

On the reclassification of species assigned to *Candida* and other anamorphic ascomycetous yeast genera based on phylogenetic circumscription

Heide-Marie Daniel · Marc-André Lachance ·
Cletus P. Kurtzman

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Abstract Multigene phylogenies have been instrumental in revising the classification of ascosporic (teleomorph) yeasts in a natural system based on lines of descent. Although many taxonomic changes have already been implemented for teleomorph taxa, this is not yet the case for the large genus *Candida* and smaller anascosporic (anamorph) genera. In view of the recently introduced requirement that a fungal species or higher taxon be assigned only a single valid name under the new International Code of Nomenclature for algae, fungi, and plants (Melbourne Code), the current species of *Candida* and other anamorph yeast genera must undergo revision to make genus membership consistent with phylogenetic affinities. A review of existing data and analyses shows that certain *Candida* species may be assigned to teleomorph

genera with high confidence using multigene phylogenies. *Candida* species that form well-circumscribed phylogenetic clades without any teleomorph member justify the creation of new genera. However, a considerable number of *Candida* species sit at the end of isolated and often long branches, and hence cannot be assigned to larger species groups. They should be maintained in *Candida* sensu lato until studied by multigene analyses in datasets with comprehensive taxon sampling. The principle of name stability has to be honoured to the largest extent compatible with a natural classification of *Candida* species.

Keywords *Candida* · Reclassification · Ascomycetous yeasts · Dual nomenclature · Melbourne Code

H.-M. Daniel (✉)
Mycothèque de l'Université catholique de Louvain
(BCCM/MUCL), Earth and Life Institute, Mycology
Laboratory, Université catholique de Louvain, Croix du
Sud 2 bte L7.05.06, 1348 Louvain-la-Neuve, Belgium
e-mail: heide-marie.daniel@uclouvain.be

M.-A. Lachance
Department of Biology, University of Western Ontario,
London, ON N6A 5B7, Canada

C. P. Kurtzman
Bacterial Foodborne Pathogens and Mycology Research
Unit, National Center for Agricultural Utilization
Research, Agricultural Research Service, U.S.
Department of Agriculture, Peoria, IL 61604, USA

Introduction

Ascomycetous yeasts without known sexual states have been classified according to mode of cell division and occurrence of unique cellular morphologies. Three types of cell division have been observed; bipolar, with budding only at the poles of the cell (e.g., *Kloeckera*, *Schizoblastosporion*); multipolar or multilateral, in which budding occurs at many sites on the cell wall (e.g., *Botryozyma*, *Candida*, *Myxozyma*, *Saitoella*, *Trigonopsis*); and fission, in which the new cell wall develops without constriction of the

parent cell wall as in bud formation (e.g., *Schizosaccharomyces*). Distinctive cell morphologies occur in several genera, such as *Brettanomyces* (ogival-shaped cells) and one species of *Trigonopsis* (triangular cells). Presence or absence of pseudohyphae or true hyphae has also been used to define genera. Asexual yeasts that divide by multilateral budding but have no distinctive cellular morphology have been assigned to the genus *Candida*. This system of classification allowed morphologically indistinguishable species to be grouped in a single genus, in parallel to the more intricate system used for sexually reproducing species, which were assigned to genera based primarily on ascus and ascospore morphology.

DNA-based studies showed that phenotypic characteristics alone are inadequate in building a stable, informative, and emendable classification system, likely due to evolutionary parallelisms and reversals (Kurtzman and Robnett 1994; Guzmán et al. 2013). Multi-gene sequence analysis, such as for the Saccharomycetaceae (Kurtzman and Robnett 2003), has shown that circumscription of yeast genera from phenotypic characters is often not congruent with their delineation based on molecular phylogenies. In contrast, the classification of asexually reproducing yeasts was rarely addressed in molecular phylogenetic studies because their inclusion in *Candida* and other anamorphic genera satisfied the requirements of longstanding rules under the International Code of Botanical Nomenclature. However, a recent change in the rules for naming pleomorphic fungi now requires that a fungal species or higher taxon be assigned only a single valid name under the new Code [*International Code of Nomenclature for algae, fungi, and plants* (Melbourne Code) (McNeill et al. 2012)]. As a consequence, the current species of *Candida* and other asexual yeast genera must undergo revision to make genus membership consistent with phylogenetic affinities. In the case of species that currently possess both anamorph and teleomorph names, a decision will be required regarding which name to retain. In the previous system, the teleomorph name had priority, but the new Code places both names on an equal footing and reaffirms instead the principles of historical priority and common usage.

In the discussion that follows, we examine anamorphic ascomycetous yeast genera (Tables 1, 2) and consider the impact of phylogenetic circumscription and changes in the Code on their standing. The genus

Table 1 Anamorph-teleomorph connections among ascomycetous yeasts

Anamorphic genus	Teleomorphic genus
Saccharomycotina	
<i>Aciculoconidium</i>	Unknown. Near <i>Kodamaea</i> .
<i>Blastobotrys</i>	<i>Trichomonascus</i>
<i>Botryozyma</i>	<i>Ascobotryozyma</i>
<i>Brettanomyces</i>	<i>Dekkera</i>
<i>Candida</i>	Many genera
<i>Geotrichum</i>	<i>Dipodascus</i> and <i>Galactomyces</i>
<i>Kloeckera</i>	<i>Hanseniaspora</i>
<i>Macrorhabdus</i>	Unknown.
<i>Myxozyma</i>	<i>Lipomyces</i>
<i>Saprochaete</i>	<i>Magnusiomyces</i>
<i>Schizoblastosporion</i>	<i>Nadsonia</i>
<i>Trigonopsis</i>	Unknown. Near <i>Botryozyma</i> and <i>Tortispora</i> .
Taphrinomycotina	
<i>Lalaria</i>	<i>Taphrina</i>
<i>Saitoella</i>	Unknown. Near <i>Taphrina</i> and <i>Protomyces</i> .

Candida is of major concern because it has experienced a disproportionate increase in size relative to other genera. The most recent treatment of the genus recognized 314 species of multiple phylogenetic affiliations and listed 51 additional species names without discussion (Lachance et al. 2011). Since then, the number of new species assigned to *Candida* has continued to increase. After consultation of the ascomycetous yeast sequence database YeastIP (<http://genome.jouy.inra.fr/yeastip/>) (Weiss et al. 2013), Mycobank (<http://www.mycobank.org/>) (Crous et al. 2004) on February 11 2014, and the SCOPUS literature database, we here account for 434 *Candida* species and discuss their classification. Importantly, the genus *Candida* and its many species have served as major vehicles for crucial information regarding treatment options for opportunistic pathogenic species, artisanal and industrial processes, food regulations, enzyme production, osmophily, thermotolerance, substrate specificities, and possible ecological roles. The genus has been kept intact in line with Berkhout's (1923) original intent to accommodate a variety of largely undifferentiated yeasts, while avoiding the creation of numerous phylogenetically circumscribed new genera that are impossible to recognize by phenotype (Kurtzman 2011). The new Code no longer allows

Table 2 Placement of selected anamorphic species in genera and undescribed clades of the Saccharomycotina

Family/genus or clade	Species	Genetic markers
Debaryomycetaceae		
<i>Lodderomyces/Candida albicans</i>	<i>C. albicans</i> , <i>C. blackwelliae</i> ^{a,c} , <i>C. bohioensis</i> ^c , <i>C. buenavistaensis</i> , <i>C. chauliodes</i> , <i>C. corydali</i> , <i>C. dubliniensis</i> , <i>C. frijolesensis</i> , <i>C. gigantensis</i> , <i>C. hyderabadensis</i> ^a , <i>C. jiufengensis</i> ^a , <i>C. labiduridarum</i> , <i>C. maltosa</i> , <i>C. metapsilosis</i> ^a , <i>C. morakotiae</i> ^a , <i>C. neerlandica</i> , <i>C. orthopsilosis</i> , <i>C. oxycetoniae</i> ^a , <i>C. parapsilosis</i> , <i>C. prachuapensis</i> ^a , <i>C. pseudojiufengensis</i> ^a , <i>C. sakaeensis</i> ^a , <i>C. sanyaensis</i> ^a , <i>C. saraburiensis</i> ^a , <i>C. sojae</i> , <i>C. tetrigidarum</i> , <i>C. theae</i> ^a , <i>C. tropicalis</i> , <i>C. verbasci</i> , <i>C. viswanathii</i>	SSU, D1/D2 LSU
<i>Candida glabrosa</i> clade	<i>C. fluviatilis</i> , <i>C. glabrosa</i> , <i>C. manassasensis</i> , <i>C. palmioleophila</i> , <i>C. pseudoglabrosa</i> , <i>C. saitoana</i> , <i>C. sphagnicola</i>	SSU, D1/D2 LSU
<i>Candida kruisii</i> clade	<i>C. aglyptini</i> ^c , <i>C. atbi</i> , <i>C. barrocoloradensis</i> , <i>C. cretensis</i> , <i>C. gatunensis</i> , <i>C. kruisii</i> , <i>C. lycoperdinae</i> , <i>C. pallodes</i> , <i>C. panamensis</i> , <i>C. stri</i> , <i>C. tritoma</i>	SSU, D1/D2 LSU
<i>Candida tanzawaensis</i> clade	<i>C. ambrosiae</i> , <i>C. anneliseae</i> , <i>C. atakaporum</i> , <i>C. bokatorum</i> , <i>C. bolitotheri</i> , <i>C. bibrorum</i> , <i>C. canberraensis</i> , <i>C. chickasaworum</i> , <i>C. choctaworum</i> , <i>C. emberorum</i> , <i>C. guaymorum</i> , <i>C. kunorum</i> , <i>C. maxii</i> , <i>C. panamericana</i> , <i>C. prunicola</i> , <i>C. pyralidae</i> , <i>C. taliae</i> , <i>C. tanzawaensis</i> , <i>C. terraborum</i> , <i>C. vadensis</i> ^a , <i>C. wounanorum</i> , <i>C. xylopsoci</i> , <i>C. yuchorum</i>	SSU, D1/D2 LSU
<i>Hyphopichia</i>	<i>C. fennica</i> , <i>C. gotoi</i> , <i>C. homilentoma</i> , <i>C. khmerensis</i> ^a , <i>C. pseudorhagii</i> ^a , <i>C. rhagii</i> , <i>C. wangnamkhiaoensis</i> ^a	D1/D2 LSU
<i>Kurtzmaniella</i>	<i>C. anglica</i> ^a , <i>C. boleticola</i> , <i>C. fragi</i> , <i>C. oleophila</i> , <i>C. railenensis</i> ^a , <i>C. santamariae</i> , <i>C. schatavii</i> , <i>C. zeylanoides</i>	SSU, D1/D2 LSU
<i>Yamadazyma</i>	<i>C. aaseri</i> , <i>C. amphicis</i> ^{a,c} , <i>C. andamanensis</i> ^a , <i>C. atlantica</i> , <i>C. atmosphaerica</i> , <i>C. blattariae</i> ^a , <i>C. buinensis</i> , <i>C. cerambycidarum</i> ^a , <i>C. conglobata</i> , <i>C. dendronema</i> , <i>C. diddensiae</i> , <i>C. diospyri</i> ^a , <i>C. endomychidarum</i> ^a , <i>C. friederichii</i> , <i>C. germanica</i> ^a , <i>C. gorgasii</i> ^a , <i>C. insectorum</i> , <i>C. jaroonii</i> ^a , <i>C. kanchanaburiensis</i> ^a , <i>C. khao-thaluensis</i> ^a , <i>C. keroseneae</i> ^a , <i>C. koratica</i> ^a , <i>C. lessepsii</i> ^a , <i>C. membranifaciens</i> , <i>C. michaelii</i> ^a , <i>C. naeodendra</i> ^a , <i>C. oceani</i> ^a , <i>C. olivae</i> ^a , <i>C. pseudoaaseri</i> ^a , <i>C. songkhlaensis</i> ^a , <i>C. spencermartinsiae</i> ^a , <i>C. takamatsuzukensis</i> ^a , <i>C. tallmaniae</i> ^a , <i>C. taylorii</i> ^{a,c} , <i>C. tammaniensis</i> ^a , <i>C. tenuis</i> , <i>C. trypodendroni</i> ^a , <i>C. tumulicola</i> ^a , <i>C. vaughaniae</i> ^a , <i>C. vriesiae</i> ^a	SSU, D1/D2 LSU
Metschnikowiaceae		
<i>Clavispora</i>	<i>C. aechmeae</i> , <i>C. akabanensis</i> , <i>C. asparagi</i> , <i>C. auris</i> ^a , <i>C. berkhoutiae</i> ^a , <i>C. blattae</i> , <i>C. bromeliacearum</i> , <i>C. carvajalis</i> ^a , <i>C. chanthaburiensis</i> ^a , <i>C. citri</i> ^a , <i>C. dosseyi</i> , <i>C. duobushaemulonii</i> ^a , <i>C. ecuadorensis</i> ^a , <i>C. eppingiae</i> ^a , <i>C. ezoensis</i> ^a , <i>C. flosculorum</i> , <i>C. fructus</i> , <i>C. haemulonii</i> , <i>C. heveicola</i> ^a , <i>C. intermedia</i> , <i>C. inulinophila</i> ^a , <i>C. konsanensis</i> ^a , <i>C. kutaonensis</i> ^a , <i>C. middelhoveniana</i> ^a , <i>C. mogii</i> , <i>C. musae</i> , <i>C. oregonensis</i> , <i>C. phyllophila</i> ^a , <i>C. pseudoflosculorum</i> ^a , <i>C. pseudohaemulonii</i> ^a , <i>C. pseudointermedia</i> , <i>C. rhizophorensis</i> ^{a,c} , <i>C. ruelliae</i> ^a , <i>C. sharkensis</i> ^{a,c} , <i>C. suratensis</i> ^a , <i>C. thailandica</i> , <i>C. tolerans</i> , <i>C. tsuchiya</i> , <i>C. ubatubensis</i> , <i>C. vitiphila</i> ^a	ACT1, EF1, Mcm7, RPB2

Table 2 continued

Family/genus or clade	Species	Genetic markers
<i>Kodamaea</i>	<i>C. alishanica</i> ^a , <i>C. arcana</i> , <i>C. derodonti</i> , <i>C. fukazawae</i> , <i>C. fungicola</i> , <i>C. hsintzibuensis</i> ^a , <i>C. kaohsiungensis</i> ^a , <i>C. leandrea</i> ^a , <i>C. lidongshanica</i> ^a , <i>C. loeiensis</i> ^a , <i>C. mesenterica</i> , <i>C. plutei</i> , <i>C. restingae</i> ^a , <i>C. sagramina</i> , <i>C. smagusa</i> ^a , <i>C. suecica</i> , <i>Endomyces scopularum</i> ^d	SSU, D1/D2 LSU
Pichiaceae, methanol-assimilating yeasts and near relatives		
<i>Ogataea</i>	<i>C. arabinofermentans</i> , <i>C. boidinii</i> , <i>C. chumphonensis</i> ^a , <i>C. krabiensis</i> ^a , <i>C. maris</i> , <i>C. matranensis</i> ^a , <i>C. methanosorbosa</i> , <i>C. nanaspora</i> , <i>C. nemodendra</i> , <i>C. nitratophila</i> , <i>C. ortonii</i> ^a , <i>C. ovalis</i> , <i>C. piceae</i> , <i>C. pini</i> , <i>C. rishiriensis</i> ^{a, c} , <i>C. sithepensis</i> ^a , <i>C. sonorensis</i> , <i>C. succiphila</i> , <i>C. suzukii</i> , <i>C. xyloterini</i> ^b	LSU, SSU, <i>EF1α</i> , mtSSU
Phaffomycetaceae		
<i>Cyberlindnera</i>	<i>C. adriatica</i> , <i>C. easanensis</i> ^a , <i>C. hungchunana</i> ^a , <i>C. maesa</i> ^a , <i>C. maritima</i> , <i>C. mengyuniae</i> ^a , <i>C. mycetangii</i> , <i>C. nakhonratchasimensis</i> ^a , <i>C. pattaniensis</i> ^a , <i>C. stauntonica</i> ^a , <i>C. takata</i> ^a , <i>C. taoyuanica</i> ^a , <i>C. variovaarae</i>	LSU, SSU, <i>EF1α</i>
<i>Wickerhamomyces</i>	<i>C. dajiaensis</i> ^a , <i>C. jianshihensis</i> ^a , <i>C. namnaoensis</i> , <i>C. odintsovae</i> , <i>C. peoriensis</i> , <i>C. ponderosae</i> , <i>C. quercuum</i> , <i>C. silvicultrix</i> , <i>C. ulmi</i> , <i>C. yuanshanica</i> ^{a, c}	LSU, SSU, <i>EF1α</i>
Trichomonascaceae and <i>Starmerella</i>		
<i>Starmerella</i>	<i>C. apicola</i> , <i>C. apis</i> , <i>C. batistae</i> , <i>C. bombi</i> , <i>C. cellae</i> , <i>C. davenportii</i> , <i>C. etchellsii</i> , <i>C. floricola</i> , <i>C. floris</i> , <i>C. geochares</i> , <i>C. gropengiesseri</i> , <i>C. khaoyaiensis</i> , <i>C. kuoi</i> , <i>C. lactis-condensi</i> , <i>C. magnoliae</i> , <i>C. potachaoreniae</i> , <i>C. powellii</i> , <i>C. ratchasimensis</i> , <i>C. riodocensis</i> , <i>C. sirachaensis</i> , <i>C. sorbosivorans</i> , <i>C. stellata</i> , <i>C. stigmati</i> , <i>C. tilneyi</i> , <i>C. vaccinii</i>	D1/D2 LSU
<i>Trichomonascus</i>	<i>C. allociferii</i> ^a , <i>C. mucifera</i> ^a , <i>Blastobotrys adenivorans</i> , <i>B. attinorum</i> ^a , <i>B. americana</i> , <i>B. arbuscula</i> , <i>B. aristata</i> , <i>B. capitulata</i> , <i>B. chiropterorum</i> , <i>B. elegans</i> , <i>B. illinoiensis</i> , <i>B. indianensis</i> , <i>B. malaysiensis</i> , <i>B. mokoena</i> , <i>B. muscicola</i> , <i>B. nivea</i> , <i>B. parvus</i> , <i>B. peoriensis</i> , <i>B. proliferans</i> , <i>B. raffinosisfermentans</i> , <i>B. robertii</i> ^a , <i>B. serpentis</i> ^a , <i>B. terrestris</i>	LSU, mtSSU, COX2
<i>Wickerhamiella</i>	<i>C. alocasiicola</i> ^a , <i>C. azyma</i> , <i>C. azymoides</i> ^a , <i>C. bombiphila</i> ^a , <i>C. drosophilae</i> , <i>C. galacta</i> , <i>C. hasegawae</i> ^a , <i>C. infanticola</i> , <i>C. jalapaonensis</i> ^a , <i>C. kazuoi</i> ^a , <i>C. musiphila</i> ^a , <i>C. pararugosa</i> , <i>C. parazyza</i> ^a , <i>C. sergipensis</i> ^a , <i>C. sorbophila</i> , <i>C. spandovensis</i> , <i>C. vanderwaltii</i>	LSU, mtSSU, COX2

Additional groupings are discussed in the text. Genetic markers used to circumscribe the genera or clades are mentioned

^a Placement by D1/D2 LSU sequence analyses

^b Placement by SSU and D1/D2 LSU sequence analyses

^c Spelling corrected according to www.indexfungorum.org

^d Among the only three available cultures of *E. scopularum*, one was attributed to *Pezizomycotina* (Euascomycetes) (CBS 131.86) while two (CBS 154.92, CBS 155.92) clustered with *Candida* species that belong to the *Kodamaea* clade in analyses of SSU and D1/D2 LSU sequences (Suh et al. 2001), and represent a *Kodamaea* species

maintenance of the status quo and implementation of the new rules is underway, as exemplified in the reclassification of anamorphic species in teleomorph-typified genera such as *Alloascoidea* (Kurtzman and Robnett 2013b), *Ambrosiozyma* (Kurtzman and Robnett, 2013c), *Diddensiella* (Péter et al. 2012), *Scheffersomyces* (Urbina

and Blackwell 2012a, b), *Starmerella* (Duarte et al. 2012), and *Yarrowia* (Groenewald and Smith 2013; Nagy et al. 2013), and the reclassification of ascosporic *Asco-botryozyma* species into the anamorphic genus *Botryozyma* (Lachance and Kurtzman 2013). When newly discovered asexual species are described as members of

teleomorphic genera or former anamorphs are reassigned to them, authors increasingly add the mention of f.a., *forma asexualis*, to draw attention to the fact that the sexual state is unknown, as suggested by Lachance (2012).

In this review, we discuss the placement of anamorphic species in currently recognized genera and consider assignment of divergent species to new phylogenetically circumscribed genera. As part of this analysis, we shall also examine assignment of genera to families. Although family-level classification in ascomycetous yeasts is not completely resolved, a phylogenetic analysis using small (SSU) and large subunit (LSU) rRNA, translation elongation factor (*EF1 α*), RNA polymerase II, subunits B1 and B2 (*RPB1*, *RPB2*) gene sequences (referred to as ‘five-gene analysis’) that included representatives of almost all known genera lends support to the backbone of a phylogenetic tree (Fig. 1, Kurtzman and Robnett 2013a) that reflects the family classification proposed by Kurtzman (2011).

Debaryomycetaceae

Ascosporic genera that are presently assigned to the Debaryomycetaceae include *Debaryomyces*, *Kurtzmaniella*, *Lodderomyces*, *Meyerozyma*, *Millerozyma*, *Priceomyces*, *Scheffersomyces*, *Schwanniomyces*, *Spathaspora*, *Wickerhamia*, and *Yamadazyma* (Kurtzman 2011). *Hyphopichia* was placed among these genera by the five-gene analysis (Fig. 1, Clade 6) in contrast to its earlier classification in the Metschnikowiaceae. Yeasts in this family are characterized by ubiquinone Q-9, but at present, most species relationships in this family have only been analyzed using D1/D2 LSU and SSU sequence data (Kurtzman and Suzuki 2010) and branch support is oftentimes weak.

Candida, the most prominent genus in the Debaryomycetaceae, is typified by *C. vulgaris*, a synonym of *C. tropicalis*, and will be restricted to the monophyletic group that includes *C. tropicalis*, *C. albicans*, the ascosporic species *Lodderomyces elongisporus*, and 28 additional species (Ji et al. 2009; Lachance et al. 2011; Nitiyon et al. 2011; Chang et al. 2012a; Limtong et al. 2012b; Hui et al. 2013; Sipiczki 2013) (Table 2). Consistent with the Code, the genus name for species in this clade should be *Candida* as it is widely used, in contrast to *Lodderomyces*, which is encountered only

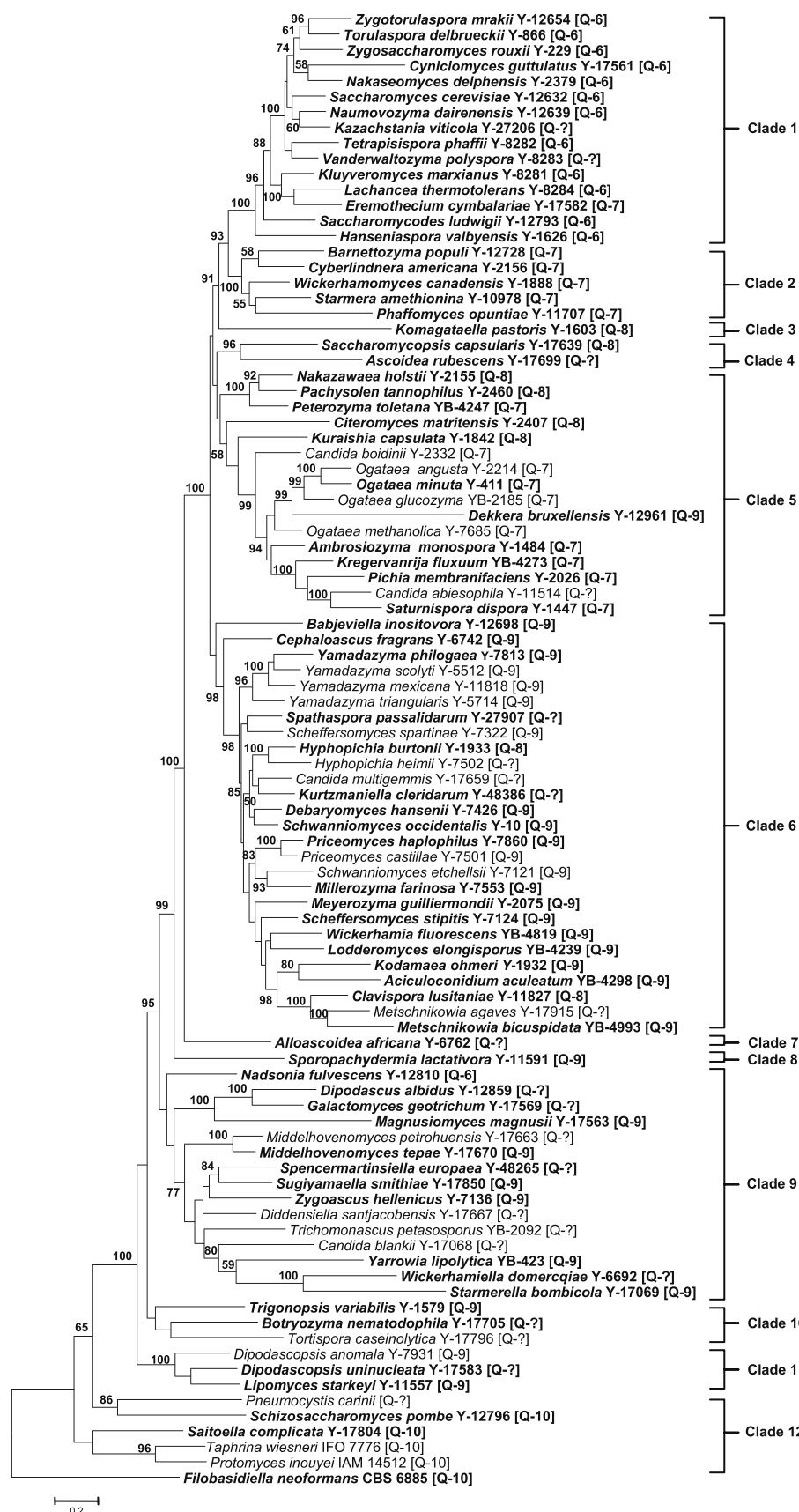
infrequently. Numerous new species have been added to this clade and the expansion suggests that *C. tropicalis* and *C. albicans* might occupy distinct sister clades. This prospect argues strongly for the retypification of *Candida* on the widely recognized species *C. albicans*.

Many *Candida* species can be assigned to presently described genera, but the genus also contains species with no known phylogenetic affinities in existing genera. Among these are the *C. glaebosa* clade, which includes seven described species (Table 2) and appears to be a neighbor of the *C. tropicalis*, *Spathaspora*, and *Scheffersomyces* clades (Kurtzman and Suzuki 2010; Kachalkin and Yurkov 2012; Suh et al. 2013). Members of the *C. glaebosa* clade appear similar in their responses on common growth tests and sugar fermentation is often slow, weak or absent. *Candida ascalaphidarum* was most similar to *C. palmioleophila*, a member of this clade based on D1/D2 LSU sequences, although of uncertain affiliation when adding SSU sequences to the analysis (Nguyen et al. 2007).

The *C. kruisii* clade includes 11 species (Suh et al. 2006; Lachance et al. 2011) (Table 2), all of which are associated with mushrooms and the beetles feeding on them. The species belong to three subclades, two of which differ in growth reaction to cycloheximide, but the subclades appear to represent a single genus. The large *C. tanzawaensis* clade, which presently includes 23 species (Kurtzman 2001; Suh et al. 2004; Lachance et al. 2011) (Table 2), is also associated with beetles and wood-decaying mushrooms. The species assimilate xylose, which suggests an ecological role in the decomposition of wood-derived carbohydrates. Basal to the *C. tanzawanaensis* clade are *C. caryicola* and *C. tibetensis* with the even more distant neighbors *C. linzhiensis* and *C. sequanensis* (Lachance et al. 2011). The assignment of these four species to two or more separate genera should await additional gene sequences to confirm their phylogenetic position. *Candida sake* and *C. alai* also represent monotypic lineages that may represent separate genera (Lachance et al. 2011), but their placement also must await additional gene sequence analyses.

Placement of the ascosporic genus *Hyphopichia* is weakly supported in the Debaryomycetaceae from the five-gene analysis (Fig. 1, Clade 6). The *Hyphopichia* clade includes seven *Candida* species (Limtong et al. 2012a) (Table 2), most of which are on long branches

Fig. 1 Phylogenetic relationships among type species of ascomycetous yeast genera and reference taxa determined from maximum likelihood analysis using concatenated gene sequences for SSU rRNA, LSU rRNA, *EF-1 α* , *RPB1* and *RPB2* (from Kurtzman and Robnett 2013a). *Filobasidiella neoformans* was the designated outgroup species in the analysis. Names in bold font are type species of currently recognized genera, whereas names in standard font are not type species. Bootstrap values (1,000 replicates) >50 % are given at branch nodes. Strain accession numbers are NRRL unless otherwise indicated. Designations in brackets indicate the coenzyme Q value for each species. *Alloascoidea*, *Diddensiella* and *Tortispora* are newly described ascosporic genera (Kurtzman and Robnett 2013b; Lachance and Kurtzman 2013; Péter et al. 2012) and *Middelhovenomyces* is a newly described anamorphic genus (Kurtzman and Robnett 2014). The new anamorphic genera *Danielozyma* (near *Kodamaea*) and *Deakozyma* (near *Yarrowia*) (Kurtzman and Robnett 2014) are not included in this analysis



when analyzed from D1/D2 LSU sequences. The *Kurtzmaniella* clade includes eight species of *Candida* (Kurtzman 2011; Lachance et al. 2011) (Table 2). Other species that may be members or neighbors of this clade include *C. aurita*, *C. natalensis*, *C. quercitrusa*, *C. multigemmis* and *C. sophiae-reginae*. *Candida pseudofarinosa* is to be assigned to *Millerozyma* based on *ACT1*, *RPB1* and *RPB2* sequences (Mallet et al. 2012) and *C. psychrophila* to *Debaryomyces* based on high D1/D2 LSU similarity (Kurtzman 2011).

Candida athensensis, *C. carpophila*, *C. neustonensis*, and *C. smithsonii* are assigned to the *Meyerozyma* clade based on D1/D2 LSU sequences, although with high bootstrap support (Chang et al. 2010; Lachance et al. 2011). The rarely isolated *C. elateridarum* and the osmophilic *C. glucosophila* join the clade on long, unsupported branches. *Candida fermenticarenis* and *C. northwykensis* appear to be members of *Priceomyces* based on D1/D2 LSU, supported by SSU sequence analysis for the former species (Kurtzman and Suzuki 2010; Ravella et al. 2011).

The genus *Scheffersomyces* has been revised and *Candida* species were included based on a multilocus phylogenetic analysis (Urbina and Blackwell 2012a, b). An analysis with extended taxon sampling indicated polyphyly of the genus, also reflected by either xylose or cellobiose fermenting ability, calling for a limitation of *Scheffersomyces* to the clade comprising the type species *Sch. stipitis* as well as *Sch. cryptocercus*, *Sch. illinoensis*, *Sch. insectosa*, *Sch. lignosus*, *Sch. parashehatae*, *Sch. quercinus*, *Sch. segobiensis*, *Sch. shehatae*, *Sch. virginianus*, and *Sch. xylosifermentans* (Suh et al. 2013). The species *C. broadrunensis*, *C. thasaenensis*, *Sch. amazonensis*, *Sch. coipomoensis*, *Sch. ergatensis*, *Sch. gosinicus*, *Sch. lignicola*, *Sch. queiroziae*, and *Sch. spartinae* need to be reclassified.

The genus *Spathaspora* is composed of a core group that is well supported by phylogenetic analyses of D1/D2 LSU sequences and includes *C. jeffriesii*, *C. materiae*, *Sp. arborariae*, *Sp. brasiliensis*, *Sp. passalidarum*, and *Sp. suhii* (Cadete et al. 2013). *Spathaspora xylofermentans* and *Sp. roraimanensis* share the unique ascospore morphology of this group, but form variable associations with species such as *C. sake* or *C. alai* and *C. insectamans*, all likely to represent independent genera because of long branch lengths. Other weakly associated species include *C. lyxosophila*, *C. xylanilytica*, and *C. subhashii*

(Boonmak et al. 2011). The redefinition of *Spathaspora* requires the use of gene sequences providing higher resolution than D1/D2 LSU.

The genus *Yamadazyma* presently has 11 assigned species. However, sequence analysis has identified 40 phylogenetically related *Candida* species (Burgaud et al. 2011; Groenewald et al. 2011a; Junyapate et al. 2014; Lachance et al. 2011; Nagatsuka et al. 2009) (Table 2), which will expand *Yamadazyma* into one of the larger genera of the Debaryomycetaceae.

Metschnikowiaceae

Most genera in the Metschnikowiaceae clade (*Aciculoconidium*, *Clavispora*, *Kodamaea*, *Metschnikowia*) resemble those of Debaryomycetaceae in ubiquinone Q-9 formation and both families were placed in the same large Clade 6 by the five-gene analysis (Fig. 1). The Metschnikowiaceae form a well-supported cluster with exclusion of *Hyphopichia*. *Clavispora* is an exception in possessing ubiquinone Q-8. The genera *Metschnikowia* and *Clavispora* are distinguished by their ubiquinones and ascospore morphology, although these traits are not known for all members. The evolutionary rates of D1/D2 LSU sequences are highly diverse in the *Metschnikowia/Clavispora* clade and phylogenetic analyses using housekeeping genes are required to circumscribe both genera reliably. An analysis using four coding genes confirmed some, but not all groups derived by D1/D2 LSU analysis, although some species placements still remain to be resolved (Guzmán et al. 2013). The analysis delineated four groups, two of which comprised *Metschnikowia* species and included *C. chrysomelidarum*, *C. gelsemii*, *C. golubevii*, *C. hawaiiiana*, *C. ipomoeae*, *C. kipukae*, *C. kofuensis*, *C. picachoensis*, *C. pimensis*, *C. rancensis*, and *C. torresii* with reasonable to high statistical support. *Candida wancherniae* could be assigned to one of these groups based on D1/D2 LSU similarity to *M. agaves* (Nakase et al. 2009b). *Candida danieliae* and *C. hainanensis* were only loosely connected to members of these groups by long branches and their placement needs to be ascertained by multigene analysis (Wang et al. 2008; Groenewald et al. 2011b). A distinct group was formed by *C. picinguabensis* and *C. saopaulonensis* with *C. melibiosica* joined on a long branch, to which *C. bambusicola*, *C. nongkhaisensis*, *C. robnettiae*,

C. succicola, *C. tocantinsensis*, *C. touchengensis*, and *C. baotianensis* may potentially be added based on D1/D2 sequence similarity (Nakase et al. 2011a; Groenewald et al. 2011b; Barbosa et al. 2012; Hui et al. 2012). Phylogenetic analyses identified 40 species of *Candida* as likely members of the *Clavispora* clade (Wang et al. 2008; James et al. 2009; Satoh et al. 2009; Fell et al. 2011; Groenewald et al. 2011b; Nakase et al. 2011b; Ribeiro et al. 2011; Yuan et al. 2012; Cendejas-Bueno et al. 2012; Sarawan et al. 2013; James et al. 2013; Limtong and Kaewwichian 2013) (Table 2).

The *Kodamaea* clade is well recognizable from combined D1/D2 LSU and SSU analyses and 16 species of *Candida* are members of this clade (Suh and Blackwell 2005; Hsieh et al. 2010; Lachance and Kurtzman 2011; Nakase et al. 2011c) (Table 2). *Candida catenulata*, *C. mesorugosa*, *C. neorugosa*, *C. pseudorugosa*, *C. ranongensis*, *C. rugosa*, *C. savonica*, *C. scorzettiae*, and *C. tanticharoeniae* were shown on common branches in different combinations based on D1/D2 LSU and these nine species may be either members or sisters of *Kodamaea* (Li et al. 2006; Nakase et al. 2010a; Am-In et al. 2011; Paredes et al. 2012; Chaves et al. 2013). A similar placement was shown for *C. catenulata* and *C. rugosa* by multigene phylogenetic analyses (Tsui et al. 2008) and needs confirmation by multigene analyses with an extended taxon sampling.

The anamorphic genus *Aciculoconidium* is characterized by multilateral budding and branched septate hyphae that form needle-shaped blastoconidia (Smith 2011a). The single known species, *A. aculeatum*, has been isolated from fruit flies but not from other substrates. An ascospore state for *Aciculoconidium* is unknown, but phylogenetic analysis places it as a neighbor to the genus *Kodamaea* (Fig. 1, Clade 6).

*Candida litseae*¹ and *C. ontarioensis* represent an isolated lineage that initially appeared somewhat closely related to *Sporopachydermia* based on an analysis that included LSU, mtSSU and *COX2* (Kurtzman and Robnett 2007). A new analysis based on SSU, D1/D2 LSU, *EF1 α* , *RPB1* and *RPB2* confirms the isolation of these two species, which justified their placement in the new genus *Danielozyma* (Kurtzman and Robnett 2014), and also shows them somewhat related to Metschnikowiaceae.

Pichiaceae, methanol-assimilating yeasts and near relatives

Three genera of the Pichiaceae (*Kregervanrija*, *Pichia*, *Saturnispora*) form a well-supported group in the five-gene analysis, although *Dekkera/Brettanomyces* occur in the neighboring methanol-assimilating yeasts on a long branch (Fig. 1, Clade 5). The extended group of Pichiaceae, methanol-assimilating yeasts and their near relatives received variable support (Kurtzman and Robnett 2013a). Genera of this group were phylogenetically circumscribed by SSU, LSU, and *EF1 α* gene sequences (Kurtzman et al. 2008). The asexual genus *Brettanomyces* was described in 1921, but discovery of ascospore formation in certain species resulted in placement of those species in the teleomorphic genus *Dekkera* in 1964 as dictated by the *International Code of Botanical Nomenclature*, then in force [see Smith (2011b) for species characteristics]. Species of *Brettanomyces* are noteworthy for production of acetic acid from glucose, a characteristic that markedly shortens longevity in culture. Species of the clade often spoil wine, beer, and soft drinks, but have more recently been regarded as contributors to diversified aromas. Because the name *Brettanomyces* is commonly used in the food and beverage industries, the genus name *Brettanomyces* should have priority over *Dekkera*.

The genus *Nakazawaea* is expected to be enlarged by *C. anatomiae*, *C. ishiwadae*, *C. peltata*, *C. populi*, and *C. wickerhamii* according to SSU, LSU, mtSSU, and *EF1 α* analyses (Kurtzman 2011). The addition of *C. laoshanensis*, *C. molendinolei*, *C. pomicola* and *C. wyomingensis* is suggested by D1/D2 LSU sequences (Lachance et al. 2011). Following the genus concept applied by the transfer of various *Pichia* and *Williopsis* species to *Ogataea*, the transfer of 20 *Candida* species to *Ogataea* is expected (Nakase et al. 2010b; Kurtzman and Robnett 2010; Koo-wadjanakul et al. 2011; Lachance et al. 2011) (Table 2). However, the *Ogataea* clade that formed the base for the above genus circumscription was not statistically supported. Two supported subclades were formed at the exclusion of *C. boidinii* which had an isolated position that became more pronounced by using *RPB1* and *RPB2* instead of mtSSU sequences. The *Ogataea* clade and apparently related *Candida* species need further study before reclassification is done. Other *Candida* species that may be more distantly related to *Ogataea* and *Kuraishia* include

¹ Spelling corrected according to www.indexfungorum.org

C. borneonana, *C. cidri*, *C. hungarica* and *C. ogatae* (Péter et al. 2009; Sipiczki 2012). In addition, *C. cylindracea*, *C. floccosa*, and *C. pseudocylindracea* are located on long branches basal to the *Ogataea* clade (Lachance et al. 2011; Wang et al. 2009a). *Candida wuzhishanensis* belongs to the *Ambrosiomyces* clade (Wang et al. 2009a).

Multigene phylogenetic analysis of *C. californica*, *C. ethanolica*, *C. inconspicua*, *C. pseudolambica*, *C. rugopelliculosa*, and *C. thaimueangensis* placed these species in the *Pichia* clade (Kurtzman et al. 2008), whereas *C. awuue*,² *C. cabralensis*, and *C. phayaonensis* were added by D1/D2 LSU analyses (Limtong et al. 2012c; Flórez et al. 2010; Nielsen et al. 2010). *Candida diversa*, *C. halmiae*, *C. sekii*, and *C. siamensis* appear to be members of the closely related genus *Saturnispora* while *Candida sanitii*, *C. silvae*, and *C. suwanaritii* occupied a more basal position in the *Saturnispora* clade (Nielsen et al. 2010; Limtong et al. 2010a; Boonmak et al. 2009). Two basal clades consisting of (1) *C. abiesophila*, *C. asiatica* and (2) *C. ficus*, *C. silvatica* might represent neighbouring genera (Limtong et al. 2010b; Kurtzman 2006).

Phaffomycetaceae

Genera of the Phaffomycetaceae (*Komagataella*, *Phaffomyces*) also include *Barnettozyma*, *Cyberlindnera*, *Phaffomyces*, *Starmera* and *Wickerhamomyces* based on the five-gene analysis (Fig. 1, Clades 2 and 3). The *Barnettozyma* clade includes *C. norvegica* and *C. montana* with minimal support, while D1/D2 LSU sequences also indicate *C. qinlingensis* and *C. sanyiensis* as possible members (Liu et al. 2008; Kurtzman 2011; Lachance et al. 2011). *Cyberlindnera* includes the 13 species listed in Table 2 (Jindamorakot et al. 2004; Kurtzman et al. 2008; Chang et al. 2012c). *Phaffomyces* includes *C. orba* and *C. coquimbensis*, and *Wickerhamomyces* includes the 10 species listed in Table 2 (Cardinali et al. 2012; Nakase et al. 2012; Kurtzman et al. 2008; Liu et al. 2008). *C. solani* took different positions in and around the *Wickerhamomyces*/*Cyberlindnera* clade depending on datasets. The *Starmera* clade appears to include *C. berthetii*, *C. dendrica*, *C. laemsonensis*, and *C. stellimalicola*

(Am-In et al. 2011; Kurtzman et al. 2008). Whether the basal species *C. freyschussii* and *C. galis* belong to the Phaffomycetaceae is uncertain (Lachance et al. 2011).

Saccharomycodaceae

Saccharomycodaceae include *Hanseniaspora*, *Kloeckera*, and *Saccharomycodes* (Kurtzman 2011). *Kloeckera* represents the asexual state of the widely known ascosporic genus *Hanseniaspora*. Asexual reproduction is by bipolar budding and phylogenetic analysis using SSU, 5.8S/alignable ITS, LSU rRNA, *EF-1 α* , mtSSU and *COX2* sequences placed *Kloeckera*/*Hanseniaspora* near the bipolar budding genus *Saccharomycodes*, but not near *Wickerhamia* or *Nadsonia*, which also divide by bipolar budding (Kurtzman and Robnett 2003, also seen in Fig. 1, Clade 1). *Hanseniaspora* was described in 1912 and presently has 13 assigned species (Cadez and Smith 2011a), whereas *Kloeckera*, which was described in 1928, has three assigned species (Cadez and Smith 2011b; Jindamorakot et al. 2009; Chang et al. 2012b). Based on taxonomic priority and number of assigned species, *Hanseniaspora* should be considered the valid genus name for the *Kloeckera*/*Hanseniaspora* clade.

Saccharomycopsidaceae

Saccharomycopsis as the only genus of the family has been phylogenetically circumscribed by SSU, LSU rRNA, and *EF-1 α* sequence analysis with strong bootstrap support and includes *C. amapae* and *C. lasenensis* (Kurtzman and Smith 2011a). All members of the clade share the requirement of sulfur in organic form and most species are capable of necrotrophic mycoparasitism (Lachance et al. 2000).

Saccharomycetaceae

Genera of the Saccharomycetaceae (*Cyniclomyces*, *Eremothecium*, *Kazachstania*, *Kluyveromyces*, *Lachancea*, *Nakaseomyces*, *Naumovozyma*, *Saccharomyces*, *Tetrapisispora*, *Torulaspora*, *Vanderwaltozyma*, *Zygosaccharomyces*, *Zygotorulaspora*) were phylogenetically circumscribed by SSU, 5.8S/alignable ITS, LSU rRNA, *EF-1 α* , mtSSU rRNA, and *COX2* gene sequences

² Spelling corrected according to www.indexfungorum.org

(Kurtzman and Robnett 2003) and appear to be members of a well supported family according to the five-gene phylogenetic analysis (Fig. 1, Clade 1). Species produce ubiquinone Q-6 with the exception of *Eremothecium*, which ranges from Q-7 to Q-9. *Candida* species that are members of this family include *C. humilis*, *C. milleri* and *C. pseudohumilis* in the genus *Kazachstania* (Kurtzman and Robnett 2003; Wang et al. 2009b; Lachance et al. 2011) and *C. braccarensis*, *C. castellii*, *C. glabrata*, *C. kungkrabaensis*, *C. nivariensis*, and *C. uthaithanina* in the genus *Nakaseomyces* (Lachance 2011a; Limtong et al. 2011).

Dipodascaceae, *Magnusiomyces*, and *Saprochaete*

Dimorphic arthroconidial yeasts were taxonomically revised based on ITS sequences resulting in three groups: *Galactomyces* and its *Geotrichum* anamorphs, *Dipodascus* and its *Geotrichum* anamorphs and *Magnusiomyces* with the anamorphic genus *Saprochaete* (de Hoog and Smith 2004, 2011a, b). All three clades were grouped on a single branch in the five-gene analysis (Fig. 1, Clade 9). Species recognition by ITS sequences was complicated by intra-strain sequence heterogeneities and D1/D2 LSU and *ACT1* sequences were used to revise the *Galactomyces geotrichum*/*Geotrichum candidum* species complex (Groenewald et al. 2012). From the preceding analyses, these arthroconidial yeasts appear to constitute three genera.

Geotrichum was described in 1832 (de Hoog and Smith 2011a), *Dipodascus* in 1892 and *Galactomyces* in 1977. Because the type species of *Geotrichum* (*G. candidum*) is in the *Galactomyces* clade and *Geotrichum* is so widely known, perhaps *Geotrichum* should be the genus name of choice for this clade. If this were the approach taken, species of *Geotrichum* in the second clade could be transferred to *Dipodascus*. As for the *Magnusiomyces/Saprochaete* clade, *Saprochaete* has taxonomic priority (1970 vs. 1977), but *Magnusiomyces* is better known and the preferred genus name for species of this clade.

Trichomonascaceae, *Yarrowia* and *Starmerella*

The genera of Trichomonascaceae (*Blastobotrys*, *Sugiyamaella*, *Trichomonascus*, *Wickerhamiella*, *Zygoascus*) have been circumscribed by LSU, mtSSU

and *COX2* gene sequences (Kurtzman and Robnett 2007). *Deakozyma*, *Middelhovenomyces*, *Starmerella* and *Yarrowia* appear to be related to the Trichomonascaceae based on five-gene analyses (Fig. 1, Clade 9, Kurtzman and Robnett 2014). Ubiquinone Q-9 is present in those members of the group for which it has been determined.

Starmerella includes only two sexually reproducing species placed by D1/D2 LSU analysis in a large clade of nutritionally highly similar yeasts predominantly isolated from bees and their environment, which comprises *C. apicola* and 24 additional species (Sipiczki 2009; Nakase et al. 2010c; Daniel et al. 2013) (Table 2). A bifurcation divides the bootstrap-supported *C. magnoliae* subclade from the *Starmerella* clade (Lachance 2011b), but there is no compelling argument for a genus-level separation at this time. *Candida spenceri* is likely to be a member of the *Starmerella* clade, but the type strain sequence deposited in GenBank as AB537437 is identical to multiple strains of *C. potachaoreniae* and shows only two substitutions to its type strain sequence (Nakase et al. 2010c).

The *Yarrowia* clade was circumscribed by ITS and D1/D2 LSU sequences and represents species renown for the efficient secretion of metabolites, in particular lipases (Groenewald and Smith 2013). The potential assignments of *C. galli*, *C. hollandica*, *C. osloensis*,³ and *C. phangngaensis*² to the genus *Yarrowia* appear reliable, but the divergent species *C. alimentaria*, *C. hispaniensis* and *C. bentonensis* need further analysis before they can be assigned to a genus (Nagy et al. 2013). *Candida incommunis* is another divergent species and appears weakly associated with *Yarrowia* based on SSU sequence analysis (Suzuki et al. 1999; Suzuki and Nakase 1999).

The *Sugiyamaella* clade was strongly supported by LSU, mtSSU, *COX2* sequence analysis, leading to the interpretation of the clade as one genus (Kurtzman 2007a; Kurtzman and Robnett 2007). Thirteen *Candida* species comprised in this clade were assigned to *Sugiyamaella* (Urbina et al. 2013), while *C. qingdaonensis* also belongs to this clade (Wang et al. 2010). The wood-associated genus *Spencermartinsiella*, including *C. cellulocola*, has been circumscribed by D1/D2 LSU sequences (Péter et al. 2011; Dlačhy et al. 2012).

³ Spelling corrected according to www.indexfungorum.org

In culture, colonies of *Trichomonascus/Blastobotrys* species often appear mold-like (Smith et al. 2011). Hyphal growth is abundant but budding cells are sometimes absent. Some species produce blastoconidia with setae, which are long, tail-like extensions of the cell wall. Multigene phylogenetic analysis placed species of *Arxula*, *Blastobotrys*, and *Sympodiomyces* species in the *Trichomonascus* clade along with certain *Stephanoascus* and *Candida* species (Ueda-Nishimura and Mikata 2002; Kurtzman and Robnett 2007; Smith et al. 2011) (Table 2). *Trichomonascus* is the oldest genus name followed by *Blastobotrys*, *Sympodiomyces* and *Arxula*, respectively. Because none of the names is widely used, *Trichomonascus* should become the accepted genus name on the basis of priority of description. Species of this clade metabolize compounds such as adenine, xanthine, glycine, uric acid, putrescine and branched chain aliphatic compounds (Middelhoven and Kurtzman 2003), and some of the species are able to transform *Fusarium* T-2 mycotoxin to T-2 glucoside (McCormick et al. 2012).

Wickerhamiella species are often isolated from flowers and associated insects and are a phenotypically homogenous group of nutritionally specialised species that show remarkably small cell sizes. In view of the phenotypic and ecological homogeneity, a high degree of sequence variability is observed in the clade, which includes 17 *Candida* species (Badotti et al. 2013) (Table 2). *C. versatilis* was suggested as a member of the clade, but warrants further analyses because of its particular high evolutionary rate. Basal to *Wickerhamiella* is a small clade that includes *C. aurangiensis*, *C. salmanticensis*, and *C. tartarivorans* and appears to represent a new genus (Kurtzman and Robnett 2007).

The *Zygoascus* clade, as circumscribed by LSU, mtSSU, and *COX2* sequence analysis, includes *C. polysorbophila*, and D1/D2 LSU sequence similarity suggests that *C. bituminiphila*, *C. lundiana*, *C. patagonica*, and *C. suthepensis* might also be members of the clade (Kurtzman and Robnett 2007; Saksinchai et al. 2012). The divergent species *C. blankii*, *C. digboiensis*, *C. ghanaensis*, and *C. tunisiensis* may be candidates as type species of new genera. On the basis of multigene analysis, *C. petrohuensis* and *C. tepae*, which are well isolated from other known species (Kurtzman and Robnett 2013a; Eddouzi et al. 2013) represent the new genus *Middelhovenomyces* (Kurtzman and Robnett 2014).

Lipomycetaceae

The three genera of the Lipomycetaceae, *Dipodascopsis*, *Lipomyces*, and *Myxozyma*, are phenotypically united by production of intracellular lipids and extracellular starch-like compounds, and phylogenetic analyses of either D1/D2 LSU or multigene sequences of SSU, LSU, mtSSU and *EF-1 α* separate the genera from other members of the Saccharomycotina (Kurtzman et al. 2007). Subclades include species of both the ascosporic *Lipomyces* (Smith and Kurtzman 2011), and the anamorphic *Myxozyma* (van der Walt et al. 1981; Kurtzman and Smith 2011b), whereas *Dipodascopsis* is separate from these two genera. Differences in ascospore morphology and ubiquinone isoprene chain length among members of *Lipomyces* have provided a basis for naming monotypic genera such as *Limtongia* and *Kockiozyma* (Jindamorakot et al. 2011, 2012). Internal branch support for many species assigned to *Lipomyces/Myxozyma* is weak and it seems preferable to reexamine species from larger datasets before any additional taxonomic changes are made.

Trigonopsidaceae

The family Trigonopsidaceae, with the assigned genera *Botryozyma* (= *Ascobotryozyma*), *Tortispora*, and *Trigonopsis* was introduced to accommodate members of an early diverging lineage of Saccharomycetales (Fig. 1, Clade 10, Lachance and Kurtzman 2013). Species of the genus *Botryozyma* and its ascosporic state *Ascobotryozyma* produce pseudohyphae that are unique because they form an ovoid or elongated basal cell, which give the assemblage a ‘T-like’ appearance (Kerrigan and Smith 2011a, b). The species are associated with nematodes living in rotting grapes and slime fluxes of trees, and the ‘T-cells’ help attach the yeasts to the cuticle of nematodes, although apparently not as parasites. Where known, ascospores formed by species of this clade are elongated and curved.

The genus *Trigonopsis* was described from a single species, *T. variabilis*, where some strains produce both typical ellipsoid budding cells and distinctive triangular cells. *Trigonopsis* appeared phylogenetically isolated from other yeast genera (Kurtzman and Robnett 1998, 2013a), but further analyses placed *C. cantarellii*, *C. vinaria* and the newly described species

T. californica in the *Trigonopsis* clade (Kurtzman 2007b). None of these three species form typical triangular cells, thus eliminating cell morphology as a synapomorphy for circumscription of *Trigonopsis*. The genus *Tortispora* was introduced to accommodate the ascospore *T. ganteri* as well as *C. caseinolytica* and six new asexual species, all of which share the capability to hydrolyse casein and grow on 1-butanol as sole carbon source (Lachance and Kurtzman 2013).

Saccharomycetales *incertae sedis*

Description of the genus *Schizoblastosporion* was based on the single species *S. starkeyi-henricii*, which is characterized by bipolar budding but absence of ascospore formation (Smith 2011c). Phylogenetic analysis placed *S. starkeyi-henricii* in the *Nadsonia* clade (Kurtzman and Robnett 1998), and the species was later transferred to this genus to comply with the new Code (Kurtzman and Robnett 2013b). Phylogenetic placement of *Nadsonia* is uncertain, but the genus may be an early diverging member of the large clade delimited by *Dipodascus* and *Starmerella* (Fig. 1, Clade 9).

The genus *Macrorhabdus*, represented by the single species *M. ornithogaster*, was discovered as a parasite of budgerigars and other birds and becomes established in areas of the stomach (Phalen et al. 2011). The effect on birds is somewhat unclear, but infection may cause a wasting disease. The species has special requirements for laboratory cultivation. Reproduction is by fission and when viewed under the microscope, the cells initially appeared to represent a ‘megabacterium’. Gene sequence analysis, however, showed *Macrorhabdus* to be a fungus and placed this taxon as an early diverging member of the Saccharomycotina (Tomaszewski et al. 2003).

The family assignment of the possibly related *C. chilensis*, *C. heliconia*, *C. nonsorbophila*, *C. sinolaborantium*, and *C. temnochilae* is uncertain. Suggested placements are in Debaryomycetaceae close to the *Yamadazyma* clade by SSU and D1/D2 LSU or in Pichiaceae basal to *Nakazawaea* by D1/D2 LSU analysis (Suh et al. 2005; Nakase et al. 2009a; Lachance et al. 2011).

The species *C. anutae*, *C. argentea*, *C. entomophila*, *C. insectalens*, *C. silvanorum*, and *C. sorboxylosa* do not yet show reliable links to existing genera or known

groups in D1/D2 LSU based phylogenetic analyses. Their placements remain speculative and should be resolved by inclusion in multiple gene phylogenies using a representative taxon sampling.

Taphrinomycotina

Commonly known yeast genera assigned to the Taphrinomycotina include *Taphrina*, *Schizosaccharomyces*, *Pneumocystis*, *Protomyces* and *Saitoella* (Kurtzman 2011; Sugiyama and Hamamoto 2011). Of these, only *Saitoella* does not have a known ascospore state. Two species are known for *Saitoella*, *S. complicata*, from Himalayan soil, and *S. coloradoensis*, from tree frass collected in Colorado, USA. *Saitoella* is well separated from the preceding genera, but its relationship with the poorly characterized plant pathogenic genera *Burenia*, *Protomycopsis*, *Taphridium* and *Volkartia* is unknown.

Species of the ascospore genus *Taphrina* are plant pathogens, but may be grown on common agar media (Fonseca and Rodrigues 2011). Typically, species of *Taphrina* are only isolated from infected plants, but discovery of asexual states of new species of *Taphrina* on leaf surfaces and in leaf litter showed that *Taphrina* species may occur in nature as saprophytes (Fonseca and Inácio 2011). Because these new species did not form ascospores in culture, they were placed in the anamorphic genus *Lalaria*. In view of the requirements of the new Code, species of *Lalaria* will be assigned to the genus *Taphrina*.

Conclusion

The assignment of asexual yeast species to existing or newly created genera is straightforward in some cases and complicated in others. Genera that consist of a tight network of closely related species may only require re-analysis of alignments that incorporate all potential new members plus representatives of closely related genera, using available sequences. By contrast, a number of *Candida* species cannot be phylogenetically placed on the basis of D1/D2 LSU sequences alone, the only marker for which a continuously updated public database is available. Such species appear to lack close relatives and are found on long, isolated branches in phylogenetic trees. Analysis of

multi-gene datasets that include representatives of all known phylogenetic groups is hoped to facilitate stable generic assignments. In the interim, species without a resolved phylogenetic position should remain in the genus *Candida* as *Candida* sensu lato species. Prudence is needed in reassigning problematic anamorphic yeast species if users and taxonomists alike are to be spared the confusion of multiple name changes.

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References

- Am-In S, Limtong S, Yongmanitchai W, Jindamorakot S (2011) *Candida andamanensis* sp. nov., *Candida laemsonensis* sp. nov. and *Candida ranongensis* sp. nov., anamorphic yeast species isolated from estuarine waters in a Thai mangrove forest. *Int J Syst Evol Microbiol* 61:454–461
- Badotti F, Silva PAB, Mendonça MC, Gomes FCO, Morais PB, Lachance MA, Rosa CA (2013) *Wickerhamiella dulcicola* sp. nov. and *Wickerhamiella cachassae* sp. nov., yeasts isolated from cachaca fermentation in Brazil. *Int J of Syst Evol Microbiol* 63:1169–1173
- Barbosa AC, Morais CG, Morais PB, Rosa LH, Pimenta RS, Lachance MA, Rosa CA (2012) *Wickerhamiella pagnoccae* sp. nov. and *Candida tocaninsensis* sp. nov., two ascomycetous yeasts from flower bracts of *Heliconia psittacorum* (Heliconiaceae). *Int J Syst Evol Microbiol* 62:459–464
- Berkhout CM (1923) De Schimmelgeslachten *Monilia*, *Oidium*, *Oospora* en *Torula*. Thesis, Utrecht
- Boonmak C, Jindamorakot S, Kawasaki H, Yongmanitchai W, Suwanarit P, Nakase T, Limtong S (2009) *Candida siamensis* sp. nov., an anamorphic yeast species in the *Saturnispora* clade isolated in Thailand. *FEMS Yeast Res* 9:668–672
- Boonmak C, Limtong S, Jindamorakot S, Somjit Am-In, Yongmanitchai W, Suzuki K-I, Nakase T, Kawasaki H (2011) *Candida xylanilytica* sp. nov., a xylan-degrading yeast species isolated from Thailand. *Int J Syst Evol Microbiol* 61:1230–1234
- Burgaud G, Arzur D, Sampaio JP, Barbier G (2011) *Candida oceani* sp. nov., a novel yeast isolated from a Mid-Atlantic ridge hydrothermal vent (–2300 meters). *Antonie Van Leeuwenhoek* 100:75–82
- Cadete RM, Melo MA, Zilli JE, Vital MJS, Mouro A, Prompt AH, Gomes FCO, Stambuk BU, Lachance MA, Rosa CA (2013) *Spathaspora brasiliensis* sp. nov., *Spathaspora suhii* sp. nov., *Spathaspora roraimanensis* sp. nov. and *Spathaspora xylofermentans* sp. nov., four novel D-xylose-fermenting yeast species from Brazilian Amazonian forest. *Antonie Van Leeuwenhoek* 103:421–431
- Cadez N, Smith MTh (2011a) *Hanseniaspora* Zikes (1912). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 421–434
- Cadez N, Smith MTh (2011b) *Kloeckera* Janke (1928). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 1287–1289
- Cardinali G, Antonielli L, Corte L, Roscini L, Ganter PF (2012) *Candida coquimbensis* sp. nov., a link between Australian and Nearctic/Neotropical *Phaffomyces*. *Int J Syst Evol Microbiol* 62:3067–3071
- Cendejas-Bueno E, Kolecka A, Alastruey-Izquierdo A, Theelen B, Groenewald M, Kostrzewa M, Cuenca-Estrella M, Gómez-López A, Boekhout T (2012) Reclassification of the *Candida haemulonii* complex as *Candida haemulonii* (*C. haemulonii* group I), *C. duobushaemulonii* sp. nov. (*C. haemulonii* group II), and *C. haemulonii* var. *vulnera* var. nov.: three multiresistant human pathogenic yeasts. *J Clin Microbiol* 50:3641–3651
- Chang CF, Lee CF, Liu SM (2010) *Candida neustonensis* sp. nov., a novel ascomycetous yeast isolated from the sea surface microlayer in Taiwan. *Antonie Van Leeuwenhoek* 97:35–40
- Chang CF, Lin YC, Chen SF, Carvaja-Barriga EJ, Barahona PP, James SA, Bond CJ, Roberts IN, Lee CF (2012a) *Candida theae* sp. nov., a new anamorphic beverage-associated member of the *Lodderomyces* clade. *Int J Food Microbiol* 153:10–14
- Chang CF, Huang LY, Chen SF, Lee CF (2012b) *Kloeckera taiwanica* sp. nov., an ascomycetous apiculate yeast species isolated from mushroom fruiting bodies. *Int J Syst Evol Microbiol* 62:1434–1437
- Chang CF, Liu YR, Chen SF, Naumov GI, Naumova ES, Lee CF (2012c) Five novel species of the anamorphic genus *Candida* in the *Cyberlindnera* clade isolated from natural substrates in Taiwan. *Antonie Van Leeuwenhoek* 102:9–21
- Chaves GM, Terçarioli GR, Padovan ACB, Rosas RC, Ferreira RC, Melo ASA, Colombo AL (2013) *Candida mesorugosa* sp. nov., a novel yeast species similar to *Candida rugosa*, isolated from a tertiary hospital in Brazil. *Med Mycol* 51:231–242
- Crous PW, Gams W, Stalpers JA, Robert V, Stegehuis G (2004) MycoBank: an online initiative to launch mycology into the 21st century. *Stud Mycol* 50:19–22
- Daniel HM, Rosa CA, São Thiago-Calaça PS, Antonini Y, Bastos EMAF, Evrard E, Huret S, Fidalgo-Jiménez A, Lachance MA (2013) *Starmerella neotropicalis* f.a., sp. nov., a yeast species found in bees and pollen. *Int J Syst Evol Microbiol* 63:3896–3903
- de Hoog GS, Smith MTh (2004) Ribosomal gene phylogeny and species delimitation in *Geotrichum* and its teleomorphs. *Stud Mycol* 50:489–515
- de Hoog GS, Smith MTh (2011a) *Geotrichum* Link: Fries (1832). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 1279–1286

- de Hoog GS, Smith MTh (2011b) *Saprochaete* Coker & Shanor ex D.T.S. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 1317–1325
- Dlauchy D, Lee C-F, Péter G (2012) *Spencermartinsiella ligniputridi* sp. nov., a yeast species isolated from rotten wood. Int J Syst Evol Microbiol 62:2799–2804
- Duarte FL, Pimentel NH, Teixeira A, Fonseca A (2012) *Saccharomyces bacillaris* is not a synonym of *Candida stellata*: reinstatement as *Starmerella bacillaris* comb. nov. Antonie Van Leeuwenhoek 102:653–658
- Eddouzi J, Hofstetter V, Groenewald M, Manai M, Sanglard D (2013) Characterisation of a new clinical yeast species, *Candida tunisiensis* sp. nov., isolated from a strain collection from Tunisian hospitals. J Clin Microbiol 51:31–39
- Fell JW, Statzell-Tallman A, Scorzetti G, Gutiérrez MH (2011) Five new species of yeasts from fresh water and marine habitats in the Florida Everglades. Antonie Van Leeuwenhoek 99:533–549
- Flórez AB, Belloch C, Álvarez-Martín P, Querol A, Mayo B (2010) *Candida cabralensis* sp. nov., a yeast species isolated from traditional Spanish blue-veined Cabrales cheese. Int J Syst Evol Microbiol 60:2671–2674
- Fonseca Á, Inácio J (2011) *Lalaria* R.T. Moore emend. Á. Fonseca (2004). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 1291–1298
- Fonseca Á, Rodrigues MG (2011) *Taphrina* Fries (1832). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 823–858
- Groenewald M, Smith MTh (2013) The teleomorph state of *Candida deformans* Langeron & Guerra and description of *Yarrowia yakushimensis* comb. nov. Antonie Van Leeuwenhoek 103:1023–1028
- Groenewald M, Robert V, Smith MTh (2011a) The value of the D1/D2 and internal transcribed spacers (ITS) domains for the identification of yeast species belonging to the genus *Yamadazyma*. Persoonia 26:40–46
- Groenewald M, Robert V, Smith MT (2011b) Five novel *Wickerhamomyces*- and *Metschnikowia*-related yeast species, *Wickerhamomyces chaumierensis* sp. nov., *Candida pseudoflosculorum* sp. nov., *Candida danieliae* sp. nov., *Candida robnetiae* sp. nov. and *Candida eppingiae* sp. nov., isolated from plants. Int J Syst Evol Microbiol 61:2015–2022
- Groenewald M, Coutinho T, Smith MTh, van der Walt JP (2012) Species reassignment of *Geotrichum bryndzae*, *Geotrichum phurueaensis*, *Geotrichum silvicola* and *Geotrichum vulgare* based on phylogenetic analyses and mating compatibility. Int J Syst Evol Microbiol 62:3072–3080
- Guzmán B, Lachance MA, Herrera CM (2013) Phylogenetic analysis of the angiosperm-floricolous insect-yeast association: have yeast and angiosperm lineages co-diversified? Mol Phylogenet Evol 68:161–175
- Hsieh CW, Huang LY, Tschen EFT, Chang CF, Lee CF (2010) Five novel anamorphic, ascomycetous yeast species associated with mushrooms and soil. FEMS Yeast Res 10:948–956
- Hui FL, Ke T, Niu QH, Du PC (2012) *Candida baotianensis* sp. nov., an ascomycetous yeast species from forest soil in China. J Gen Appl Microbiol 58:59–63
- Hui FL, Niu QH, Ke T, Li YX, Lee CF (2013) *Candida sanyaensis* sp. nov., an ascomycetous yeast species isolated from soil. Antonie Van Leeuwenhoek 103:47–52
- James SA, Carvajal Barriga EJ, Bond CJ, Cross K, Núñez NC, Portero PB, Roberts IN (2009) *Candida carvajalis* sp. nov., an ascomycetous yeast species from the Ecuadorian Amazon jungle. FEMS Yeast Res 9:784–788
- James SA, Barriga EJC, Barahona PP, Cross K, Bond CJ, Roberts IN (2013) *Candida ecuadorensis* sp. nov., an ascomycetous yeast species found in two separate regions of Ecuador. Int J Syst Evol Microbiol 63:393–397
- Ji ZH, Jia JH, Bai FY (2009) Four novel *Candida* species in the *Candida albicans/Lodderomyces elongisporus* clade isolated from the gut of flower beetles. Antonie Van Leeuwenhoek 95:23–32
- Jindamorakot S, Am-in S, Thuy TT, Duy ND, Kawasaki H, Potacharoen W, Limtong S, Tanticharoen M, Nakase T (2004) *Candida easanensis* sp. nov. *Candida pattaniensis* sp. nov. and *Candida nakhonratchasimensis* sp. nov., three new species of yeasts isolated from insect frass in Thailand. J Gen Microbiol 50:261–269
- Jindamorakot S, Ninomiya S, Limtong S, Yongmanitchai W, Tuntirungkij M, Potacharoen W, Tanaka K, Kawasaki H, Nakase T (2009) Three new species of bipolar budding yeasts of the genus *Hanseniaspora* and its anamorph *Kloeckera* isolated in Thailand. FEMS Yeast Res 9:1327–1337
- Jindamorakot S, Am-In S, Yukphan P, Yamada Y (2011) *Limtongia* gen. nov. for *Zygozoma smithiae* (Lipomycetaceae). Ann Microbiol 61:689–693
- Jindamorakot S, Yukphan P, Yamada Y (2012) *Kockiozoma* gen. nov., for *Zygozoma suomiensis*: the phylogeny of the Lipomycetaceae yeasts. Ann Microbiol 62:1831–1840
- Junyapate K, Jindamorakot S, Limtong S (2014) *Yamadazyma ubonensis* f.a., sp. nov., a novel xylitol-producing yeast species isolated in Thailand. Antonie Van Leeuwenhoek 105:471–480
- Kachalkin AV, Yurkov AM (2012) Yeast communities in *Sphagnum* phyllosphere along the temperature-moisture ecocline in the boreal forest-swamp ecosystem and description of *Candida sphagnicola* sp. nov. Antonie Van Leeuwenhoek 102:29–43
- Kerrigan J, Smith MTh (2011a) *Ascobotryozyma* J. Kerrigan & M.Th. Smith. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 319–323
- Kerrigan J, Smith MTh (2011b) *Botryozyma* Shann & M.Th. Smith (1992). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 979–982
- Koowadjanakul N, Jindamorakot S, Yongmanitchai W, Limtong S (2011) *Ogataea phyllophila* sp. nov., *Candida chumphonensis* sp. nov. and *Candida matranensis* sp. nov., three methylotrophic yeast species from phylloplane in Thailand. Antonie Van Leeuwenhoek 100:207–217
- Kurtzman CP (2001) Six new anamorphic ascomycetous yeasts near *Candida tanzawaensis*. FEMS Yeast Res 1:177–185
- Kurtzman CP (2006) New species and new combinations in the yeast genera *Kregervanrija* gen.nov., *Saturnispora* and *Candida*. FEMS Yeast Research 6:288–297

- Kurtzman CP (2007a) Eleven new species of *Sugiyamaella* and *Candida* from forest habitats. FEMS Yeast Res 7:1046–1063
- Kurtzman CP (2007b) New anamorphic yeast species: *Candida infanticola* sp. nov., *Candida polysorbophila* sp. nov., *Candida transvaalensis* sp. nov. and *Trigonopsis californica* sp. nov. Antonie Van Leeuwenhoek 92:221–231
- Kurtzman CP (2011) Discussion of teleomorphic and anamorphic ascomycetous yeasts and yeast-like taxa. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 293–307
- Kurtzman CP, Robnett CJ (1994) Synonymy of the yeast genera *Wingea* and *Debaryomyces*. Antonie Van Leeuwenhoek 66:337–342
- Kurtzman CP, Robnett CJ (1998) Identification and phylogeny of ascomycetous yeasts from analysis of nuclear large subunit (26S) ribosomal DNA partial sequences. Antonie Van Leeuwenhoek 73:331–371
- Kurtzman CP, Robnett CJ (2003) Phylogenetic relationships among yeasts of the ‘*Saccharomyces* complex’ determined from multigene sequence analyses. FEMS Yeast Res 3:417–432
- Kurtzman CP, Robnett CJ (2007) Multigene phylogenetic analysis of the *Trichomonascus*, *Wickerhamiella* and *Zygoascus* yeast clades, and the proposal of *Sugiyamaella* gen. nov. and 14 new species combinations. FEMS Yeast Res 7:141–151
- Kurtzman CP, Robnett CF (2010) Systematics of methanol assimilating yeasts and neighboring taxa from multigene sequence analysis and the proposal of *Peterozyma* gen. nov., a new member of the Saccharomycetales. FEMS Yeast Res 10:353–361
- Kurtzman CP, Robnett CJ (2013a) Relationships among genera of the Saccharomycotina (Ascomycota) from multigene phylogenetic analysis of type species. FEMS Yeast Res 13:23–33
- Kurtzman CP, Robnett CJ (2013b) *Alloascoidea hylecoeti* gen. nov., comb. nov., *Alloascoidea africana* comb. nov., *Ascoidea tarda* sp. nov., and *Nadsonia starkeyi-henricii* comb. nov., new members of the Saccharomycotina (Ascomycota). FEMS Yeast Res 13:423–432
- Kurtzman CP, Robnett CJ (2013c) Description of *Ambrosiozyma oregonensis* sp. nov., and reassignment of *Candida* species of the *Ambrosiozyma* clade to *Ambrosiozyma kashinagacola* f.a., comb. nov., *Ambrosiozyma llanquihensis* f.a., comb. nov., *Ambrosiozyma maleeae* f.a., comb. nov., *Ambrosiozyma pseudovanderkliftii* f.a., comb. nov., and *Ambrosiozyma vanderkliftii* f.a., comb. nov. Int J Syst Evol Microbiol 63:3877–3883
- Kurtzman CP, Robnett CJ (2014) Three new anascosporic genera of the Saccharomycotina: *Danielozyma* gen. nov., *Deakozyma* gen. nov. and *Middelhovenomyces* gen. nov. Antonie van Leeuwenhoek 105:933–942
- Kurtzman CP, Smith MTh (2011a) *Saccharomycopsis* Schöning (1903). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 751–763
- Kurtzman CP, Smith MTh (2011b) *Myxozyma* van der Walt, Weijman & von Arx (1981). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 1303–1312
- Kurtzman CP, Suzuki M (2010) Phylogenetic analysis of ascomycetous yeasts that form coenzyme Q-9 and the proposal of the new genera *Babjeviella*, *Meyerozyma*, *Millerozyma*, *Priceomyces*, and *Scheffersomyces*. Mycoscience 51:2–14
- Kurtzman CP, Albertyn J, Basehoar-Powers E (2007) Multigene phylogenetic analysis of the Lipomycetaceae and proposed transfer of *Zygozyma* species to *Lipomyces* and *Babjevia anomala* to *Dipodascopsis*. FEMS Yeast Res 7:1027–1034
- Kurtzman CP, Robnett CJ, Basehoar-Powers (2008) Phylogenetic relationships among species of *Pichia*, *Issatchenkia* and *Williopsis* determined from multigene sequence analysis, and the proposal of *Barnettozyma* gen. nov., *Lindnera* gen. nov. and *Wickerhamomyces* gen. nov. FEMS Yeast Res 8:939–954
- Lachance MA (2011a) *Nakaseomyces* Kurtzman (2003). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 633–636
- Lachance MA (2011b) *Starmerella* Rosa & Lachance (1998). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 811–815
- Lachance MA (2012) In defense of yeast sexual life cycles: the forma asexualis—an informal proposal. Yeast News! 61: 24–25
- Lachance MA, Kurtzman CP (2011) *Kodamaea* Y. Yamada, T. Suzuki, Matsuda & Mikata emend. Rosa, Lachance, Starmer, Barker, Bowles & Schlag-Edler. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 483–490
- Lachance MA, Kurtzman CP (2013) The yeast genus *Tortispora* gen. nov., description of *Tortispora ganteri* sp. nov., *Tortispora mauiana* f.a., sp. nov., *Tortispora agaves* f.a., sp. nov., *Tortispora sangerardii* f.a., sp. nov., *Tortispora cuajiniquilana* f.a., sp. nov., *Tortispora starmeri* f.a., sp. nov., and *Tortispora phaffii* f.a., sp. nov., reassignment of *Candida caseinolytica* to *Tortispora caseinolytica* f.a., comb. nov., emendation of *Botryozyma*, and assignment of *Botryozyma*, *Tortispora* gen. nov., and *Trigonopsis* to the family Trigonopsidaceae fam. nov. Int J Syst Evol Microbiol 63:3104–3114
- Lachance MA, Pupovac-Velikonja A, Natarajan S, Schlader B (2000) Nutrition and phylogeny of predacious yeasts. Can J Microbiol 46:495–505
- Lachance MA, Boekhout T, Scorzetti G, Fell JW, Kurtzman CP (2011) *Candida* Berkhout. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 987–1278
- Li J, Xu YC, Bai FY (2006) *Candida pseudorugosa* sp. nov., a novel yeast species from sputum. J Clin Microbiol 44: 4486–4490
- Limtong S, Kaewwichian R (2013) *Candida phyllophila* sp. nov. and *Candida vitiphila* sp. nov., two novel yeast species from grape phylloplane in Thailand. J Gen Appl Microbiol 59:191–197
- Limtong S, Kaewwichian R, Am-In S, Boonmak C, Jindamorakot S, Yongmanitchai W, Srisuk N, Kawasaki H, Nakase T (2010a) Three anamorphic yeast species *Candida sanitii* sp. nov., *Candida sekii* sp. nov. and *Candida*

- suwanaritii*, three novel yeasts in the *Saturnispora* clade isolated in Thailand. FEMS Yeast Res 10:114–122
- Limtong S, Kaewwichian R, Am-In S, Nakase T, Lee CF, Yongmanitchai W (2010b) *Candida asiatica* sp. nov., an anamorphic ascomycetous yeast species isolated from natural samples from Thailand, Taiwan, and Japan. Antonie Van Leeuwenhoek 98:475–481
- Limtong S, Jindamorakot S, Am-In Kaewwichian R, Nitiyon S, Yongmanitchai W, Nakase T (2011) *Candida uthaithanina* sp. nov., an anamorphic yeast species in *Nakaseomyces* clade isolated in Thailand. Antonie Van Leeuwenhoek 99:865–871
- Limtong S, Kaewwichian R, Jindamorakot S, Yongmanitchai W, Nakase T (2012a) *Candida wangnamkhiaoensis* sp. nov., an anamorphic yeast species in the *Hyphopichia* clade isolated in Thailand. Antonie Van Leeuwenhoek 102: 23–28
- Limtong S, Koowadjanakul N, Jindamorakot S, Yongmanitchai W, Nakase T (2012b) *Candida sirachaensis* sp. nov. and *Candida sakaeensis* sp. nov. two anamorphic yeast species from phylloplane in Thailand. Antonie Van Leeuwenhoek 102:221–229
- Limtong S, Nitiyon Rungluk Kaewwichian, Jindamorakot S, Am-In S, Yongmanitchai W (2012c) *Wickerhamomyces xylosica* sp. nov. and *Candida phayaonensis* sp. nov., two xylose-assimilating yeast species from soil. Int J Syst Evol Microbiol 62:2786–2792
- Liu CH, Young SS, Chang TC, Lee CF (2008) *Candida dajiaensis* sp. nov., *Candida yuanshanicus* sp. nov., *Candida jianshihensis* sp. nov., and *Candida sanyiensis* sp. nov., four anamorphic, ascomycetous yeast species isolated from soil in Taiwan. FEMS Yeast Res 8:815–822
- Mallet S, Weiss S, Jacques N, Leh-Louis V, Sacerdot C, Casaregola S (2012) Insights into the life cycle of yeasts from the CTG clade revealed by the analysis of the *Millerozyma (Pichia) farinosa* species complex. PLoS ONE 7:e35842
- McCormick SP, Price NPJ, Kurtzman CP (2012) Glucosylation and other biotransformations of T-2 toxin by yeasts of the *Trichomonascus* clade. Appl Environ Microbiol 78:8694–8702
- McNeill J, Barrie FR, Buck WR, Demoulin V, Greuter W, Hawksworth DL, Herendeen PS, Knapp S, Marhold K, et al (2012) International Code of Nomenclature for Algae, Fungi, and Plants (Melbourne Code). Regnum Veg, 154. Koelz Scientific Books, Koenigstein, Germany
- Middelhoven WJ, Kurtzman CP (2003) Relation between phylogeny and physiology in some ascomycetous yeasts. Antonie Van Leeuwenhoek 83:69–74
- Nagatsuka Y, Kiyuna T, Kigawa R, Sano C, Miura S, Sugiyama J (2009) *Candida tumulicola* sp. nov. and *Candida takamatsuzukensis* sp. nov., novel yeast species assignable to the *Candida membranifaciens* clade, isolated from the stone chamber of the Takamatsuzuka tumulus. Int J Syst Evol Microbiol 59:186–194
- Nagy E, Niss M, Dlauchy D, Arneborg N, Nielsen DS, Péter G (2013) *Yarrowia divulgata* f.a., sp. nov., a yeast species from animal-related and marine sources. Int J Syst Evol Microbiol 63:4818–4823
- Nakase T, Jindamorakot S, Am-In S, Ninomiya S, Kawasaki H, Limtong S (2009a) *Candida nonsorbophila* sp. nov., a new ascomycetous yeast species isolated in Thailand. FEMS Yeast Res 9:663–667
- Nakase T, Jindamorakot S, Ninomiya S, Imanishi Y, Kawasaki H (2009b) *Candida wancherniae* sp. nov. and *Candida morakotiae* sp. nov., two novel ascomycetous anamorphic yeast species found in Thailand. J Gen Appl Microbiol 55:93–100
- Nakase T, Jindamorakot S, Imanishi Y, Am-In S, Ninomiya S, Kawasaki H, Limtong S (2010a) *Candida tanticharoeniae* sp. nov., a novel anamorphic yeast species found in Thailand. J Gen Appl Microbiol 56:89–92
- Nakase T, Imanishi Y, Ninomiya S, Takashima M (2010b) *Candida rishirensis* sp. nov., a novel methylotrophic anamorphic yeast species isolated from soil on Rishiri island in Japan. J Gen Appl Microbiol 56:169–173
- Nakase T, Jindamorakot S, Imanishi Y, Am-In S, Ninomiya S, Kawasaki H, Limtong S (2010c) *Candida potacharoeniae* sp. nov. and *Candida spenceri* sp. nov., two novel galactose-containing ascomycetous anamorphic yeast species isolated in Thailand. J Gen Appl Microbiol 56:287–295
- Nakase T, Jindamorakot S, Am-In S, Lee CF, Limtong S (2011a) Four novel species of the anamorphic yeast genus *Candida* found in Thailand and Taiwan. J Gen Appl Microbiol 57:231–242
- Nakase T, Jindamorakot S, Am-In S, Lee CF, Imanishi Y, Limtong S (2011b) Three novel species of the anamorphic yeast genus *Candida* in the *Candida intermedia* clade found in Japan, Thailand and Taiwan. J Gen Appl Microbiol 57:73–81
- Nakase T, Jindamorakot S, Am-In S, Kawasaki H (2011c) *Candida loeiensis* sp. nov., a novel anamorphic yeast species found in Thailand. J Gen Appl Microbiol 57: 387–391
- Nakase T, Jindamorakot S, Am-In S, Ninomiya S, Kawasaki H (2012) *Wickerhamomyces tratensis* sp. nov. and *Candida namnaoensis* sp. nov., two novel ascomycetous yeast species in the *Wickerhamomyces* clade found in Thailand. J Gen Appl Microbiol 58:145–152
- Nguyen NH, Suh S-O, Blackwell M (2007) Five novel *Candida* species in insect-associated yeast clades isolated from *Neuroptera* and other insects. Mycologia 99:842–858
- Nielsen DS, Jakobsen M, Jespersen L (2010) *Candida halmiae* sp. nov., *Geotrichum ghanense* sp. nov. and *Candida awuuii* sp. nov., isolated from Ghanaian cocoa fermentations. Int J Syst Evol Microbiol 60:1460–1465
- Nitiyon S, Boonmak C, Am-In S, Jindamorakot S, Kawasaki H, Yongmanitchai W, Limtong S (2011) *Candida saraburiensis* sp. nov. and *Candida prachuapensis* sp. nov., xylose-utilizing yeast species isolated in Thailand. Int J Syst Evol Microbiol 61:462–468
- Paredes K, Sutton DA, Cano J, Fothergill AW, Lawhon SD, Zhang S, Watkins JP, Guarro J (2012) Molecular identification and antifungal susceptibility testing of clinical isolates of the *Candida rugosa* species complex and proposal of the new species *Candida neorugosa*. J Clin Microbiol 50:2397–2403
- Péter G, Tornai-Lehoczki J, Dlauchy D (2009) *Candida ogatae* sp. nov., an anamorphic member of the *Kuraishia* clade. FEMS Yeast Res 9:328–333
- Péter G, Dlauchy D, Tornai-Lehoczki J, Suzuki M, Kurtzman CP (2011) *Spencermartinsiella europaea* gen. nov., sp. nov., a new member of the family Trichomonascaceae. Int J Syst Evol Microbiol 61:993–1000

- Péter G, Dlauchy D, Price NP, Kurtzman CP (2012) *Diddensia caesifluorescens* gen. nov., sp. nov., a riboflavin producing yeast species of the family Trichomonascaceae. *Int J Syst Evol Microbiol* 62:3081–3087
- Phalen DN, Hannafusa Y, Tomaszewski EK (2011) *Macrorhabdus* Tomaszewski, Logan, Snowden, Kurtzman & Phalen. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 1299–1301
- Ravella SR, Donovan N, James SA, Shivaji S, Arunasri K, Bond CJ, Roberts IN, Hobbs PJ (2011) *Candida northwykensis* sp. nov., A novel yeast isolated from the gut of the click beetle *Melanotus villosus*. *Curr Microbiol* 63:115–120
- Ribeiro AJR, De Carvalho PMB, De S, Cabral A, MacRae A, Mendonça-Hagler LCS, Berbara RLL, Hagler AN (2011) *Candida middelhoveniana* sp. nov., a new yeast species found on the rhizoplane of organically cultivated sugarcane. *Antonie Van Leeuwenhoek* 100:341–347
- Saksinchai S, Suzuki M, Lumyong S, Ohkuma M, Chantawannakul P (2012) Two new species of the genus *Candida* in the *Zygoascus* clade, *Candida lundiana* sp. nov. and *Candida suthepensis* sp. nov., isolated from raw honey in Thailand. *Antonie Van Leeuwenhoek* 101:633–640
- Sarawan S, Mahakhan P, Jindamorakot S, Vichitphan K, Vichitphan S, Sawaengkaew J (2013) *Candida konsanensis* sp. nov., a new yeast species isolated from *Jasminum adenophyllum* in Thailand with potentially carboxymethyl cellulase-producing capability. *World J Microbiol Biotechnol* 29:1481–1486
- Satoh K, Makimura K, Hasumi Y, Nishiyama Y, Uchida K, Yamaguchi H (2009) *Candida auris* sp. nov., a novel ascomycetous yeast isolated from the external ear canal of an inpatient in a Japanese hospital. *Microbiol Immunol* 53:41–44
- Sipiczki M (2009) *Candida stigmatis* sp. nov., a new anamorphic yeast species isolated from flowers. *FEMS Yeast Res* 10:362–365
- Sipiczki M (2012) *Candida borneonana* sp. nov., a methanol-assimilating anamorphic yeast isolated from decaying fruit. *Int J Syst Evol Microbiol* 62:2303–2306
- Sipiczki M (2013) Detection of yeast species also occurring in substrates associated with animals and identification of a novel dimorphic species in *Verbascum* flowers from Georgia. *Antonie Van Leeuwenhoek* 103:567–576
- Smith MTh (2011a) *Aciculoconidium* D.S. King & S.-C. Jong (1976). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 955–957
- Smith MTh (2011b) *Schizoblastosporion* Ciferri (1930). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 1329–1330
- Smith MTh, Kurtzman CP (2011) *Lipomyces* Lodder & Kreger-van Rij (1952). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 545–560
- Smith MTh, de Hoog GS, Statzell-Tallman A, Kurtzman CP (2011) *Blastobotrys* von Klopotek (1967). In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 959–977
- Sugiyama J, Hamamoto M (2011) *Saitoella* S. Goto, Sugiyama, Hamamoto & Komagata. In: Kurtzman CP, Fell JW, Boekhout T (eds) The yeasts, a taxonomic study, 5th edn. Elsevier Science B.V., Amsterdam, pp 1313–1315
- Suh S-O, Blackwell M (2005) Four new yeasts in the *Candida mesenterica* clade associated with basidiocarp-feeding beetles. *Mycologia* 97:167–177
- Suh S-O, Kurtzman CP, Blackwell M (2001) The status of *Endomyces scopularum*—a filamentous fungus and two yeasts. *Mycologia* 93:317–322
- Suh S-O, McHugh JV, Blackwell M (2004) Expansion of the *Candida tanzawaensis* yeast clade: 16 novel *Candida* species from basidiocarp-feeding beetles. *Int J Syst Evol Microbiol* 54:2409–2429
- Suh S-O, Nguyen NH, Blackwell M (2005) Nine new *Candida* species near *C. membranifaciens* isolated from insects. *Mycol Res* 109:1045–1056
- Suh S-O, Nguyen NH, Blackwell M (2006) A yeast clade near *Candida kruisii* uncovered: nine novel *Candida* species associated with basidioma-feeding beetles. *Mycol Res* 110:1379–1394
- Suh S-O, Houseknecht JL, Gujjari P, Zhou JJ (2013) *Scheffersomyces parashaehatae* f.a., sp. nov., *Scheffersomyces xylosifermentans* f.a., sp. nov., *Candida broadrunensis* sp. nov. and *Candida manassasensis* sp. nov., novel yeasts associated with wood-ingesting insects, and their ecological and biofuel implications. *Int J Syst Evol Microbiol* 63:4330–4339
- Suzuki M, Nakase T (1999) A phylogenetic study of ubiquinone Q-8 species of the genera *Candida*, *Pichia*, and *Citeromyces* based on 18S ribosomal DNP sequence divergence. *J Gen Appl Microbiol* 45:239–246
- Suzuki M, Sung-Oui S, Sugita T, Nakase T (1999) A phylogenetic study on galactose-containing *Candida* species based on 18S ribosomal DNA sequences. *J Gen Appl Microbiol* 45:229–238
- Tomaszewski EK, Logan KS, Snowden KF, Kurtzman CP, Phalen DN (2003) Phylogenetic analysis identifies the ‘megabacterium’ of birds as a novel anamorphic ascomycetous yeast, *Macrorhabdus ornithogaster* gen. nov., sp. nov. *Int J Syst Evol Microbiol* 53:1201–1205
- Tsui CKM, Daniel HM, Robert V, Meyer W (2008) Re-examining the phylogeny of clinically relevant *Candida* species and allied genera based on multigene analyses. *FEMS Yeast Res* 8:651–659
- Ueda-Nishimura K, Mikata K (2002) Species distinction of the ascomycetous heterothallic yeast-like fungus *Stephanoascus ciferrii* complex: description of *Candida allociferrii* sp. nov. and reinstatement of *Candida mucifera* Kocková-Kratochvílová et Sláviková. *Int J Syst Evol Microbiol* 52:463–471
- Urbina H, Blackwell M (2012a) Multilocus phylogenetic study of the *Scheffersomyces* yeast clade and characterization of the N-terminal region of xylose reductase gene. *PLoS ONE* 7:e39128
- Urbina H, Blackwell M (2012b) New combinations in *Scheffersomyces*: *S. amazonensis* and *S. ergatensis*. *Mycotaxon* 123:233–234
- Urbina H, Frank R, Blackwell M (2013) *Scheffersomyces cryptocercus*: a new xylose-fermenting yeast associated

- with the gut of wood roaches and new combinations in the *Sugiyamaella* yeast clade. *Mycologia* 105:650–660
- van der Walt JP, Weijman ACM, von Arx JA (1981) The anamorphic yeast genus *Myxozyma* gen. nov. *Sydowia. Ann Mycol Ser II* 34:191–198
- Wang SA, Jia JH, Bai FY (2008) *Candida alocasiicola* sp. nov., *Candida hainanensis* sp. nov., *Candida heveicola* sp. nov. and *Candida musiphila* sp. nov., novel anamorphic, ascomycetous yeast species isolated from plants. *Antonie Van Leeuwenhoek* 94:257–265
- Wang C, Wang QM, Jia JH, Bai FY (2009a) *Candida pseudocylindracea* sp. nov. and *Candida wuzhishanensis* sp. nov. from Hainan island, southern China. *Mycosystema* 28:79–85
- Wang QM, Xu J, Wang H, Li J, Bai FY (2009b) *Torulaspora quercuum* sp. nov. and *Candida pseudohumilis* sp. nov., novel yeasts from human and forest habitats. *FEMS Yeast Res* 9:1322–1326
- Wang SA, Li FL, Bai FY (2010) *Candida laoshanensis* sp. nov. and *Candida qingdaonensis* sp. nov., anamorphic, ascomycetous yeast species isolated from decayed wood. *Int J Syst Evol Microbiol* 60:1697–1701
- Weiss S, Samson F, Navarro D, Casaregola S (2013) YeastIP: a database for identification and phylogeny of ascomycetous yeasts. *FEMS Yeast Res* 13:117–125
- Smith MTh (2011c) *Brettanomyces* Kufferath & van Laer (1921). In: Kurtzman CP, Fell JW, Boekhout T (eds) *The yeasts, a taxonomic study*, 5th edn. Elsevier Science B.V., Amsterdam, pp 983–986
- Yuan B, Hu N, Sun J, Wang SA, Li FL (2012) Purification and characterization of a novel extracellular inulinase from a new yeast species *Candida kutaonensis* sp. nov. *KRFIT. Appl Microbiol Biotechnol* 96:1517–1526