Five novel *Wickerhamomyces*- and *Metschnikowia*-related yeast species, *Wickerhamomyces chaumierensis* sp. nov., *Candida pseudoflosculorum* sp. nov., *Candida danieliae* sp. nov., *Candida robnettiae* sp. nov. and *Candida eppingiae* sp. nov., isolated from plants

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On the basis of nucleotide divergences in the D1/D2 domain of the 26S rRNA gene and the internal transcribed spacers (ITS) domain of the rRNA gene, five novel yeast species, *Wickerhamomyces chaumierensis* sp. nov. (CBS 8566<sup>T</sup> = JCM 17246<sup>T</sup>), *Candida pseudoflosculorum* sp. nov. (CBS 8584<sup>T</sup> = JCM 17242<sup>T</sup>), *Candida danieliae* sp. nov. (CBS 8533<sup>T</sup> = JCM 17247<sup>T</sup>), *Candida robnettiae* sp. nov. (CBS 8580<sup>T</sup> = JCM 17243<sup>T</sup>) and *Candida eppingiae* sp. nov. (CBS 8586<sup>T</sup> = JCM 17241<sup>T</sup>), isolated from plants in Thailand and Guyana, are proposed in this study.

Plants have been recognized for many years as important substrates, from which novel yeast species can be isolated, and insects have been identified as key vectors for the introduction and dispersal of yeasts on plants (Ganter, 2006). Studies of beetles associated with ephemeral flowers have resulted in the inclusion of a number of novel species in the genus *Wickerhamomyces* (Kurtzman et al., 2008) and the dramatic increase of described species of the genus *Metschnikowia* (Lachance et al., 1999; 2003) and the formerly monotypic genus *Kodamaea* (Kurtzman & Robnett, 1998; Rosa et al., 1999).

Two closely related species, *Pichia pijperi* and *Candida solani*, were placed in the *Pichia anomala* phylogenetic clade on the basis of nucleotide divergences in the D1/D2 domain (Kurtzman & Robnett, 1998), but were later transferred to the *Wickerhamomyces* clade (Kurtzman et al., 2008) due to nucleotide divergences in the EF-1α, LSU and SSU rRNA gene regions. The newly described genus *Wickerhamomyces* accommodated 17 phylogenetically related species, which were formerly assigned to the genera *Pichia*, *Williopsis* and *Hansenula*. Although *P. pijperi* and *C. solani* were placed basal to the rest of the species present in the *Wickerhamomyces* clade (Kurtzman & Robnett, 1998; Kurtzman et al., 2008), they were included in the genus *Wickerhamomyces* due to a lack of well-supported unique characteristics.

Many species of the genus *Metschnikowia* are associated with flowers, some are parasitic in invertebrates and some are found in aquatic habitats (Ganter, 2006). Kurtzman & Robnett (1998) showed that the genus *Metschnikowia* and three sister groups, *Clavispora*, *Yarrowia* and *Cynidiomyces*, were weakly associated and characterized by highly divergent species, *Pichia ohmeri* also being present in this diverse group. This species was first described as a member of the genus *Pichia* by Kreger-van Rij (1970); however, Billon-Grand (1989) introduced the genus *Yamadazyma* to accommodate 16 *Pichia* species including *P. ohmeri*. All of the species assigned to the newly described genus *Yamadazyma* were characterized by the presence of the CoQ<sub>9</sub> system and hat-shaped ascospores. However, on the basis of rRNA sequence analyses, *P. ohmeri* was not closely related to other species of either genus, *Pichia* or *Yamadazyma*, and, therefore, was placed by Yamada et al. (1995) in the genus *Kodamaea*, closely related to the genus *Metschnikowia*. The apparent paraphyly of the genus *Metschnikowia* with respect to the genus *Clavispora* was mentioned by Lachance et al. (2006) as a motive for nomenclatural revision. Any revisions should be made with caution since high rates of rRNA gene sequence divergence are observed in the clade; the formation of ascospores by *Metschnikowia lachancei* that are intermediate in morphology between typical *Metschnikowia* and

**Abbreviations:** CI, consistency index; ITS, internal transcribed spacers; nr, nuclear ribosomal; RC, rescaled consistency index; RI, retention index; TL, tree length.

The GenBank/EMBL/DDBJ accession numbers for the ITS and D1/D2 regions of strains CBS 8533<sup>T</sup>, CBS 8565<sup>T</sup>, CBS 8580<sup>T</sup>, CBS 8584<sup>T</sup> and CBS 8586<sup>T</sup> are HM156530, HM156503, HM156522, HM156519 and HM156531, and HM156539, HM156533, HM156541, HM156536 and HM156540, respectively.

A supplementary figure is available with the online version of this paper.
Clavispora ascospores and the absence of mating reactions between species of Clavispora should also be taken into account.

In this study, four strains isolated from plants in Guyana and one from plants in Thailand were characterized on the basis of their phylogenetic positions and their morphological and physiological characteristics. Five novel species, one teleomorphic and four anamorphic, are proposed as members of the Wickerhamomyces and Metschnikowia clades, respectively.

Strains were collected from flower surfaces and tree exudates during an expedition of the British Mycological Society to Khao Yai National Park, Thailand, in August 1997, and to La Chaumiere, Guyana, in January 1997. The protocols described by Robert et al. (1998) were used for sample collection, enrichment and isolation. Samples were collected in sterile syringes and enriched in glucose (dextrose)–yeast–peptone (DYP) broth, adjusted to pH 3.5. Strains were isolated on DYP agar supplemented with chloramphenicol (200 mg l⁻¹). The origin and original denomination of the strains studied are listed in Table 1. DNA was extracted from cultures grown on GPYA medium (4 % glucose, 0.5 % yeast autolysate, 2 % agar) for 3 days using the FastDNA kit (Bio 101) with the ‘FastPrep’ Instrument (Q-Biogene). Primers V9G (de Hoog & Gerrits van den Ende, 1998) and LR5 (Vilgalys & Hester, 1990) were used to amplify the partial nuclear ribosomal (nr)RNA gene that included the D1/D2 domain of the large-subunit nrDNA as well as the internal transcribed spacers (ITS) domain (ITS 1, ITS 2 and the intervening 5.8S nrRNA gene) as described by Knutsen et al. (2007). The PCR products were separated by electrophoresis at 80 V for 40 min on a 0.8 % (w/v) agarose gel containing 0.1 μg ethidium bromide ml⁻¹ in 1x TAE buffer (0.4 M Tris, 0.05 M NaAc, 0.01 M EDTA; pH 7.85) and examined under UV-light. The amplicons were sequenced in both directions using the primers LR0R (Vilgalys & Hester, 1990) and LR5 for the D1/D2 domain, whereas the primers V9G and ITS4 (White et al., 1990) were used for the ITS domain. A BigDye Terminator version 3.1 Cycle Sequencing kit (Applied Biosystems) was used according to the manufacturer’s recommendations and the products were analysed on an ABI Prism 3730XL DNA Sequencer (Perkin–Elmer). A consensus sequence was computed from the forward and reverse sequences with the program SeqMan from the Lasergene package (DNASTAR). All sequences were assembled and aligned using MAFFT (version 6, Katoh et al., 2002) and manually adjusted or improved by eye where necessary using Sequence Alignment Editor (version 2.0a11; Rambaut, 2002).

The sequence data were analysed using the program PAUP version 4.0b10 (Swofford, 2003) and the resulting trees were printed as described by Groenewald et al. (2008). Maximum-parsimony analyses were performed using the heuristic search option with 1000 random taxon additions and the robustness of the trees was evaluated by bootstrap calculations based on 1000 replications. Other calculations were made, including tree length (TL), consistency index (CI), retention index (RI) and rescaled consistency index (RC). Neighbour-joining analyses using different substitution models, including HKY85, Kimura two-parameter and uncorrected ‘p’ models, were also performed. All analyses were done where gaps were treated as either missing data or fifth character states (new state); large gaps were both included and excluded in different analyses. The sequences were deposited in GenBank and sequence alignments were deposited in TreeBASE (www.treebase.org).

Colony and cell morphology were determined after growth for 3 days at 25 °C on GPYA for all strains tested (Table 1). Physiological characteristics were determined using the API 32 C system (bioMérieux) according to the manufacturer’s instructions and assimilation of nitrogen compounds and fermentation of glucose were tested using the methods described by Yarrow (1998) for all strains tested (Table 2); data were retrieved after 5 days. Growth at 30–40 °C was determined by incubation on GPYA for 7 days. All tests were replicated.

<table>
<thead>
<tr>
<th>Strain</th>
<th>Substrate, Region, Country of isolation</th>
<th>Mating</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Candida danieliae sp. nov.</strong></td>
<td>Gum produced by an unknown tree, Khao Thalu, Thailand</td>
<td>A</td>
</tr>
<tr>
<td>CBS 8533T</td>
<td>Gum produced by an unknown tree, Khao Thalu, Thailand</td>
<td>A</td>
</tr>
<tr>
<td>CBS 8534</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Wickerhamomyces chaumieriensis sp. nov.</strong></td>
<td>Surface of an unknown flower, La Chaumiere, Guyana</td>
<td>S</td>
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<tr>
<td>CBS 8565T</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Candida robnettiae sp. nov.</strong></td>
<td>Surface of an unknown flower, La Chaumiere, Guyana</td>
<td>A</td>
</tr>
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<td>CBS 8580T</td>
<td></td>
<td></td>
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<tr>
<td><strong>Candida pseudoflosculorum sp. nov.</strong></td>
<td>Surface of an unknown flower, La Chaumiere, Guyana</td>
<td>A</td>
</tr>
<tr>
<td>CBS 8584T</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Candida eppingiae sp. nov.</strong></td>
<td>Surface of an unknown flower, La Chaumiere, Guyana</td>
<td>A</td>
</tr>
<tr>
<td>CBS 8586T</td>
<td></td>
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</tr>
</tbody>
</table>

Table 1. Details of strains used in this study

s, Self-sporulating; A, anamorph.
and cadaverine, the fermentation of glucose and growth at 30 °C. All strains were negative for the assimilation of melibiose, lactose, +,-, Negative; maturity.

Strains: 1, CBS 8533T; 2, CBS 8534T; 3, CBS 8565T; 4, CBS 8580T; 5, CBS 8584T; 6, CBS 8586T. All strains were positive for the assimilation of D-glucose, sucrose, maltose, trehalose, melezitose, ethylamine and cadaverine, the fermentation of glucose and growth at 30 °C. All strains were negative for the assimilation of melibiose, lactose, L-rhamnose, L-arabinose, erythritol, inositol, D-glucuronate, nitrate, D-glucosamine HCl and tryptophan and for growth at 40 °C.

Table 2. Physiological characteristics of the novel strains related to species of the genera Wickerhamomyces and Metschnikowia

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>1</th>
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<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
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<tr>
<td>Assimilation of:</td>
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<tr>
<td>Raffinose</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>+</td>
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<tr>
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<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
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</tr>
<tr>
<td>Methyl-α-D-glucopyranoside</td>
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<td>+</td>
<td>+</td>
<td>+</td>
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<td>−</td>
<td>−</td>
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</tr>
<tr>
<td>D-Sorbitol</td>
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<td>+</td>
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<tr>
<td>Gluconoamline</td>
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<td>+</td>
<td>−</td>
<td>−</td>
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<td>Potassium-2-Ketogluconate</td>
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<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
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<tr>
<td>L-Lysine</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
</tr>
<tr>
<td>Cycloheximide (0.01%)</td>
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<td>−</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>+</td>
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<tr>
<td>Growth at:</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>33 °C</td>
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<td>−</td>
<td>−</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>36 °C</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>+</td>
</tr>
</tbody>
</table>

Ascospore production of all the novel strains was examined. Four different agar media were tested, namely 5 % Difco malt extract, V8, diluted V8 (1/20) and YM (Yarrow, 1998). The cultures were incubated at 25 °C and inspected at 3–7-day intervals for 2 months. All cultures were tested individually. Ascospore production was also examined in a mixed culture of strains CBS 8533T and CBS 8534.

Ascospore production

The results of ascospore production tests are presented in Table 1. Of the six newly isolated strains, one strain, CBS 8565T, was found to be self-sporulating on V8 agar, whereas no ascospores were observed in the remaining five isolates or in the crossing of CBS 8533T with CBS 8534 (Fig. 1).

After 3 days of incubation on V8 agar, unconjugated ascii with 2–4 ascospores that were ovoid to hat-shaped with a subequatorial ledge were observed (Fig. 1b–c) in strain CBS 8565T. The ascospores may have been released at maturity.

Physiology

Physiological characteristics of the six novel strains are presented in Table 2. Strains CBS 8533T and CBS 8534 were identical in their fermentation and assimilation abilities and both could grow at 37 °C. Strain CBS 8584T, which was phylogenetically closely related to Candida flosculorum (Fig. 2 and Fig. S1, available in IJSEM Online), differed from strain CBS 10566T, the type strain of C. flosculorum (Rosa et al., 2007), in its ability to grow in 0.01 % cycloheximide and assimilate lactic acid, raffinose, trehalose, L-mannitol, D-glucanate and D-sorbitol; C. flosculorum could assimilate L-sorbose whereas strain CBS 8584T lacked that ability. Previously, Rosa et al. (2007) tested additional isolates of C. flosculorum and all had identical physiological profiles to that of the type strain CBS 10566T. Strain CBS 8565T differed from the rest of the strains studied as it was unable to assimilate potassium-2-ketogluconate and D-mannitol and had a maximum growth temperature of 30 °C.

Sequence comparison

The D1/D2 alignment (deposited in TreeBASE), containing 75 strains, including the outgroup sequence, had a total length of 575 characters, of which 241 were constant, 31 were parsimony-uninformative and 303 were parsimony-informative. Parsimony analysis resulted in 97 equally most-parsimonious trees, the first of which is shown in Fig. 2. The 97 trees obtained differed only with respect to the order of some of the species within the different clades. Neighbour-joining analyses using different substitution models, performed on this alignment when the gaps were included and treated as missing, produced a similar tree topology (data not shown). When the gaps at alignment positions 380–508 were excluded from the analyses, the tree topology for the clades was similar to that obtained when all gaps were included.

The ITS alignment (deposited in TreeBASE), containing 43 strains including the outgroup sequence, had a total length of 535 characters of which 159 were constant, 67 were parsimony-uninformative and 309 were parsimony-informative. All gaps were included and treated as missing data. The parsimony analysis resulted in 12 equally most-parsimonious trees, one of which is shown in Supplementary Fig. S1. The 12 trees obtained differed only with respect to the order of the species within the different clades. For this alignment, when gaps were treated as fifth character states in the parsimony analysis, a similar tree topology was found for the clades.

In both the D1/D2- and ITS-based phylogenetic trees presented in this study (Fig. 2 and Supplementary Fig. S1), three supported clades were found, one containing species of the genus Wickerhamomyces (88 % and 99 % bootstrap support in D1/D2- and ITS-based trees, respectively), one containing species of the genus Kodamaea (100 % bootstrap for both analyses) and one containing species of the genera Metschnikowia and Clavispora (92 % and >50 % bootstrap support in D1/D2- and ITS-based trees,
respectively). The species represented by strains CBS 8533T, CBS 8580T and CBS 8586T could be distinguished from their close relatives using only the D1/D2 domain (TreeBASE). However, strain CBS 8584T differed from C. flosculorum (CBS 10566T) by only three substitutions in the 465 nt region available for the D1/D2 domain but differed by 27 substitutions and one gap in the 349 nt region available for the ITS domain. The differences observed in the ITS sequences as well as the physiological differences discussed above were found to be significant enough for strain CBS 8584T and C. flosculorum CBS 10566T to be considered two distinct species. The data showed that the clade in which species of the genera Metschnikowia and Clavispora reside is still unresolved and additional data are required to clarify the phylogenetic relationships among the different anamorphic and teleomorphic species within this clade. The novel anamorphic species (including strains CBS 8534, CBS 8533T, CBS 8580T, CBS 8584T, CBS 8586T) were, therefore, described as being part of the Metschnikowia/Clavispora clade until additional differential characteristics can be identified that might distinguish species within this clade from one another. Lachance et al. (2006) argued against the subdivision of Metschnikowia into smaller genera on the basis of rRNA gene sequence data, as suggested by Mendonça-Hagler et al. (1993), due to their highly divergent nature and the fact that some form of mating reaction was observed between species in this clade. Finding teleomorphic stages of the anamorphic species within this clade may also widen our understanding of the biological relationships that exist among species within this highly divergent clade.

The Wickerhamomyces clade could, however, be divided into two groups in both the D1/D2- and ITS-based phylogenetic trees (Fig. 2 and Supplementary Fig. S1), with W. pijperi and C. solani in group 1 (99 % and 96 % bootstrap support in D1/D2- and ITS-based trees, respectively) and the rest of the Wickerhamomyces isolates in group 2 (66 % and 100 % bootstrap support). This clustering was consistent for all the analyses and gap treatments performed. Strain CBS 8565T was described as being a species of the genus Wickerhamomyces as ascospore formation was observed as being direct, similar to other species of the genus Wickerhamomyces (Kurtzman et al., 2008), and it clustered in group 1, together with W. pijperi and C. solani as its closest relatives.

Taxonomy

The novel strains described in this study clustered in two different teleomorphic clades in both the LSU and ITS phylogenies: the Wickerhamomyces clade, containing (among others) strain CBS 8565T, and the Metschnikowia/Clavispora clade, containing strains CBS 8534, CBS 8533T, CBS 8580T, CBS 8584T, CBS 8586T. Based on the evidence provided in this study, the five novel strains represent novel yeast species, for which the names Wickerhamomyces chaumierensis sp. nov. (CBS 8565T), Candida pseudoflosculorum sp. nov. (CBS 8584T), Candida robnettiae sp. nov. (CBS 8580T), Candida danieliae sp. nov. (CBS 8533T) and Candida eppingiae sp CBS 8586T. nov. are proposed.

Latin diagnosis of Wickerhamomyces chaumierensis M. Groenew., V. Robert et M.Th. Smith sp. nov.

Post 3 dies 25 °C in agaro cum dextroso, peptono et extracto levedinis, cultura alba, glabra, butyrosa, hebes, convexa. Cellulæ vegetativæ ovoidæ, ellipsoidæ vel elongatae,
Augustum at 30 °C at non at 33 °C. Typus: CBS 8565T (=JCM 17246T) excisata et virus in collectione culturarum Centraalbureau voor Schimmelcultures, Trajectum ad Rhenum praeservantur.

Description of Wickerhamomyces chaumierensis M. Groenew., V. Robert & M.Th. Smith sp. nov.

Wickerhamomyces chaumierensis (chaumier.en’sis. N.L. n. Fr. fem. adj. chaumierensis from Chaumiere, referring to the collection site La Chaumiere in Guyana, from where the type strain was isolated).

After 3 days at 25 °C on glucose–yeast extract–peptone agar, white, smooth, butyrous, dull and convex colonies are formed. Cells are ovoid, ellipsoidal to elongate, 3–9 × 5–21 μm and occur singly, in pairs or in short chains. Pseudohyphae are formed. On V8 agar after 3 days, ascii are formed directly and contain 2–4 ascospores that are hat-shaped to ovoid with an indistinct subequatorial ledge. Ascospores are not produced. Maximum temperature for growth is 30 °C. The results of tests for fermentation of glucose and growth on various carbon and nitrogen compounds are presented in Table 2.

The type strain, CBS 8565T (=JCM 17246T), is deposited as a dried specimen and as a living strain in the culture collection of the Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands.

Latin diagnosis of Candida pseudoflosculorum M. Groenew., V. Robert & M.Th. Smith sp. nov.


Description of Candida robbettiae M. Groenew., V. Robert & M.Th. Smith sp. nov.

Candida robbettiae (robb.net’ti.aae. N.L. fem. n. robbettiae named after Christie J. Robnett for her valuable contribution to yeast taxonomy).

After 3 days at 25 °C on glucose–yeast extract–peptone agar, the culture is white, butyrous, glossy, glabrous and convex. The cells are globose, ellipsoidal to elongate, 1.5–6 × 3–11 μm and occur singly or in pairs. Pseudohyphae are formed. Ascospores are not produced. Maximum temperature for growth is 37 °C. The results of tests for fermentation of glucose and growth on various carbon and nitrogen compounds are presented in Table 2.

The type strain, CBS 8580T (=JCM 17243T), is deposited as a dried specimen and as a living strain in the culture collection of the Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands.
collection of the Centraalbureau voor Schimmelcultures, Trajectum ad Rhenum praeservantur.

Latin diagnosis of *Candida danieliae* M. Groenew., V. Robert et M.Th. Smith sp. nov.


Description of *Candida danieliae* M. Groenew., V. Robert & M.Th. Smith sp. nov.

*Candida danieliae* (da.ni.e’li.ae. N.L. fem. n. *danieliae* named after Heide-Marie Daniel for her valuable contribution to phylogenetic studies done within the genus *Candida*).

After 3 days at 25 °C on glucose–yeast extract–peptone agar, the culture is white, smooth, butyrous, glossy and convex. The cells are ovoid, 1.5–5 × 2–6 μm and occur singly or in pairs. Pseudohyphae are formed. Maximum temperature for growth is 37 °C. The results of tests for fermentation of glucose and growth on various carbon and nitrogen compounds are presented in Table 2.

The type strain, CBS 8533T (=JCM 17247T), is deposited as a dried specimen and as a living strain, in the culture collection of the Centraalbureau voor Schimmecultures, Utrecht, The Netherlands.

Latin diagnosis of *Candida eppingiae* M. Groenew., V. Robert et M.Th. Smith sp. nov.


Description of *Candida eppingiae* M. Groenew., V. Robert & M.Th. Smith sp. nov.

*Candida eppingiae* (ep.pin’gi.ae. N.L. fem. n. *eppingiae* named after Wendy Epping at the CBS yeast collection for her valued technical assistance).

After 3 days at 25 °C on glucose–yeast extract–peptone agar, the culture is white, smooth, butyrous, glossy and convex. The cells are ovoid, ellipsoidal or elongate, 1.5–4 × 2–8 μm, single, pairs or short chains. Pseudohyphae are formed. Ascospores are not formed. Maximum temperature for growth is 37 °C. The results of tests for fermentation of glucose and growth on various carbon and nitrogen compounds are presented in Table 2.

The type strain, CBS 8586T (=JCM 17241T), is deposited as a dried specimen and as a living strain, in the culture collection of the Centraalbureau voor Schimmecultures, Utrecht, The Netherlands.

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References


