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Phylogenomic analysis of the *Candida auris-Candida haemuli* clade and related taxa in the *Metschnikowiaceae,* and proposal of thirteen new genera, fifty-five new combinations and nine new species

F. Liu[1], Z.-D. Hu[1], X.-M. Zhao[1], W.-N. Zhao[1], Z.-X. Feng[1], A. Yurkov[2], S. Alwasel[3], T. Boekhout[3,4], K. Bensch[5], F.-L. Hui[6], F.-Y. Bai[7], Q.-M. Wang[1,8,9,*]

Key words

AAI
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Abstract *Candida* is a polyphyletic genus of asexually reproducing yeasts in the *Saccharomycotina* with more than 400 species that occur in almost all families of the subclass and its name is strongly connected with the infectious disease candidiasis. During the last two decades, approximately half of the *Candida* species have been reassigned into more than 36 already existing genera and 14 newly proposed genera, but the polyphyletic feature of the genus largely remained. *Candida auris* is an important, globally emerging opportunistic pathogen that has caused life-threatening outbreaks in healthcare facilities worldwide. This species belongs to the *Candida auris-Candida haemuli* (CAH) clade in the *Metschnikowiaceae*, a clade that contains multidrug-resistant clinically relevant species, but also species isolated from natural environments. The clade is phylogenetically positioned remotely from the type species of the genus *Candida* that is *Candida vulgaris* (currently interpreted as a synonym of *Candida tropicalis*) and belongs to the family *Debaryomycetaceae*. Although previous phylogenetic and phylogenomic studies confirmed the position of *C. auris* in the *Metschnikowiaceae*, these analyses failed to resolve the position of the CAH clade within the family and its delimitation from the genera *Clavispora* and *Metschnikowia*. To resolve the position of the CAH clade, phylogenomic and comparative genomics analyses were carried out to address the phylogenetic position of *C. auris* and related species in the *Metschnikowiaceae* using several metrics, such as the average amino acid identity (AAI) values, the percentage of conserved proteins (POCP) and the presence-absence patterns of orthologs (PAPO). Based on those approaches, 13 new genera are proposed for various *Candida* and *Hyphopichia* species, including members of the CAH clade in the *Metschnikowiaceae*. As a result, *C. auris* and related species are reassigned to the genus *Candidozyma*. Fifty-five new combinations and nine new species are introduced and this will reduce the polyphyly of the genus *Candida*.

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INTRODUCTION

The genus *Candida* contains ascomycetous yeasts that belong to *Saccharomycotina* without a known sexual state and that reproduce asexually by budding and that may form pseudohyphae or true hyphae and lack distinctive morphological features that distinguish it from other asexually (and sexually) reproducing ascomycetous yeast genera (Lachance et al. 2011). For a long time, the genus served as a dustbin genus for many asexual ascomycetous yeast species that did not show any distinct properties that could be used for their placement in a specific genus. This broad definition of the genus and the past classification system with dual naming for sexual and asexual morphs has made this genus large and phylogenetically heterogeneous. In the fifth edition of *The Yeasts*, *a taxonomic study* (Lachance et al. 2011) and Daniel et al. (2014), 365 and 434 species were recognized in the genus *Candida*, respectively. Many molecular phylogenetic studies (e.g., Kurtzman & Robnett 1998, Kurtzman 2011a, Lachance et al. 2011, Daniel et al. 2014) indicated that *Candida* is a highly polyphyletic genus with its members distributed in almost all families of *Saccharomycotina*. Some species of *Candida* are of major importance in the medical field, and among the most important opportunistic pathogens (Lachance et al. 2011, Stavrou et al. 2019, Takashima & Sugita 2022), e.g., *Candida albicans*, *Candida dublinenesis*, *Candida glabrata* (also known as *Nakaseomyces glabratus*, see below),

[1] School of Life Sciences, Institute of Life Sciences and Green Development, Hebei University, Baoding 071002, Hebei, China; corresponding author e-mail: wangqm@hbu.edu.cn.
[2] Leibniz Institute DSMZ-German Collection of Microorganisms and Cell Cultures, Braunschweig, Germany.
[3] College of Sciences, King Saud University, Riyadh, Saudi Arabia.
[4] The Yeasts Foundation, Amsterdam, The Netherlands.
[5] Westerdijk Institute of Fungal Biodiversity, Uppsalalaan 8, 3584 CT Utrecht, The Netherlands.
[6] School of Life Science and Agricultural Engineering, Nanyang Normal University, Nanyang 473061, China.
[7] State Key Laboratory of Mycology, Institute of Microbiology, Chinese Academy of Sciences, Beijing 100101, China.
[8] Hebei Basic Science Center for Biotic Interaction, Hebei University, Baoding 071002, Hebei, China.
[9] Key Laboratory of Microbial Diversity Research and Application of Hebei Province, Hebei University, Baoding 071002, Hebei, China.

Candida parapsilosis and *Candida tropicalis*. Besides, many emerging species have been identified (Stavrou et al. 2019), such as *Candida auris*. Following the implementation of the 'One Fungus, one name' principle by the International Code of Nomenclature for algae, fungi, and plants (ICNafp; McNeill et al. 2012), *C. glabrata* has recently been transferred to the genus *Nakaseomyces* in the *Saccharomycetaceae* (as *N. glabratus*) (Takashima & Sugita 2022). Fortunately, the clinically most relevant species *C. albicans*, *C. dubliniensis*, *C. parapsilosis* and *C. tropicalis* belong to the core of the genus that is represented by its nomenclatural type species, *Candida vulgaris* (a synonym of *C. tropicalis*) in the family *Debaryomycetaceae* (Lachance et al. 2011, Daniel et al. 2014).

Candida auris, an emerging fungal opportunist, was firstly isolated from the external ear canal of a Japanese patient in 2009 and placed in the *Candida haemuli* clade (also known as the *Candida haemulonii* clade, CAH) in the family *Metschnikowiaceae* (Satoh et al. 2009, Cendejas-Bueno et al. 2012), which from a phylogenetic perspective is distantly related to *C. tropicalis*. This species has been isolated around the world and causes a threat to global health due to its high mortality and resistance to multiple antifungal drugs (Clancy & Nguyen 2017, Lockhart et al. 2017, Rabaan et al. 2023). A few other species closely related to *C. auris* also may cause infections, i.e., *Candida khanbhai*, *C. haemuli* (also known as *C. haemulonii*), *Candida duobushaemuli* (also known as *Candida duobushaemulonii*), *Candida pseudohaemuli* (also known as *Candida pseudohaemulonii*) and *Candida vulturna* were found to be resistant to multiple antifungal drugs, mainly amphotericin B and with a reduced susceptibility to various azoles (Cendejas-Bueno et al. 2012, Sipiczki & Tap 2016, Muthusamy et al. 2022, De Jong et al. 2023). Other species belonging to the clade, such as *Candida chanthaburiensis*, *Candida konsanensis*, *Candida heveicola* and *Candida ruelliae*, were isolated from natural habitats, i.e., flowers and tree bark (Saluja & Prasad 2008, Wang et al. 2008, Limtong & Yongmanitchai 2010, Sarawan et al. 2013). Although *C. auris*, *C. haemuli* and *C. vulturna* are mostly obtained prominent from humans and animals, some isolates originated from plants or marine substrates (Van Uden & Kolipinski 1962, Sipiczki & Tap 2016, Arora et al. 2021, Yadav et al. 2022). Sipiczki & Tap (2016) and Klaps et al. (2020) published three new species as *C. vulturna pro tempore*, *Candida ohialehuae pro tempore* and *Candida metrosideri pro tempore* in the CAH clade. The authors indicated that the placement in the genus *Candida* was provisional considering the distant relationships of those new species with the core *Candida* species in the *Lodderomyces* clade, where the type species of the genus *Candida* is placed. However, this made the names formally invalid according to Art. 36.1(a) (ICNafp Shenzhen code; Turland et al. 2018) as indicated in Index Fungorum and MycoBank. Recently, De Jong et al. (2023) validated the names *C. chanthaburiensis*, *C. konsanensis*, *C. metrosideri*, *C. ohialehuae* and *C. vulturna*, and described a new species *Candida khanbhai* in the CAH clade, but they did not revise the taxonomy of the CAH clade.

Recently, genome-based metrics, i.e., the average amino acid identity (AAI) values and the percentage of conserved proteins (POCP), have been used to characterize genera in prokaryotes (Luo et al. 2014, Varghese et al. 2015, Parks et al. 2018, 2022, Hayashi Sant'Anna et al. 2019, Meier-Kolthoff & Göker 2019, Barco et al. 2020, Nouioui & Sangal 2022). Such approaches and the presence-absence patterns of orthologs (PAPO) were also employed to delimit yeast genera using presently well-recognized genera in the *Saccharomycetaceae* as an example (Liu et al. 2024). From the above study, a range of 80–92 % POCP values and a range of 60–70 % AAI values might be estimated thresholds to discriminate genera in *Saccharomycetaceae* (Liu et al. 2024).

The recent addition of so-called *Candida* species in the CAH clade by Sipiczki & Tap (2016) and Klaps et al. (2020), prompted us to carry out a phylogenomic and comparative genome analysis of the CAH clade and related species using some genome-based metrics that have been used in the studies of Takashima et al. (2019) and Liu et al. (2024), such as the AAI, the POCP and the PAPO. The genomes of 150 species including 154 strains in the *Metschnikowiaceae* have been analyzed to resolve the taxonomy of the CAH clade. A new genus, *Candidozyma*, is proposed to accommodate the members of the CAH clade. Furthermore, our analyses revealed 12 other lineages in the *Metschnikowiaceae* for which new generic names are proposed.

MATERIALS AND METHODS

Ribosomal DNA (rDNA) phylogenetic analysis

The sequences of the ITS (including 5.8S) and the D1/D2 domains of the large subunit (LSU) (Table S1) were downloaded from the NCBI nucleotide database (https://www.ncbi.nlm.nih.gov/nucleotide/) and aligned using the MAFFT program G-INS-i (Katoh & Standley 2013). Three datasets, the ITS, the D1/D2 and the combined ITS + D1/D2 sequences were used to construct Maximum Likelihood (ML) trees with the GTR+G+I model using the software of RAxML v. 8.2.12 (Stamatakis 2014) with 1 000 bootstrap replicates.

Genome sequencing, assemblies and annotation

DNA from yeast colonies of 14 strains, viz., *C. chanthaburiensis* NBRC 102176^T, *Candida eppingiae* JCM 17241^T, *C. haemuli* SLLAear13-1, *C. heveicola* SLLAear14-10, *C. khanbhai* AFear10, CBS 16213^T, CBS 16555, *C. konsanensis* NBRC 109082^T, *Candida linzhiensis* AS 2.3073^T, *Candida melibiosica* JCM 9558^T, *C. ruelliae* CBS 10815^T, *Candida* sp. XZY238F3, *Danielozyma pruni* NYUN 218101^T and *Metahyphopichia laotica* CBS 13022^T, was extracted using the method described by Wang & Bai (2008). Genomic libraries (150 bp paired-end) were constructed following the manufacturer's protocols of TruSeq DNA Nano library prep kit (Illumina) and sequenced on an Illumina HiSeq 2000 platform using TruSeq SBS Kit (Illumina). The adapter sequence and low-quality reads were removed with default parameters using Fastp v. 0.20.1 (Chen et al. 2018). SPAdes v. 3.15.0 (Bankevich et al. 2012) was used to assemble the genomes of the above 14 yeast strains with the following parameters: "--memory 800 -k 21,33,55,77,99 --careful --cov-cutoff auto". Quast v. 5.0.2 (Gurevich et al. 2013) was assessed for genome quality. Gene prediction was done using GeneMark-ES (Ter-Hovhannisyan et al. 2008).

Phylogenomic analysis and comparative genomics

Phylogenetic relationships of members of the CAH clade and related taxa in *Metschnikowiaceae* were evaluated by identifying single-copy homologs. BUSCO v. 5.3.2 (Manni et al. 2021) was used to evaluate the integrity and obtain a single copy of the BUSCO sequence. Genomes with less than 60 % BUSCO completeness were eliminated and 155 genomes (154 strains in *Metschnikowiaceae* and 1 strain in *Debaryomycetaceae* as outgroup) were retained (Table 1). Alignment of single-copy BUSCO sequences was done using MAFFT v. 7.475 (Katoh & Standley 2013) with L-INS-I model. The maximum Likelihood (ML) tree was constructed using IQ-TREE v. 2.1.2 (Minh et al. 2020) with MFP as the model and 1 000 ultrafast bootstrap repeats (-m MFP -B 1000 -redo -mredo -nt AUTO). The phylo-

Table 1 List of yeast strains and genomes used in this study.

Species	Strain	Assembly	Complete BUSCOs	Complete and single-copy BUSCOs (S)	No. proteins	Total length	GC (%)	Clade	Source
Candida berkhoutiae	CBS 11722^T	GCA_030578995.1	93.20 %	93.10 %	5390	12617291	44.99	*C. blattae* clade	NCBI
Candida blattae	NRRL Y-27698^T	GCA_003706955.2	93.80 %	93.70 %	5661	12022277	49.77	*C. blattae* clade	NCBI
Candida dosseyi	NRRL Y-27950^T	GCA_030573325.1	93.60 %	93.50 %	5642	11984081	49.87	*C. blattae* clade	NCBI
Candida ecuadorensis	CBS 12653^T	GCA_030579155.1	90.40 %	90.30 %	5610	12617072	48.07	*C. blattae* clade	NCBI
Candida ezoensis	CBS 11753^T	GCA_030569115.1	92.70 %	92.60 %	5346	12574817	45.14	*C. blattae* clade	NCBI
Candida flosculorum	NRRL Y-48731^T	GCA_030568875.1	93.70 %	93.60 %	5422	12064463	48.2	*C. blattae* clade	NCBI
Candida intermedia	CBS 572^T	GCA_900106115.1	95.70 %	95.60 %	5931	13162108	43.53	*C. blattae* clade	NCBI
Candida inulinophila	CBS 11725^T	GCA_030562885.1	93.60 %	93.50 %	5405	13306216	46.04	*C. blattae* clade	NCBI
Candida middelhoveniana	CBS 12306^T	GCA_030557965.1	93.50 %	93.30 %	5495	12832034	44.96	*C. blattae* clade	NCBI
Candida pseudoflosculorum	CBS 8584^T	SRR16989025	93.30 %	93.20 %	5422	12171906	48.07	*C. blattae* clade	NCBI
Candida pseudointermedia	NRRL Y-10939^T	GCA_030557285.1	94.60 %	94.50 %	5658	13085940	43.47	*C. blattae* clade	NCBI
Candida sharkensis	NRRL Y-48380^T	GCA_030567015.1	94.10 %	94.00 %	5998	14008157	43.46	*C. blattae* clade	NCBI
Candida suratensis	CBS 10928^T	GCA_030566815.1	89.70 %	89.60 %	5803	13760921	47.91	*C. blattae* clade	NCBI
Candida thailandica	CBS 10610^T	GCA_022023595.1	90.70 %	90.50 %	5491	16310147	45.96	*C. blattae* clade	NCBI
Candida tsuchiyae	NRRL Y-17840^T	GCA_030566995.1	93.40 %	93.30 %	5288	12514726	46.31	*C. blattae* clade	NCBI
Clavispora xylosa	NYNU 174173^T	GCA_023158955.1	71.30 %	71.20 %	5045	15305418	50.87	*C. blattae* clade	NCBI
Candida citri	CBS 11858^T	GCA_030571295.1	92.70 %	92.60 %	5323	13045557	43.4	*C. citri* clade	NCBI
Candida danieliae	CBS 8533^T	GCA_030579135.1	90.80 %	90.70 %	5344	11795114	50	*C. danieliae* clade	NCBI
Candida entomophila	NRRL Y-7783^T	GCA_030555945.1	92.10 %	91.70 %	5261	10209960	54.43	*C. entomophila* clade	NCBI
Candida sp.	CBS 14106	SRR16974439	95.90 %	95.60 %	5658	11453389	51.23	*C. entomophila* clade	NCBI
Candida eppingiae	JCM 17241^T	NMDC60137102	85.50 %	85.40 %	5217	11274499	50.9	*C. eppingiae* clade	this study
Candida kutaoensis	CBS 11388^T	GCA_030562905.1	78.00 %	77.80 %	4631	9654364	55.76	*C. kutaoensis* clade	NCBI
Candida baotianmanensis	CBS 11898^T	GCA_030556145.1	85.00 %	84.90 %	5066	11060496	55.16	*C. melibiosica* clade	NCBI
Candida melibiosica	JCM 9558^T	NMDC60137103	85.40 %	85.30 %	5049	11018273	55.36	*C. melibiosica* clade	this study
Candida rhizophorensis	NRRL Y-48382^T	GCA_030573355.1	86.40 %	86.30 %	5165	11723898	51.63	*C. melibiosica* clade	NCBI
Candida oregonensis	NRRL Y-5850^T	GCA_003707785.2	95.30 %	95.10 %	5471	10887972	47.46	*C. oregonensis* clade	NCBI
Clavispora reshetovae	CBS 11556^T	GCA_030558395.1	92.80 %	92.30 %	6224	13479832	46.44	*C. oregonensis* clade	NCBI
Candida bambusicola	CBS 11723^T	GCA_030563705.1	91.40 %	91.30 %	5105	12107016	42.59	*C. succicola* clade	NCBI
Candida nongkhaiensis	CBS 11724^T	GCA_030563825.1	91.60 %	91.40 %	5266	12680896	39.96	*C. succicola* clade	NCBI
Candida picinguabensis	NRRL Y-27814^T	GCA_030582875.1	92.10 %	92.00 %	5146	11996333	44.14	*C. succicola* clade	NCBI
Candida robnettiae	CBS 8580^T	GCA_030568975.1	90.80 %	90.70 %	5040	12701715	40.48	*C. succicola* clade	NCBI
Candida saopauloensis	NRRL Y-27815^T	GCA_030582915.1	92.00 %	91.90 %	5099	12020785	44.26	*C. succicola* clade	NCBI
Candida succicola	CBS 11726^T	GCA_030563905.1	91.20 %	91.10 %	5077	12130308	43.04	*C. succicola* clade	NCBI
Candida touchengensis	CBS 10585^T	GCA_030566735.1	91.30 %	91.30 %	5147	12016383	45.07	*C. succicola* clade	NCBI
Metschnikowia saccharicola	CBS 12575^T	GCA_030569455.1	91.80 %	91.70 %	5151	12154026	40.63	*C. succicola* clade	NCBI
Candida savonica	NRRL Y-17077^T	GCA_030570115.1	95.20 %	95.00 %	5537	12643935	50.52	*C. tanticharoeniae* clade	NCBI
Candida tanticharoeniae	CBS 11574^T	GCA_030558325.1	93.90 %	93.70 %	5366	12225802	51.84	*C. tanticharoeniae* clade	NCBI
Candida mogii	NRRL Y-17032^T	GCA_030573315.1	87.20 %	87.10 %	4970	11074207	46.2	*C. tolerans* clade	NCBI
Candida tolerans	NRRL Y-48705	GCA_030582955.1	90.30 %	90.20 %	5291	12803081	42	*C. tolerans* clade	NCBI
Candida aechmeae	NRRL Y-48456	GCA_030583085.1	90.30 %	90.20 %	5287	11247228	49.06	*C. ubatubensis* clade	NCBI
Candida ubatubensis	NRRL Y-27812	GCA_030567085.1	88.60 %	88.50 %	5266	11259751	49.93	*C. ubatubensis* clade	NCBI
Candida linzhiensis	AS 2.3073^T	NMDC60137104	95.40 %	95.00 %	5881	14916200	30.02	*C. sequanensis* clade	this study
Candida sequanensis	NRRL Y-17682^T	GCA_030557975.1	94.50 %	94.30 %	5902	15045357	31.4	*C. sequanensis* clade	NCBI
Candida sp.	XZY238F3	NMDC60146131	94.70 %	94.50 %	5758	14038224	33.86	*C. sequanensis* clade	this study
Candida auris	B11221	GCA_002775015.1	94.40 %	94.00 %	5521	12741178	45.32	CAH clade	NCBI
Candida chanthaburiensis	NBRC 102176^T	NMDC60046445	90.20 %	90.00 %	5338	13025691	46.68	CAH clade	this study
Candida duobushaemuli	B09383	GCA_002926085.1	88.80 %	88.50 %	5173	12580400	46.84	CAH clade	NCBI
Candida haemuli	SLLAear13-1	NMDC60046450	91.60 %	91.40 %	5515	13278047	45.2	CAH clade	this study
Candida haemuli var. *haemuli*	B11899	GCA_002926055.1	90.40 %	90.30 %	5249	13314323	45.19	CAH clade	NCBI
Candida haemuli var. *vulneris*	K1	GCA_012184645.1	93.50 %	93.40 %	5502	13207566	45.21	CAH clade	NCBI
Candida heveicola	AS 2.3483^T	GCA_003708405.1	89.90 %	89.50 %	5274	13065558	47.2	CAH clade	NCBI
Candida heveicola	SLLAear14-10	NMDC60046449	90.60 %	90.20 %	5323	13075462	47.2	CAH clade	this study

Table 1 (cont.)

Species	Strain	Assembly	Complete BUSCOs	Complete and single-copy BUSCOs (S)	No. proteins	Total length	GC (%)	Clade	Source
Candida khanbhai	AFear10	NMDC60046448	90.30 %	90.10 %	5201	12119318	47.52	CAH clade	this study
Candida khanbhai	CBS 16213^T	NMDC60137105	89.80 %	89.60 %	5223	12474519	47.44	CAH clade	this study
Candida khanbhai	CBS 16555	NMDC60137106	90.10 %	89.90 %	5250	12332639	47.56	CAH clade	this study
Candida konsanensis	NBRC 109082^T	NMDC60046446	90.20 %	89.90 %	5344	13069910	46.71	CAH clade	this study
Candida pseudohaemuli	UZ153 17	GCA_002933435.1	90.10 %	89.90 %	5412	12690930	47.14	CAH clade	NCBI
Candida ruelliae	CBS 10815^T	NMDC60046447	88.40 %	88.30 %	5359	13541693	46.84	CAH clade	this study
Candida vulturna	CBS 14366^T	GCA_030585165.1	90.80 %	90.60 %	5423	12642490	46.97	CAH clade	NCBI
Candida asparagi	NRRL Y-48714^T	GCA_030573135.1	89.40 %	89.30 %	5047	11455834	48.68	*Clavispora* s.str. clade	NCBI
Candida carvajalis	NRRL Y-48694^T	GCA_030581635.1	89.50 %	89.30 %	4949	11240520	48.27	*Clavispora* s.str. clade	NCBI
Candida phyllophila	CBS 12671^T	SRR16989024	90.40 %	90.00 %	5263	12079776	48.02	*Clavispora* s.str. clade	NCBI
Candida vitiphila	CBS 12672^T	GCA_030557995.1	91.80 %	91.60 %	5038	11158879	48.2	*Clavispora* s.str. clade	NCBI
Clavispora fructus	NRRL Y-17072^T	GCA_003707795.1	88.00 %	87.20 %	4931	11424019	49.03	*Clavispora* s.str. clade	NCBI
Clavispora lusitaniae	CBS 6936^T	GCA_001673695.2	95.10 %	95.00 %	5537	11992787	44.53	*Clavispora* s.str. clade	NCBI
Clavispora opuntiae	NRRL Y-11820^T	GCA_030574075.1	92.40 %	92.30 %	5181	11556692	42.54	*Clavispora* s.str. clade	NCBI
Clavispora paralusitaniae	NYNU 161120^T	GCA_022058765.1	87.10 %	86.70 %	5259	12616965	44.51	*Clavispora* s.str. clade	NCBI
Clavispora santaluciae	A1.5	GCA_022577645.1	91.00 %	90.50 %	4978	11018616	49.7	*Clavispora* s.str. clade	NCBI
Danielozyma ontarioensis	NRRL YB-1246^T	GCA_003706395.1	95.40 %	95.10 %	5544	10694567	46.57	*Danielozyma*	NCBI
Danielozyma pruni	NYUN 218101^T	NMDC60146132	92.60 %	92.50 %	5403	11944991	58.53	*Danielozyma*	this study
Debaryomyces hansenii	CBS 767^T	GCA_000006445.2	98.70 %	98.30 %	6272	12152486	36.35	*Debaryomycetaceae*	NCBI
Hyphopichia gotoi	NRRL Y-27225^T	GCA_003708205.1	96.10 %	95.70 %	5823	13294060	40.54	*H. heimii* clade	NCBI
Hyphopichia heimii	NRRL Y-7502^T	GCA_003706925.2	95.60 %	95.40 %	5863	12888973	40.37	*H. heimii* clade	NCBI
Hyphopichia pseudorhagii	NRRL YB-2076^T	GCA_030449045.1	95.70 %	95.50 %	5759	12489910	40.75	*H. heimii* clade	NCBI
Hyphopichia rhagii	NRRL Y-2594^T	GCA_003708185.2	95.60 %	95.40 %	5646	12379694	40.79	*H. heimii* clade	NCBI
Hyphopichia burtonii	NRRL Y-1933^T	GCA_001661395.1	94.60 %	94.20 %	5996	12403110	34.99	*Hyphopichia* s.str. clade	NCBI
Hyphopichia buzzinii	CBS 14300^T	GCA_030556945.1	95.80 %	95.40 %	5829	12668805	41.65	*Hyphopichia* s.str. clade	NCBI
Hyphopichia fennica	NRRL Y-7505^T	GCA_030444945.1	96.10 %	95.80 %	5838	13952948	32.58	*Hyphopichia* s.str. clade	NCBI
Hyphopichia homilentoma	JCM 1507^T	GCA_001599095.1	94.40 %	94.00 %	5536	12176763	49.52	*Hyphopichia* s.str. clade	NCBI
Hyphopichia khmerensis	CBS 9784^T	GCA_030569195.1	95.50 %	95.30 %	5712	13329260	32.4	*Hyphopichia* s.str. clade	NCBI
Hyphopichia pseudoburtonii	makgeolli	GCA_003856775.1	95.00 %	94.60 %	5831	15547333	36	*Hyphopichia* s.str. clade	NCBI
Hyphopichia wangnamkhiaoensis	CBS 11695^T	GCA_030578475.1	95.90 %	95.50 %	5829	14591231	37.39	*Hyphopichia* s.str. clade	NCBI
Candida wancherniae	NRRL Y-48709^T	GCA_003708715.2	85.90 %	85.80 %	4721	10260097	53.15	*M. agaves* clade	NCBI
Metschnikowia agaves	UWOPS 92-207.1^T	GCA_008065245.1	92.10 %	92.00 %	5172	11121255	44.54	*M. agaves* clade	NCBI
Metschnikowia sp.	yHMJ9	GCA_030444895.1	90.50 %	90.30 %	5327	11908917	51.39	*M. agaves* clade	NCBI
Metschnikowia aberdeeniae	SUB 05-213.1	GCA_002370615.1	91.20 %	91.00 %	5098	10651211	48.54	*M. arizonensis* clade	NCBI
Metschnikowia amazonensis	UFMG-CM-6309^T	GCA_008065195.1	87.90 %	87.70 %	6691	19103064	40.43	*M. arizonensis* clade	NCBI
Metschnikowia arizonensis	UWOPS 99-103.4	GCA_002370875.1	92.20 %	92.10 %	5716	16199712	41.67	*M. arizonensis* clade	NCBI
Metschnikowia borealis	UWOPS 96-101.1	GCA_002370855.1	91.10 %	91.00 %	6591	20526619	43.08	*M. arizonensis* clade	NCBI
Metschnikowia bowlesiae	UWOPS 12-619.1	GCA_002370295.1	89.30 %	89.20 %	5773	17200370	48.58	*M. arizonensis* clade	NCBI
Metschnikowia cerradonensis	UFMG 03-T67.1^T	GCA_002370635.1	92.70 %	92.50 %	6559	20691529	42.89	*M. arizonensis* clade	NCBI
Metschnikowia colocasiae	UWOPS 03-202.1	GCA_002370175.1	91.10 %	90.90 %	5546	14917106	47.01	*M. arizonensis* clade	NCBI
Metschnikowia continentalis	UWOPS 95-402.1^T	GCA_002370835.1	92.50 %	92.30 %	6934	22098529	42.3	*M. arizonensis* clade	NCBI
Metschnikowia cubensis	MUCL 45753^T	GCA_002374405.1	91.20 %	91.10 %	6383	20567312	43.53	*M. arizonensis* clade	NCBI
Metschnikowia dekortorum	UWOPS 01-142b3^T	GCA_002374455.1	89.80 %	89.60 %	5524	16339066	48.73	*M. arizonensis* clade	NCBI
Metschnikowia drakensbergensis	EBD-CdVSA10-2A	GCA_002370475.1	91.80 %	91.70 %	5255	11864716	48.2	*M. arizonensis* clade	NCBI
Metschnikowia hamakuensis	UWOPS 04-199.1	GCA_002370815.1	90.30 %	90.20 %	6157	18736887	43.9	*M. arizonensis* clade	NCBI
Metschnikowia hawaiiana	NRRL Y-27473^T	GCA_003708615.1	91.40 %	91.30 %	5019	11848248	48.16	*M. arizonensis* clade	NCBI
Metschnikowia hawaiiensis	UWOPS 87-2203.2	GCA_002370325.1	89.70 %	89.60 %	6019	18360083	44.5	*M. arizonensis* clade	NCBI
Metschnikowia hibisci	UWOPS 95-797.2^T	GCA_002374725.1	91.80 %	91.70 %	5187	11402227	42.13	*M. arizonensis* clade	NCBI
Metschnikowia ipomoeae	NRRL Y-27455^T	GCA_030566495.1	92.20 %	92.10 %	6257	19124835	43.62	*M. arizonensis* clade	NCBI
Metschnikowia ipomoeae	UWOPS 10-104.1	GCA_002374715.1	92.60 %	92.40 %	6211	19000479	43.55	*M. arizonensis* clade	NCBI
Metschnikowia kamakouana	UWOPS 04-112.5^T	GCA_002374535.1	92.00 %	91.90 %	5713	15746623	44.81	*M. arizonensis* clade	NCBI
Metschnikowia kipukae	UWOPS 00-669.2^T	GCA_002370135.1	92.20 %	92.00 %	5181	11229551	45.13	*M. arizonensis* clade	NCBI

Table 1 (cont.)

Species	Strain	Assembly	Complete BUSCOs	Complete and single-copy BUSCOs (S)	No. proteins	Total length	GC (%)	Clade	Source
Metschnikowia lochheadii	UWOPS 03-167a3	GCA_002374545.1	92.40 %	92.30 %	6647	20911142	41.89	*M. arizonensis* clade	NCBI
Metschnikowia matae	UFMG-CM-Y395^T	GCA_002374375.1	92.30 %	92.20 %	6851	21250408	40.91	*M. arizonensis* clade	NCBI
Metschnikowia mauinuiana	UWOPS 04-110.4	GCA_002370755.1	91.20 %	91.00 %	5961	17251389	43.88	*M. arizonensis* clade	NCBI
Metschnikowia orientalis	UWOPS05-269.1	GCA_002893685.1	88.30 %	88.20 %	4975	12453693	49.39	*M. arizonensis* clade	NCBI
Metschnikowia proteae	EBD-T1Y1^T	GCA_002370515.1	91.50 %	91.40 %	5263	12400777	48.51	*M. arizonensis* clade	NCBI
Metschnikowia santaceciliae	UWOPS 01-517a1^T	GCA_002374485.1	92.20 %	92.00 %	6644	20559367	43.32	*M. arizonensis* clade	NCBI
Metschnikowia similis	UWOPS 03-133.4	GCA_002370765.1	88.60 %	88.50 %	5637	17255585	48.72	*M. arizonensis* clade	NCBI
Metschnikowia shivogae	UWOPS 04-310.1^T	GCA_002374645.1	91.30 %	91.10 %	5108	10759625	49.88	*M. arizonensis* clade	NCBI
Candida golubevii	NRRL Y-48707^T	GCA_003708755.1	91.40 %	91.40 %	5532	14776713	45.12	*M. bicuspidata* clade	NCBI
Metschnikowia andauensis	CBS 10809^T	GCA_030568715.1	66.50 %	65.90 %	8207	17931512	45.44	*M. bicuspidata* clade	NCBI
Metschnikowia anglica	CBS 15342^T	GCA_030573055.1	93.00 %	92.90 %	5379	13582273	47.05	*M. bicuspidata* clade	NCBI
Metschnikowia australis	UFMG-CM-Y6158	GCA_002073855.1	87.60 %	87.50 %	4828	14350488	47.21	*M. bicuspidata* clade	NCBI
Metschnikowia baotianmanensis	CBS 15869	GCA_030565705.1	88.70 %	73.70 %	7503	19862458	45.9	*M. bicuspidata* clade	NCBI
Metschnikowia bicuspidata	NRRL YB-4993^T	GCA_001664035.1	92.70 %	92.30 %	5838	16055203	47.85	*M. bicuspidata* clade	NCBI
Metschnikowia chrysomelidarum	NRRL Y-27749^T	GCA_030582795.1	89.90 %	89.40 %	6328	16371206	44.48	*M. bicuspidata* clade	NCBI
Metschnikowia chrysoperlae	NRRL Y-27615^T	GCA_030674525.1	81.50 %	81.20 %	7409	17268004	46.24	*M. bicuspidata* clade	NCBI
Metschnikowia corniflorae	NRRL Y-27750^T	GCA_030581935.1	84.20 %	82.40 %	7901	28064570	44.83	*M. bicuspidata* clade	NCBI
Metschnikowia fructicola	NRRL Y-27328^T	GCA_030556695.1	83.00 %	66.50 %	8438	20112834	45.77	*M. bicuspidata* clade	NCBI
Metschnikowia gelsemii	NRRL Y-48212^T	GCA_030561745.1	92.90 %	92.70 %	6021	18115406	43.39	*M. bicuspidata* clade	NCBI
Metschnikowia gruessii	NRRL Y-17809^T	GCA_030563445.1	90.20 %	90.10 %	7143	22233920	42.45	*M. bicuspidata* clade	NCBI
Metschnikowia henanensis	CBS 12677^T	GCA_030674755.1	81.40 %	64.90 %	8030	20688651	46.77	*M. bicuspidata* clade	NCBI
Metschnikowia kofuensis	NRRL Y-27226^T	GCA_030564885.1	87.70 %	78.70 %	7168	18128511	45.35	*M. bicuspidata* clade	NCBI
Metschnikowia koreensis	CBS 8854^T	GCA_030569435.1	92.30 %	92.10 %	6024	14348919	41.75	*M. bicuspidata* clade	NCBI
Metschnikowia krissii	NRRL Y-5389^T	GCA_030561945.1	89.30 %	89.20 %	4865	13288520	45.31	*M. bicuspidata* clade	NCBI
Metschnikowia kunwiensis	NRRL Y-48698^T	GCA_030583255.1	84.70 %	84.50 %	5080	14222198	48.91	*M. bicuspidata* clade	NCBI
Metschnikowia lachancei	NRRL Y-27242^T	GCA_030572615.1	90.40 %	86.70 %	8305	23926579	42.49	*M. bicuspidata* clade	NCBI
Metschnikowia lunata	NRRL Y-7131^T	GCA_030583235.1	92.00 %	91.90 %	5953	16680955	44.15	*M. bicuspidata* clade	NCBI
Metschnikowia noctiluminum	NRRL Y-27753^T	GCA_030578735.1	90.30 %	88.80 %	6171	16712092	44.81	*M. bicuspidata* clade	NCBI
Metschnikowia peoriensis	CBS 15345^T	GCA_030573015.1	91.10 %	81.50 %	7691	17708309	41.8	*M. bicuspidata* clade	NCBI
Metschnikowia persimmonesis	KIOM_G15050	GCA_014905795.1	78.00 %	73.80 %	6939	16473584	45.81	*M. bicuspidata* clade	NCBI
Metschnikowia picachoensis	NRRL Y-27607^T	GCA_030556465.1	91.00 %	87.20 %	7540	21509105	44.7	*M. bicuspidata* clade	NCBI
Metschnikowia pimensis	NRRL Y-27619^T	GCA_030556455.1	91.00 %	90.60 %	6503	18519651	44.73	*M. bicuspidata* clade	NCBI
Metschnikowia pulcherrima	NRRL Y-7111^T	GCA_030583425.1	90.60 %	90.40 %	6048	15504344	45.81	*M. bicuspidata* clade	NCBI
Metschnikowia aff. *pulcherrima*	APC 1.2	GCA_004217705.1	89.40 %	89.20 %	5800	15801215	45.88	*M. bicuspidata* clade	NCBI
Metschnikowia reukaufii	MR1	GCA_003401635.1	89.90 %	89.50 %	5978	15552339	41.85	*M. bicuspidata* clade	NCBI
Metschnikowia rubicola	CBS 15344^T	GCA_030557065.1	87.80 %	83.10 %	7583	18345891	45.69	*M. bicuspidata* clade	NCBI
Metschnikowia shanxiensis	NRRL Y-48710^T	GCA_030578695.1	86.40 %	76.10 %	7440	17950602	45.74	*M. bicuspidata* clade	NCBI
Metschnikowia sinensis	NRRL Y-48711^T	GCA_030583125.1	89.70 %	89.30 %	6121	15503712	45.76	*M. bicuspidata* clade	NCBI
Metschnikowia vanudenii	NRRL Y-17036^T	GCA_030583145.1	93.50 %	93.20 %	6550	20514424	42.71	*M. bicuspidata* clade	NCBI
Metschnikowia viticola	NRRL Y-48693^T	GCA_030556725.1	82.00 %	81.70 %	6090	16028048	45.27	*M. bicuspidata* clade	NCBI
Metschnikowia zobellii	gsMetZobe1.1	GCA_939531405.1	88.40 %	88.20 %	4913	13653384	47.69	*M. bicuspidata* clade	NCBI
Candida hainanensis	NRRL Y-48715^T	GCA_030561765.1	89.90 %	89.90 %	5012	10423758	50.33	*M. caudata* clade	NCBI
Metschnikowia caudata	EBD-CdVSA08-1^T	GCA_008065185.1	84.50 %	84.40 %	4576	10906389	55.99	*M. caudata* clade	NCBI
Metschnikowia lopburiensis	CBS 12574^T	GCA_030563105.1	90.70 %	90.70 %	4975	10450139	50.35	*M. caudata* clade	NCBI
Metschnikowia drosophilae	UWOPS83-1135.3^T	GCA_002893735.1	90.70 %	90.60 %	4905	10543888	52.8	*M. drosophilae* clade	NCBI
Metschnikowia laotica	CBS 12961^T	GCA_030563125.1	82.00 %	81.90 %	5449	10521976	49.27	*M. drosophilae* clade	NCBI
Metschnikowia torresii	CBS 5152^T	GCA_002893725.1	90.40 %	90.30 %	4994	10913326	51.24	*M. drosophilae* clade	NCBI
Metahyphopichia laotica	CBS 13022^T	NMDC60146133	95.30 %	95.00 %	5622	11063518	42.17	*Metahyphopichia*	this study
Metahyphopichia silvanorum	NRRL Y-7782^T	GCA_030574095.1	95.10 %	94.90 %	5700	11457544	38.51	*Metahyphopichia*	NCBI
Metschnikowia sp.	yHQL527	GCA_030578455.1	91.50 %	91.10 %	5516	11974810	35.23	*Metahyphopichia*	NCBI
Metschnikowia sp.	yHKB443	GCA_030444905.1	77.20 %	77.00 %	4528	11390856	53.78	*Metschnikowia* sp. yHKB443	NCBI

Table 2 List of the AAI, POCP and PAPO values of genera and clades in *Metschnikowiaceae*.

Genera and clades	AAI	POCP	PAPO (unique genes)
C. blattae clade+*Candida citri*	69.25–98.86 %	83.47–99.07 %	0
C. blattae clade	70.19–98.86 %	83.47–99.07 %	2
C. entomophila clade	67.93–67.93 %	88.63–88.63 %	4
C. melibiosica clade	72.05–97.51 %	89.13–98.18 %	15
C. oregonensis clade	72.8–72.8 %	89.11–89.11 %	4
C. succicola clade	70.79–96.43 %	89.21–98.64 %	11
C. tanticharoeniae clade	83.56–83.56 %	96.84–96.84 %	55
C. tolerans clade	71.98–71.98 %	89.12–89.12 %	22
C. ubatubensis clade	91.22–91.22 %	97.48–97.48 %	52
CAH clade	74.67–100.0 %	90.87–99.65 %	24
CAH clade+*C. tolerans* clade	64.14–100.0 %	81.38–99.65 %	3
Clavispora	65.0–94.98 %	77.05–95.37 %	0
Clavispora s.str. clade	67.26–94.98 %	88.35–96.19 %	6
Hyphopichia	63.8–95.63 %	82.11–98.59 %	0
Hyphopichia s.str. clade	65.53–81.68 %	83.07–94.87 %	4
H. heimii clade+*C. sequanensis* clade	65.74–95.63 %	83.00–98.59 %	0
C. sequanensis clade	71.95–81.98 %	89.07–92.47 %	13
H. heimii clade	80.42–95.63 %	95.13–98.59 %	41
Metahyphopichia	68.78–73.3 %	90.16–92.21 %	11
Metschnikowia	57.46–99.37 %	55.16–98.91 %	0
M. arizonensis clade	69.02–99.78 %	71.01–98.29 %	4
M. arizonensis clade+*M. caudata* clade	63.23–99.78 %	63.38–98.75 %	0
M. caudata clade	78.73–99.02 %	92.82–98.75 %	12
M. drosophilae clade+*Metschnikowia* sp. yHKB443	62.86–91.0 %	74.64–97.79 %	0
M. drosophilae clade	84.44–91.0 %	94.66–97.79 %	43
M. bicuspidata clade+*M. agaves* clade+*Candida danieliae*	64.5–99.37 %	71.33–98.91 %	0
M. bicuspidata clade+*M. agaves* clade	64.5–99.37 %	71.33–98.91 %	1
M. agaves clade	73.43–74.58 %	88.37–90.80 %	5
M. bicuspidata clade	67.98–99.37 %	72.26–98.91 %	2
Danielozyma	74.43–74.43 %	92.98–92.98 %	16

genomic tree and the final alignment are saved in the TreeBASE (www.treebase.org, No. 31145).

CompareM v. 0.1.2 (https://github.com/dparks1134/CompareM) was used to assess the AAI values (Liu et al. 2024) among *Metschnikowiaceae* with default parameters. The method for calculating the percentage of conserved protein (POCP) was done according to Qin et al. (2014). The proteomes of each combination of two strains were compared using Blastp (Tatusova & Madden 1999). The conserved proteins were identified based on aligned length (50 %), identity (> 40 %) and e-value ($< 1 \times 10^{-5}$). POCP was calculated as the ratio of conserved proteins to the total number of two proteomes as published on GitHub (https://github.com/hoelzer/pocp) and was used to verify the results.

Presence-absence patterns of orthologs (PAPO) were made according to the method described by Takashima et al. (2019).

Table 3 List of the genus-specific OGs (unique genes) to use as diagnostic characters for the newly proposed genera.

Clade	OGs to use in describing genus as diagnostic characters
C. sequanensis clade	OG0009095
C. blattae clade	OG0005896
C. entomophila clade	OG0010431; OG0010436
C. eppingiae clade	OG0008853; OG0014363; OG0014397; OG0007521
CAH clade	OG0005701; OG0005971; OG0005961
C. kutaoensis clade	OG0010973; OG0011060; OG0011082; OG0011085; OG0011093
Clavispora s.str. clade	OG0006565; OG0006567
C. melibiosica clade	OG0007152
C. oregonensis clade	OG0011188
C. succicola clade	OG0006718; OG0006721
C. tanticharoeniae clade	OG0011372; OG0011374; OG0011341
C. tolerans clade	OG0009123
C. ubatubensis clade	OG0006898
H. heimii clade	OG0007683; OG0008295; OG0007296

OrthoFinder v. 2.5.4 (Emms & Kelly 2019) was used to identify the orthologous genes (OGs) that were indicated as 0 (zero) in case of 'absence' OGs and 1 (one) as 'presence' OGs. We identified the number of unique and shared proteins in the CAH clade, and the other 23 clades in the *Metschnikowiaceae* (Table 2), to clarify the boundaries between the clades. The core genome was considered as the conserved OGs within a clade and the pan genome was considered as the OGs found in at least one strain in a clade and the unique genome was the OGs found in all strains of a clade but not in any other clades. The software eggNOG-mapper v. 2.0 (Cantalapiedra et al. 2021) was used to annotate the unique groups of orthologous genes (OGs) to obtain the function of genes in eggNOG, KEGG, Gene Ontology (GO) and Pfam domain. We selected OG with the same annotation function or OG with more than 30 % identity as the genus-specific OGs (Table 3). The identity of OG is calculated using EMBOSS water alignment tool (Madeira et al. 2019).

RESULTS AND DISCUSSION

Genome assemblies and annotation

The newly sequenced genomes of *C. chanthaburiensis* NBRC 102176^T, *C. eppingiae* JCM 17241^T, *C. haemuli* SLLAear13-1, *C. heveicola* SLLAear14-10, *C. khanbhai* AFear10, CBS 16213^T, CBS 16555, *C. konsanensis* NBRC 109082^T, *C. linzhiensis* AS 2.3073^T, *C. melibiosica* JCM 9558^T and *C. ruelliae* CBS 10815^T, *Candida* sp. XZY238F3, *Danielozyma pruni* NYUN 218101^T and *Metahyphopichia laotica* CBS 13022^T were assembled and ranged in size from 11.02 Mb to 14.92 Mb, and the number of predicted genes varied between 5 049 and 5 881. For detailed information on these genomes see Table 1.

Phylogenomic analysis

A total of 304 single-copy orthologue sequences were obtained from single-copy BUSCO proteins collected from 155 strains in the *Metschnikowiaceae* and *Debaryomycetaceae* (Table 1), which were used to construct the ML genome-based tree

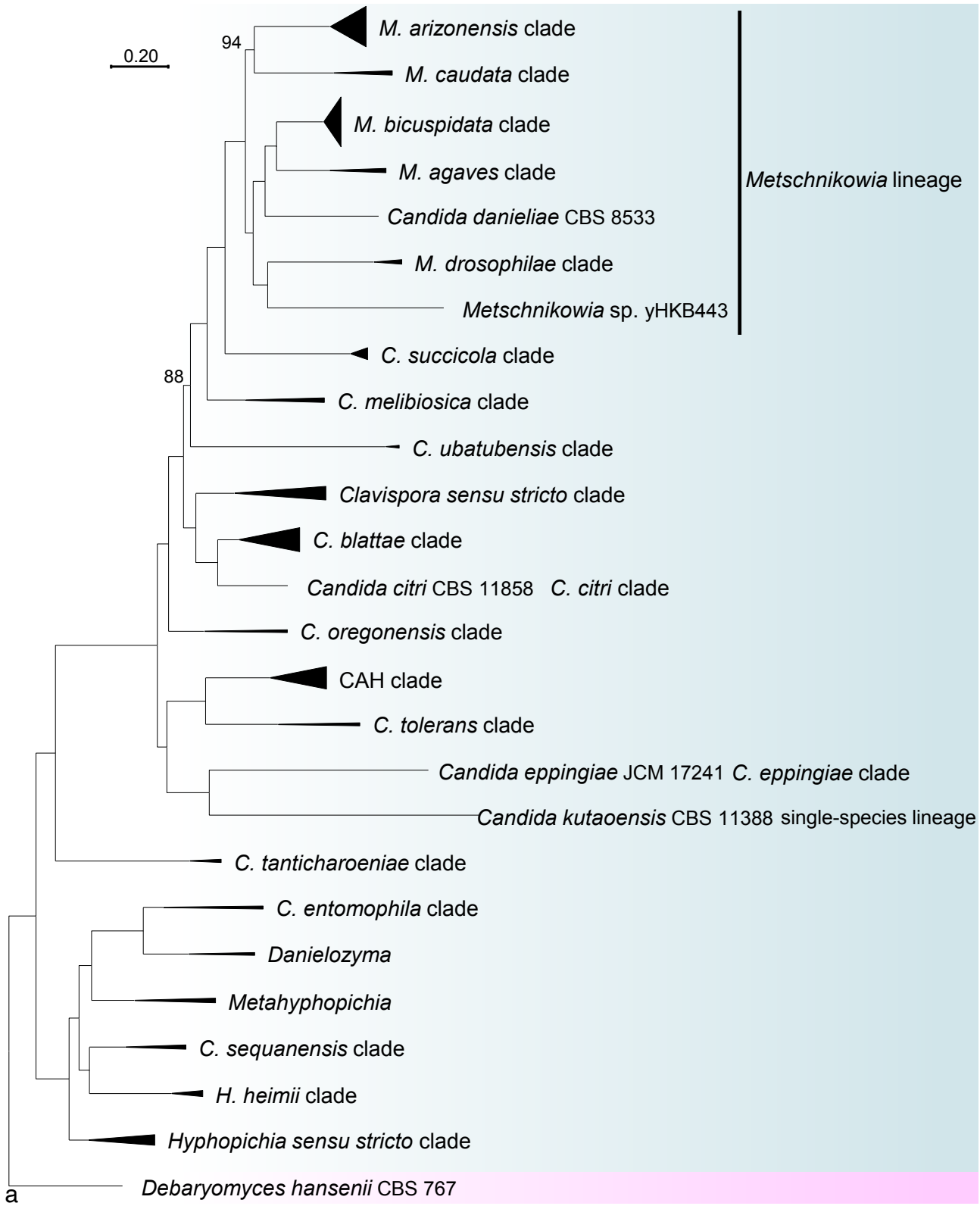

Fig. 1 Phylogenomic tree inferred using the 304 single copy orthologue proteins showed the phylogenetic relationship between the genera and clades in the *Metschnikowiaceae*. Bootstrap percentages of maximum likelihood analysis below 100 % from 1 000 bootstrap replicates are shown on the major branches. Bar = 0.2 substitutions per nucleotide position. a. An outline of the phylogeny of *Metschnikowiaceae* showing the phylogenetic relationship of the genera and clades; b. a subtree of *Metschnikowia* lineage, *C. melibiosica* clade and *C. succicola* clade; c. a tree of CAH clade, *C. citri* clade, *C. blattae* clade, *C. entomophila* clade, *C. eppingiae* clade, *C. oregonensis* clade, *C. sequanensis* clade, *C. tanticharoeniae* clade, *C. tolerans* clade, *C. ubatubensis* clade, *Candida kutaoensis* single-species lineage, *Clavispora* s.str. clade, *Danielozyma*, *Metahyphopichia*, *Hyphopichia* s.str. clade and *H. heimii* clade.

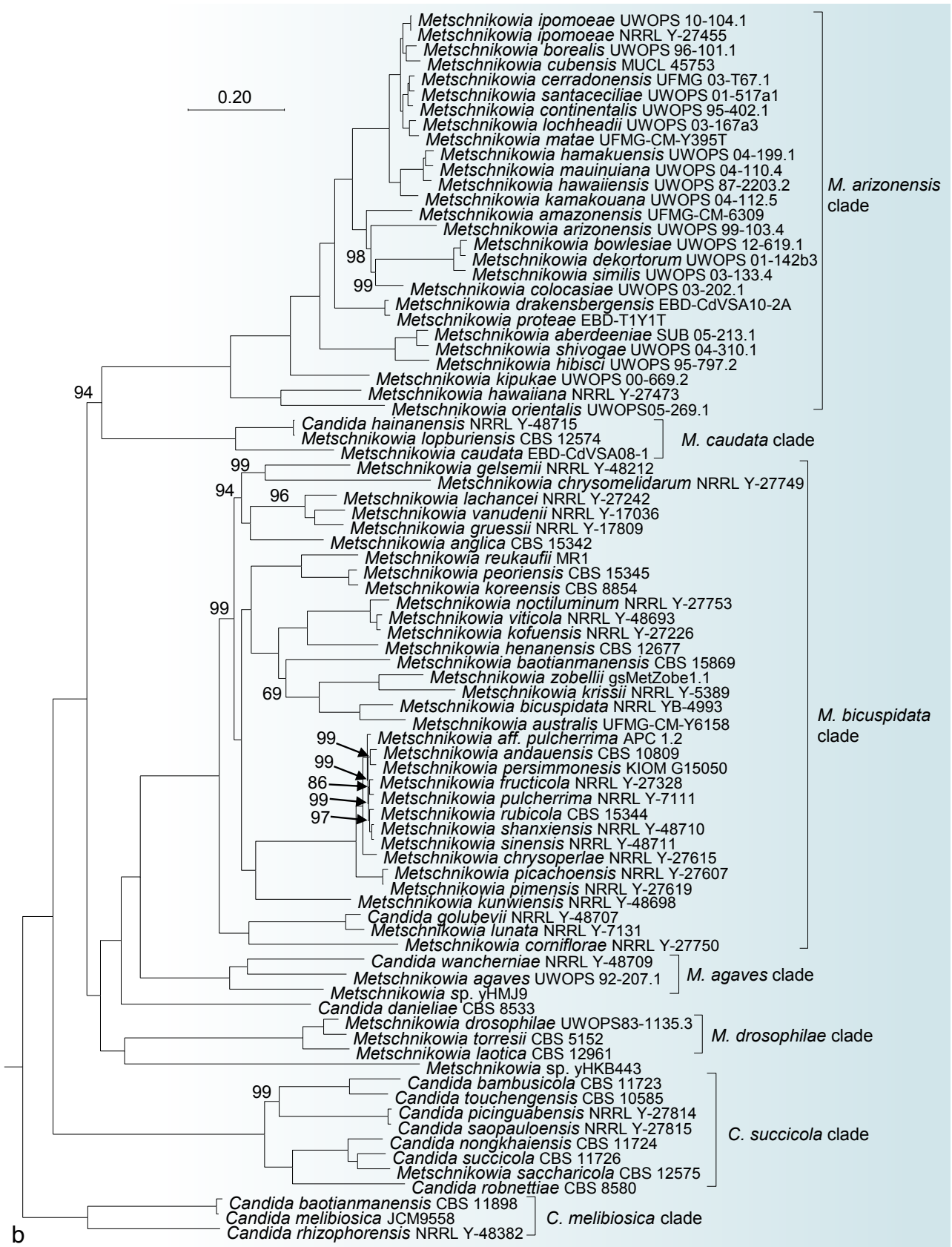
0.20
Metschnikowia ipomoeae UWOPS 10-104.1
Metschnikowia ipomoeae NRRL Y-27455
Metschnikowia borealis UWOPS 96-101.1
Metschnikowia cubensis MUCL 45753
Metschnikowia cerradonensis UFMG 03-T67.1
Metschnikowia santaceciliae UWOPS 01-517a1
Metschnikowia continentalis UWOPS 95-402.1
Metschnikowia lochheadii UWOPS 03-167a3
Metschnikowia matae UFMG-CM-Y395T
Metschnikowia hamakuensis UWOPS 04-199.1
Metschnikowia mauinuiana UWOPS 04-110.4
Metschnikowia hawaiiensis UWOPS 87-2203.2
Metschnikowia kamakouana UWOPS 04-112.5
Metschnikowia amazonensis UFMG-CM-6309
Metschnikowia arizonensis UWOPS 99-103.4
Metschnikowia bowlesiae UWOPS 12-619.1
Metschnikowia dekortorum UWOPS 01-142b3
Metschnikowia similis UWOPS 03-133.4
Metschnikowia colocasiae UWOPS 03-202.1
Metschnikowia drakensbergensis EBD-CdVSA10-2A
Metschnikowia proteae EBD-T1Y1T
Metschnikowia aberdeeniae SUB 05-213.1
Metschnikowia shivogae UWOPS 04-310.1
Metschnikowia hibisci UWOPS 95-797.2
Metschnikowia kipukae UWOPS 00-669.2
Metschnikowia hawaiiana NRRL Y-27473
Metschnikowia orientalis UWOPS05-269.1
M. arizonensis clade
Candida hainanensis NRRL Y-48715
Metschnikowia lopburiensis CBS 12574
Metschnikowia caudata EBD-CdVSA08-1
M. caudata clade
Metschnikowia gelsemii NRRL Y-48212
Metschnikowia chrysomelidarum NRRL Y-27749
Metschnikowia lachancei NRRL Y-27242
Metschnikowia vanudenii NRRL Y-17036
Metschnikowia gruessii NRRL Y-17809
Metschnikowia anglica CBS 15342
Metschnikowia reukaufii MR1
Metschnikowia peoriensis CBS 15345
Metschnikowia koreensis CBS 8854
Metschnikowia noctiluminum NRRL Y-27753
Metschnikowia viticola NRRL Y-48693
Metschnikowia kofuensis NRRL Y-27226
Metschnikowia henanensis CBS 12677
Metschnikowia baotianmanensis CBS 15869
Metschnikowia zobellii gsMetZobe1.1
Metschnikowia krissii NRRL Y-5389
Metschnikowia bicuspidata NRRL YB-4993
Metschnikowia australis UFMG-CM-Y6158
Metschnikowia aff. pulcherrima APC 1.2
Metschnikowia andauensis CBS 10809
Metschnikowia persimmonesis KIOM G15050
Metschnikowia fructicola NRRL Y-27328
Metschnikowia pulcherrima NRRL Y-7111
Metschnikowia rubicola CBS 15344
Metschnikowia shanxiensis NRRL Y-48710
Metschnikowia sinensis NRRL Y-48711
Metschnikowia chrysoperlae NRRL Y-27615
Metschnikowia picachoensis NRRL Y-27607
Metschnikowia pimensis NRRL Y-27619
Metschnikowia kunwiensis NRRL Y-48698
Candida golubevii NRRL Y-48707
Metschnikowia lunata NRRL Y-7131
Metschnikowia corniflorae NRRL Y-27750
M. bicuspidata clade
Candida wancherniae NRRL Y-48709
Metschnikowia agaves UWOPS 92-207.1
M. agaves clade
Metschnikowia sp. yHMJ9
Candida danieliae CBS 8533
Metschnikowia drosophilae UWOPS83-1135.3
Metschnikowia torresii CBS 5152
Metschnikowia laotica CBS 12961
M. drosophilae clade
Metschnikowia sp. yHKB443
Candida bambusicola CBS 11723
Candida touchengensis CBS 10585
Candida picinguabensis NRRL Y-27814
Candida saopauloensis NRRL Y-27815
Candida nongkhaiensis CBS 11724
Candida succicola CBS 11726
Metschnikowia saccharicola CBS 12575
Candida robnettiae CBS 8580
C. succicola clade
Candida baotianmanensis CBS 11898
Candida melibiosica JCM9558
Candida rhizophorensis NRRL Y-48382
C. melibiosica clade
b

Fig. 1 (cont.)


0.20
Metschnikowia lineage
88
C. succicola clade
C. melibiosica clade
Candida ubatubensis NRRL Y-27812
Candida aechmeae NRRL Y-48456
C. ubatubensis clade
Candida asparagi NRRL Y-48714
Clavispora fructus NRRL Y-17072
Candida carvajalis NRRL Y-48694
Candida phyllophila CBS 12671
Candida vitiphila CBS 12672
Clavispora santaluciae A1.5
Clavispora lusitaniae CBS 6936
Clavispora paralusitaniae NYNU 161120
Clavispora opuntiae NRRL Y-11820
Clavispora sensu stricto clade
Candida berkhoutiae CBS 11722
Candida middelhoveniana CBS 12306
Candida ezoensis CBS 11753
Candida inulinophila CBS 11725
Candida tsuchiyae NRRL Y-17840
98
Candida intermedia CBS 141442
Candida pseudointermedia NRRL Y-10939
Candida blattae NRRL Y-27698
Candida dosseyi NRRL Y-27950
Candida ecuadorensis CBS 12653
Candida suratensis CBS 10928
Candida flosculorum NRRL Y-48731
Candida pseudoflosculorum CBS 8584
Candida sharkensis NRRL Y-48380
Candida thailandica CBS 10610
Clavispora xylosa NYNU 174173
C. blattae clade
Candida citri CBS 11858
C. citri clade
Candida oregonensis NRRL Y-5850
C. oregonensis clade
Clavispora reshetovae CBS 11556
Candida chanthaburiensis NBRC 102176
Candida konsanensis NBRC 109082
Candida heveicola AS 2.3483
Candida heveicola SLLAear14-10
Candida khanbhai CBS 16213
Candida khanbhai CBS 16555
Candida khanbhai AFear10
Candida duobushaemuli B09383
Candida vulturna CBS 14366
Candida pseudohaemuli UZ153 17
Candida haemuli B11899
Candida haemuli var. vulneris K1
Candida haemuli SLLAear13-1
Candida ruelliae CBS 10815
Candida auris B11221
CAH clade
Candida mogii NRRL Y-17032
Candida tolerans NRRL Y-48705
C. tolerans clade
Candida eppingiae JCM 17241
C. eppingiae clade
Candida kutaoensis CBS 11388 single-species lineage
Candida savonica NRRL Y-17077
Candida tanticharoeniae CBS 11574
C. tanticharoeniae clade
Candida entomophila NRRL Y-7783
Candida sp. CBS 14106
C. entomophila clade
Danielozyma ontarioensis NRRL YB-1246
Danielozyma pruni NYUN 218101
Danielozyma
Metahyphopichia laotica CBS 13022
Metschnikowia sp. yHQL527
Metahyphopichia silvanorum NRRL Y-7782
Metahyphopichia
Candida linzhiensis AS 2.3073
Candida sequanensis NRRL Y-17682
Candida sp. XZY238F3
C. sequanensis clade
Hyphopichia gotoi NRRL Y-27225
Hyphopichia heimii NRRL Y-7502
Hyphopichia pseudorhagii NRRL YB-2076
Hyphopichia rhagii NRRL Y-2594
H. heimii clade
Hyphopichia burtonii NRRL Y-1933
Hyphopichia khmerensis CBS 9784
Hyphopichia fennica NRRL Y-7505
Hyphopichia pseudoburtonii makgeolli
Hyphopichia wangnamkhiaoensis CBS 11695
Hyphopichia buzzinii CBS 14300
Hyphopichia homilentoma JCM 1507
Hyphopichia sensu stricto clade
C
Debaryomyces hansenii CBS 767

Fig. 1 (cont.)

(Fig. 1). The BUSCO completeness of 155 genomes used in the analysis exceeded 60 %. Six *Candida* species and six *Metschnikowia* species, namely *Candida akabanensis*, *C. bromeliacearum*, *C. metrosideri*, *C. ohialehuae*, *C. xinjiangensis*, *C. xylosifermentans*, *Metschnikowia colchici*, *M. maroccana*, *M. miensis*, *M. persici*, *M. rancensis* and *M. taurica* were not included in the phylogenomic analysis as no genome data were available. Phylogenetic trees including those species for which a genome is lacking were constructed based on ITS, D1/D2 and ITS+D1/D2 rDNA sequences (Fig. S1–S3). In phylogenomic analyses, the bootstrap values obtained for the branches in the phylogenetic trees are expected to be high because phylogenomic-based analysis minimizes sampling error (Salichos & Rokas 2013, Lachance 2022), hence lower bootstrap values indicate potential incongruences between gene loci in phylogenomic analyses. For this reason, only bootstraps < 100 % are shown on the nodes of the phylogenomic tree. The genera *Danielozyma* and *Hyphopichia* were assigned to the family *Debaryomycetaceae* (Groenewald et al. 2023), but our phylogenomic analysis showed that these two genera formed a well-supported lineage with other lineages in *Metschnikowiaceae* (Fig. 1). Hence, we conclude that these two genera belong to *Metschnikowiaceae*, which is in agreement with the earlier results by Kurtzman (2011a), Shen et al. (2018) and Opulente et al. (2023).

Our phylogenomic analysis showed that genera *Clavispora*, *Hyphopichia*, *Metschnikowia* and *Candida* in the *Metschnikowiaceae* are heterogenous and to some extent polyphyletic (Fig. 1a–c). They occurred in 21 clades or single species lineage, namely the *C. blattae* clade, the *C. citri* clade, the *C. entomophila* clade, the *C. eppingiae* clade, the *C. melibiosica* clade, the *C. oregonensis* clade, the *C. sequanensis* clade, the *C. succicola* clade, the *C. tanticharoeniae* clade, the *C. tolerans* clade, the *C. ubatubensis* clade, the CAH clade, the *Clavispora* s.str. clade, the *Hyphopichia* s.str. clade, the *H. heimii* clade, the *M. agaves* clade, the *M. arizonensis* clade, the *M. bicuspidata* clade, the *M. caudata* clade, the *M. drosophilae* clade and the *C. kutaoensis* single-species lineage (Fig. 1a–c).

The genus *Clavispora* contains seven species at present (Drumonde-Neves et al. 2020, Chai et al. 2022). Several *Candida* species were placed close to *Clavispora* species in previous analyses, but not transferred to the genus as it was preferred by those authors to await further phylogenetic analyses using housekeeping genes to circumscribe both genera reliably (Daniel et al. 2014). Based on a phylogenetic analysis of concatenated *ACT1*, *EF2*, *Mcm7* and *RPB2* sequences, Guzmán et al. (2013) showed that the genus *Clavispora* is not monophyletic. The LSU rDNA analysis placed *Clavispora reshetovae* (Yurkov et al. 2009) in a distinct lineage from the clade containing the nomenclatural type of the genus, *Clavispora lusitaniae*, and the species *Clavispora opuntiae* (Guzmán et al. 2013). The phylogenomic analysis in this study supported the polyphyletic nature of *Clavispora* (Fig. 1a, c). Four *Clavispora* species, viz., *Cl. fructus*, *Cl. lusitaniae*, *Cl. opuntiae* and *Cl. paralusitaniae*, and four *Candida* species, viz., *C. asparagi*, *C. carvajalis*, *C. phyllophila* and *C. vitiphila*, formed a well-supported clade (Fig. 1c). The *Clavispora* s.str. clade clustered with the *C. citri* clade and the *C. blattae* clade consisting of 15 more *Candida* species, namely *C. berkhoutiae*, *C. blattae*, *C. dosseyi*, *C. ecuadorensis*, *C. ezoensis*, *C. flosculorum*, *C. inulinophila*, *C. intermedia*, *C. middelhoveniana*, *C. pseudointermedia*, *C. pseudoflosculorum*, *C. sharkensis*, *C. suratensis*, *C. thailandica*, *C. tsuchiyae* and *Clavispora xylosa*. *Clavispora reshetovae* and *Candida oregonensis* formed a well-supported clade, namely the *C. oregonensis* clade that is positioned in a separate branch in the phylogenomic tree, namely at position basal to *Metschnikowia* and *Clavispora* (Fig. 1a, c). It is important to note that the *C. blattae* clade included the recently described asexual species *Cl. xylosa* (Chai et al. 2022). Based on the results of our phylogenomic analysis, it is possible either to merge the *C. blattae* clade with the genus *Clavispora* or to classify them as two different genera and transfer *Cl. xylosa* to a newly erected genus for the *C. blattae* clade. Members of the *Clavispora* s.str. clade contain CoQ8 as the major component of ubiquinone system (Lachance 2011a, Lachance et al. 2011, Limtong & Kaewwichian 2013), whereas species in the *C. blattae* clade, i.e., *C. berkhoutiae*, *C. ezoensis*, *C. intermedia*, *C. inulinophila*, *C. pseudointermedia*, *C. thailandica* and *C. tsuchiyae* have CoQ9 (Jindamorakot et al. 2007, Lachance et al. 2011, Nakase et al. 2011). In the past the CoQ composition has been used as an additional criterion to classify yeasts at the generic level (Yamada & Kondo 1972, Yamada et al. 1976, Billon-Grand 1985, 1989, Suzuki & Nakase 1986), and this biochemical characteristic has also been used to support the circumscription of several genera of basidiomycetous yeasts (Wang et al. 2015a, b, Takashima et al. 2019).

A few discrepancies between the phylogenomic and the combined ribosomal ITS and LSU rDNA-based tree (Fig. S1) have been observed. While the entire clade comprising *Clavispora* s.str. clade, the *C. blattae* clade, the *C. citri* clade and the *C. oregonensis* clade received good support in both analyses (100 % in the phylogenomic tree and 91 % in the rDNA analysis, respectively), the two analyses showed different phylogenetic relationships within this large clade (Fig. 1, S1). Specifically, *C. citri* and *C. xylosifermentans* occupied a basal position in the ITS+D1/D2 rDNA tree and other species were distributed between two moderately supported clades, namely the *C. blattae* clade (77 % support) and a second cluster of clades (76 % support) comprising the *C. melibiosica* clade, the *C. oregonensis* clade, the *C. ubatubensis* clade and the *Clavispora* s.str. clade (Fig. S1). The position of the *C. citri* clade was remarkably different between our phylogenomic analysis (Fig. 1) and the ITS+D1/D2 rDNA tree (Fig. S1).

Based on the phylogenomic analysis alone, the discrepancy between the two phylogenetic analyses brought some uncertainty to the question whether it is reasonable to merge *C. citri* with the *C. blattae* clade. Therefore, we evaluated other genome-based statistics. No clade-specific OGs were found for the *C. blattae* clade + *C. citri* in the PAPO analysis described below, which suggests that it is better to separate *C. citri* from the *C. blattae* clade as it indicates that no genomic synapomorphic genes occur in the *C. blattae* clade + *C. citri.* However, considering the unavailability of a genome of *C. xylosifermentans*, the second known member of the clade, we presently keep the taxonomic position of the *C. citri* clade, and suggest to resolve the position of this clade in the future.

All *Metschnikowia* species that produce needle-shaped ascospores and four related *Candida* species, namely *C. danieliae*, *C. golubevii*, *C. hainanensis* and *C. wancherniae*, formed a well-supported lineage, namely the *Metschnikowia* lineage, in our phylogenomic analysis (Fig. 1a, b). The genus *Metschnikowia* includes two groups that produce large spores and small spores, respectively (Lachance 2011b, Guzmán et al. 2013, Lachance et al. 2016, Lee et al. 2018). The large-spored group included the *M. arizonensis* clade and the *M. caudata* clade, while the small-spored group contained *C. danieliae*, the *M. agaves* clade, the *M. bicuspidata* clade, the *M. drosophilae* clade and *Metschnikowia* sp. yHKB443 (Fig. 1b). The *M. caudata* clade, the *M. drosophilae* clade and *Metschnikowia* sp. yHKB443 clustered together in the previous analysis of Opulente et al. (2023) that used a phylogenomic analysis indicated that the taxonomic relationships of those clades need to be addressed further by exploring more taxa. Therefore, the reclassification of the *Metschnikowia* lineage was not further considered in this study.

Kaewwichian et al. (2012) described *Metschnikowia saccharicola*, a species with no known sexual morph, based on a combined analysis of the ITS and D1/D2 rDNA sequences. Our rDNA sequence and phylogenomic analyses showed that this species is part of a highly supported (100 % support in both analyses) clade (Fig. 1b, S1), namely the *C. succicola* clade, with *Candida bambusicola*, *C. nongkhaiensis*, *C. picinguabensis*, *C. robnettiae*, *C. saopauloensis*, *C. succicola*, *C. tocantinsensis* and *C. touchengensis*. However, the clade was located outside the core *Metschnikowia* lineage, suggesting that the placement of *M. saccharicola* in the genus *Metschnikowia* needs to be reconsidered. Notably, all members of the *C. succicola* clade are asexually reproducing species as far as presently known. In our phylogenomic analysis, this clade occurred as the first branching lineage to the core *Metschnikowia* lineage (Fig. 1a, b).

Within the *Metschnikowiaceae* the *Candida* species occur dispersed. Besides the *Candida* species in the above-discussed *C. blattae* clade, the *C. citri* clade, the *C. oregonensis* clade, the *C. succicola* clade, the *Clavispora* s.str. clade and the *Metschnikowia* lineage, more than 20 *Candida* species occurred in eight well-supported clades and one single-species lineage (Fig. 1b, c). Among them, *C. baotianmanensis*, *C.melibiosica* and *C. rhizophorensis* formed a separate lineage, namely the *C. melibiosica* clade, which occurred as the first branching lineage in the *Metschnikowia* lineage and the *C. succicola* clade (Fig. 1b). Daniel et al. (2014) concluded that the *C. melibiosica* clade and the *C. succicola* clade formed two lineages that were separated by long distances from the core *Metschnikowia* clade and suggested that they might be considered as two new genera. Our data support this notion (Fig.1, S1). *Candida aechmeae* and *C. ubatubensis* formed a small clade on a long branch that was placed outside the *Metschnikowia* lineage, the *C. melibiosica* clade and the *C. succicola* clade in the *Metschnikowiaceae* (Fig. 1). A search among public sequences revealed at least five undescribed potential new species in the *C. ubatubensis* clade represented by strains *Candida* sp. UFMGCMY6390, *Candida* sp. MCB1C2(5), *Candida* sp. UFMGF12, *Candida* aff. *ubatubensis* IMUFRJ 51945 and '*Clavispora'* sp. UFMGCMY3120 (Fig. S2), which indicated that new species in the *C. ubatubensis* clade might be described in the future.

The phylogenomic analysis showed that the CAH clade received good support and was phylogenetically positioned remotely from the genera *Clavispora*, *Danielozyma*, *Hyphopichia*, *Metschnikowia* (Fig. 1a, c). As far as is known at present, members of the CAH clade reproduce asexually, unlike the phylogenetic closely related genera *Clavispora* and *Metschnikowia* that reproduce sexually with asci and ascospores. Two species, *C. mogii* and *C. tolerans*, formed a well-supported clade closely related to the CAH clade (Fig. 1c). Until now, the phylogenetic position of these species remained uncertain. Sugita & Nakase (1999) placed *C. mogii* in a basal position with affinities to the genus *Clavispora* based on the analysis of the small subunit (SSU) rDNA sequence, whereas Kurtzman & Robnett (1998) suggested a weak connection to *C. haemuli* (CAH clade) based on a phylogenetic analysis of sequences of the D1/D2 domains of LSU rDNA. Our ITS+D1/D2 rDNA sequence analyses showed that *C. mogii* and *C. tolerans* formed a well-supported (100 % support) clade distinct from the CAH clade together with sequences of four unpublished and potentially new species labelled as *Candida* cf. *tolerans* UWO(PS)99-704.2, *Candida* sp. 1A1, '*Clavispora'* sp. 111180 and '*Clavispora'* sp. 111221 (Fig. S1).

A previous phylogenetic analysis of D1/D2 LSU rDNA sequences indicated that *C. savonica* and *C. tanticharoeniae* were closely related to the genus *Kodamaea* in *Debaryomycetaceae* (Nakase et al. 2010), but our phylogenomic analysis showed that they occupied a basal position in the *Metschnikowiaceae* with high statistical support (Fig. 1c). Phylogenetic analysis of combined ITS and D1/D2 sequence data showed that three other and potentially new species occurred in the *C. tanticharoeniae* clade (Fig S2, S3). Both *C. eppingiae* and *C. kutaoensis* formed a single-species lineage on a long branch adjacent to the CAH and *C. tolerans* clades (Fig. 1c), but this topology received low bootstrap support in analyses based on rDNA sequences (Groenewald et al. 2011, Yuan et al. 2012; Fig. S1–S3). Although *C. bromeliacearum* was not included in our phylogenomic analysis due to the lack of genome data, this species and *C. eppingiae* clustered together with high (100 % BP) support in the combined ITS+D1/D2 rDNA-based tree constructed by Groenewald et al. (2011), suggesting that *C. bromeliacearum* and *C. eppingiae* belong together to this clade. An unpublished strain *Candida* sp. UWO(PS)00-137.1 clustered with the *C. eppingiae* clade in our D1/D2 LSU rDNA-based phylogenetic analysis (Fig. S2) and likely represents another member of the *C. eppingiae* clade. Opulente et al. (2023) previously observed that *C. kutaoensis* occurred on a long branch next to the *C. ubatubensis* clade. Based on the D1/D2 LSU rDNA sequence analysis (Fig. S2) *Candida* aff. *kutaonensis* UCDFST: 62-304 likely represents a different species than *C. kutaoensis* because its D1/D2 sequence differs from that of the type strain of *C. kutaoensis* by more than 4 % of the nucleotides.

Hyphopichia species were placed in two clades in this and a previous phylogenomic analysis (Opulente et al. 2023; Fig. 1c). Specifically, the nomenclatural type *H. burtonii*, *H. buzzinii*, *H. fennica*, *H. homilentoma*, *H. khmerensis*, *H. lachancei*, *H. pseudoburtonii* and *H. wangnamkhiaoensis* formed the *Hyphopichia* s.str. clade (Fig. 1c, S1, S2). The second clade comprised *H. heimii*, *H. gotoi*, *H. rhagii*, *H. paragotoi* and *H. pseudorhagii*, and is called the *H. heimii* clade (Fig. 1c, S1, S2). *Candida linzhiensis* and *C. sequanensis* grouped together and formed the *C. sequanensis* clade with high support and positioned in a basal position to the *H. heimii* clade (Fig. 1c). Together the *H. heimii* and *C. sequanensis* clades built a larger well-supported clade with *Danielozyma*, the *C. entomophila* clade and *Metahyphopichia* (Fig. 1c), which agrees with the result of Opulente et al. (2023). A controversial position of *Danielozyma ontarioensis* was found in the phylogenetic analyses by Shen et al. (2018) and Li et al. (2021) based on genome data as the species occurred nested in the genus *Hyphopichia*. In our phylogenomic analysis, *Danielozyma* was found to be closely related to *C. entomophila* and *Candida* sp. CBS 14106 that clustered together with high support. Our analyses also revealed two potentially new species in this clade represented by strains labelled as *Danielozyma* aff. *ontarioensis* UCDFST:681027.2 and *Danielozyma* sp. DMKUSK8 (Fig. S1). The combined ITS+D1/D2 sequence analysis showed that *Candida xinjiangensis* described by Zhu et al. (2017) and *C. entomophila* formed a well-supported clade closely related to the genus *Danielozyma* but lacking statistical support (Fig. S1). The D1/D2 rDNA sequence analysis indicated that four strains, namely *Candida* sp. UFMG-CM-Y7109, *Candida* sp. UFMG-CM-Y6230, *Candida* sp. UFMG-CM-Y605 and *Candida* sp. GE17L14 may represent three new species in the *C. entomophila* clade (Fig. S2). Daniel et al. (2014) concluded that *C. entomophila* did not cluster confidently with any existing genera in the phylogenetic analysis of D1/D2 rDNA sequences. The data presented above and the results of our phylogenomic analysis suggested that the *C. entomophila* clade may represent a new genus comprising at least five species. Sipiczki & Tap (2016) described *Metahyphopichia*, a genus closely related to *Danielozyma* and *Hyphopichia*. Recently, *Candida silvanorum* was

transferred to *Metahyphopichia* (Khunnamwong et al. 2022). Our phylogenomic analysis showed that *Metahyphopichia laotica*, *Metahyphopichia silvanorum* and '*Metschnikowia'* sp. yHQL527 clustered together closely related to the genus *Danielozyma* and the *C. entomophila* clade (Fig. 1c).

Delineation of genera based on genomic-based metrics

Although the taxonomic relationship of most clades in the *Metschnikowiaceae* was well resolved based on the above phylogenomic analysis, the results revealed several small clades that were found to be closely related to existing genera or clades occurring on rather long branches, i.e., i) the CAH clade and the *C. tolerans* clade; and ii) the *H. heimii* clade and the *C. sequanensis* clade. Recently, several genomic metrics have been explored to test phylogenetic hypotheses (Takashima et al. 2019, Liu et al. 2024). Here we explored the use of these genomics-based statistical analyses, namely the AAI, POCP and PAPO approaches, which have been recently used to test the boundaries of generally well-accepted genera in the *Saccharomycetaceae* (Liu et al. 2024), to address the taxonomic relationship between the various genera and clades in the *Metschnikowiaceae* in more detail.

In the AAI analysis, species in the genera *Clavispora*, *Hyphopichia* and *Metschnikowia* had 65.0–94.98 %, 63.8–95.63 % and 57.46–99.37 % AAI values, respectively (Table 2, S2), which all are lower than the observed values (about 70 %) for well-accepted genera in the *Saccharomycetaceae* (Liu et al. 2024). The AAI values of the *C. blattae* clade, the *C. entomophila* clade, the *C. melibiosica* clade, the *C. oregonensis* clade, the *C. sequanensis* clade, the *C. succicola* clade, the *C. tanticharoeniae* clade, the *C. tolerans* clade, the *C. ubatubensis* clade, the CAH clade, the *Clavispora* s.str. clade, the *Hyphopichia* s.str. clade, the *H. heimii* clade, the *M. agaves* clade, the *M. caudata* clade, the *M. arizonensis* clade, the *M. bicuspidata* clade, the *M. drosophilae* clade, the *Danielozyma* clade and the *Metahyphopichia* clade were all within in the range suggested by Liu et al. (2024) (Table 2, S2).

Protein sequence similarity was analyzed among 150 yeast species belonging to the 23 clades or genera using the POCP method (Table 2, S3). The results showed that the POCP values in the *C. blattae* clade, the *C. entomophila* clade, the *C. melibiosica* clade, the *C. oregonensis* clade, the *C. sequanensis* clade, the *C. succicola* clade, the *C. tanticharoeniae* clade, the *C. tolerans* clade, the *C. ubatubensis* clade, the CAH clade, the *Clavispora* s.str. clade, the *Hyphopichia* s.str. clade, the *H. heimii* clade, the *M. agaves* clade, the *M. caudata* clade, the *M. drosophilae* clade, the genus *Danielozyma* and *Metahyphopichia* were > 80 % (Table 2). However, the *M. arizonensis* clade and the *M. bicuspidata* clade had POCP values of 71.01–98.29 % and 72.26–98.91 %, respectively, which are lower than values observed for well-accepted genera of *Saccharomycetaceae* with POCP > 80 % (Liu et al. 2024). The range of the POCP values for all species presently classified in the genus *Metschnikowia* was larger, namely 55.16 % to 98.91 % (Table 2). The analysis indicated that the genus *Metschnikowia* is genetically far more heterogeneous than any of its closely related genera or clades, possibly due to the presence of lineages that are phylogenetically very different, i.e., those containing large-spored and small-spored species, respectively (Guzmán et al. 2013, Lachance et al. 2016, Lee et al. 2018). Our data suggest that this genus needs to be reclassified in the future.

The PAPO analysis has been used by Takashima et al. (2019) and Liu et al. (2024) to delimit yeast genera in *Trichosporonales* and *Saccharomycetaceae*, respectively. With this method, the number of unique genes (also known as unique orthologs and genus-specific genes) present in clades and genera is examined. Here, we performed this analysis using 154 strains of species belonging to *Metschnikowiaceae*. We identified unique, core, and pan-genomics genes based on OrthoFinder OGs results (Table S3). More than two unique genes were found in the *C. blattae* clade, the *C. entomophila* clade, the *C. melibiosica* clade, the *C. oregonensis* clade, the *C. sequanensis* clade, the *C. succicola* clade, the *C. tanticharoeniae* clade, the *C. tolerans* clade, the *C. ubatubensis* clade, the CAH clade, the *Clavispora* s.str. clade, the *Hyphopichia* s.str. clade, the *H. heimii* clade, the *M. agaves* clade, the *M. caudata* clade, the *M. arizonensis* clade, the *M. bicuspidata* clade, the *M. drosophilae* clade, the *Danielozyma* clade and the *Metahyphopichia* clade. No unique genes were found in the genera *Clavispora*, *Hyphopichia* and *Metschnikowia*, indicating that these genera are genetically more diverse than any other such group, suggesting that these genera are in need of reclassification.

The above results indicate that the three genera *Clavispora*, *Hyphopichia* and *Metschnikowia* display a notable degree of genomic heterogeneity. Previous research showed that the relative evolutionary divergence (RED) in genera *Clavispora* (RED = 0.903), *Hyphopichia* (RED = 0.859) and *Metschnikowia* (RED = 0.914) is closer to that of family-level ranks in *Fungi*, median RED = 0.889 (Li et al. 2021), which is an indication that these genera are underclassified. Further investigation of the AAI and POCP values of the genera *Clavispora* and *Metschnikowia* showed that these were lower than those obtained for any other closely related clade or genus (Table 2). The phylogenomic analysis indicated that *Clavispora* was polyphyletic, and *Cl. reshetovae* and *Cl. xylosa* belonged to the *C. oregonensis* clade and the *C. blattae* clade, respectively. The high heterogeneity of the genomic indices suggests that the genus *Clavispora* should be restricted to the *Clavispora* s.str. clade containing the type species *Cl. lusitaniae*. The situation with the genus *Metschnikowia* is less trivial. The genus is monophyletic, although it contains two large clades comprising species having large spores and small spores, respectively. The divergence of the genus at the level of rDNA sequences has been acknowledged before, as well as the similarity of growth responses and ecology (Lachance 2011b). The phylogenomic analysis performed in our study resolved the two major clades but they seem to be still heterogeneous (Fig. 1b). The *M. caudata* clade was found to be separated from most other species of the large-spored clade. Similarly, the small-spored clade contained three well-supported clades, namely the *M. bicuspidata* clade, the *M. agaves* clade, and the *M. drosophilae* clade. When we analyzed these five clades within the genus *Metschnikowia* separately, the number of unique genes increased to two and more, the AAI values were close to 70 %, and the POCP values were higher than 80 %, except for the two large *M. arizonensis* and *M. bicuspidata* clades (Table 2), the cores of the large- and small-spored clades, respectively. These results showed that the genus *Metschnikowia* as it is presently recognized is characterized by significant genetic and phylogenetic divergence that may have various causes. For instance, the rates of sequence divergence may differ between older and newer phylogenetic lineages, as well as those undergoing hybridization and speciation (e.g., Shen et al. 2018). In particular, a strong effect is observed in lineages with short generation times, such as microorganisms including yeasts (e.g., Shen et al. 2018, Steenwyk & Rokas 2023). However, evolutionary rates among protein-coding genes of different yeast classes are rather universal, with only a minor shift toward higher rates in 'younger' gene classes (Wolf et al. 2009). A recent RED analysis (Groenewald et al. 2023) showed that the RED values obtained for families *Metschnikowiaceae*, *Saccharomycodaceae* (incl. *Hanseniaspora*) and *Saccharomycetaceae* are in the same range as those of other major fungal lineages. While relatively similar evolutionary divergence levels can be consistent across large lineages (e.g.,

taxonomic ranks of family and order), specific genetic features involved in genome recombination may further contribute to unique divergence patterns in single genera. Recently, it has been demonstrated that the ascomycetous yeast genus *Hanseniaspora* exhibits high molecular evolutionary rates and is characterized by extensive loss of cell-cycle and DNA repair genes (Steenwyk et al. 2019). Among the two lineages in the genus, the fast-evolving one lost more genes associated with the cell cycle and genome integrity. The phenomenon may not be restricted to *Hanseniaspora*, but also be present in other lineages of ascomycetous yeasts. Whether or not other lineages characterized by a high genetic divergence, like the aforementioned *Metschnikowia*, underwent an accelerated evolution due to reduced repair mechanisms requires further investigation.

The CAH and *C. tolerans* clades, and the *H. heimii* and *C. sequanensis* clades formed two well-supported lineages, respectively (Fig. 1). However, no unique genes were observed for the *H. heimii* + *C. sequanensis* clade. The CAH clade + *C. tolerans* clade had three unique genes, but their respective AAI values were rather low, 64.14–100.0 % (Table 2). Considering phylogenetic distance, low similarity in genetic composition and overall sequence similarity, we conclude that *H. heimii* and *C. sequanensis* should preferably be accommodated in different genera. The phenotypic comparison (see Taxonomy section) revealed that the CAH clade and the *C. tolerans* clade can be distinguished by the assimilation of melezitose, which is positive for the CAH clade and negative for the *C. tolerans* clade.

Due to the lack of a sufficient number of genome sequences for species belonging to the *C. eppingiae* clade and *C. kutaoensis* single-species lineage, results of AAI, POCP and PAPO values were not available. However, the phylogenomic and the rDNA sequence analyses (Fig. 1, S1–S3) both suggest that the two clades represent two distinct lineages in the *Metschnikowiaceae*.

Morphological, biochemical, and physiological characteristics have traditionally served as primary criteria for circumscribing yeast genera. With a growing number of species, features associated with sexual reproduction and other diagnostic characteristics, including ascospore morphology and rare physiological properties do not apply universally to all species anymore (e.g., Giménez-Jurado et al. 2003, Garcia-Acero et al. 2024). While most species may still exhibit the major traits in common (plesiomorphies), this tendency potentially increases the heterogeneity within genera and complicates the demarcation of generic boundaries. The family *Metschnikowiaceae* contains three teleomorphic genera, *Clavispora*, *Hyphopichia* and *Metschnikowia*. The morphological characteristics of these yeasts, particularly those pertaining to sexual reproduction, exhibit greater diversity compared to a few distinctive physiological and biochemical characteristics, such as glucose fermentation, assimilation of nitrate and major respiratory ubiquinone system (Kurtzman 2011b, Lachance 2011a, b). In the absence of sexual morphology, identifying physiological attributes for clades consisting solely of asexual species (such as the former *Candida*) poses a significant challenge, as larger clades tend to exhibit fewer shared traits in common. A few morphological and physiological features alone may not always suffice for the accurate circumscription of asexual genera (as seen in examples from basidiomycetous genera like *Bullera*, *Cryptococcus*, *Dioszegia*, *Rhodotorula* and *Sporobolomyces*). In such cases, additional methods such as molecular techniques may be necessary for the definitive classification of these yeasts. For the resolved in the phylogenomic analysis *Candida* clades of *Metschnikowiaceae*, molecular metrics remain the most reliable tool for identification. Maintaining *Candida* species outside the family *Debaryomycetaceae* is not sustainable due to the increasing heterogeneity of the genus and the growing uncertainty in identification at the genus level with the discovery of new species. Accommodating asexual species within sexual genera is feasible to a certain extent. However, clades that cannot be assigned to any previously described genus would necessitate the creation of a new name, like the previously described *Danielozyma* and *Metahyphopichia* (Kurtzman & Robnett 2014, Sipiczki et al. 2016).

Taking together the results of our phylogenomic analysis, the statistical evaluation of the variability of genomic metrics, and phenotypic characters, we propose 13 new genera in the *Metschnikowiaceae* to improve the taxonomy of these ascomycetous yeasts (see Taxonomy section below). The representative unique genes (genus-specific protein families, OGs) of each clade (Table 3) were used to diagnose the new genera in the taxonomy section. Detailed information on those OGs is given in Table S4.

Benefits of renaming yeast taxa

Changing the name of fungi may be confusing for the end-users in the applied field, be it clinical or industrial, and this certainly may be true in a short time frame. A concern was raised about the disconnect between newly introduced names and the practical needs of end-users (e.g., De Hoog et al. 2023). However, the long-term negative effects of newly introduced names were not supported by several recent surveys (Chang et al. 2021, Chen et al. 2021, Kidd et al. 2022, 2023, Carroll et al. 2023). Appropriate and accurate name changes that reflect the proper evolutionary relationships among organisms may provide benefits for the broader user community (Lücking et al. 2021). Such changes support the fundamental disciplines of taxonomy and nomenclature, ensuring the communication of accurate information to the end-users (Carroll et al. 2023).

Fungal taxonomy, including that of yeasts, has experienced many name changes in the recent past. Application of new techniques and tools led to changing generic concepts by adapting broader or more narrow circumscriptions of genera like *Saccharomyces*, *Kluyveromyces* and *Pichia* to name a few (Kurtzman 2003, Kurtzman et al. 2008). The concern about renaming, splitting, and lumping genera is understandable. However, the history of the genus *Candida* is different from that of many other yeast genera. The broad definition of the genus that is based on a few phenotypic characteristics, namely the absence of a sexual state, together with the past concept of 'dual nomenclature' (Hawksworth et al. 2011, Lücking et al. 2021) has made this genus large and phylogenetically heterogeneous (Daniel et al. 2014). The polyphyletic nature of the genus *Candida* has been recognized over the last decades (Lachance et al. 2011, Daniel et al. 2014) and attempts to reclassify this genus have been made (Takashima & Sugita 2022). The CAH clade is phylogenetically related to the genera *Clavispora* and *Metschnikowia*, and distantly positioned from the *C. albicans* clade (or *Lodderomyces* clade) representing the genus *Candida* in the strict sense as *C. vulgaris*, a current synonym under *C. tropicalis* and the type of the genus, belongs to the *C. albicans*/*Lodderomyces* clade. Because of the significant phylogenetic distance between the CAH clade and the *C. albicans*/*Lodderomyces* clade, the separation of the CAH clade from the genus *Candida* into its own genus is warranted. A wide range of knowledge suggests that apart from their morphological appearance on some culture media, members of the CAH and the *C. albicans*/*Lodderomyces* clade do not share common characteristics, including many physiological properties and resistance to antimycotics (see below). The proposal presented here is based on solid data and widely accepted taxonomic practice in mycology and zymology. Below we propose a new genus *Candidozyma* to accommodate the species in the CAH clade.

Species in a phylogenetically defined genus usually share genetic properties and evolutionary traits, including phenotypic ones. In other words, species within different genera have gained different genetic and phenotypic characteristics from distinct and not necessarily closely related recent ancestors during evolution. As such, genera can be seen as centers of speciation in which the species are genetically more closely related than species from other such centers. Thus, a generic name is used to communicate traits that are common for a species or strains in the genus, i.e., synapomorphies. This is very much true for the genus *Candida* which is most referred to as representing yeasts of clinical importance. However, among single-celled fungi, i.e., the yeasts, such phenotypic expressions may not always be clear. Here it may help to consider non-standard datasets, such as antifungal susceptibility data. For example, the *Candida* species that belong to different families, such as *C. albicans* (*Debaryomycetaceae*) and *C. auris* (*Metschnikowiaceae*) have different antifungal susceptibility patterns (Schmalreck et al. 2014, Stavrou et al. 2019, Kidd et al. 2023). Therefore, separating distantly related species, like those of the CAH clade from those of the *C. albicans*/*Lodderomyces* clade, into a new genus confirms that these yeasts possess diverse properties and require distinct treatment options (Schmalreck et al. 2014, Stavrou et al. 2019, Lücking et al. 2021). Furthermore, organisms bearing the same generic name are expected to share similar properties, including those useful for biotechnological and agricultural applications, fermentations, and biological safety concerns. In the field of fungal biotechnology, appropriate fungal name changes can help to predict and search for novel production organisms and their applications (Kurtzman et al. 2015) and may assist researchers to identify and track the different species of yeast with their intrinsic properties, which can help in identifying novel production organisms that may have been previously overlooked or misidentified (Houbraken et al. 2014). The case of renaming so-called *Candida* species that do not belong to the core *C. albicans*/*Lodderomyces* clade will also be beneficial for the application of such organisms in biotechnology, for example, due to a separation from pathogenic clades containing important opportunists. Presently, the name *Candida* is strongly associated with candidiasis, an infection caused by several human opportunistic yeasts. Renaming the bulk of species that presently are classified in the genus *Candida* may boost their biotechnological applications, facilitate general acceptance and ease the authorization process for use in production processes.

TAXONOMY

Validated taxa

Among species considered in the present study, three species names are presently indicated in the nomenclatural repositories Index Fungorum and MycoBank as invalid according to 40.7 of the ICNafp Shenzhen Code (Turland et al. 2018). The interpretation of the wording of the ICNafp applied to descriptions of yeast fungi has been a matter of recent debate. A group of yeast taxonomists argued that they disagree with some strict and literal interpretations of the ICNafp requirements and wordings, which made a few hundred names of yeast species (and some genera) invalid, despite that they have been documented, safely preserved and with accessible authentic type material in their descriptions (Yurkov et al. 2021). By co-incidence, the names of several species revised in the present study are controversially declared invalid. In addition, it turned out that the orthography of the epithet '*haemulonii*', for which also other orthographic variants were in use, e.g., '*haemuloni*' and '*haemulonis*', needs a correction. The epithet refers to the fish genus *Haemulon*, a word derived from the Greek neuter noun haema (= blood). Like other Greek-derived genera (e.g., *Rhododendron*, *Agropyron*) it is latinized as 2nd declension neuter noun with the correct genitive case '*haemuli*'. Epithets derived from this name will be corrected as *C. haemuli*, *C. pseudohaemuli* and *C. pseuduobushaemuli*.

Australozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852145

Etymology. The genus is named based on the yeasts in this lineage having been isolated from the southern Hemisphere.

Type species. *Australozyma succicola* (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. succicola* clade, which is in a separate lineage from the *C. melibiosica* clade and the *Metschnikowia* lineage (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein families OG0006718 and OG0006721 (Table 3, S4).

Sexual reproduction not known. Colonies white to grayish white, butyrous, smooth. Multilateral budding cells present. Hyphae not produced, but pseudohyphae present or not. Growth in the presence of 50 % glucose (osmotolerance) and 15 % NaCl (halotolerance). The major ubiquinon coenzyme Q-9.

Notes — The genus *Australozyma* differs from its closely related genus *Helenozyma* (i.e., the *C. melibiosica* clade) by lack of assimilation of N-acetyl-D-glucosamine, whereas the genus *Helenozyma* can use this compound (Table S5).

Australozyma bambusicola (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852146

Basionym. *Candida bambusicola* Nakase et al., J. Gen. Appl. Microbiol. 57: 234. 2011.

Australozyma nongkhaiensis (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852147

Basionym. *Candida nongkhaiensis* Nakase et al., J. Gen. Appl. Microbiol. 57: 237. 2011.

Australozyma picinguabensis (Ruivo et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852148

Basionym. *Candida picinguabensis* Ruivo et al., Int. J. Syst. Evol. Microbiol. 56: 1149. 2006.

Australozyma robnettiae (M. Groenew. et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852149

Basionym. *Candida robnettiae* M. Groenew. et al., Int. J. Syst. Evol. Microbiol. 61: 2020. 2011.

Australozyma saccharicola Kaewwich. ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *sp. nov.* — MycoBank MB 852211

Holotype. NBRC 108904 (preserved in a metabolically inactive state), National Institute of Technology and Evaluation (NITE), Kisarazu, Chiba, Japan.

Synonym. *Metschnikowia saccharicola* Kaewwich., Antonie van Leeuwenhoek 102: 746. 2012. Nom. inval., Art. 40.7 (Melbourne).

For a description see Antonie van Leeuwenhoek 102: 746. 2012.

Australozyma saopauloensis (Ruivo et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852160

Basionym. *Candida saopauloensis* Ruivo et al. (as '*saopaulonensis*'), Int. J. Syst. Evol. Microbiol. 56: 1150. 2006.

Australozyma succicola (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852161

Basionym. *Candida succicola* Nakase et al., J. Gen. Appl. Microbiol. 57: 238. 2011.

Australozyma touchengensis (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852162

Basionym. *Candida touchengensis* Nakase et al., J. Gen. Appl. Microbiol. 57: 240. 2011.

Candidozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 848168.

Etymology. The genus is named for the asexual morphology like that found in the genus *Candida*.

Type species. *Candidozyma auris* (Satoh & Makimura) Q.M. Wang, Yurkov, Boekhout, & F.Y. Bai.

This genus is proposed to accommodate members of the CAH clade, which is closely related to the *C. tolerans* clade (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2) and the presence of genus-specific protein families OG0005701, OG0005971 and OG0005961 (Table 3, S4).

Sexual reproduction not known, but most mating and meiosis genes are conserved and MTLa and MTLα mating loci are present in different populations (Muñoz et al. 2018). Therefore, mating might be expected, and a sexual state might be inducible under appropriate conditions. Colonies cream to yellowish cream, white, butyrous. Budding multilateral. Pseudohyphae and hyphae are usually not produced, but occur in special conditions, such as when growing aerobically.

Notes — The genus *Candidozyma* differs from its closely related genus *Osmozyma* (i.e., the *C. tolerans* clade) by assimilation of melezitose, whereas the genus *Osmozyma* does not assimilate this compound (Table S5). Most species in the *Candidozyma* are clinically important and are resistant to multiple antifungal drugs, which seems to be a unique feature compared to other genera in the *Metschnikowiaceae*.

Candidozyma auris (Satoh & Makimura) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848169

Basionym. *Candida auris* Satoh & Makimura, Microbiol. Immunol. 53: 43. 2009.

Synonym. *Candida auris* Satoh & Makimura ex F. Hagen, Med. Mycol. 61: myad009, 7. 2023. Nom. illegit., Art 53.

Candidozyma chanthaburiensis (Limtong et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848170

Basionym. *Candida chanthaburiensis* Limtong et al., Med. Mycol. 61: myad009, 7. 2023.

Synonym. *Candida chanthaburiensis* Limtong & Yongman., Antonie van Leeuwenhoek 98: 383. 2010. Nom. inval., Art. 40.7 (Shenzhen).

Candidozyma duobushaemuli (Cend.-Bueno et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848171

Basionym. *Candida duobushaemuli* Cend.-Bueno et al. (as '*duobushaemulonii*'), J. Clin. Microbiol. 50: 3646. 2012.

Candidozyma haemuli (Uden & Kolip.) Q.M. Wang, Yurkov, Boekhout, F.Y. Bai, *comb. nov.* — MycoBank MB 848173

Basionym. *Torulopsis haemuli* Uden & Kolip. (as '*haemulonii*'), Antonie van Leeuwenhoek 28: 78. 1962.

Synonym. *Candida haemuli* (Uden & Kolip.) S.A. Mey. & Yarrow (as '*haemulonii*'), Int. J. Syst. Bacteriol. 28: 612. 1978.

Candidozyma haemuli* var. *vulneris (Cend.-Bueno et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848174

Basionym. *Candida haemuli* var. *vulneris* Cend.-Bueno et al., J. Clin. Microbiol. 50: 3648. 2012.

Candidozyma heveicola (F.Y. Bai & S.A. Wang) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848175

Basionym. *Candida heveicola* F.Y. Bai & S.A. Wang, Antonie van Leeuwenhoek 94: 263. 2008.

Candidozyma khanbhai (A.W. de Jong & F. Hagen) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848176

Basionym. *Candida khanbhai* A.W. de Jong & F. Hagen, Med. Mycol. 61: myad009, 5. 2023.

Candidozyma konsanensis (Sarawan et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848177

Basionym. *Candida konsanensis* Sarawan et al., Med. Mycol. 61: myad009, 7. 2023.

Synonym. *Candida konsanensis* Sarawan et al., World J. Microbiol. Biotechnol. 29: 1483. 2013. Nom. inval., Arts 40.7, F.5.1 (Shenzhen).

Candidozyma metrosideri (J. Klaps et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848178

Basionym. *Candida metrosideri* J. Klaps et al., Med. Mycol. 61: myad009, 7. 2023.

Synonym. *Candida metrosideri* J. Klaps et al., PLoS ONE 15: e0240093, 11. 2020. Nom. inval., Art. 36.1(a) (Shenzhen).

Candidozyma ohialehuae (J. Klaps et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848179

Basionym. *Candida ohialehuae* Klaps et al., Med. Mycol. 61: myad009, 7. 2023.

Synonym. *Candida ohialehuae* J. Klaps et al., PLoS ONE 15: e0240093, 11. 2020. Nom. inval., Art. 36.1(a) (Shenzhen).

Candidozyma pseudohaemuli (Sugita, M. Takash. et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848180

Basionym. *Candida pseudohaemuli* Sugita, M. Takash. et al. (as '*pseudohaemulonii*'), Microbiol. Immunol. 50: 472. 2006.

Candidozyma ruelliae (Saluja & G.S. Prasad) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848181

Basionym. *Candida ruelliae* Saluja & G.S. Prasad, FEMS Yeast Res. 8: 664. 2008.

Candidozyma vulturna (Sipiczki et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848182

Basionym. *Candida vulturna* Sipiczki et al., Med. Mycol. 61: myad009, 7. 2023.

Synonym. *Candida vulturna* Sipiczki & Tap, Int. J. Syst. Evol. Microbiol. 66: 4014. 2016. Nom. inval., Arts 36.1(b), 40.7 (Shenzhen).

Clavispora Rodr. Mir., Antonie van Leeuwenhoek 45: 480. 1979, emend. Q.M. Wang, Yurkov, Boekhout & F.Y. Bai

Type species. *Clavispora lusitaniae* Rodr. Mir.

This genus is emended to accommodate the *Clavispora* s.str. clade including sexual and asexual members (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). Genus-specific protein families OG0006565, OG0006567 (Table 3).

Sexual reproduction is observed in some species. For sexual taxa, conjugation of haploid cells of opposite mating types usually precedes ascus formation. Bud-parent conjugation is also possible. Ascospores usually clavate, rarely ovoid to spherical. One or two (rarely three or four) ascospores per ascus (Lachance 2011a). The spore wall may have small warts, which are visible by electron microscopy. Colonies white to cream, butyrous. Budding multilateral. Pseudohyphae may be formed but hyphae are not formed. The major ubiquinone is coenzyme Q-8.

Clavispora asparagi (F.Y. Bai & H.Z. Lu) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852163

Basionym. *Candida asparagi* F.Y. Bai & H.Z. Lu, Int. J. Syst. Evol. Microbiol. 54: 1413. 2004.

Clavispora carvajalis (S.A. James et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852164

Basionym. *Candida carvajalis* S.A. James et al., FEMS Yeast Res. 9: 786. 2009.

Clavispora phyllophila Limtong & Kaewwich. ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *sp. nov.* — MycoBank MB 852212

Holotype. CBS 12671 (preserved in a metabolically inactive state), Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands.

Synonym. *Candida phyllophila* Limtong & Kaewwich., Curr. Microbiol. 59: 194. 2013. Nom. inval., Art. 40.7 (Melbourne).

For a description see Curr. Microbiol. 59: 194. 2013.

Clavispora vitiphila (Limtong & Kaewwich.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852165

Basionym. *Candida vitiphila* Limtong & Kaewwich., Curr. Microbiol. 59: 195. 2013.

Gaillardinia Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852166

Etymology. The genus is named in honor of Claude Gaillardin for his contribution to yeast genomics.

Type species. *Gaillardinia entomophila* (D.B. Scott et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. entomophila* clade, which is in a separate lineage closely related to *Danielozyma* and *Metahyphopichia* (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein families OG0010431, OG0010436 (Table 3).

Sexual reproduction not known. Colonies white, butyrous, smooth. Multilateral budding cells and blastoconidia are present. Pseudohyphae and hyphae are present. Spherical to ellipsoidal asexual endospores are formed in hyphal strands. The major ubiquinone is coenzyme Q-8.

Notes — The genus *Gaillardinia* differs from *Danielozyma* and *Metahyphopichia* by assimilation of L-rhamnose, lactose and soluble starch (Table S5). All members of *Gaillardinia* do not use soluble starch, but the species of *Danielozyma* and *Metahyphopichia* assimilate this compound.

Gaillardinia entomophila (D.B. Scott et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852167

Basionym. *Candida entomophila* D.B. Scott et al., Antonie van Leeuwenhoek 37: 456. 1971.

Gaillardinia xinjiangensis (X.F. Zhu et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852168

Basionym. *Candida xinjiangensis* X.F. Zhu et al., Arch Microbiol. 199: 379. 2017.

Danielia Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB848188

Etymology. The genus is named in honor of Heide-Marie Daniel for her contribution to yeast taxonomy.

Type species. *Danielia oregonensis* (Phaff & Carmo Souza) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the *C. oregonensis* clade, which was resolved as a separate lineage in *Metschnikowiaceae* (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein family OG0011188 (Table 3, S4).

Ascus formation may be preceded by conjugation between independent cells or between a parent cell and a bud. Asci with two ovoid ascospores with a small ring, and after maturation, ascospores are liberated from the ascus and tend to agglutinate (Yurkov et al. 2009). Colonies white to cream, butyrous. Multilateral budding cells present. Hyphae not formed. Pseudohyphae present or not.

Danielia oregonensis (Phaff & Carmo Souza) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848189

Basionym. *Candida oregonensis* Phaff & Carmo Souza, Antonie van Leeuwenhoek 28: 206. 1962.

Danielia reshetovae (Yurkov et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852214

Basionym. *Clavispora reshetovae* Yurkov et al., Persoonia 23: 183. 2009.

Helenozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852177

Etymology. The genus is named in honor of Helen R. Buckley for her contribution to yeast taxonomy.

Type species. *Helenozyma melibiosica* (H.R. Buckley & Uden) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. melibiosica* clade, which is in a separate lineage near *C. succicola* clade and *Metschnikowia* lineage (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein family OG0007152 (Table 3, S4).

Asci present with one or two ellipsoidal to elongate ascospores or absent. Colonies white, butyrous, smooth. Multilateral budding cells present. Hyphae not produced, pseudohyphae present. The major ubiquinon coenzyme Q-9.

Notes — The genus *Helenozyma* differs from its closely related genus *Australozyma* (i.e., the *C. succicola* clade) by assimilation of N-acetyl-D-glucosamine. The former assimilates it, but the latter does not (Table S5).

Helenozyma baotianmanensis F.L. Hui & T. Ke ex Q.M. Wang, Yurkov, Boekhoutt & F.Y. Bai, *sp. nov.* — MycoBank MB 852234

Holotype. CGMCC 2.4378 (preserved in a metabolically inactive state), China General Microbiological Culture Collection Center, Beijing, China.

Synonym. *Candida baotianmanensis* F.L. Hui & T. Ke, J. Gen. Appl. Microbiol. 58: 61. 2012. Nom. inval., Art. 40.7 (Melbourne).

For a description see J. Gen. Appl. Microbiol. 58: 61. 2012.

Helenozyma melibiosica (H.R. Buckley & Uden) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852178

Basionym. *Candida melibiosica* H.R. Buckley & Uden, Mycopathol. Mycol. Appl. 36: 264. 1968.

Helenozyma rhizophorensis (Fell et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852179

Basionym. *Candida rhizophorensis* Fell et al. (as '*rhizophoriensis*'), Antonie van Leeuwenhoek 99: 545. 2011.

Hermanozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB852180

Etymology. The genus is named in honor of Herman J. Phaff for his contribution to yeast taxonomy.

Type species. *Hermanozyma ubatubensis* (Ruivo et al., Pagnocca, Lachance & C.A. Rosa) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. ubatubensis* clade, which is in a separate lineage affinity with *C. melibiosica* clade, *C. succicola* clade and *Metschnikowia* lineage (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein families OG0006898 (Table 3, S4).

Sexual reproduction not known. Colonies white to cream, butyrous, smooth. Multilateral budding cells present. Hyphae and pseudohyphae present or not.

Notes — The genus *Hermanozyma* differs from its closely related genera *Australozyma* (i.e., the *C. succicola* clade) and *Helenozyma* (i.e., *C. melibiosica* clade) by assimilation of erythritol and L-rhamnose, whereas the latter two genera cannot use those carbon sources (Table S5).

Hermanozyma aechmeae (Landell & P. Valente) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852181

Basionym. *Candida aechmeae* Landell & P. Valente, Int. J. Syst. Evol. Microbiol. 60: 246. 2010.

Hermanozyma ubatubensis (Ruivo et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852182

Basionym. *Candida ubatubensis* Ruivo et al., Int. J. Syst. Evol. Microbiol. 55: 2216. 2005.

Isabelozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852183

Etymology. The genus is named in honor of Isabel Spencer-Martins for her contribution to yeast taxonomy.

Type species. *Isabelozyma heimii* (Pignal) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *H. heimii* clade, which is in a separate lineage related to the *C. sequanensis* clade (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein family OG0007683, OG0008295 and OG0007296 (Table 3, S4).

If sexual reproduction is present, asci are formed with one to four hat-shaped ascospores. Colonies white to tannish white, butyrous, smooth to somewhat convoluted. Multilateral budding cells and blastoconidia present. Hyphae not formed, pseudohyphae present.

Notes — The genus *Isabelozyma* differs from its relative *Soucietia* (i.e., the *C. sequanensis* clade) by positive assimilation of sucrose, whereas the genus *Soucietia* does not use sucrose (Table S5).

Isabelozyma gotoi (Nakase & M. Suzuki) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852184

Basionym. *Candida gotoi* Nakase & M. Suzuki, Microbiol. Culture Coll. 13: 110. 1997.
Synonym. *Hyphopichia gotoi* (Nakase & M. Suzuki) L.R. Ribeiro et al., Antonie van Leeuwenhoek 110: 992. 2017.

Isabelozyma heimii (Pignal) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852185

Basionym. *Pichia heimii* Pignal, Antonie van Leeuwenhoek 36: 525. 1970.
Synonym. *Hyphopichia heimii* (Pignal) Kurtzman, Antonie van Leeuwenhoek 88: 123. 2005.

Isabelozyma paragotoi F.L. Hui et al. ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *sp. nov.* — MycoBank MB 852235

Holotype. CICC 33048 (preserved in a metabolically inactive state), China Centre of Industrial Culture Collection, Beijing, China.

Synonym. *Hyphopichia paragotoi* F.L. Hui et al., Int. J. Syst. Evol. Microbiol. 65: 2879. 2015. Nom. inval., Art. 40.7 (Melbourne).

For a description see Int. J. Syst. Evol. Microbiol. 65: 2879. 2015.

Isabelozyma pseudorhagii (Kurtzman) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852186

Basionym. *Candida pseudorhagii* Kurtzman, Antonie van Leeuwenhoek 88: 123. 2005.
Synonym. *Hyphopichia pseudorhagii* (Kurtzman) L.R. Ribeiro et al., Antonie van Leeuwenhoek 110: 992. 2017.

Isabelozyma rhagii (Diddens & Lodder) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB852188

Basionym. *Candida tropicalis* var. *rhagii* Diddens & Lodder, Die Hefasammlung des 'Centraalbureau voor Schimmelcultures': Beitrage zu einer Monographie der Hefearten. II. Teil. Die anaskosporogenen Hefen. Zweite Halfte: 488. 1942.

Synonym. *Hyphopichia rhagii* (Diddens & Lodder) L.R. Ribeiro et al., Antonie van Leeuwenhoek 110: 992. 2017.

Osmozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852189

Etymology. The genus is named because of the osmotolerant character of the species in this lineage.

Type species. *Osmozyma mogii* (Vidal-Leir.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. tolerans* clade, which are in a separate lineage closely related to the CAH clade (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein family OG0009123 (Table 3, S4).

Sexual reproduction not known. Colonies white, butyrous, smooth. Multilateral budding cells and blastoconidia are present. Hyphae not produced, pseudohyphae are present. Growth in the presence of 50 % glucose (osmotolerance) and 15 % NaCl (halotolerance). The major ubiquinone is coenzyme Q-9.

Notes — The related genus *Candidozyma* (the CAH clade) differs from *Osmozyma* by assimilation of melezitose, which is not utilized by the latter (Table S5).

Osmozyma mogii (Vidal-Leir.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852190

Basionym. *Candida mogii* Vidal-Leir., Antonie van Leeuwenhoek 33: 342. 1967.

Osmozyma tolerans Lachance et al. ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *sp. nov.* — MycoBank MB 852236

Holotype. CBS 8613 (preserved in a metabolically inactive state), Westerdijk Fungal Biodiversity Institute, Utrecht, the Netherlands.

Synonym. *Candida tolerans* Lachance et al., Canad. J. Microbiol. 45: 173. 1999. Nom. inval., Art. 40.3 (Melbourne).

For a description see Canad. J. Microbiol. 45: 173. 1999.

Soucietia Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852191

Etymology. The genus is named in honor of Jean-Luc Souciet for his contribution to yeast genomics.

Type species. *Soucietia sequanensis* (Saëz & Rodr. Mir.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. sequanensis* clade, which is in a separate lineage closely related to the *H. heimii* clade (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein family OG0009095 (Table 3, S4).

Sexual reproduction not known. Colonies white, butyrous, smooth. Multilateral budding cells and blastoconidia are present. Hyphae and pseudohyphae are present.

Notes — The genus *Soucietia* differs from its closely related genus *Isabelozyma* (i.e., the *H. heimii* clade) by lack of assimilation of sucrose, but that can be used by the latter (Table S5).

Soucietia linzhiensis (F.Y. Bai & Z.W. Wu) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852192

Basionym. *Candida linzhiensis* F.Y. Bai & Z.W. Wu, Int. J. Syst. Evol. Microbiol. 56: 1155. 2006.

Soucietia sequanensis (Saëz & Rodr. Mir.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852193

Basionym. *Candida sequanensis* Saëz & Rodr. Mir., Antonie van Leeuwenhoek 50: 379. 1984.

Sungouiella Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 848198

Etymology. The genus is named in honor of Sung-Oui Suh for his contribution to yeast taxonomy.

Type species. *Sungouiella intermedia* (Cif. & Ashford) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. blattae* clade, which is in a separate lineage closely related to *Clavispora* s.str. clade (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales, Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein family OG0005896 (Table 3).

Sexual reproduction not known. Colonies white, cream, yellowish gray, butyrous. Multilateral budding cells present. Hyphae not formed, pseudohyphae present. The major ubiquinone coenzyme Q-9.

Notes — The genus *Sungouiella* has CoQ 9 as major ubiquinone, which differs from the presence of CoQ 8 formed by its relative *Clavispora* s.str. (Table S5).

Sungouiella akabanensis (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848199

Basionym. *Candida akabanensis* Nakase et al., Microbiol. Cult. Collect. 10: 36. 1994.

Sungouiella berkhoutiae (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852425

Basionym. *Candida berkhoutiae* Nakase et al., J. Gen. Appl. Microbiol. 57: 76. 2011.

Sungouiella blattae (N.H. Nguyen et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848201

Basionym. *Candida blattae* N.H. Nguyen et al., Mycologia 99: 853. 2008.

Sungouiella dosseyi (N.H. Nguyen et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852196

Basionym. *Candida dosseyi* N.H. Nguyen et al., Mycologia 99: 853. 2008.

Sungouiella ecuadorensis (S.A. James) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852197

Basionym. *Candida ecuadorensis* S.A. James (as '*ecuadoriensis*'), Int. J. Syst. Evol. Microbiol. 63: 396. 2013.

Sungouiella ezoensis (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852198

Basionym. *Candida ezoensis* Nakase et al., J. Gen. Appl. Microbiol. 57: 78. 2011.

Sungouiella flosculorum (C.A. Rosa et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852199

Basionym. *Candida flosculorum* C.A. Rosa et al., Int. J. Syst. Evol. Microbiol. 57: 2972. 2007.

Sungouiella intermedia (Cif. & Ashford) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848202

Basionym. *Blastodendrion intermedium* Cif. & Ashford (as '*intermedius*'), Porto Rico J. Publ. Health Trop. Med. 5: 103. 1929.
Synonym. *Candida intermedia* (Cif. & Ashford) Langeron & Guerra, Ann. Parasitol. Humaine Comp. 16: 461. 1938.

Sungouiella inulinophila (Nakase et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852200

Basionym. *Candida inulinophila* Nakase et al., J. Gen. Appl. Microbiol. 57: 79. 2011.

Sungouiella middelhoveniana (J.R.A. Ribeiro et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852201

Basionym. *Candida middelhoveniana* J.R.A. Ribeiro et al., Antonie van Leeuwenhoek 100: 343. 2011.

Sungouiella pseudoflosculorum (M. Groenew. et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852202

Basionym. *Candida pseudoflosculorum* M. Groenew. et al., Int. J. Syst. Evol. Microbiol. 61: 2020. 2011.

Sungouiella pseudointermedia (Nakase et al.) Q.M. Wang, Yurkov, Boekhout, F.Y. Bai, *comb. nov.* — MycoBank MB 848203

Basionym. *Candida pseudointermedia* Nakase et al., J. Gen. Appl. Microbiol. 22: 178. 1976.

Sungouiella sharkensis (Fell et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852203

Basionym. *Candida sharkensis* Fell et al. (as '*sharkiensis*'), Antonie van Leeuwenhoek 99: 542. 2011.

Sungouiella suratensis Limtong & Yongman. ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *sp. nov.* — MycoBank MB 852237

Holotype. CBS 10928 (preserved in a metabolically inactive state), Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands.

Synonym. *Candida suratensis* Limtong & Yongman., Antonie van Leeuwenhoek 98: 386. 2010. Nom. inval., Art. 40.7 (Melbourne).

For a description see Antonie van Leeuwenhoek 98: 386. 2010.

Sungouiella thailandica Jindam. et al. ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *sp. nov.* — MycoBank MB 848219

Holotype. NBRC 102562 (preserved in a metabolically inactive state), National Institute of Technology and Evaluation (NITE), Kisarazu, Chiba, Japan.

Synonym. *Candida thailandica* Jindam. et al., FEMS Yeast Res. 7: 1411. 2007. Nom. inval., Art. 40.7 (Shenzhen).

For a description see Jindamorak et al., FEMS Yeast Res. 7: 1411. 2007.

Sungouiella tsuchiyae (Nakase & M. Suzuki) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852204

Basionym. *Candida tsuchiyae* Nakase & M. Suzuki, J. Gen. Appl. Microbiol. 31: 508. 1985.

Sungouiella xylosa (F.L. Hui & C.Y. Chai) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 848204

Basionym. *Clavispora xylosa* F.L. Hui & C.Y. Chai, Frontiers Microbiol. 13(no. 1019599): 7. 2022.

Tanozyma Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852206

Etymology. The genus is named in honor of Chen Shuhui Tan for her contributions to The Yeasts, A taxonomic Study, and her contributions to the cryopreservation of microbes.

Type species. *Tanozyma kutaoensis* S.A. Wang & F.L. Li ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. kutaoensis* single-species lineage, which is in a separate lineage positioned near the *C. eppingiae* clade (Fig. 1a, c). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis and the presence of genus-specific protein families OG0010973, OG0011060, OG0011082, OG0011085, OG0011093 (Table 3, S4).

Sexual reproduction not known. Colonies white, butyrous, smooth. Multilateral budding cells present. Hyphae not produced, pseudohyphae are present.

Tanozyma kutaoensis S.A. Wang & F.L. Li ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *sp. nov.* — MycoBank MB 852216

Holotype. AS 2.4027 (preserved in a metabolically inactive state), China General Microbiological Culture Collection Center, Beijing, China.

Synonym. *Candida kutaoensis* S.A. Wang & F.L. Li (as '*kutaonensis*'), Appl. Microbiol. Biotechn. 96: 1522. 2012. Nom. inval., Art. 40.7 (Melbourne).

For a description see Appl. Microbiol. Biotechn. 96: 1522. 2012.

Gabaldonia Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852207

Etymology. The genus is named in honor of Toni Gabaldón for his contribution to yeast genomics and biology, especially of hybrids.

Type species. *Gabaldonia eppingiae* (M. Groenew. et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. eppingiae* clade, which is in a separate branch closely to the *C. kutaoensis* single-species lineage (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis and the presence of genus-specific protein families OG0008853, OG0014363, OG0014397 and OG0007521 (Table 3, S4).

Sexual reproduction not known. Colonies white, butyrous, smooth. Multilateral budding cells and blastoconidia present. Hyphae not present, pseudohyphae present.

Gabaldonia eppingiae (M. Groenew. et al.) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB852208

Basionym. *Candida eppingiae* M. Groenew. et al., Int. J. Syst. Evol. Microbiol. 61: 2021. 2011.

Wilhelminamyces Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *gen. nov.* — MycoBank MB 852209

Etymology. The genus is named in honor of Wilhelmina Ch. Slooff for her contribution to yeast taxonomy.

Type species. *Wilhelminamyces savonicus* (Sonck) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai.

This genus is proposed for the species in the *C. tanticharoeniae* clade, which is in a separate lineage near the *C. eppingiae* clade and the *C. kutaoensis* single-species lineage (Fig. 1a, b). Member of the *Metschnikowiaceae* (*Serinales*, *Pichiomycetes*). The genus is mainly circumscribed by the phylogenomic analysis, the genome-based metrics AAI, POCP and PAPO (Table 2), and the presence of genus-specific protein families OG0011372, OG0011374 and OG0011341 (Table 3, S4).

Sexual reproduction not known. Colonies white to brownish grey, butyrous, smooth. Multilateral budding cells and blastoconidia present. Hyphae not present, pseudohyphae present. The major ubiquinone coenzyme Q-9.

Wilhelminamyces savonicus (Sonck) Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *comb. nov.* — MycoBank MB 852210

Basionym. *Candida savonica* Sonck, Antonie van Leeuwenhoek 40: 543. 1974.

Wilhelminamyces tanticharoeniae Nakase et al. ex Q.M. Wang, Yurkov, Boekhout & F.Y. Bai, *sp. nov.* — MycoBank MB 852215

Holotype. BCC 11806 (preserved in a metabolically inactive state), BIOTEC Culture Collection, Pathumthani, Thailand.

Synonym. *Candida tanticharoeniae* Nakase et al., J. Gen. Appl. Microbiol. 56: 90. 2010. Nom. inval., Art. 40.7 (Melbourne).

For a description see J. Gen. Appl. Microbiol. 56: 90. 2010.

Contributions

Q.-M.W. conceived and designed the project. W.-N.Z. and Z.-X.F. and F.-L.H. performed yeast isolation and phenotypic comparison. F.L., Z.-D.H. and X.-M.Z. performed genomic metrics analysis. K.B. worked on nomenclatural matters. Q.-M.W., A.Y., T.B., S.A. and F.-Y.B. wrote the paper. Q.-M.W., A.Y. and T.B. revised the paper.

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Declaration on conflict of interest The authors declare that there is no conflict of interest.

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Supplementary material

Fig. S1–S3, Table S1–S5 and all OGs used in the description of genera genus as diagnostic characters are deposited in the Figshare repository: https://doi.org/10.6084/m9.figshare.25132418. The genome sequences of 14 strain have been deposited in National Microbiology Data Center (NMDC) with project number NMDC10018537, NMDC10018368 and NMDC10018700 (https://nmdc.cn/resource/en/genomics/project/detail/NMDC10018537, https://nmdc.cn/resource/en/genomics/project/detail/NMDC10018368, https://nmdc.cn/resource/en/genomics/project/detail/NMDC10018700).

Table S1 List of yeast species and Genbank numbers used in the ITS and D1/D2 analyses.

Table S2 The matrix of AAI and POCP values in the *Metschnikowiaceae*. The upper right corner represents the AAI values and the lower left corner represents the POCP values.

Table S3 The PAPO analysis of the clades in the *Metschnikowiaceae*.

Table S4 The annotation results of clade-specific OGs of the 17 clades/genera or single species lineages in the *Metschnikowiaceae*.

Table S5 The phenotypic characteristics of different genera and clades in *Metschnikowiaceae*.

Fig. S1 Phylogenetic tree inferred using the ITS and D1/D2 domain of 26S rDNA gene showed the positions of the genera and clades in the *Metschnikowiaceae*. Bootstrap percentages of maximum likelihood analysis over 50 % from 1000 bootstrap replicates are shown on the major branches. Bar = 0.05 substitutions per nucleotide position.

Fig. S2 Phylogenetic tree inferred using the D1/D2 domain of 26S rDNA gene showed the positions of the genera and clades in the *Metschnikowiaceae*. Bootstrap percentages of maximum likelihood analysis over 50 % from 1000 bootstrap replicates are shown on the major branches. Bar = 0.05 substitutions per nucleotide position.

Fig. S3 Phylogenetic tree inferred using the ITS gene showed the positions of the genera and clades in the *Metschnikowiaceae*. Bootstrap percentages of maximum likelihood analysis over 50 % from 1000 bootstrap replicates are shown on the major branches. Bar = 0.05 substitutions per nucleotide position.