Yamadazyma insecticola f.a., sp. nov. and Yamadazyma epiphylla f.a., sp. nov., two novel yeast species

Sasitorn Jindamorakot,1 Somjit Am-In,1 Rungluk Kaewwichian1† and Savitree Limtong2,3

Two yeast strains representing two novel yeast species were isolated from frass of an unidentified insect (ST-78T) and the external surfaces of rice leaves (YE170T) collected in Thailand. The two strains were genetically, morphologically and phenotypically distinct from recognized species and were found to represent two novel species of the genus Yamadazyma although formation of ascospores was not observed. In terms of pairwise sequence similarity of the D1/D2 region of the large subunit rRNA gene, the closest relative of strain ST-78T was Candida lessepsii CBS 9941T but with 3.8 % nucleotide substitutions, while the closest relative of strain YE170T was strain ST-78T but with 4.3 % nucleotide substitutions. Analysis of the sequences of the internal transcribed spacer 1 and 2 (ITS1–2) regions revealed that strain ST-78 differed from C. lessepsii CBS 9941T by 8.8 % nucleotide substitutions and from strain YE170T by 9.4 % nucleotide substitutions. The result of pairwise sequence similarity of the D1/D2 and ITS1–2 regions together with phylogenetic analysis indicated that strains ST-78T and YE170T represented two novel species within the Yamadazyma clade. The names Yamadazyma insecticola f.a., sp. nov. (type strain ST-78T = BCC 8314T = NBRC 110421T = CBS 13382T; MycoBank no. MB810546) and Yamadazyma epiphylla f.a., sp. nov. (type strain YE170T = BCC 63466T = NBRC 110423T = CBS 13384T; MycoBank no. MB810547) are proposed for the two novel yeast species.

The genus Yamadazyma was described by Billon-Grand (1989) to accommodate species that were transferred from the genus Pichia, which formed hat-shaped ascospores that were released from the ascus at maturity and had coenzyme Q-9 as their major ubiquinone (Kurtzman & Robnett, 1998). Phylogenetic analysis of the D1/D2 region of the large subunit rRNA gene placed the species assigned to the genus Yamadazyma in several clades and indicated that the genus is polyphyletic (Kurtzman & Robnett, 1998); it was therefore not generally accepted. Analysis of the D1/

D2 region of the LSU rRNA gene and the nearly complete small subunit rRNA gene supported transferring some species that had been assigned to the genus Yamadazyma by Billon-Grand (1989) to the newly described genera Babjevella, Meyerozyma, Millerozyma and Preisomyces. Thereafter, the genus Yamadazyma became a well-supported clade (Kurtzman & Suzuki, 2010) and a generally accepted genus in the family Debaryomycetaceae, order Saccharomycetales (Kurtzman, 2011). In Kurtzman (2011), Yamadazyma philoegae, the type species of the genus, as well as Y. aktivaensis, Y. mexicana, Y. nakazawae, Y. scolyti, Y. triangularis and 28 Candida species are placed in the Yamadazyma clade. Since then, many novel species of the genus Candida in this clade have been described, for example Candida kanchanaburiensis, C. khao-thaluensis, C. vaughaniae, C. tallmaniae, C. oceani, C. sirachaiensis, C. sakaeoensis, C. phyllophilla and C. vitiphila (Nakase et al., 2008; Burgaud et al., 2011; Groenewald et al., 2011; Lintong et al., 2012; Lintong & Kaewwichian, 2013). Recently, five species of the genus Yamadazyma, namely

†Present address: Microbiology Program, Department of Science, Faculty of Science and Technology, Bansomdejchaopraya Rajabhat University, Bangkok 10600, Thailand.

Abbreviations: ITS, internal transcribed spacer; LSU, large subunit.

The GenBank/EMBL/DDBJ accession numbers for the sequences of the D1/D2 region of the large subunit rRNA gene and the ITS1–2 regions of Yamadazyma insecticola ST-78T are DQ400379 and LC006081, respectively, and of Yamadazyma epiphylla YE170T are LC006026 and LC006082, respectively.
Y. terventina, Y. siamensis, Y. phyllophia, Y. paraphyllophia and Y. ubonensis, were proposed from strains isolated in Italy, Taiwan and Thailand (Ciafardini et al., 2013; Kaewwichian et al., 2013; Junyapate et al., 2014). At the time of writing, the Yamadazyma clade consists of 11 species of the genus Yamadazyma and more than 30 species of the genus Candida (Lachance et al., 2011; Kurtzman, 2011). The habitats of species belonging to the Yamadazyma clade are very diverse and include water, plants, animals, and the guts of termites and other insects (Suh et al., 2005; Ganter, 2006).

In the present paper, two yeast strains isolated from frass of an unidentified insect (ST-78T) and the external surfaces of rice leaves (YE170T) collected in Thailand are described and considered to represent two novel species of the genus Yamadazyma, Yamadazyma insecticola f.a., sp. nov. and Yamadazyma epiphylla f.a., sp. nov.

### Yeast isolation

Strain ST-78T was isolated from frass of an unidentified insect by direct streaking on yeast extract-malt extract (YM) agar (0.3 % yeast extract, 0.3 % malt extract, 0.5 % peptone and 2.0 % agar) supplemented with 100 μg chloramphenicol ml⁻¹ and 200 μg sodium propionate ml⁻¹ in a Petri dish. Strain YE170T was isolated by the plating of leaf washings as described by Inácio et al. (2002). A rice leaf sample (10 g) was aseptically suspended in 50 ml of 0.85 % saline solution in a 250 ml Erlenmeyer flask and shaken on a rotary shaker at 25 °C for 1 h to detach yeast cells from the surfaces. An aliquot (0.1 ml) of the washing solution was then spread on YM agar supplemented with 100 μg chloramphenicol ml⁻¹ and 250 μg sodium propionate ml⁻¹, and incubated at 25 °C until yeast colonies appeared. Purification of yeast strains was performed by cross streaking on YM agar. Purified yeast strains were suspended in YM broth supplemented with 10 % (v/v) glycerol and maintained at −80 °C.

### DNA sequencing and phylogenetic analysis

The nucleotide sequences of the D1/D2 region of the LSU rRNA gene and the internal transcribed spacer 1 and 2 (ITS1–2) regions were amplified from genomic DNA extracted from cells. DNA extraction, PCR primers, PCR reaction conditions and the sequencing of amplicons were determined according to the methods outlined by Kurtzman & Robnett (1998) and White et al. (1990). Amplification of the D1/D2 region of the LSU rRNA gene was carried out by PCR with the forward primer NLI (5’-GCATATCAATTACGGGAGAAAAG-3’) and the reverse primer NLR4 (5’-GGTCCGTGT-TTCAAGACGG-3’) (Kurtzman & Robnett, 1998). The ITS1–2 regions were amplified with forward primer ITS5 (5’-GGAATGTAAAGCTGAAACAGG-3’) and reverse primer ITS4 (5’-TCCCTCGCTATTGATATGC-3’) (White et al., 1990). Sequence divergence of the D1/D2 region of the LSU rRNA gene and the ITS1–2 regions of the yeast strains was compared with similar sequences in the GenBank database by the nucleotide BLAST analysis tool (Altschul et al., 1997). The phylogenetic placement of the proposed novel species along with neighbouring taxa was analysed using the concatenated sequences of the ITS1–2 and the D1/D2 regions of the LSU rRNA gene. The sequences of the novel strains and related species retrieved from GenBank (accession numbers indicated in Fig. 1) were aligned using the program MUSCLE (Edgar, 2004) and phylogenetic trees were reconstructed by using the maximum-likelihood method based on the Kimura two-parameter model. Evolutionary analyses were conducted in MEGA6 (Tamura et al., 2013).

### Phenotypic characterization

The strains were characterized morphologically, biochemically and physiologically according to the standard methods given by Kurtzman (2011). Pseudohypha and hypha formation was investigated on YM agar, corn meal agar (CMA) and potato dextrose agar (PDA) and on slide culture after growth at 25 °C for 7 days. Ascospore formation was investigated on YM agar, acetate agar, 5 % malt extract agar, CMA, Gorodkowa agar and Fowell’s acetate agar after growth at 15 and 25 °C for 4 weeks. Carbon assimilation tests were conducted in a liquid medium according to the method described by Kurtzman (2011). Nitrogen assimilation was examined on solid media with starved inocula (Nakase & Suzuki, 1986a). The ability to grow at various temperatures was determined in YM broth using a metal block bath. Ubiquinone was extracted from yeast cells grown in yeast peptone glucose broth (1.0 % yeast extract, 2.0 % peptone and 2.0 % glucose) at 25 °C on a rotary shaker at 150 r.p.m. for 3 days. The cells were washed with distilled water and then freeze-dried. Ubiquinone extraction and purification were performed as described by Nakase & Suzuki (1986b). Ubiquinone isoprenologues were identified by HPLC (Waters 2690) with a Cosmosil column (Waters 5C18) and eluted with a 2:1 (v/v) ratio of methanol/2-propanol as the mobile phase at a flow rate of 1 ml min⁻¹ and the eluent was analysed using a UV spectrophotometer (Waters 996 photodiode array detector) at 275 nm.

### Novel species delineation and phylogenetic placement

In terms of pairwise alignment, the sequence of strain ST-78T was related most closely to Candida lessepsii CBS 9941T, but with 3.8 % nucleotide substitutions (20 nt substitutions, two indels out of 535 nt) in the D1/D2 region of the LSU rRNA gene and 8.8 % nucleotide substitutions (49 nt substitutions, two indels out of 579 nt) in the D1/D2 region of the LSU rRNA gene. Strain YE170T was related most closely to strain ST-78T but with 4.3 % nucleotide substitutions (22 nt substitutions, five indels out of 521 nt) and 9.4 % nucleotide substitutions (56 nt substitutions, 24 indels out of 623 nt) in the D1/D2 region of the LSU rRNA gene and the ITS1–2 regions, respectively. Its closest...
**Fig. 1.** Phylogenetic tree showing the positions of *Yamadazyma insecticola* f.a., sp. nov. (ST-78\(^T\)) and *Yamadazyma epiphylla* f.a., sp. nov. (YE170\(^T\)) with respect to closely related species based on the concatenated sequences of the ITS1–2 regions and the D1/D2 region of the LSU rRNA gene. The phylogenetic tree was reconstructed from evolutionary distance data with Kimura's two-parameter correction, using the maximum-likelihood method by MEGA software version 6.0. Numbers indicate percentages of bootstrap sampling, derived from 1000 samples. Numbers in parentheses are GenBank accession numbers. *Babjeviella inositovora* NRRL Y-12698\(^T\) was the outgroup in the analysis. Bar, 0.01 substitutions per site.
recognized relatives were Candida amphixiae CBS 9877T and Candida tammaniensis CBS 8504T, but with 4.5% nucleotide substitutions (23 nt substitutions, eight indels out of 524 nt) and 6.2% nucleotide substitutions (38 nt substitutions, 25 indels out of 640 nt) in the D1/D2 region of the LSU rRNA gene and the ITS1–2 regions, respectively. Therefore, BLAST similarity searches with the D1/D2 region of the LSU and ITS1–2 regions clearly indicated that strains ST-78T and YE170T were representatives of two novel species.

Phylogenetic analysis based on the concatenated sequences of the ITS1–2 regions and D1/D2 region of the LSU rRNA gene using the maximum-likelihood method indicated that strains ST-78T and YE170T represented two novel species placed in the Yamadazyma clade (Fig. 1). The phylogenetically closest relative of strain ST-78T was Y. triangularis. Strain YE170T was distinct from strain ST-78T and placed in a subclade that contained C. lessepsii, the closest relative of strain ST-78T in terms of pairwise sequence similarity of the sequence of the D1/D2 region of the LSU rRNA gene. The affinity of the subclades containing the two novel species with the subclade containing the type species of the genus Yamadazyma was supported by bootstrap values of 51 and 65%, respectively. The phylogenetic analysis indicated the reciprocal monophony of the two novel species with respect to related species. Because the phylogenetic tree was reconstructed from the concatenated sequences of the ITS1–2 regions and the D1/D2 region of the LSU rRNA gene, the two novel species did not show the same relationship as the result of pairwise sequence similarity of the sequences of the D1/D2 region of the LSU rRNA gene. No differences were detected between the neighbour-joining and maximum-parsimony methods, particularly with regard to the position of strains ST-78T and YE170T. A phylogenetic species concept therefore applies.

According to the recent International Code of Nomenclature for algae, fungi, and plants, the most important requirement is the adoption of 'one fungus, one name' (Miller et al., 2011). Consequently, although the formation of ascospores was not observed, the two novel species are described based on a single strain each and sexual spore reproduction was not observed, the novel species are assigned to the genus Yamadazyma, and the designation forma asexualis (f.a.) is included following the recommendation of Lachance (2012). We propose the names Yamadazyma insecticola f.a., sp. nov. (type strain ST-78T, MycoBank accession no. MB810546) and Yamadazyma epiphylla f.a., sp. nov. (type strain YE170T, MycoBank accession no. MB8810547) for these species.

Physiologically, Y. insecticola and Y. epiphylla can be differentiated from each other and from their closest known relatives not only based on analysis of the sequences of the D1/D2 region of the LSU rRNA gene and the ITS1–2 regions but also based on several phenotypic characteristics (Table 1). Y. insecticola does not assimilate melibiose, raffinose or DL-lactic acid and does not grow at 40°C while Y. epiphylla assimilates these compounds and grows at 40°C. Y. insecticola grows in 60% glucose and with 0.1% cycloheximide whereas Y. epiphylla does not. Y. insecticola can be distinguished from C. lessepsii based on several phenotypic characteristics; for example, Y. insecticola assimilates sucrose, L-sorbose, L-rhamnose and ethanol, grows in vitamin-free medium and 0.1% cycloheximide and does not ferment trehalose while C. lessepsii does not assimilate sucrose, L-sorbose or L-rhamnose, does not grow in vitamin-free medium or 0.1% cycloheximide and ferments trehalose. Phenotypic characteristics that distinguish Y. epiphylla from C. amphixiae are the inability to ferment D-galactose and trehalose of Y. epiphylla in contrast to C. amphixiae. Y. epiphylla assimilates melibiose and raffinose while C. amphixiae does not.

Members of the Yamadazyma clade exhibit an association with the gut of beetles and other insects, flowers, tree exudates, plants, mushroom, deep-sea coral, water samples, and marine and mangrove habitats (Nakase et al., 2008; Burgaud et al., 2011; Groenewald et al., 2011; Kurtzman, 2011; Lachance et al., 2011; Kaewwichian et al., 2013; Junyapate et al., 2014). According to these reports, 20

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species in the Yamadazyma clade have been isolated from the gut or frass of insects and 10 species have been obtained from plants. In the present study, two yeast strains representing two novel species of the genus Yamadazyma, Y. insecticola f.a. and Y. epiphylla f.a., were isolated from frass of an unidentified insect and the external surfaces of rice leaves. Since the first description of four yeast species isolated from insect frass reported by Phaff and do Carmo-Sousa (1962), many species have been described belonging to several genera of ascomycetous yeasts, such as Ascobotryozyma, Barnettozyma, Kuraisha, Lipomyces, Lindnera, Meyerozyma, Nakazawaea, Ogataea, Peterozyma, Pichia, Schefferomyces, Starmera, Sugiyamaella, Trichomonas, Wickerhamozyma and Yamadazyma, and some genera of basidiomycetous yeasts, such as Bulleromyces, Curvibasidium, Cryptococcus, Sporobolomyces and Trichosporon. The basidiomycetous yeasts often colonize the phylloplane at approximately 10–104 cm–2 (Shivas & Brown, 1984) and they move from leaf to leaf by passive air dispersal. In general, the phylloplane yeast community includes species of the genera Bullera, Bensingtonia, Cystoflabidium, Cryptococcus, Leucosporidium, Pseudozyma, Rhodotorula and Sporobolomyces (Starmer & Lachance, 2011). However, ascomycetous yeasts have also been obtained from the phylloplane, as reported by Limtong et al. (2014).

The strains isolated from insect frass and phylloplane have been isolated from many countries in all continents (Kurtzman et al., 2011). This indicates that insect frass and phylloplane or plants are important habitats of yeasts worldwide in terms of species distribution.

This paper describes two novel yeast species of the genus Yamadazyma based each on a single strain, supporting by several phenotypic and genetic properties that differentiate them from any recognized species. This is despite the lack of phenotypic and genetic heterogeneity information regarding the proposed species, and understanding of their species diversity, ecology and phylogeny.

**Description of Yamadazyma insecticola**

**Yamadazyma insecticola** (in.sec.ti’cola. N.L. fem adj. insecticola referring to an association between yeast and insect). After growth in YM broth at 25 °C for 3 days, cells are globose, subglobose to ovoid (2–7 × 2.5–9 μm) and occur singly, in pairs or in groups (Fig. 2a). Budding is multilateral. After growth on YM agar at 25 °C for 3 days, the streak culture is greyish white, smooth, soft to butyrous with entire margin. Pseudoconidia are formed in slide culture on YM agar, CMA and PDA after 3 days at 25 °C (Fig. 2b) and true hyphae are not formed in slide culture on those agar media after 21 days at 25 °C. Ascospores are not produced on YM agar, acetate agar, 5% malt extract agar, CMA, Gorodkowa agar and Fowell’s acetate agar at 15 or 25 °C after 4 weeks. Positive for fermentation of D-glucose, weakly positive for fermentation of D-galactose but negative for fermentation of sucrose, maltose, lactose, trehalose and raffinose. Assimilates D-glucose, D-galactose, L-sorbose (latent), sucrose, maltose, cellobiose, trehalose, melezitose, soluble starch (weakly), D-xylose, L-arabinose, D-arabinose, D-ribose (weakly), L-rhamnose, ethanol, glycerol, erythritol, ribitol, D-mannitol, D-glucitol, methyl α-D-glucoside, salicin, succinic acid, citric acid, xylitol (weakly), L-arabitol and D-gluconate, but not lactose, melibiose, raffinose, inulin, galactitol, D-glucosone-D-lactone, D-gluconate, D-galacturate, 2-keto-D-gluconate, 5-keto-D-gluconate, DL-lactic acid, inositol or hexadecane. Ethylamine-HCl, L-lysine-HCl and cadaverine are assimilated, but nitrate and nitrite are not. Growth in vitamin-free medium is positive. Growth occurs on media containing 50% (w/w) glucose, 60% glucose, 10% NaCl/5% glucose, 15% NaCl/5% glucose, 0.01% cyclohexemide and 0.1% cyclohexemide. Grows at 25, 30, 35 and 37 °C but not at 40 °C. Acid formation from glucose is positive. Starch-like compounds are not produced. Diazonium blue B and urease reactions are negative. The major ubiquinone is Q-9.

Strain ST-78T (=BCC 8314T=NBRC 110421T=CBS 13382T) is the holotype of Y. insecticola f.a., sp. nov. (MycoBank accession number MB810546). The strain was isolated from insect frass collected from Udon Thani province, Thailand. The culture is maintained by freezing and/or lyophilization.

**Description of Yamadazyma epiphylla**

**Yamadazyma epiphylla** (e.pi.phyl’la. N.L. fem. adj. epiphylla referring to an association between yeast and plant surface). After growth in YM broth at 25 °C for 3 days, cells are globose, subglobose to ovoid (2–7 × 2.5–9 μm) and occur

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**Fig. 2.** Yamadazyma insecticola f.a., sp. nov. (ST-78T): (a) budding cells in YM broth after 3 days at 25 °C; (b) pseudoconidia formed on CMA after 3 days at 25 °C. Bars, 10 μm.
singly, in pairs or in groups (Fig. 3a). Budding is multilateral. After growth on YM agar at 25 °C for 3 days, the streak culture is greyish white, smooth, soft to butyrous with entire margin. Pseudohyphae are formed in slide or streak culture after 3 days. Budding is not observed on YM agar after 3 days at 25 °C. Cells in YM broth after 3 days at 25 °C are coarse, in pairs or in groups (Fig. 3a). Cells on YM agar after 3 days at 25 °C are typically singly, in pairs or in groups (Fig. 3a). Budding is multilateral. After growth on YM agar at 25 °C for 3 days, the streak culture is greyish white, smooth, soft to butyrous with entire margin. Pseudohyphae are formed in slide culture on YM agar, CMA and PDA after 3 days at 25 °C (Fig. 3b) but true hyphae are not formed in slide culture on those agar media after 21 days at 25 °C. Ascospores are not produced on YM agar, acetate agar, 5 % malt extract agar, CMA, Gorodkowa agar or Fowell’s acetate agar at 15 or 25 °C for 4 weeks. Fermentation of D-glucose is positive but negative for D-galactose, sucrose, maltose, lactose, trehalose and raffinose. Assimilates D-glucose, D-galactose, L-sorbose (slowly), sucrose, maltose, cellobiose, trehalose, melibiose, raffinose, melezitose, soluble starch (weakly), D-xylose, L-arabinose, D-arabinose, D-ribose, L-rhamnose, ethanol, glycerol, erythritol, ribitol, D-mannitol, D-glucitol (latent), methyl α-D-glucoside, salicin, DL-lactic acid, succinic acid, citric acid, xylitol, L-arabitol and D-glucosamine, but not lactose, inulin, galactitol, D-glucosono-Δ-lactone, D-glucuronate, D-galacturonate, 2-keto-D-glucuronate, 5-keto-D-gluconate, inositol or hexadecane. Ethylamine-HCl, L-lysine-HCl and cadaverine are assimilated, but nitrate and nitrite are negative. Growth occurs on media containing 10 % NaCl/5 % glucose, 15 % NaCl/5 % glucose (weakly) and 50 % glucose but not on media containing 60 % glucose, 0.01 % cyclohexemide or 0.1 % cyclohexemide. Grows at 25, 30, 35, 37 and 40 °C but not at 42 °C. Acid formation from glucose is positive. Starch-like compounds are not produced. Diazonium blue B and urease reactions are negative. The major ubiquinone is Q-9.

Strain YE170T (=BCC 63466T=NBRC 110423T=CBS 13384T) is the holotype of *Y. epiphylla* f.a., sp. nov. (MycoBank accession number MB810547). The strain was isolated from the surfaces of rice leaves collected from Nonthaburi province, Thailand. The culture is maintained by freezing and/or lyophilization.

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