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Description of *Martiniozyma* gen. nov. and transfer of seven *Candida* species to *Saturnispora* as new combinations

Cletus P. Kurtzman

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Abstract DNA sequence analysis has shown *Candida abiesophila* (NRRL Y-11514^T, CBS 5366^T) and *Candida asiatica* (NRRL Y-63747^T, CBS 10863^T) to be members of a small clade that is phylogenetically separate from other yeasts. In view of their isolation from neighboring genera, such as *Pichia* and *Saturnispora*, the two anamorphic species are proposed for transfer to *Martiniozyma* gen. nov. (MycoBank MB 812061) with *Martiniozyma abiesophila* designated as type species (MycoBank MB 812062). In keeping with the *International Code of Nomenclature for algae, fungi, and plants*, which specifies that related anamorphic and teleomorphic species can be assigned to the same genus, the following *Candida* species are transferred to *Saturnispora* to conform with their phylogenetic placement: *Candida diversa* (NRRL Y-5713^T), *Candida halmiae* (CBS 11009^T), *Candida sanitii* (CBS 10864^T), *Candida sekii* (CBS 10931^T), *Candida siamensis* (CBS 11022^T), *Candida silvae* (NRRL Y-6725^T) and *Candida suwanaritii* (CBS 11021^T).

Keywords *Martiniozyma* gen. nov. · *Saturnispora* · New yeast species combinations

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C. P. Kurtzman (✉)
Bacterial Foodborne Pathogens and Mycology Research Unit, National Center for Agricultural Utilization Research, Agricultural Research Service, U.S. Department of Agriculture, 1815 North University Street, Peoria, IL 61604, USA
e-mail: cletus.kurtzman@ars.usda.gov

Introduction

The use of DNA sequence analysis for species identification (Kurtzman and Robnett 1998; Fell et al. 2000, and many subsequent publications) has resulted in the discovery of hundreds of new yeast species during the past 10–15 years. Depending on phylogenetic placement, new sexually reproducing species may be assigned to a known teleomorphic genus or placed in a new genus, but new asexual species related to a teleomorphic genus could not be assigned to that genus because the *International Code of Botanical Nomenclature* (Vienna Code) (McNeill et al. 2006) required that sexual (teleomorphic) and asexual (anamorphic) species be assigned to different genera. Consequently, new asexual species, even if determined from phylogenetic analysis to be members of a teleomorphic genus, had to be assigned to an anamorphic genus, such as *Candida* for ascomycetes, or perhaps *Cryptococcus* or *Rhodotorula* for basidiomycetes. Because of this practice, many anamorphic genera are often highly polyphyletic. The paradox of this requirement was resolved with introduction of a new Code, entitled the *International Code of Nomenclature for algae, fungi, and plants* (Melbourne Code) (McNeill et al. 2012), which permits related species, anamorphic or teleomorphic, to be assigned to the same genus. Many anamorphic species have been shown to be members of teleomorphic clades (Kurtzman 2011a, b; Boekhout et al. 2011), and these species can now be reassigned to those genera as new combinations. Asexual species that are assigned to sexual genera are often designated as *forma asexualis* (*f.a.*) to note that they exhibit no known sexual state despite their assignment to a telomorphic genus (e.g., Lachance and Kurtzman 2013).

In addition to reassignment of anamorphic species to presently accepted genera, other species have been shown to be phylogenetically separate from known genera and are candidates for membership in new genera. Examples include placement of phylogenetically isolated *Candida* species in the new genera *Danielozyma*, *Deakozyma* and *Middelhovenomyces* (Kurtzman and Robnett 2014).

In the present study, *Candida abiesophila* and the related species *Candida asiatica* are proposed for placement in a new genus because of their isolation from other phylogenetically circumscribed genera. The nearest described genera are *Dekkera* (anamorph *Brettanomyces*) *Pichia* and *Saturnispora*. It was also noted during this comparison that seven described species of *Candida* are members of the *Saturnispora* clade and they are proposed for placement in this genus as new combinations.

Materials and methods

Species examined in this study are given in Fig. 1, as well as in Tables 1 and 2, with GenBank accession numbers for the D1/D2 LSU rRNA and ITS sequences analyzed. Composition of culture media used in tests for ascosporulation in *Candida abiesophila* is given by Kurtzman et al. (2011). Methods for DNA isolation and sequencing of the D1/D2 LSU rRNA gene and ITS DNA are those previously reported (Kurtzman and Robnett 1998, 2003), and sequence determinations were made with an ABI 3730 automated DNA sequencer according to the manufacturer's instructions. Gene sequences were aligned using the program Muscle, which is included in MEGA, version 5.2 (Tamura et al. 2011) and alignments were visually adjusted. Sequences were analyzed with the maximum likelihood program included in MEGA and bootstrap support was determined from 1000 replicates.

Results and discussion

Candida abiesophila was initially shown from D1/D2 LSU rRNA gene sequence analysis to be phylogenetically isolated from other yeasts but closely related to the genera *Kregervanrija*, *Pichia* and *Saturnispora* (Kurtzman 2006). Analysis of concatenated gene sequences from translation elongation factor-1α (EF-1α) and the nearly entire LSU and SSU rRNAs (Kurtzman et al. 2008), as well as from concatenated gene sequences from LSU and SSU rRNAs, EF-1α, and RNA polymerase II subunit 1 (RPB1) and subunit 2 (RPB2) (Kurtzman and Robnett 2013), again showed the phylogenetic isolation of *C. abiesophila* and its placement near *Kregervanrija*, *Saturnispora* and *Pichia*. From these analyses, it has become clear that *C. abiesophila* represents the founding species of a new genus. *Candida asiatica* was described by Limtong et al. (2010a) and these authors reported from D1/D2 analysis that the most closely related species was *C. abiesophila*. As seen in Fig. 1, these two species form an isolated clade near *Pichia*, *Saturnispora*, *Dekkera*/*Brettanomyces* and *Kregervanrija*. *Candida abiesophila* is known from four strains and *C. asiatica* from six strains. *C. abiesophila* was isolated from red fir in California and Ponderosa pine in Washington, USA, but *C. asiatica* has a greater habitat range with strains from water and soil in Thailand, soil and a fern in Taiwan and figs in Japan (Table 1). In view of the phylogenetic isolation of *C. abiesophila* and *C. asiatica* from other known yeasts, their placement in a separate genus is proposed. Retention in the genus *Candida* is not an option under the new Code because these species are not closely related to *Candida tropicalis* (*C. vulgaris*), the type species of the genus *Candida*.

Candida abiesophila and *C. asiatica* differ from one another in D1/D2 LSU rRNA gene sequences at 83 positions (70 substitutions, 13 indels) for the 550 nucleotides compared, which is similar to the difference in D1/D2 substitutions shown by highly divergent species in the neighboring genera *Dekkera*/

Fig. 1 Phylogenetic relationships among species of *Dekkera*/*Brettanomyces, Martiniozyma*, *Pichia* and *Saturnispora*, which were determined from maximum likelihood analysis of D1/D2 LSU rRNA gene sequences. Bootstrap values >50 % are given at nodes and were determined from 1000 replicates. *Trichomonascus petasosporus* was the outgroup species in the analysis. Species names are followed by culture collection accession numbers and GenBank numbers. CBS, Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; NRRL, ARS Culture Collection, Peoria, IL USA. All named species are represented by the type strain (T) ▶

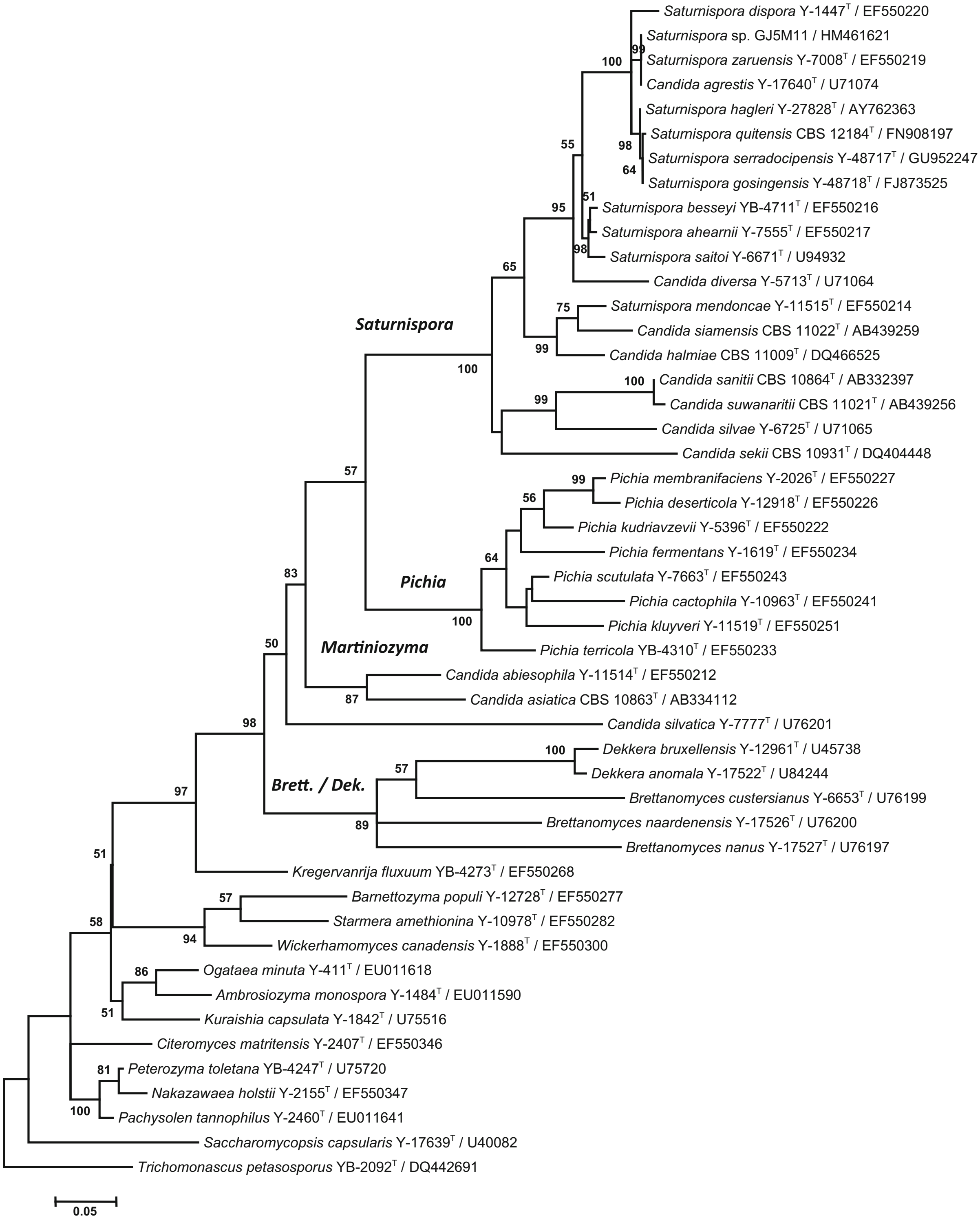
Saturnispora dispora Y-1447T / EF550220
Saturnispora sp. GJ5M11 / HM461621
99
100
Saturnispora zaruensis Y-7008T / EF550219
Candida agrestis Y-17640T / U71074
Saturnispora hagleri Y-27828T / AY762363
Saturnispora quitensis CBS 12184T / FN908197
55
98
Saturnispora serradocipensis Y-48717T / GU952247
64
Saturnispora gosingensis Y-48718T / FJ873525
51
95
Saturnispora besseyi YB-4711T / EF550216
Saturnispora ahearnii Y-7555T / EF550217
98
Saturnispora saitoi Y-6671T / U94932
65
Candida diversa Y-5713T / U71064
75
Saturnispora mendoncae Y-11515T / EF550214
Saturnispora
Candida siamensis CBS 11022T / AB439259
99
Candida halmiae CBS 11009T / DQ466525
100
100
Candida sanitii CBS 10864T / AB332397
99
Candida suwanaritii CBS 11021T / AB439256
Candida silvae Y-6725T / U71065
Candida sekii CBS 10931T / DQ404448
57
99
Pichia membranifaciens Y-2026T / EF550227
56
Pichia deserticola Y-12918T / EF550226
Pichia kudriavzevii Y-5396T / EF550222
Pichia fermentans Y-1619T / EF550234
64
83
Pichia scutulata Y-7663T / EF550243
Pichia
Pichia cactophila Y-10963T / EF550241
100
Pichia kluyveri Y-11519T / EF550251
50
Martiniozyma
Pichia terricola YB-4310T / EF550233
Candida abiesophila Y-11514T / EF550212
87
Candida asiatica CBS 10863T / AB334112
98
Candida silvatica Y-7777T / U76201
100
Dekkera bruxellensis Y-12961T / U45738
57
Dekkera anomala Y-17522T / U84244
Brett. / Dek.
97
Brettanomyces custersianus Y-6653T / U76199
89
Brettanomyces naardenensis Y-17526T / U76200
Brettanomyces nanus Y-17527T / U76197
51
Kregervanrija fluxuum YB-4273T / EF550268
57
Barnettozyma populi Y-12728T / EF550277
58
Starmera amethionina Y-10978T / EF550282
94
Wickerhamomyces canadensis Y-1888T / EF550300
86
Ogataea minuta Y-411T / EU011618
Ambrosiozyma monospora Y-1484T / EU011590
51
Kuraishia capsulata Y-1842T / U75516
Citeromyces matritensis Y-2407T / EF550346
81
Peterozyma toletana YB-4247T / U75720
Nakazawaea holstii Y-2155T / EF550347
100
Pachysolen tannophilus Y-2460T / EU011641
Saccharomycopsis capsularis Y-17639T / U40082
Trichomonascus petasosporus YB-2092T / DQ442691
0.05

Table 1 Origin of strains of *Candida abiesophila* and *C. asiatica*

Species	Strain accession number	Source
Candida abiesophila	NRRL Y-11513	Sap, red fir (*Abies concolor*), Yosemite Valley, California, USA
	NRRL Y-11514^T, CBS 5366	Sap, red fir (*Abies concolor*), Aspen Valley, California, USA
	NRRL YB-2311	Insect frass, Ponderosa pine (*Pinus ponderosa*), Chelan National Forest, Twisp, Washington, USA
	NRRL YB-2346	Insect frass, Ponderosa pine (*Pinus ponderosa*), Chelan National Forest, Twisp, Washington, USA
Candida asiatica	CBS 10863^T	Estuarine water, Laem Son National Park, Ranong Province, Thailand
	LYSM9	Soil, forest, Phu Ruea National Park, Loei Province, Thailand
	GE19S05	Soil, sea coast mountain, Fongbin, Hualein, Taiwan
	SC5L04	Leaf, turnip fern (*Angiopteris lygodiifolia*), mountain habitat, Dasi, Taoyuan, Taiwan
	JCM 11058	Sour fig fruit (*Ficus carica*), Mitsuguchi, Yasuura-cho, Toyota-gun, Hiroshima Prefecture, Japan
	JCM 11059	Sour fig fruit (*Ficus carica*), Mitsuguchi, Yasuura-cho, Toyota-gun, Hiroshima Prefecture, Japan

Strains NRRL YB-2311 and NRRL YB-2346 were discovered in the ARS Culture Collection after publication of the description of *C. abiesophila* (Kurtzman 2006). Data for *C. asiatica* is from Limtong et al. (2010a). Superscript T designates the type strain for each species

Table 2 Nucleotide differences in D1/D2 LSU rRNA gene sequences and ITS sequences for selected strain pairs and for divergent species of *Dekkera/Brettanomyces*, *Martiniozyma*, *Pichia* and *Saturnispora*

Strain pairs	NRRL no.[a]	D1/D2 LSU	D1/D2 GenBank accession no.	ITS1	ITS2	ITS GenBank accession no.
Martiniozyma clade						
C. abiesophila	Y-11514^T		EF550212			KT221053
	Y-11513	1s, 2i	KT221045	0	0	KT221052
	YB-2311	2s, 2i	KT221047	2s	0	KT221054
	YB-2346	2s, 2i	KT221048	2s	0	KT221055
C. abiesophila	Y-11514^T		EF550212			KT221053
C. asiatica	CBS 10863^T	70s, 13i	AB334112	26s, 6i[b]	48s, 11i[b]	KT221051
Saturnispora clade						
S. zaruensis	Y-7008^T		EF550219			KT221056
C. agrestis	Y-17640^T	0	U71074	0	0	KT221057
S. dispora	Y-1447^T		EF550220			
C. sekii	CBS 10931^T	62s, 31i	DQ404448			
Dekkera/Brettanomyces clade						
D. bruxellensis	Y-12961^T		U45738			
B. nanus	Y-17527^T	107s, 66i	U76197			
Pichia clade						
P. kudviavzevii	Y-5396^T		EF550222			
P. terricola	YB-4310^T	64s, 10i	EF550233			

s substitutions, *i* indels (insertions/deletions)

[a] NRRL, ARS Culture Collection, National Center for Agricultural Utilization Research, Peoria, IL, USA; CBS, Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; ^{T}, type strain

[b] Length of aligned ITS sequences for *C. abiesophila* and *C. asiatica*: ITS1 = 88 nucleotides, ITS2 = 109 nucleotides

Brettanomyces, *Pichia* and *Saturnispora* (Table 2). Nucleotide differences in D1/D2 and ITS for *C. asiatica* type strain and the four strains of *C. abiesophila* are given in Table 2. Most noticeable is that the extent of ITS substitutions between *C. abiesophila* and *C. asiatica* is much greater than for D1/D2. In an earlier study it was found that D1/D2 and ITS nucleotide substitutions in species of the Saccharomycetaceae were similar (Kurtzman and Robnett 2003). However, for species of *Citeromyces*, interspecific ITS substitutions exceeded those of D1/D2 by nearly tenfold (Kurtzman 2012). Because of varying divergence rates for ITS among different yeast clades, reliance was placed on D1/D2 divergence for considering *C. abiesophila* and *C. asiatica* as members of the same genus.

Martiniozyma Kurtzman gen. nov.

Description of the genus

Growth is by multilateral budding on a narrow base and cells may be globose, ovoid or elongate. Pseudohyphae may be formed but true hyphae are not. An ascosporic state is unknown.

Fermentation of glucose is strain variable and other sugars are not fermented. The few carbon compounds assimilated include glucose, ethanol, glycerol, mannitol and glucitol but not methanol, hexadecane or inositol. Nitrate is not utilized as a sole source of nitrogen. The genus can be separated from other members of the Saccharomycotina by gene sequence analysis.

Phylogenetic placement: Saccharomycetales, Saccharomycotina, Ascomycota. The genus *Martiniozyma* appears most closely related to *Pichia*, *Saturnispora*, *Dekkera*/*Brettanomyces* and *Kregervanrija* (Fig. 1).

Type species: *Martiniozyma abiesophila* (Kurtzman) Kurtzman.

MycoBank number: MB 812061.

Etymology: The genus is named in honor of Dr. Ann Vaughan-Martini and the late Dr. Alessandro Martini, University of Perugia, Perugia, Italy, for their many contributions to yeast systematics and yeast biology.

Martiniozyma abiesophila (Kurtzman) Kurtzman comb. nov.

Basionym: *Candida abiesophila* Kurtzman (2006). FEMS Yeast Res 6:295.

Type strain: NRRL Y-11514 (CBS 5366).

MycoBank number: MB 812062.

Martiniozyma asiatica (Limtong, Kaewwichian, Am-In, Nakase & Lee) Kurtzman comb. nov.

Basionym: *Candida asiatica* Limtong, Kaewwichian, Am-In, Nakase & Lee (2010a). Antonie van Leeuwenhoek 98:478.

Type strain: CBS 10863 (NBRC 103863).

MycoBank number: MB 812063.

In the description of *C. abiesophila* (Kurtzman 2006), the two known strains did not form ascospores when cultured alone or in combination. Since that description, two additional strains of *C. abiesophila* were discovered and in the present study the four strains were examined individually and as pairs with incubation on YM agar and 5 % malt extract agar at 17 and 25 °C. Examination for conjugation and ascospore formation was every 2 days for the first week and then weekly for 6 weeks when cultures were incubated at 25 °C and for 12 weeks for cultures at 17 °C. During this time, neither conjugations nor ascospores were observed. Similarly, Limtong et al. (2010a) reported no ascospore formation by *C. asiatica* strains, either when grown alone or in pairs. These observations suggest that the two species are heterothallic and that only one mating type has been isolated for each of the species.

Liu and Kurtzman (1991) determined relationships among Saturn-spored species assigned to *Pichia* and *Williopsis* from phylogenetic analysis of partial sequences of large and small subunit rRNAs. The *Williopsis* species were widely separated and appeared not to be members of one genus, but the *Pichia* species were closely related and interpreted to be members of a single genus. Consequently, the genus *Saturnispora* was described to accommodate the Saturn-spored species that formerly had been classified in *Pichia*. Comparisons of D1/D2 sequences showed that *Candida agrestis* was conspecific with *S. zaruensis* (Kurtzman and Robnett 1998) and that two additional *Candida* species, *C. diversa* and *C. silvae*, were also members of the *Saturnispora* clade (Kurtzman 2006). Since that time, five additional anamorphic species of the *Saturnispora* clade have been described but the Vienna Code required that they be assigned to *Candida*. With the changes in nomenclatural rules given in the Melbourne Code, these *Candida* species can be reassigned to the genus *Saturnispora*.

Species of *Candida* proposed for transfer to the genus *Saturnispora* as new combinations.

Saturnispora diversa (Ohara, Nonomura & Yunome ex van Uden & Buckley) Kurtzman *f.a.* comb. nov.

Basionym: *Candida diversa* Ohara, Nonomura & Yunome ex van Uden & Buckley (1970). The Yeasts, A Taxonomic Study, 2nd edn. p. 958.

Type strain: NRRL Y-5713 (CBS 4074).

MycoBank No.: MB 812065.

Saturnispora halmiae (Nielsen, Jakobsen & Jespersen) Kurtzman *f.a.* comb. nov.

Basionym: *Candida halmiae* Nielsen et al. (2010). Int J Syst Evol Microbiol 60: 1462.

Type strain: CBS 11009.

MycoBank No.: MB 812066.

Saturnispora sanitii (Limtong, Am-In, Kaewwichian, Boonmak, Jindamorakot, Yongmanitchai, Srisuk, Kawasaki & Nakase) Kurtzman *f.a.* comb. nov.

Basionym: *Candida sanitii* Limtong et al. (2010b). FEMS Yeast Res 10:118.

Type strain: CBS 10864.

MycoBank No.: MB 812067.

Saturnispora sekii (Limtong, Kaewwichian, Jindamorakot, Am-In, Boonmak, Yongmanitchai, Srisuk, Kawasaki & Nakase) Kurtzman *f.a.* comb. nov.

Basionym: *Candida sekii* Limtong et al. (2010b). FEMS Yeast Res 10:121.

Type strain: CBS 10931.

MycoBank No.: MB 812068.

Saturnispora siamensis (Boonmak, Jindamorakot, Kawasaki, Yongmanitchai, Suwanarit, Nakase & Limtong) Kurtzman *f.a.* comb. nov.

Basionym: *Candida siamensis* Boonmak et al. (2009). FEMS Yeast Res 9:670.

Type strain: CBS 11022.

MycoBank No.: MB 812069.

Saturnispora silvae (Vidal-Leiria & van Uden) Kurtzman *f.a.* comb. nov.

Basionym: *Candida silvae* Vidal-Leiria & van Uden (1963). Antonie van Leeuwenhoek 29:261.

Type strain: NRRL Y-6725 (CBS 5498).

MycoBank No.: MB 812070.

Saturnispora suwanaritii (Limtong, Boonmak, Kaewwichian, Am-In, Jindamorakot, Yongmanitchai, Srisuk, Kawasaki & Nakase) Kurtzman *f.a.* comb. nov.

Basionym: *Candida suwanaritii* Limtong et al. (2010b). FEMS Yeast Res 10:120.

Type strain: CBS 11021.

MycoBank No.: MB 812071.

In earlier studies, *Candida agrestis* was shown to have an identical D1/D2 sequence with *Saturnispora zaruensis* (Kurtzman and Robnett 1998) and to exhibit high nuclear DNA relatedness as determined from reassociation experiments (Mikata et al. 1999). These two studies indicated that *C. agrestis* is the same species as *S. zaruensis*. In the present study, the ITS sequences of type strains of the two species were compared and found to be identical (Table 2), again indicating conspecificity of the two taxa.

Reclassification of yeasts and other fungi following rules of the Melbourne Code will place systematics on a phylogenetic basis. At this time, there are sufficient data to reclassify many closely related yeasts, but reclassification of other more divergent taxa will need to await development of larger datasets that will arise from either sequencing additional genes or from whole genome sequencing. An example from this study is *Candida silvatica*, which appears to represent a new monotypic genus, but its phylogenetic placement is not strongly supported with present datasets (Fig. 1). This study again raises the interesting issue that many phylogenetically circumscribed genera may be unrecognized from phenotype, as seen for *Martiniozyma*, *Pichia* and *Saturnispora*.

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