrate and nitrite, whereas species of its closely related genus *Cephaloascus* do not (Table S3). Our D1/D2 LSU analysis showed that *Candida* cf. *chilensis* CBS 11766 (GenBank FN824503) represents a potential new species of *Nothofagozyma* (Fig. S9, Table S2).

Species accepted:

Nothofagozyma chilensis (Grinb. & Yarrow) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858081

Holotype: CBS 5719, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. Chile, isolated from decomposed wood of the southern beech tree (*Nothofagus* sp.).

Basionym: *Candida chilensis* Grinb. & Yarrow, Antonie van Leeuwenhoek 36: 144. 1970.

New combinations and validated taxa of *Scheffersomyces*

Scheffersomyces broadrunensis (S.O. Suh & J.J. Zhou) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858106

Holotype: ATCC MYA-4650, preserved in a metabolically inactive state at the American Type Culture Collection (ATCC), Manassas, USA. USA, VA, Broad Run, Bull Run Mountain, isolated from the gut of an unidentified tenebrionid beetle on a rotten log.

Basionym: *Candida broadrunensis* S.O. Suh & J.J. Zhou, Int. J. Syst. Evol. Microbiol. 63: 4334. 2013.

Scheffersomyces lignicola Jindam., Limtong, Yongman., Tuntir., Potach., H. Kawas. & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858107

For a description: see Jindam. et al., FEMS Yeast Res. 7: 1412. 2007.

Holotype: NBRC 102564, preserved in a metabolically inactive state at Biological Resource Center, NITE (NBRC), Tokyo, Japan. THAILAND, isolated from insect frass.

Synonyms: *Candida lignicola* Jindam., Limtong, Yongman., Tuntir., Potach., H. Kawas. & Nakase, FEMS Yeast Res. 7: 1412. 2007. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Scheffersomyces lignicola* Jindam., Limtong, Yongman., Tuntir., Potach., H. Kawas. & Nakase ex H. Urbina & M. Blackw., PLoS ONE 7: e39128, 9. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified; published as a combination, but 'basionym' (*Candida lignicola*) is invalid.

Validated taxa in *Spathaspora*

Spathaspora brasiliensis R.M. Cadete, Zilli, M.J.S. Vital, F.C.O. Gomes, Stambuk, Lachance & C.A. Rosa ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858108

For a description: see Cadete et al., Antonie van Leeuwenhoek 103: 426. 2013.

Holotype: CBS 12679, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRAZIL, isolated from rotting wood.

Synonym: *Spathaspora brasiliensis* R.M. Cadete, Zilli, M.J.S. Vital, F.C.O. Gomes, Stambuk, Lachance & C.A. Rosa, Antonie van Leeuwenhoek 103: 426. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Spathaspora suhii R.M. Cadete, Zilli, M.J.S. Vital, F.C.O. Gomes, Stambuk, Lachance & C.A. Rosa ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858109

For a description: see Cadete et al., Antonie van Leeuwenhoek 103: 428. 2013.

Holotype: CBS 12680, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRAZIL, isolated from rotting wood.

Synonym: *Spathaspora suhii* R.M. Cadete, Zilli, M.J.S. Vital, F.C.O. Gomes, Stambuk, Lachance & C.A. Rosa, Antonie van Leeuwenhoek 103: 428. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

New combinations in *Suhomyces*

Suhomyces caryicola (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858110

Holotype: NRRL YB-1499, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, IL, Peoria, isolated from a nut pod of a pignut hickory tree (*Carya glabra*).

Basionym: *Candida caryicola* Kurtzman, FEMS Yeast Res. 1: 182. 2001.

Suhomyces rongomai-pounamu (Padamsee, B.S. Weir, M.E. Petterson & P.K. Buchanan) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858111

Holotype: PDD 105303. NEW ZEALAND, Auckland, The Gardens, Totara Park, isolated from agaric mushroom surface, March 2016.

Basionym: *Candida rongomai-pounamu* Padamsee, B.S. Weir, M.E. Petterson & P.K. Buchanan, Persoonia 38: 347. 2017.

Suhomyces tibetensis (F.Y. Bai & Z.W. Wu) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858112

Holotype: CGMCC 2.3072, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Tibet, Linzhi, isolated from the flower, July 2004.

Basionym: *Candida tibetensis* F.Y. Bai & Z.W. Wu, Int. J. Syst. Evol. Microbiol. 56: 1154. 2006.

Suzukiozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***gen. nov.***

MycoBank: MB848205

Etymology: the genus is named in honor of M. Suzuki for his contribution to yeast taxonomy.

Type species: *Suzukiozyma glaebosa* (Komag. & Nakase) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *Candida glaebosa* clade, which occur in a separate clade from the genus *Diutina* (Fig. 9, Daniel et al. 2014). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0007615 and OG0007620 (Table 6).

Sexual reproduction not known. Colonies are white to cream, butyrous. Budding is multilateral. Hyphae not produced, pseudohyphae are present or not.

Note: *Suzukiozyma* differs from its closely related genus *Diutina* by a lower GC content (31.16–41.24%), whereas the genus *Diutina* has a higher GC content (41.23–53.05%) (Table S3).

Species accepted:

Suzukiozyma candida (Lodder) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848211

Holotype: CBS 940, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from the atmosphere.

Basionym: *Torulopsis candida* Lodder, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk. 32: 163. 1934.

Synonyms: *Torula candida* Saito, J. Jap. Bot. 1: 41 1922. Nom. illeg., Art. 53.1, homonym, non *Torula candida* Opiz, 1855.

≡ *Cryptococcus candidus* (Lodder) C.E. Skinner, Amer. Midl. Naturalist 43: 249. 1950.

≡ *Candida saitoana* Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 31: 85. 1985.

Suzukiozyma fluviatilis (L.R. Hedrick) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848206

Holotype: CBS 6776, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, Indiana, isolated from polluted river water.

Basionym: *Candida fluviatilis* L.R. Hedrick, Antonie van Leeuwenhoek 42: 329. 1976.

Suzukiozyma glaebosa (Komag. & Nakase) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848207

Holotype: CBS 5691, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from frozen cuttlefish.

Basionym: *Candida glaebosa* Komag. & Nakase, J. Gen. Appl. Microbiol. 11: 262. 1965.

Suzukiozyma manassasensis (S.O. Suh & J.J. Zhou) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848208

Holotype: ATCC MYA-4652, preserved in a metabolically inactive state at the American Type Culture Collection (ATCC), Manassas, USA. USA, VA, Broad Run, Bull Run Mountain, isolated from the gut of *Xylopinus saperdioides*.

Basionym: *Candida manassasensis* S.O. Suh & J.J. Zhou, Int. J. Syst. Evol. Microbiol. 63: 4336. 2013.

Suzukiozyma palmioleophila (Nakase & Itoh) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848209

Holotype: JCM 5218, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. JAPAN, isolated from soil.

Basionym: *Candida palmioleophila* Nakase & Itoh, J. Gen. Appl. Microbiol. 34: 496. 1988.

Suzukiozyma pseudoglaebosa (M. Suzuki & Nakase) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848210

Holotype: JCM 2168, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. JAPAN, isolated from soil.

Basionym: *Candida pseudoglaebosa* M. Suzuki & Nakase, Bull. Jap. Fed. Cult. Coll. 9: 130. 1993.

Suzukiozyma sphagnicola (Kachalkin & Yurkov) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, ***comb. nov.***

MycoBank: MB848212

Holotype: CBS 11774, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. RUSSIA, Tver region, Central Forest State Biosphere Reserve, isolated from *Sphagnum girgensohnii*.

Basionym: *Candida sphagnicola* Kachalkin & Yurkov, Antonie van Leeuwenhoek 102: 40. 2011.

New combinations and validated taxa in *Yamadazyma*

Yamadazyma andamanensis Am-In, Limtong, Yongman. & Jindam. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858113

For a description: see Am-In et al., Int. J. Syst. Evol.

Microbiol. 61: 459. 2011.

Holotype: CBS 10859, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Ranong province, Laem Son National Park, isolated from the estuarine water of the mangrove forest.

Synonym: *Candida andamanensis* Am-In, Limtong, Yongman. & Jindam., Int. J. Syst. Evol. Microbiol. 61: 459. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yamadazyma dushanensis F.L. Hui, Yun Wang, Y.C. Ren & Ying Li ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858116

For a description: see Wang et al., Curr. Microbiol. 71: 272. 2015.

Holotype: CBS 13914, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Nanyang, Dushan Forest Park, isolated from rotten wood, June 2014.

Synonym: *Yamadazyma dushanensis* F.L. Hui, Yun Wang, Y.C. Ren & Ying Li, Curr. Microbiol. 71: 272. 2015. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yamadazyma jaroonii Imanishi, Jindam., Mikata, Nagak., Potach., Tantich. & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB862196

For a description: see Imanishi et al., Antonie van Leeuwenhoek 94(2): 273. 2007.

Holotype: CBS 10790, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Kao-Yaow, isolated from insect frass, March 2001.

Synonym: *Candida jaroonii* Imanishi, Jindam., Mikata, Nagak., Potach., Tantich. & Nakase, Antonie van Leeuwenhoek 94(2): 273. 2007. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yamadazyma oceani Burgaud & G. Barbier ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858117

For a description: see Burgaud et al., Antonie van Leeuwenhoek 100: 79. 2011.

Holotype: CBS 11857, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. ATLANTIC OCEAN, Mid-Atlantic Ridg, isolated from an unidentified deep-sea coral.

Synonyms: *Candida oceani* Burgaud & G. Barbier, Antonie van Leeuwenhoek 100: 79. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Yamadazyma oceani* Burgaud & G. Barbier ex H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4776. 2025. Nom. inval., Art. 40.1 (Shenzhen); published as a combination, but 'basionym' (*Candida oceani*) is invalid.

Yamadazyma paraphyllophila Kaewwich., Yongman., H. Kawas., P.H. Wang & Limtong ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858118

For a description: see Kaewwichian et al., Antonie van Leeuwenhoek 103: 786. 2012.

Holotype: CBS 9928, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Pindung, NanJen-Shan Natural Reserve, isolated from the phylloplane of hengchun pencilwood (*Dysoxylum hongkongense*).

Synonym: *Yamadazyma paraphyllophila* Kaewwich., Yongman., H. Kawas., P.H. Wang & Limtong, Antonie van Leeuwenhoek 103: 786. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yamadazyma phyllophila Kaewwich., Yongman., H. Kawas., P.H. Wang & Limtong ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858119

For a description: see Kaewwichian et al., Antonie van Leeuwenhoek 103: 786. 2012.

Holotype: CBS 12572, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Nakhon Ratchasima province, isolated from the phylloplane of corn (*Zea mays*).

Synonym: *Yamadazyma phyllophila* Kaewwich., Yongman., H. Kawas., P.H. Wang & Limtong, Antonie van Leeuwenhoek 103: 786. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yamadazyma siamensis Kaewwich., Yongman., H. Kawas., P.H. Wang & Limtong ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858120

For a description: see Kaewwichian et al., Antonie van Leeuwenhoek 103: 784. 2012.

Holotype: CBS 12573, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Phetchabun province, isolated from the phylloplane sugarcane (*Saccharum officinarum*).

Synonym: *Yamadazyma siamensis* Kaewwich., Yongman., H. Kawas., P.H. Wang & Limtong, Antonie van Leeuwenhoek 103: 784. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yamadazyma songkhlaensis Imanishi, Jindam., Mikata, Nagak., Potach., Tantich. & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB862197

For a description: see Imanishi et al., Antonie van Leeuwenhoek 94(2): 274. 2007.

Holotype: CBS 10791, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Nam Tok Tone Nga-Chang Waterfall, isolated from insect frass, March 2001.

Synonym: *Candida songkhlaensis* Imanishi, Jindam., Mikata, Nagak., Potach., Tantich. & Nakase, Antonie van Leeuwenhoek 94(2): 274. 2007. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yamadazyma ubonensis Junyapate, Jindam. & Limtong ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858125

For a description: see Junyapate et al., Antonie van Leeuwenhoek 105: 477. 2014.

Holotype: CBS 12859, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Ubon Ratchathani province, isolated from the tree bark.

Synonym: *Yamadazyma ubonensis* Junyapate, Jindam. & Limtong, Antonie van Leeuwenhoek 105: 477. 2014. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Yamadazyma vrieseae Landell & P. Valente ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB862198

For a description: see Landell et al., Int. J. Syst. Evol. Microbiol. 60 (1): 247. 2010.

Holotype: CBS 10829, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRAZIL, Rio Grande do Sul, Itapuã Park, isolated from the tank water of bromeliads.

Synonym: *Candida vrieseae* Landell & P. Valente, Int. J. Syst. Evol. Microbiol. 60(1): 247. 2010. Nom. inval., Art. 40.7 (Shenzhen), more than one collection in which the type is conserved was specified.

Zhuliangozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858084

Etymology: the genus is named in honor of Dr. Zhu-Liang Yang for his contribution to fungal taxonomy, especially macrofungal taxonomic system and economic mushrooms.

Type species: *Zhuliangozyma blackwelliae* (F.Y. Bai & Z.H. Ji) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Candida blackwelliae* clade, which occur in a separate clade from the *Candida sensu stricto*, *Lodderomyces* clade, *Nematodospora*, the *Candida corydali* clade, the *Hemisphaericaspora* clade, and the single-species lineage *Scheffersomyces stambukii* (Fig. 9). Member of the *Debaryomycetaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0009199 and OG0009200 (Table 6).

Both teleomorphic and anamorphic species occur in this genus. Unconjugated asci are formed from single cells with a single greatly elongated ascospore with tapered and curved ends. Colonies are white to cream, smooth, butyrous. Budding is multilateral. Pseudohyphae are present or not.

Note: *Zhuliangozym* differs from the closely related *Candida/Lodderomyces* lineage by a higher GC content (50.46–53.88%), whereas all genera in the *Candida/Lodderomyces* lineage have a GC content lower than 45% (Table S3).

Species accepted:

Zhuliangozyma blackwelliae (F.Y. Bai & Z.H. Ji) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858085

Holotype: CGMCC 2.3639, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Beijing, Baiwangshan mountain, isolated from the gut of *Trichius succinctus*, July 2007.

Basionym: *Candida blackwelliae* F.Y. Bai & Z.H. Ji [as '*blackwellae*'], Antonie van Leeuwenhoek 95: 28. 2009.

Zhuliangozyma boniae (C.G. Morais, T.M. Batista, J. Kominek, G.R. Franco, C. Fonseca, C.T. Hittinger, M.A. Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858086

Holotype: UFMG-CM-Y306, preserved in a metabolically inactive state at the Collection of Microorganisms and Cells of Federal University of Minas Gerais (UFMG), Belo Horizonte, Minas Gerais, Brazil. BRAZIL, Rio Doce Ecological State Park, isolated from rotting wood.

Basionym: *Spathaspora boniae* C.G. Morais, T.M. Batista, J. Kominek, G.R. Franco, C. Fonseca, C.T. Hittinger, M.A. Lachance & C.A. Rosa, Int. J. Syst. Evol. Microbiol. 67: 3804. 2017.

Zhuliangozyma parablackwelliae (F.L. Hui & L.N. Huang) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858087

Holotype: NYNU 17763, preserved in a metabolically inactive state at Nanyang University, Henan province, China. CHINA, Yunnan province, Xishuangbanna Tropical Rainforest, isolated from rotting wood.

Basionym: *Candida parablackwelliae* F.L. Hui & L.N. Huang, Int. J. Syst. Evol. Microbiol. 69: 2779. 2019.

New taxa and reinstated genus in *Phaffomycetaceae* (*Phaffomycetales*, *Saccharomycetes*)

Validated taxa in *Barnettozyma*

Barnettozyma sucrosica Imanishi, A. Yamaz. & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858131

For a description: see Imanishi et al., J. Gen. Appl. Microbiol. 56: 449. 2010.

Holotype: CBS 11512, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, Rishiri Island, isolated from soil, July 2007.

Synonym: *Barnettozyma sucrosica* Imanishi, A. Yamaz. & Nakase, J. Gen. Appl. Microbiol. 56: 449. 2010. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Barnettozyma xylosica R. Kobay., A. Kanti & H. Kawas. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858132

For a description: see Kobayashi et al., Int. J. Syst. Evol. Microbiol. 67: 3974. 2017.

Holotype: NBRC 111558, preserved in a metabolically inactive state at Biological Resource Center, NITE (NBRC), Tokyo, Japan. INDONESIA, West Java, Chibodas Botanical Garden, isolated from litter, December 2014.

Synonym: *Barnettozyma xylosica* R. Kobay., A. Kanti & H. Kawas., Int. J. Syst. Evol. Microbiol. 67: 3974. 2017. Nom. inval., Art. 40.7 (Shenzhen), more than one collection in which the type is conserved was specified.

Barnettozyma xylosiphila R. Kobay., A. Kanti & H. Kawas. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858133

For a description: see Kobayashi et al., Int. J. Syst. Evol. Microbiol. 67: 3974. 2017.

Holotype: NBRC 110202, preserved in a metabolically inactive state at Biological Resource Center, NITE (NBRC), Tokyo, Japan. INDONESIA, West Sumatra, Bung Hatta Botanical Garden, isolated from decayed wood, May 2013.

Synonym: *Barnettozyma xylosiphila* R. Kobay., A. Kanti & H. Kawas., Int. J. Syst. Evol. Microbiol. 67: 3974. 2017. Nom. inval., Art. 40.7 (Shenzhen), more than one collection in which the type is conserved was specified.

Gotozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858126

Etymology: the genus is named in honor of S. Goto for his contribution to yeast taxonomy.

Type species: *Gotozyma montana* (Goto & Oguri) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Barnettozyma siamensis* clade, which occur in a separate clade from the genera *Barnettozyma sensu stricto*, *Millerago*, the *Barnettozyma wickerhamii* clade and the *Phaffomyces* clade (Figs. 15–16). Member of the *Phaffomycetaceae* (*Phaffomycetales*, *Saccharomycetes*). The genus is mainly circumscribed by phylogenomic analysis and rDNA phylogenetic analysis.

Sexual reproduction not known. Colonies are white to cream, butyrous. Budding is multilateral. Pseudohyphae are present or not. True hyphae are absent. Where known, coenzyme Q-7 is formed.

Note: *Gotozyma* spp. have higher GC% (37.35–37.83%) compared with its closely related genus *Phaffomyces* (31.11–32.3%).

Species accepted:

Gotozyma botsteinii G. Arrey, G.S. Li, R. Murphy, L. Guimaraes, S. Alizadeh, M. Poulsen & B. Regenberg ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858129

For a description: see Arrey et al., G3, Genes, Genomes, Genetics 11 (12, jkab342): 7. 2021.

Holotype: CBS 16679, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. IVORY COAST, isolated from hindgut of *Macrotermes bellicosus.*

Synonym: *Barnettozyma botsteinii* G. Arrey, G.S. Li, R. Murphy, L. Guimaraes, S. Alizadeh, M. Poulsen & B. Regenberg, G3, Genes, Genomes, Genetics: 11 (12, jkab342): 7. 2021. Nom. inval., Art. 40.8 (Shenzhen), a statement that the culture is preserved in a metabolically inactive state was not included in the protologue.

Gotozyma montana (Goto & Oguri) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858127

Holotype: CBS 8057, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from the wild grape (*Vitis coignetiae*).

Basionym: *Candida montana* Goto & Oguri, J. Gen. Appl. Microbiol. 29: 88. 1983.

Gotozyma siamensis (Polburee & Limtong) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858128

Holotype: DMKU-UbN24(1). THAILAND, Ubon Ratchathani province, Na Chaluai district, isolated from soil.

Basionym: *Barnettozyma siamensis* Polburee & Limtong, Int. J. Syst. Evol. Microbiol. 64: 3055. 2014.

Reinstated genus

Komagataea Y. Yamada, M. Matsuda, K. Maeda, Sakak. & Mikata, Biosc. Biotechn. Biochem. 58: 1243. 1994.

MycoBank: MB27298

Type species: *Komagataea pratensis* (Babeva & Reshetova) Y. Yamada, M. Matsuda, K. Maeda, Sakak. & Mikata.

Species accepted:

Komagataea norvegica (Reiersöl) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858249

Holotype: CBS 4239, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. Norway, isolated from sputum.

Basionym: *Torulopsis norvegica* Reiersöl [as '*norvegica*'], Antonie van Leeuwenhoek 24: 111. 1958.

Synonym: *Candida norvegica* (Reiersöl) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 613. 1978.

Komagataea pratensis (Babeva & Reshetova) Y. Yamada, M. Matsuda, K. Maeda, Sakak. & Mikata, Biosc. Biotechn. Biochem. 58: 1243. 1994.

MycoBank: MB362653

Basionym: *Williopsis pratensis* Babeva & Reshetova, Mikrobiologiya 48: 1041. 1979.

Synonym: *Barnettozyma pratensis* (Babeva & Reshetova) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 948. 2008.

Komagataea qinlingensis (F.Y. Bai & H.Z. Lu) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858136

Holotype: CGMCC 2.2524, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Shanxi province, Qinling, isolated from soil, October 2002.

Basionym: *Candida qinlingensis* F.Y. Bai & H.Z. Lu, Int. J. Syst. Evol. Microbiol. 54: 1411. 2004.

Komagataea salicaria (Phaff, M.W. Mill. & J.F.T. Spencer) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858250

Holotype: CBS 5456, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, isolated from slime fluxes of willows (*Salix* sp.).

Basionym: *Pichia salicaria* Phaff, M.W. Mill. & J.F.T. Spencer, Antonie van Leeuwenhoek 30: 139. 1964.

Synonym: *Barnettozyma salicaria* (Phaff, M.W. Mill. & J.F.T. Spencer) Kurtzman, Robnett & Basehoar-Powers, FEMS

Yeast Res. 8: 948. 2008.

Komagataea wickerhamii (van der Walt) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858137

Holotype: NRRL Y-2435, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. SOUTH AFRICA, isolated from the larval gut of *Cossidae*.

Basionym: *Endomycopsis wickerhamii* van der Walt, Antonie van Leeuwenhoek 25: 347. 1959.

Synonym: *Barnettozyma wickerhamii* (Van der Walt) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8(6): 948. 2008.

New taxon in *Millerago*

Millerago ficus F.L. Hui, Q.H. Niu, T. Ke & Zheng Liu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858248

For a description: see Hui et al., Int. J. Syst. Evol. Microbiol. 62(11): 2807. 2012.

Holotype: CBS 12638, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Henan province, Nanyang, isolated from the gut of larvae of *Apriona germari* in the trunk of *Ficus carica.*

Synonym: *Candida ficus* F.L. Hui, Q.H. Niu, T. Ke & Zheng Liu, Int. J. Syst. Evol. Microbiol. 62(11): 2807. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

New combination and validated taxa in *Phaffomyces*

Phaffomyces coquimbonensis Cardinali, Antonielli, L. Corte, Roscini & Ganter ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858134

For a description: see Cardinali et al., Int. J. Syst. Evol. Microbiol. 62: 3068. 2012.

Holotype: CBS 12348, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. PICHIDANGUI, isolated from a necrotic *Echinopsis chiloensis.*

Synonym: *Candida coquimbonensis* Cardinali, Antonielli, L. Corte, Roscini & Ganter, Int. J. Syst. Evol. Microbiol. 62: 3068. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Phaffomyces orbus (Starmer, Phaff, Ganter & Lachance) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858135

Holotype: UCD-FST 84-833.1. AUSTRALIA, Queensland, isolated from necrotic cladodes of *Opuntia stricta*.

Basionym: *Candida orba* Starmer, Phaff, Ganter & Lachance, Int. J. Syst. Evol. Microbiol. 51: 701. 2001.

New taxa and reinstated genus in *Wickerhamomycetaceae* (*Phaffomycetales*, *Saccharomycetes*)

Buckleya Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858138

Etymology: the genus is named in honor of H.R. Buckley for her contribution to yeast taxonomy and ecology.

Type species: *Buckleya freyschussii* (H.R. Buckley & Uden) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the single-species lineage *Candida freyschussii*, which occurs in a separate long branch from the genus *Cyberlindnera sensu stricto* clade, the *Williopsis* clade, and the *Wickerhamomyces hampshirensis* clade (Figs. 15–16). Member of the *Wickerhamomycetaceae* (*Phaffomycetales*, *Saccharomycetes*). The genus is mainly circumscribed by phylogenomic analysis, and the presence of genus-specific protein families OG0010458, OG0010457 and OG0008787 (Table 6).

Sexual reproduction not known. Colonies are white to cream, smooth and glistening. Budding is multilateral. Pseudohyphae occur, but true hyphae not observed. Coenzyme Q-7 is formed.

Note: Our D1/D2 LSU analysis showed that *Candida* sp. NIAH-01 (GenBank AB703242) represents a potential new species of *Buckleya* (Fig. S13, Table S2).

Species accepted:

Buckleya freyschussii (H.R. Buckley & Uden) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858139

Holotype: CBS 2162, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SWEDEN, isolated from wet wood pulp.

Basionym: *Candida freyschussii* H.R. Buckley & Uden, Mycopath. Mycol. Appl. 36: 263. 1968.

New combinations and validated taxa in *Hansenula*

Hansenula queroliae (C.A. Rosa, P.B. Morais, Lachance & Pimenta) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858175

Holotype: CBS 10936, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRAZIL, Tocantins, isolated from larva of *Anastrepha mucronata* from fruit of *Peritassa campestris*.

Basionym: *Wickerhamomyces queroliae* C.A. Rosa, P.B. Morais, Lachance & Pimenta, Int. J. Syst. Evol. Microbiol. 59: 1234. 2009.

Hansenula silvicultrix (van der Walt, D.B. Scott & Klift) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858176

Holotype: CBS 6269, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from frass of bostrichid beetle (*Sinoxylon ruficorne*) infesting sweet thorn (*Acacia karroo*).

Basionym: *Candida silvicultrix* van der Walt, D.B. Scott & Klift, Mycopathol. Mycol. Appl. 47: 234. 1972.

Hansenula spegazzinii Masiulionis & Pagnocca ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858177

For a description: see Masiulionis & Pagnocca, Int. J. Syst. Evol. Microbiol. 66: 2144. 2016.

Holotype: CBS 12756, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the

Netherlands. ARGENTINA, Santa Fe province, Santurce, isolated from the fungus garden of an ant nest of *Acromyrmex lundii*, September 2009.

Synonym: *Wickerhamomyces spegazzinii* Masiulionis & Pagnocca, Int. J. Syst. Evol. Microbiol. 66: 2144. 2016. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Hansenula sylviae Moschetti & J.P. Samp. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858178

For a description: see Francesca et al., Int. J. Syst. Evol. Microbiol. 63: 4828. 2013.

Holotype: CBS 12888, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. ITALY, Sicily, island of Ustica, isolated from a trans-Saharan migratory bird (*Sylvia communis*), 2012.

Synonym: *Wickerhamomyces sylviae* Moschetti & J.P. Samp., Int. J. Syst. Evol. Microbiol. 63: 4828. 2013. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Liangdongia Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858142

Etymology: the genus is named in honor of Liang-Dong Guo for his contribution of fungal taxonomy and ecology, especially of endophytic and mycorrhizal fungi.

Type species: *Liangdongia dryadoides* (D.B. Scott & van der Walt) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Starmera dryadoides* clade, which occur in a separate clade distinct from the *Starmera sensu stricto* clade (Fig. 15). Member of the *Wickerhamomycetaceae* (*Phaffomycetales*, *Saccharomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0007703 and OG0007714 (Table 6).

Both teleomorphic and anamorphic species occur. Asci are unconjugated, or originate from conjugation between independent cells or between a cell and its bud, with one to four hat-shaped or hemispheroidal ascospores. Colonies are white to cream, tannish-yellow, smooth, glistening and butyrous. Budding is multilateral. Pseudohyphae are present, but true hyphae are not observed. Where known, coenzyme Q-7 is formed.

Note: *Liangdongia* spp. are different from those of the closely related genus *Starmera sensu stricto* by their ability to grow on 0.1% cycloheximide (Table S3).

Species accepted:

Liangdongia berthetii (Boidin, Pignal, Mermiér & Arpin) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858143

Holotype: CBS 5452, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CAMEROON, isolated from gum arabic on a tree.

Basionym: *Candida berthetii* Boidin, Pignal, Mermiér & Arpin, Cah. Maboké 1: 100. 1963.

Synonym: *Starmera berthetii* (Boidin, Pignal, Mermiér & Arpin) H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4761. 2025.

Liangdongia dendrica (van der Walt, Klift & D.B. Scott) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858144

Holotype: CBS 6151, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. South Africa, isolated from frass of *Cerambycidae* larvae infesting *Cryptocarya latifolia*.

Basionym: *Torulopsis dendrica* van der Walt, Klift & D.B. Scott, Antonie van Leeuwenhoek 37: 461. 1971.

Synonyms: *Candida dendrica* (van der Walt, Klift & D.B. Scott) S.A. Mey. & Yarrow, Int. J. Syst. Bacteriol. 28: 612. 1978.

≡ *Starmera dendrica* (Van der Walt, Klift & D.B. Scott) H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4761. 2025.

Liangdongia dryadoides (D.B. Scott & van der Walt) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858145

Holotype: CBS 6154, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from tunnels of *Platypus externedentatus* in *Ficus sycomorus* and *Ficus hippopotami*.

Basionym: *Hansenula dryadoides* D.B. Scott & van der Walt, Antonie van Leeuwenhoek 37: 171. 1971.

Synonym: *Starmera dryadoides* (D.B. Scott & van der Walt) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 951. 2008.

Liangdongia ilhagrandensis (C.G. Morais, A.R.O. Santos, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858146

Holotype: CBS 16316, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRAZIL, Atlantic Rain Forest, isolated from rotting wood.

Basionym: *Starmera ilhagrandensis* C.G. Morais, A.R.O. Santos, Lachance & C.A. Rosa, Int. J. Syst. Evol. Microbiol. 70: 4382. 2020.

Liangdongia laemsonensis Am-In, Limtong, Yongman. & Jindam. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858147

For a description: see Am-In et al., Int. J. Syst. Evol. Microbiol. 61: 458. 2011.

Holotype: BCC 35154, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Science and Technology Development Agency (NSTDA), Pathumthani, Thailand. THAILAND, Ranong province, Laem Son National Park, isolated from estuarine water collected from a mangrove forest.

Synonyms: *Candida laemsonensis* Am-In, Limtong, Yongman. & Jindam., Int. J. Syst. Evol. Microbiol. 61: 458. 2011. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Starmera laemsonensis* Am-In, Limtong, Yongman. & Jindam. ex H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4762. 2025.

Liangdongia nongkratonensis (Nakase & Jindam.) Q.M. Wang,

Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858148

Holotype: BCC 11772, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Science and Technology Development Agency (NSTDA), Pathumthani, Thailand. THAILAND, Nakhonratchasima province, Nong Kratone, isolated from insect frass in a tropical rain forest, February 2001.

Basionym: *Pichia nongkratonensis* Nakase & Jindam., Mycoscience 46: 193. 2005.

Synonym: *Starmera nongkratonensis* (Nakase & Jindam.) H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4762. 2025.

Liangdongia prunicorticola (Y.J. Qiu, H.Y. Zhu & F.Y. Bai) Q.M. Wang, ***comb. nov.***

MycoBank: MB862244

Holotype: CGMCC 2.8558, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Hubei province, Shennongjia Forestry District, Tangchaogumu, isolated from bark of a *Prunus brachypoda* tree, April, 2024.

Basionym: *Starmera prunicorticola* Y.J. Qiu, H.Y. Zhu & F.Y. Bai, Mycosphere 16(1): 4759. 2025.

Note: The ITS+LSU D1/D2 sequence analysis showed that *S. prunicorticola* was closely related to *Starmera quercuum* (Qiu et al. 2025), indicating that *S. prunicorticola* belongs to the *Starmera dryadoides* clade; therefore, this species was transferred to the genus *Liangdongia.*

Liangdongia quercuum (Phaff & E.P. Knapp) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858149

Holotype: CBS 2283, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, California, Mather, isolated from slime flux of a black oak (*Quercus kelloggii*).

Basionym: *Pichia quercuum* Phaff & E.P. Knapp [as '*quercibus*'], Antonie van Leeuwenhoek 22: 126. 1956.

Synonym: *Starmera quercuum* (Phaff & E.P. Knapp) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 951. 2008.

Reinstated genus

Petasospora Boidin & Abadie, Bull. Trimestriel Soc. Mycol. France 70: 364. 1955. [1954]

MycoBank: MB3845

Type species: *Petasospora rhodanensis* (C. Ramírez & Boidin) Boidin & Abadie, Bull. Trimestriel Soc. Mycol. France 70: 365. 1955. [1954]

Species accepted:

Petasospora adriatica (Čadež, Cardinali, Ciafardini & G. Péter) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858182

Holotype: CBS 12504, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SLOVENIA, Koper, isolated from the sediment of extra virgin olive oil.

Basionym: *Candida adriatica* Čadež, Cardinali, Ciafardini & G. Péter, Int. J. Syst. Evol. Microbiol. 62: 2299. 2012.

Synonym: *Cyberlindnera adriatica* (Čadež, Cardinali, Ciafardini & G. Péter) H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4737. 2025.

Petasospora americana (Wick.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858183

Holotype: NRRL Y-2156, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, California, isolated from frass of *Insecta*, under bark of *Pinus jeffreyi*.

Basionym: *Hansenula bimundalis* var. *americana* Wick., Mycopathol. Mycol. Appl. 26(1): 97. 1965.

Synonym: Cyberlindnera americana (Wick.) Minter, Mycotaxon 110: 473. 2009.

Petasospora amylophila (Kurtzman, M.J. Smiley, C.J. Johnson, Wick. & Fuson) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858184

Holotype: NRRL YB-1287, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Michigan, isolated from frass in insect tunnels in loblolly pine (*Pinus taeda*).

Basionym: *Pichia amylophila* Kurtzman, M.J. Smiley, C.J. Johnson, Wick. & Fuson, Int. J. Syst. Bacteriol. 30(1): 209. 1980.

Synonym: *Cyberlindnera amylophila* (Kurtzman, M.J. Smiley, C.J. Johnson, Wick. & Fuson) Minter, Mycotaxon 110: 473. 2009.

Petasospora bimundalis (Wick. & Santa María) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858185

Holotype: NRRL Y-5343, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. SPAIN, isolated from larva of the beetle *Ergates faber* in Scotch pine (*Pinus sylvestris*).

Basionym: *Hansenula bimundalis* Wick. & Santa María, Mycopathol. Mycol. Appl. 26(1): 96. 1965.

Synonym: *Cyberlindnera bimundalis* (Wick. & Santa María) Minter, Mycotaxon 110: 474. 2009.

Petasospora dasilvae (K.O. Barros, R.M. Souza, Palladino, R.M. Cadete, A.R.O. Santos, Góes-Neto, Berkov, Zilli, M.J.S. Vital, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858186

Holotype: CBS 16129, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. BRAZIL, Roraima, São João da Baliza, isolated from rotting wood.

Basionym: *Cyberlindnera dasilvae* K.O. Barros, R.M. Souza, Palladino, R.M. Cadete, A.R.O. Santos, Góes-Neto, Berkov, Zilli, M.J.S. Vital, Lachance & C.A. Rosa, Int. J. Syst. Evolut. Biol. 71(9, no. 4986): 7. 2021.

Petasospora easanensis Jindam., Thuy & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858187

For a description: see Jindamorakot et al., J. Gen. Appl. Microbiol. 50: 263. 2004.

Holotype: JCM 12476, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. THAILAND, Amnat Charoen, Nong Laung, isolated from insect frass, February 1997.

Synonym: *Candida easanensis* Jindam., Thuy & Nakase, J. Gen. Appl. Microbiol. 50: 263. 2004. Nom. inval., Art. 40.6 (Melbourne).

≡ *Cyberlindnera easanensis* Jindam., Thuy & Nakase ex H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4737. 2025.

Petasospora euphorbiae (van der Walt & A. Opperman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858188

Holotype: CBS 8033, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, Groblersdal, isolated from the insect-infested spurge (*Euphorbia ingens*).

Basionym: *Pichia euphorbiae* Van der Walt & A. Opperman, Antonie van Leeuwenhoek 49: 55. 1983.

Synonym: *Cyberlindnera euphorbiae* (van der Walt & A. Opperman) Minter, Mycotaxon 110: 474. 2009.

Petasospora euphorbiiphila (van der Walt) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858189

Holotype: CBS 8083, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, Transvaal, isolated from the insect-infested decaying tissue of spurge (*Euphorbia ingens*).

Basionym: *Hansenula euphorbiiphila* Van der Walt [as '*euphorbiaphila*'], Antonie van Leeuwenhoek 48: 467. 1982.

Synonym: *Cyberlindnera euphorbiiphila* (Van der Walt) Minter, Mycotaxon 110: 474. 2009.

Petasospora fabianii (Wick.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858197

Holotype: NRRL Y-1871, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Illinois, isolated from a fermentor inoculated with *Aerobacter aerogenes* for the production of butylene glycol.

Basionym: *Hansenula fabianii* Wick., Mycopathol. Mycol. Appl. 26(1): 84. 1965.

Synonym: *Cyberlindnera fabianii* (Wick.) Minter, Mycotaxon 110: 474. 2009.

Petasospora hubeiensis (Y.J. Qiu, H.Y. Zhu & F.Y. Bai) Q.M. Wang, ***comb. nov.***

MycoBank: MB862241

Holotype: CGMCC 2.8539, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Hubei province, Shennongjia Forestry District, Tanjiawan, isolated from bark of a tree, July, 2023.

Basionym: *Cyberlindnera hubeiensis* Y.J. Qiu, H.Y. Zhu & F.Y. Bai, Mycosphere 16(1): 4732. 2025.

Note: The ITS+LSU D1/D2 sequence analysis showed *C. hubeiensis* was closely related to *Cyberlindnera mycetangii*, *Cyberlindnera rhodanensis* and *Cyberlindnera rhizosphaerae* (Qiu et al. 2025), indicating that *C. hubeiensis* belongs to the *Petasospora* clade; therefore, this species was transferred into the genus *Petasospora.*

Petasospora hungchunana C.F. Lee ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858198

For a description: see Chang et al., Antonie van Leeuwenhoek 102: 17. 2012.

Holotype: CBS 12243, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Pingtung, Hengchun, isolated from decayed wood, October 2009.

Synonym: *Candida hungchunana* C.F. Lee, Antonie van Leeuwenhoek 102: 17. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Petasospora juglandicorticola (Y.J. Qiu, H.Y. Zhu & F.Y. Bai) Q.M. Wang, ***comb. nov.***

MycoBank: MB862242

Holotype: CGMCC 2.8538, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Hubei province, Shennongjia Forestry District, Duidongping, isolated from the bark of a *Juglans* tree, April, 2024.

Basionym: *Cyberlindnera juglandicorticola* Y.J. Qiu, H.Y. Zhu & F.Y. Bai, Mycosphere 16(1): 4734. 2025.

Note: The ITS+LSU D1/D2 sequence analysis showed that *C. juglandicorticola* was closely related to *Cyberlindnera americana, Cyberlindnera bimundalis* and *Cyberlindnera nakhonratchasimensis* (Qiu et al. 2025), *indicating* that *C. juglandicorticola* belongs to the *Petasospora* clade; therefore, this species was transferred into the genus *Petasospora.*

Petasospora japonica (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858199

Holotype: NRRL YB-2750, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. JAPAN, isolated from the frass of *Abies firma*.

Basionym: *Pichia japonica* Kurtzman, Mycologia 79(3): 413. 1987.

Synonym: *Cyberlindnera japonica* (Kurtzman) Minter, Mycotaxon 110: 474. 2009.

Petasospora maesae C.F. Lee ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858200

For a description: see Chang et al., Antonie van Leeuwenhoek 102: 12. 2012.

Holotype: CBS 12240, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Kaohsiung, Maolin, isolated from the leaf of *Maesa japonica*, January 2008.

Synonym: *Candida maesae* C.F. Lee [as '*maesa*'], Antonie van Leeuwenhoek 102: 12. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Petasospora maritima (Siepmann) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858201

Holotype: CBS 5107, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. Atlantic Ocean, isolated from the eggs of shrimp.

Basionym: *Trichosporon maritimum* Siepmann, Veröff. Inst. Meeresf. Bremerhaven 8: 89. 1962.

Synonyms: *Cyberlindnera maritima* (Siepmann) Brysch-Herzb., Dlauchy, M. Seidel & G. Péter, Int. J. Syst. Evol. Microbiol. 71(2, no. 4477): 6. 2021.

≡ *Candida maritima* (Siepmann) Uden & H.R. Buckley, Mycotaxon 17: 298. 1983.

Petasospora meyerae (van der Walt) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858202

Holotype: CBS 7076, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, Groblersdal, isolated from rotting insect-infested spurge (*Euphorbia ingens*).

Basionym: *Pichia meyerae* van der Walt, Antonie van Leeuwenhoek 48(4): 385. 1982.

Synonym: *Cyberlindnera meyerae* (van der Walt) Minter, Mycotaxon 110: 475. 2009.

Petasospora mississippiensis (Kurtzman, M.J. Smiley, C.J. Johnson, Wick. & Fuson) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858203

Holotype: NRRL YB-1294, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Mississippi, isolated from the insect frass, loblolly pine (*Pinus taeda*).

Basionym: *Pichia mississippiensis* Kurtzman, M.J. Smiley, C.J. Johnson, Wick. & Fuson, Int. J. Syst. Bacteriol. 30: 212. 1980.

Synonym: *Cyberlindnera mississippiensis* (Kurtzman, M.J. Smiley, C.J. Johnson, Wick. & Fuson) Minter, Mycotaxon 110: 475. 2009.

Petasospora mycetangii (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858204

Holotype: NRRL Y-6843, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Kansas, isolated from the mycetangia of ambrosia beetles.

Basionym: *Candida mycetangii* Kurtzman, Int. J. Syst. Evol. Microbiol. 50: 400. 2000.

Synonym: *Cyberlindnera mycetangii* (Kurtzman) Brysch-Herzb., Dlauchy, M. Seidel & G. Péter, Int. J. Syst. Evol. Microbiol. 71(2, no. 4477): 6. 2021.

Petasospora nakhonratchasimensis Jindam. & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858205

For a description: see Jindamorakot et al., J. Gen. Appl. Microbiol. 50: 266. 2004.

Holotype: JCM 12474, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. THAILAND, isolated from the insect frass.

Synonyms: *Candida nakhonratchasimensis* Jindam. & Nakase, J. Gen. Appl. Microbiol. 50: 266. 2004. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Cyberlindnera nakhonratchasimensis* Jindam. & Nakase ex Brysch-Herzb., Dlauchy, M. Seidel & G. Péter, Int. J. Syst. Evol. Microbiol. 71(2, no. 4477): 6. 2021. Nom. inval., Art. 40.6 (Melbourne), published as a combination, but 'basionym' (*Candida nakhonratchasimensis*) is invalid.

Petasospora pattaniensis Jindam., Duy & Nakase ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858206

For a description: see Jindamorakot et al., J. Gen. Appl. Microbiol. 50: 265. 2004.

Holotype: JCM 12475, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. THAILAND, isolated from the insect frass.

Synonym: *Candida pattaniensis* Jindam., Duy & Nakase, J. Gen. Appl. Microbiol. 50: 265. 2004. Nom. inval., Art. 40.6 (Melbourne).

≡ *Cyberlindnera pattaniensis* Jindam., Duy & Nakase ex H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4737. 2025.

Petasospora petersonii (Wick.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858207

Holotype: NRRL YB-3808, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Illinois, isolated from the lung tissue of a human cadaver preserved with embalming fluid.

Basionym: *Hansenula petersonii* Wick., Mycologia 56(3): 404. 1964.

Synonym: *Cyberlindnera petersonii* (Wick.) Minter, Mycotaxon 110: 475. 2009.

Petasospora rhizosphaerae (Mestre, C.A. Rosa & S.B. Fontenla) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858208

Holotype: CRUB 1796, preserved as a lyophilized preparation in the Centro Regional Universitario Bariloche (CRUB), Bariloche, Argentina. ARGENTINA, Rio Negro, isolated from a *Nothofagus pumilio* forest.

Basionym: *Lindnera rhizosphaerae* Mestre, C.A. Rosa & S.B. Fontenla, Int. J. Syst. Evol. Microbiol. 61(4): 988. 2011.

Synonym: *Cyberlindnera rhizosphaerae* (Mestre, C.A. Rosa & S.B. Fontenla) P.M. Kirk & Offord, Index Fungorum 9: 1. 2012.

Petasospora rhodanensis (C. Ramírez & Boidin) Boidin & Abadie, Bull. Trimestriel. Soc. Mycol. France 70: 365. 1955. [1954]

MycoBank: MB302613

Basionym: *Saccharomyces rhodanensis* C. Ramírez & Boidin, Rev. Mycol. (Paris) 18(2): 152. 1953.

Synonym: *Cyberlindnera rhodanensis* (C. Ramírez & Boidin) Minter, Mycotaxon 110: 475. 2009.

Petasospora shennongjiaensis (Y.J. Qiu, H.Y. Zhu & F.Y. Bai) Q.M. Wang, ***comb. nov.***

MycoBank: MB862243

Holotype: CGMCC 2.8543, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Hubei province, Shennongjia Forestry District, Shennong Tianchi, isolated from pieces of wood/bark from a tree, April, 2024.

Basionym: *Cyberlindnera shennongjiaensis* Y.J. Qiu, H.Y. Zhu & F.Y. Bai, Mycosphere 16(1): 4735. 2025.

Note: The ITS+LSU D1/D2 sequence analysis showed that *C. shennongjiaensis* was closely related to *Cyberlindnera mycetangii*, *Cyberlindnera maritima* and *Cyberlindnera sylvatica* (Qiu et al. 2025), indicating that *C. shennongjiaensis* belongs to the *Petasospora* clade; therefore, this species was transferred into the genus *Petasospora.*

Petasospora stauntonica C.F. Lee ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858209

For a description: see Chang et al., Antonie van Leeuwenhoek 102: 19. 2012.

Holotype: CBS 12241, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Kaohsiung, Taoyuan, isolated from the leaf of *Stauntonia purpurea*, May 2008.

Synonym: *Candida stauntonica* C.F. Lee, Antonie van Leeuwenhoek 102: 19. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

≡ *Cyberlindnera stauntonica* C.F. Lee ex H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4737. 2025.

Petasospora sylvatica (Brysch-Herzb., Dlauchy, M. Seidel & G. Péter) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858210

Holotype: CBS 16335, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. GERMANY, Württemberg, isolated from a slime flux of *Fagus sylvatica*, 2019.

Basionym: *Cyberlindnera sylvatica* Brysch-Herzb., Dlauchy, M. Seidel & G. Péter, Int. J. Syst. Evol. Microbiol. 71(2, no. 4477): 5. 2021.

Petasospora taoyuanica C.F. Lee ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB862180

For a description: see Chang et al., Antonie van Leeuwenhoek 102(1): 16. 2012.

Holotype: CBS 12242, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Kaohsiung, Taoyuan, isolated from soil, May 2008.

Synonym: *Candida taoyuanica* C.F. Lee, Antonie van Leeuwenhoek 102(1): 16. 2012. Nom. inval., Art. 40.7 (Melbourne).

≡ *Cyberlindnera taoyuanica* C.F. Lee ex H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4737. 2025.

Petasospora veronae (K. Kodama) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858211

Holotype: NRRL Y-7818, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA.

Basionym: *Pichia veronae* K. Kodama, J. Ferment. Technol. 52(9): 612. 1974.

Synonym: *Cyberlindnera veronae* (K. Kodama) Minter, Mycotaxon 110: 476. 2009.

Petasospora wuzhiensis (S.A. Wang & F.Y. Bai) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858212

Holotype: CGMCC 2.3480, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Hainan province, Wuzhi mountain, isolated from a leaf of herbaceous plant, November 2006.

Basionym: *Lindnera wuzhiensis* S.A. Wang & F.Y. Bai, J. Gen. Appl. Microbiol. 56: 411. 2011.

Synonym: *Cyberlindnera wuzhiensis* (S.A. Wang & F.Y. Bai) P.M. Kirk & Offord, Index Fungorum 9: 1. 2012.

Petasospora xishuangbannaensis (Jun Zheng, Y.F. Lu, X.J. Liu & F.L. Hui) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858213

Holotype: NYNU 16752, preserved in a metabolically inactive state at Nanyang University, Henan province, China. CHINA, Yunnan province, Mengla, Menglun, isolated from rotting wood.

Basionym: *Cyberlindnera xishuangbannaensis* Jun Zheng, Y.F. Lu, X.J. Liu & F.L. Hui, Int. J. Syst. Evol. Microbiol. 67(12): 5052. 2017.

Petasospora xylebori (Ninomiya, Mikata, H. Kajim. & H. Kawas.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858214

Holotype: NBRC 11048, preserved in a metabolically inactive state at NITE Biological Resource Center (NBRC), Tokyo, Japan. JAPAN, Miyagi prefecture, isolated from a gallery in *Fagus crenata* infested by an ambrosia beetle (*Xyleborus* sp.).

Basionym: *Cyberlindnera xylebori* Ninomiya, Mikata, H. Kajim. & H. Kawas., Int. J. Syst. Evol. Microbiol. 63(7): 2708. 2013.

Petasospora xylosilytica (R.M. Cadete, C.F. Lee, Kurtzman, Zilli, M.J.S. Vital, Lachance & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858215

Holotype: NRRL YB-2097, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, South Carolina, isolated from wood frass.

Basionym: *Cyberlindnera xylosilytica* R.M. Cadete, C.F. Lee, Kurtzman, Zilli, M.J.S. Vital, Lachance & C.A. Rosa, Int. J. Syst. Evol. Microbiol. 65: 2970. 2015.

Ruyongia Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858150

Etymology: the genus is named after Dr. Ru-Yong Zheng for her contribution to fungal taxonomy, especially of *Mucoromycetes*.

Type species: *Ruyongia chambardii* (C. Ramírez & Boidin)

Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Wickerhamomyces chambardii* clade, which occurs in a separate clade from other lineages in the *Phaffomycetales* (Fig. 15). Member of the *Wickerhamomycetaceae* (*Phaffomycetales*, *Saccharomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0007319 and OG0007880 (Table 6).

Both teleomorphic and anamorphic species occur. Asci are unconjugated and form one to four hat-shaped ascospores. Colonies are white to tannish-white, butyrous, glistening. Budding is multilateral. Pseudohyphae are present or not, but true hyphae are not observed. Where known, coenzyme Q-7 is formed.

Species accepted:

Ruyongia chambardii (C. Ramírez & Boidin) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858152

Holotype: CBS 1900, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. ITALY, isolated from tanning liquor.

Basionym: *Saccharomyces chambardii* C. Ramírez & Boidin [as '*chambardi*'], Bull. Mens. Soc. Linn. Lyon 23: 152. 1954.

Synonym: *Wickerhamomyces chambardii* (C. Ramírez & Boidin) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 952. 2008.

Ruyongia mori (F.L. Hui, Liang Chen, X.Y. Chu, Niu & T. Ke) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858154

Holotype: NYNU 1216, preserved in a metabolically inactive state at Nanyang University, Henan province, China. CHINA, Henan province, Nanyan, isolated from the trunk of a white mulberry tree (*Morus alba*).

Basionym: *Wickerhamomyces mori* F.L. Hui, Liang Chen, X.Y. Chu, Niu & T. Ke, Int. J. Syst. Evol. Microbiol. 63: 1177. 2013.

Ruyongia namnaoensis (Nakase, Jindam., Am-In, Ninomiya & H. Kawas.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858155

Holotype: BCC 15093, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Science and Technology Development Agency (NSTDA), Pathumthani, Thailand. THAILAND, Petchabun province, Nam Nao National Park, isolated from insect frass of an unidentified tree, November 2001.

Basionym: *Candida namnaoensis* Nakase, Jindam., Am-In, Ninomiya & H. Kawas., J. Gen. Appl. Microbiol. 58: 150. 2012.

Ruyongia patagonica (V. de García, Brizzio, C.A. Rosa, Libkind & van Broock) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858156

Holotype: CBS 11398, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. ARGENTINA, Patagonia, Nahuel Huapi National Park, isolated from sap exudate on cut branches of *Nothofagus dombeyi* and glacier meltwater river.

Basionym: *Wickerhamomyces patagonicus* V. de García, Brizzio, C.A. Rosa, Libkind & van Broock, Int. J. Syst. Evol. Microbiol. 60: 1695. 2010.

Ruyongia ponderosae (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858158

Holotype: NRRL YB-2307, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Washington, Twisp, Chelan National Forest, isolated from the frass of an unidentified beetle that had tunneled into a Ponderosa pine (*Pinus ponderosa*).

Basionym: *Candida ponderosae* Kurtzman, Antonie van Leeuwenhoek 79: 360. 2001.

Ruyongia rarassimilans (Endoh, M. Suzuki, Omoto & Benno) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858159

Holotype: JCM 14993, preserved in a metabolically inactive state at the Japan Collection of Microorganisms (JCM), Ibaraki, Japan. JAPAN, Kyoto Pref., isolated from the body surface of *Platypus quercivorus*, 2004.

Basionym: *Pichia rarassimilans* Endoh, M. Suzuki, Omoto & Benno, J. Gen. Appl. Microbiol. 54: 183. 2008.

Ruyongia tratensis (Nakase, Jindam., Am-In, Ninomiya & H. Kawas.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858160

Holotype: BCC 15102, preserved in a metabolically inactive state at the BIOTEC Culture Collection (BCC), National Science and Technology Development Agency (NSTDA), Pathumthani, Thailand. THAILAND, Trat province, Waeru Mangrove Forest, isolated from a flower of *Sonneratia caseolaris*, January 2002.

Basionym: *Wickerhamomyces tratensis* Nakase, Jindam., Am-In, Ninomiya & H. Kawas., J. Gen. Appl. Microbiol. 58: 148. 2012.

Taiozyma Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858163

Etymology: the genus is named in honor of Dr. Fang-Lan Tai for his contribution to fungal taxonomy.

Type species: *Taiozyma bovis* (Uden & Carmo Souza) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Wickerhamomyces bovis* clade, which occurs in a separate clade from other lineages in the *Phaffomycetales* and closely related to *Phaffomycetaceae* (Fig. 15). Member of the *Wickerhamomycetaceae* (*Phaffomycetales*, *Saccharomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0006108 and OG0006424 (Table 6).

Both teleomorphic and anamorphic species occur. Asci unconjugated and generally with one to four hat-shaped ascospores. Colonies are tannish-white, creamy to brownish, butyrous, smooth. True hyphae are not observed.

Pseudohyphae are present or not. Where known, coenzyme Q-7 is formed.

Species accepted:

Taiozyma bovis (Uden & Carmo Souza) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858164

Holotype: CBS 2616, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. PORTUGAL, isolated from the cecum of a cow.

Basionym: *Pichia bovis* Uden & Carmo Souza, J. Gen. Microbiol. 16: 385. 1957.

Synonym: *Wickerhamomyces bovis* (Uden & Carmo Souza) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 952. 2008.

Taiozyma dajiaensis C.F. Lee & C.H. Liu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858165

For a description: see Liu et al., FEMS Yeast Res. 8: 818. 2008.

Holotype: CBS 10590, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Taichung, Dajiae, isolated from forest soil, 2006.

Synonym: *Candida dajiaensis* C.F. Lee & C.H. Liu, FEMS Yeast Res. 8: 818. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Taiozyma odintsovae (Babeva, Reshetova, Blagod. & Galimova) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858166

Holotype: CBS 6026, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. RUSSIA, isolated from sap of birch (*Betula verrucosa*).

Basionym: *Candida odintsovae* Babeva, Reshetova, Blagod. & Galimova, Mikrobiologiya 58: 632. 1989.

Taiozyma onychis (Yarrow) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858167

Holotype: CBS 5587, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. NETHERLANDS, isolated from nail infection of *Homo sapiens.*

Basionym: *Pichia onychis* Yarrow, Antonie van Leeuwenhoek 31: 465. 1965.

Synonym: *Wickerhamomyces onychis* (Yarrow) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 952. 2008.

Taiozyma peoriensis (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858168

Holotype: NRRL YB-1497, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Illinois, isolated from the stump of *Ulmus*.

Basionym: *Candida peoriensis* Kurtzman [as '*peoriaensis*'], Antonie van Leeuwenhoek 79: 359. 2001.

Taiozyma rabaulensis (Soneda & S. Uchida) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858169

Holotype: CBS 6797, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. PAPUA NEW GUINEA, New Britain, Rabaul, isolated from feces of an African snail.

Basionym: *Pichia rabaulensis* Soneda & S. Uchida, Bull. Natl. Sci. Mus. Tokyo, 14: 451. 1971.

Synonym: *Wickerhamomyces rabaulensis* (Soneda & S. Uchida) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 952. 2008.

Taiozyma yuanshanica C.F. Lee & Chun H. Liu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858170

For a description: see Liu et al., FEMS Yeast Res. 8: 818. 2008.

Holotype: CBS 10589, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Ilan, Yuanshan, isolated from forest soil, 2006.

Synonym: *Candida yuanshanica* C.F. Lee & Chun H. Liu [as '*yuanshanicus*'], FEMS Yeast Res. 8: 818. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Reinstated genus

Waltiozyma H.B. Mull. & Kock, S. African J. Sci. 82: 491. 1986.

MycoBank: MB22415

Type species: *Waltiozyma mucosa* (Wick. & Kurtzman) H.B. Mull. & Kock

Species accepted:

Waltiozyma chaumierensis (M. Groenew., V. Robert & M.T. Sm.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858251

Holotype: CBS 8565, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. GUYANA, La Chaumiere, isolated from the surface of a flower.

Basionym: *Wickerhamomyces chaumierensis* M. Groenew., V. Robert & M.T. Sm., Int. J. Syst. Evol. Microbiol. 61: 2018. 2011.

Waltiozyma mucosa (Wick. & Kurtzman) H.B. Mull. & Kock, S. African J. Sci. 82: 491. 1986.

MycoBank: MB432175

Basionym: *Pichia mucosa* Wick. & Kurtzman, Mycologia 63: 1014. 1971.

Synonym: *Wickerhamomyces mucosus* (Wick. & Kurtzman) Kurtzman, Robnett & Basehoar-Powers [as '*mucosa*'], FEMS Yeast Res. 8: 952. 2008.

Waltiozyma pijperi (van der Walt & Tscheuschner) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858252

Holotype: CBS 2887, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. SOUTH AFRICA, isolated from buttermilk.

Basionym: *Pichia pijperi* van der Walt & Tscheuschner, Antonie van Leeuwenhoek 23: 189. 1957.

Synonym: *Wickerhamomyces pijperi* (van der Walt & Tscheuschner) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 952. 2008.

Waltiozyma solani (Lodder & Kreger-van Rij) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858253

Holotype: CBS 1908, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THE NETHERLANDS, isolated from the potato-starch mill.

Basionym: *Candida solani* Lodder & Kreger-van Rij, Yeasts, a taxonomic study, [Edn 1] (Amsterdam): 672. 1952.

Waltiozyma xylosica Limtong, Nitiyon, Kaewwich., Jindam., Am-In & Yongman ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858254

For a description: see Limtong et al., Int. J. Syst. Evol. Microbiol. 62: 2790. 2012.

Holotype: CBS 12320, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Phayao province, Mueang Phayao district, isolated from soil, December 2008.

Synonym: *Wickerhamomyces xylosicus* Limtong, Nitiyon, Kaewwich., Jindam., Am-In & Yongman. [as '*xylosica*'], Int. J. Syst. Evol. Microbiol. 62: 2790. 2012. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

New combinations and validated taxa in *Wickerhamomyces*

Wickerhamomyces jianshihensis C.F. Lee & C.H. Liu ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858179

For a description: see Liu et al., FEMS Yeast Res. 8: 820. 2008.

Holotype: CBS 10588, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Hsinchu, Jianshih, isolated from forest soil, 2006.

Synonym: *Candida jianshihensis* C.F. Lee & C.H. Liu, FEMS Yeast Res. 8: 820. 2008. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Wickerhamomyces quercuum (Nakase) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858180

Holotype: CBS 6422, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. JAPAN, isolated from the exudate of konara oak (*Quercus serrata*).

Basionym: *Candida quercuum* Nakase, J. Gen. Appl. Microbiol. 17(6): 476. 1971.

Wickerhamomyces ulmi (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858181

Holotype: CBS 8670, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, Illinois, isolated from insect frass on elm (*Ulmus* sp.).

Basionym: *Candida ulmi* Kurtzman, Int. J. Syst. Evol. Microbiol. 50: 402. 2000.

Reinstated genus

Williopsis Zender, Bull. Soc. Bot. Genève 17: 298. 1925.

MycoBank: MB5781

Type species: *Williopsis saturnus* (Klöcker) Zender.

Species accepted:

Williopsis culbertsonii Q.M. Wang, Hulfachor, K. Sylvester & Hittinger ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858256

For a description: see Sylvester et al., FEMS Yeast Res. 15: 10. 2015.

Holotype: CBS 13898, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, Michigan, isolated from soil, associated with *Fagus grandifolia*.

Synonym: *Cyberlindnera culbertsonii* Q.M. Wang, Hulfachor, K. Sylvester & Hittinger, FEMS Yeast Res. 15: 10. 2015. Nom. inval., Art. 40.7 (Melbourne), more than one collection in which the type is conserved was specified.

Williopsis dauci (A.M. Glushakova, M.A. Tomashevskaya & Kachalkin) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858283

Holotype: KBP Y-6686, preserved in a metabolically inactive state. RUSSIA, Moscow region, from a carrot sample bought on the local market, February 2020.

Basionym: *Cyberlindnera dauci* A.M. Glushakova, M.A. Tomashevskaya & Kachalkin, Persoonia 45: 343. 2020.

Williopsis galapagoensis (Guamán-Burneo, R.M. Cadete, P. Portero, E.J. Carvajal & C.A. Rosa) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858284

Holotype: CLQCA-24SC-025, preserved in a metabolically inactive state at the Catholic University Yeasts Collection (CLQCA), Galápagos. GALÁPAGOS, Santa Cruz Island, isolated from rotting wood.

Basionym: *Cyberlindnera galapagoensis* Guamán-Burneo, R.M. Cadete, P. Portero, E.J. Carvajal & C.A. Rosa, Antonie van Leeuwenhoek 108: 927. 2015.

Williopsis jadinii (Sartory, R. Sartory, J. Weill & J. Mey.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858257

Holotype: NRRL Y-1542, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. FRANCE, isolated from pus from a human abscess.

Basionym: *Saccharomyces jadinii* Sartory, R. Sartory, J. Weill & J. Mey., Compt. Rend. Hebd. Séances Acad. Sci. 194: 1688. 1932.

Synonyms: *Cyberlindnera jadinii* (Sartory, R. Sartory, J. Weill & J. Mey.) Minter, Mycotaxon 110: 474. 2009.

≡ *Candida utilis* (Henneberg) Lodder & Kreger-van Rij, Yeasts, a taxonomic study, [Edn 1] (Amsterdam): 546. 1952.

Williopsis lachancei (Phaff, Starmer & Kurtzman) Q.M. Wang,

Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858258

Holotype: NRRL Y-27008, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Hawaii, isolated from the rotting bark of *Tetraplasandra hawaiiensis*.

Basionym: *Pichia lachancei* Phaff, Starmer & Kurtzman, Int. J. Syst. Bacteriol. 49: 1296. 1999.

Synonym: *Cyberlindnera lachancei* (Phaff, Starmer & Kurtzman) Minter, Mycotaxon 110: 474. 2009.

Williopsis maclurae (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858259

Holotype: NRRL Y-5377, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, Illinois, Peoria, isolated from decaying fruits of the osage orange tree (*Maclura pomifera*).

Basionym: *Pichia maclurae* Kurtzman, Int. J. Syst. Evol. Microbiol. 50: 398. 2000.

Synonym: *Cyberlindnera maclurae* (Kurtzman) Minter, Mycotaxon 110: 475. 2009.

Williopsis mengyuniae (Jian He & Bo Chen) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858261

Holotype: CGMCC 2.3681, preserved in a metabolically inactive state at the China General Microbiological Culture Collection Center (CGMCC), Beijing, China. CHINA, Jiangsu province, isolated from sulfonylurea-contaminated soil, September 2006.

Basionym: *Candida mengyuniae* Jian He & Bo Chen, Int. J. Syst. Evol. Microbiol. 59: 1240. 2009.

Williopsis misumaiensis (Y. Sasaki & Tak. Yoshida ex Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858260

Holotype: NRRL Y-17389, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. JAPAN, isolated from orchard soil.

Basionym: *Pichia misumaiensis* Y. Sasaki & Tak. Yoshida ex Kurtzman, Int. J. Syst. Evol. Microbiol. 50: 399. 2000.

Synonym: *Cyberlindnera misumaiensis* (Y. Sasaki & Tak. Yoshida ex Kurtzman) Minter, Mycotaxon 110: 475. 2009.

Williopsis mrakii (Wick.) G.I. Naumov & Vustin, Dokl. Akad. Nauk S.S.S.R. 259: 721. 1981.

MycoBank: MB108625

Basionym: *Hansenula mrakii* Wick., Tech. Bull. U.S. Dep. Agric. 1029: 40. 1951.

Synonym: *Cyberlindnera mrakii* (Wick.) Minter, Mycotaxon 110: 475. 2009.

Williopsis samutprakarnensis Poomtien, Jindam., Limtong, Pinphan. & Thaniy. ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858263

For a description: see Poomtien et al., Antonie van Leeuwenhoek 103: 235. 2013.

Holotype: CBS 12528, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Samutprakarn province, Bangplee, isolated from the wastewater of a cosmetic factory, February 2009.

Synonym: *Cyberlindnera samutprakarnensis* Poomtien, Jindam., Limtong, Pinphan. & Thaniy., Antonie van Leeuwenhoek 103: 235. 2013. Nom. inval., Art. 40.7 (Melbourne).

Williopsis sargentensis (Wick. & Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858264

Holotype: NRRL YB-4139, preserved as a lyophilized preparation in the ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA. USA, New Hampshire, Peterborough, isolated from the water of a small lake.

Basionym: *Pichia sargentensis* Wick. & Kurtzman, Mycologia 63: 1016. 1971.

Synonym: *Cyberlindnera sargentensis* (Wick. & Kurtzman) Minter, Mycotaxon 110: 476. 2009.

Williopsis saturnus (Klöcker) Zender, Bulletin de la Société Botanique de Genéve 17: 298. 1925.

MycoBank: MB277517

Basionym: *Saccharomyces saturnus* Klöcker, Meddel. Carlsberg Lab. 6: 77. 1903.

Synonyms: *Cyberlindnera saturnus* (Klöcker) Minter, Mycotaxon 110: 476. 2009.

≡ *Lindnera saturnus* (Klöcker) Kurtzman, Robnett & Bas.-Powers, FEMS Yeast Res. 8: 951. 2008.

Williopsis suaveolens (Klöcker) G.I. Naumov, Vustin & Babeva, Mikrobiologiya 54: 242. 1985.

MycoBank: MB103900

Basionym: *Pichia suaveolens* Klöcker, Zentralblatt für Bakteriologie und Parasitenkunde, Abteilung 2 35: 371. 1912.

Synonyms: *Cyberlindnera suaveolens* (Klöcker) Minter, Mycotaxon 110: 476. 2009.

≡ *Lindnera suaveolens* (Klöcker) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 951. 2008.

≡ *Williopsis saturnus* var. *suaveolens* (Klöcker) Kurtzman, Antonie van Leeuwenhoek 60: 18. 1991.

Williopsis subsufficiens (Wick.) Vustin, G.I. Naumov, Babeva & T.I. Naumova, Dokl. Akad. Nauk SSSR 267: 1481-1484. 1982.

MycoBank: MB456651

Basionym: *Hansenula saturnus* var. *subsufficiens* Wick., Mycopath. Mycol. Appl. 37: 30. 1969.

Synonyms: *Cyberlindnera subsufficiens* (Wick.) Minter, Mycotaxon 110: 476. 2009.

≡ *Lindnera subsufficiens* (Wick.) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 951. 2008.

≡ *Williopsis saturnus* var. *subsufficiens* (Wick.) Kurtzman, Antonie van Leeuwenhoek 60: 18. 1991.

Williopsis takata C.F. Lee ex Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***sp. nov.***

MycoBank: MB858267

For a description: see Chang et al., Antonie van Leeuwenhoek 102: 14. 2012.

Holotype: CBS 12244, preserved in a metabolically

inactive state at the Westerdijk Institute, Utrecht, the Netherlands. CHINA, Taiwan province, Nantou, Shueili, isolated from soil, November 2007.

Synonyms: *Candida takata* C.F. Lee, Antonie van Leeuwenhoek 102: 14. 2012. Nom. inval., Art. 40.7 (Melbourne).

≡ *Cyberlindnera takata* C.F. Lee ex H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4737. 2025.

Williopsis tropicalis (Boontham, Limtong, C.A. Rosa, M.R. Lopes, M.J.S. Vital & Srisuk) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858268

Holotype: CBS 14558, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. THAILAND, Samutprakarn province, isolated from the soil.

Basionym: *Cyberlindnera tropicalis* Boontham, Limtong, C.A. Rosa, M.R. Lopes, M.J.S. Vital & Srisuk, Int. J. Syst. Evol. Microbiol. 67: 2572. 2017.

Williopsis vartiovaarae (Capr.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858269

Holotype: CBS 4289, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. FINLAND, isolated from the soil.

Basionym: *Torulopsis vartiovaarae* Capr., Can. J. Microbiol. 7: 683. 1961.

Synonyms: *Candida vartiovaarae* (Capr.) Uden & H.R. Buckley [as '*vartriovaarai*'], Mycotaxon 17: 298. 1983.

≡ *Cyberlindnera vartiovaarae* (Capr.) H.Y. Zhu, Y.J. Qiu, P.J. Han & F.Y. Bai, Mycosphere 16(1): 4738. 2025.

Xingzhongia Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***gen. nov.***

MycoBank: MB858171

Etymology: the genus is named in honor of Dr. Xing-Zhong Liu for his contribution to fungal taxonomy.

Type species: *Xingzhongia hampshirensis* (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai.

This genus is proposed for the species in the *Wickerhamomyces hampshirensis* clade, which occur as a separate clade from the genus *Cyberlindnera*, the *Williopsis* clade, and the single-species lineages *Candida freyschussii* (Figs. 15–16). Member of the *Wickerhamomycetaceae* (*Phaffomycetales*, *Saccharomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 1), and the presence of genus-specific protein families OG0012666 and OG0012668 (Table 6).

Asci are unconjugated, or result from conjugation between a cell and its bud, and they have one to four hat-shaped ascospores. Colonies are white to cream, slightly glistening and butyrous. Budding is multilateral. Pseudohyphae occur, but true hyphae do not. Where known, coenzyme Q-7 is formed.

Note: *Xingzhongia* spp. have lower GC% (36.81–39.18%) compared to its closely related genera, i.e., *Cyberlindnera* (39.64–51.79%) and *Buckleya* (42.53%).

Species accepted:

Xingzhongia hampshirensis (Kurtzman) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858172

Holotype: CBS 7208, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. USA, New Hampshire, Camp Sargent, isolated from frass in a dead, cut oak (*Quercus* sp.).

Basionym: *Pichia hampshirensis* Kurtzman, Mycologia 79: 412. 1987.

Synonym: *Wickerhamomyces hampshirensis* (Kurtzman) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 952. 2008.

Xingzhongia scolytoplatypi (Ninomiya, Mikata, H. Kajim. & H. Kawas.) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858173

Holotype: NBRC 11029, preserved in a metabolically inactive state at NITE Biological Resource Center (NBRC), Tokyo, Japan. JAPAN, Iwate Prefecture, isolated from the gallery of *Scolytoplatypus shogun* in *Fagus crenata.*

Basionym: *Wickerhamomyces scolytoplatypi* Ninomiya, Mikata, H. Kajim. & H. Kawas., Int. J. Syst. Evol. Microbiol. 63: 2708. 2013.

Xingzhongia strasburgensis (C. Ramírez & Boidin) Q.M. Wang, Boekhout, Yurkov, G. Péter & F.Y. Bai, ***comb. nov.***

MycoBank: MB858174

Holotype: CBS 2939, preserved in a metabolically inactive state at the Westerdijk Institute, Utrecht, the Netherlands. FRANCE, isolated from tanned leather.

Basionym: *Saccharomyces strasburgensis* C. Ramírez & Boidin, Rev. Mycol. (Paris) 18: 154. 1953.

Synonym: *Wickerhamomyces strasburgensis* (C. Ramírez & Boidin) Kurtzman, Robnett & Basehoar-Powers, FEMS Yeast Res. 8: 952. 2008.

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Author contributions

Wang QM and Boekhout T conceived and designed the project. Zhao XM and Liu F performed the phylogenomic and genomic metrics analyses. Liu MM, Bai J and Zhao YJ worked on the taxonomy and compared the phenotypic data. Liu JH, Zhang YX, Wang JC, Zhang XH, Cui TX, Liu ZQ and Li HZ edited the phylogenetic trees. Bensch K worked on nomenclatural matters. Blackwell M supplied the phenotypic data of *Candida* sp. BG02-7-18-018A-2-2. Wang QM, Boekhout T and Liu MM wrote the paper. Wang QM, Boekhout T, Yurkov A, Liu MM, Péter G and Bai FY revised and edited the paper. The authors are solely responsible for the content of this work.

ORCID

Miao-Miao Liu: https://orcid.org/0009-0001-1001-4612
Xue-Mei Zhao: https://orcid.org/0009-0004-0682-7436
Qi-Ming Wang: https://orcid.org/0000-0002-2180-8135

Conflict of interest statement

The authors declare no other competing interests.

Data availability

The tree and sequence alignment files, and the genome (or subgenome) datasets for calculating the impact of reductive evolution, HTGs, hybridization (or alloaneuploidy) and introgressions on the values of genomic metrics are deposited in the Figshare repository: https://doi.org/10.6084/m9.figshare.28558733.

Supplementary Information

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