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SHORT COMMUNICATION

Limtongia gen. nov. for *Zygozyma smithiae* (Lipomycetaceae)

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Abstract Teleomorphic species of the genus *Zygozyma* and anamorphic species of the genus *Myxozyma* were examined phylogenetically. In phylogenetic trees based on 18S rRNA-, 26S rRNA-, mitochondrial small subunit rRNA- and EF-1α-gene sequences and concatenated sequences of the latter four regions, derived from the neighbor-joining method, the four species of the genus *Zygozyma* constituted four clusters, respectively, with low bootstrap values, indicating that all four species can be distinguished from one another at the generic level. The name of *Limtongia* was newly suggested for *Zygozyma smithiae*, and *Limtongia smithiae* was proposed as new combination.

Keywords Lipomycetaceous yeast · *Limtongia* gen. nov. · *Limtongia smithiae* comb. nov. · Phylogeny · *Zygozyma smithiae*

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Introduction

The genus *Zygozyma* van der Walt et von Arx was introduced with a single species, *Zygozyma oligophaga* van der Walt et von Arx (van der Walt et al. 1987). Subsequently, the following three species were described: *Zygozyma arxii* van der Walt, Smith et Yamada (van der Walt et al. 1989), *Zygozyma suomiensis* Smith, van der Walt et Yamada (Smith et al. 1989) and *Zygozyma smithiae* van der Walt, Wingfield et Yamada (van der Walt et al. 1990). In total, four species have been proposed in the Lipomycetaceous yeasts.

The genus *Zygozyma* was characterized morphologically by producing allantoid to cymbiform ascospores, and physiologically by producing extracellular amyloid material (Smith 1998b; van der Walt et al. 1987). Yamada and Nogawa (1990, 1995a) had already determined the partial sequences of 18S and 26S rRNAs of Lipomycetaceous yeasts, and found that *Zygozyma oligophaga* holds a unique phylogenetic position in three regions of determined sequence within the 18S and 26S rRNAs. The results obtained suggested that the genus *Zygozyma* should be restricted to only the species *Zygozyma oligophaga*, the type species of the genus *Zygozyma*, and the remaining three species of the genus should be divided into two or more taxa.

This paper proposes *Limtongia* as a new genus for *Zygozyma smithiae*, with the new combination of *Limtongia smithiae* by use of phylogenetic, genetic, chemotaxonomic and phenotypic data.

Materials and methods

All the sequence data used in this study were cited in Kurtzman and Robnett (2003) and Kurtzman et al. (2007,

2008). The base sequences of 18S rRNA genes, 26S rRNA genes, EF-1α genes and mitochondrial small subunit rRNA genes obtained were aligned either in pairs or as a group. Multiple alignments were performed with the program Clustal X (version 1.8, Thompson et al. 1997). Alignment gaps and unidentified bases were eliminated. Distance matrices for the aligned sequences were calculated by the two-parameter method of Kimura (1980). Phylogenetic trees were constructed by the neighbor-joining method (Saitou and Nei 1987). The robustness of individual branches was estimated by bootstrapping with 1,000 replications (Felsenstein 1985) using the program MEGA (version 4.0, Tamura et al. 2007). The type strains of *Saccharomyces cerevisiae*, *Kluyveromyces polysporus* (= *Vanderwaltozyma polysporus*), *Kuraishia capsulata* and *Citeromyces matritensis* were used as outgroups.

Result and discussion

Phylogenetic trees of *Zygozyma* and *Myxozyma* species based on 18S rRNA-, 26S rRNA-, mitochondrial small subunit rRNA- and EF-1α-gene sequences, as well as concatenated sequences of the latter four regions, were constructed by the neighbor-joining method (Fig. 1).

In the phylogenetic tree based on 18S rRNA gene sequences (Fig. 1a), the type strain of *Zygozyma suomiensis* (Q-8) and the type strains of some *Myxozyma* species constituted a small cluster with a bootstrap value of 100%. On the other hand, the type strain of *Zygozyma smithiae* (Q-9) was connected to the type strains of the *Myxozyma* species with a bootstrap value of 48%, and the resulting cluster was then connected to the type strain of *Zygozyma arxii* (Q-9; = *Kawasakia arxii*) with a bootstrap value of 52%. Between the cluster containing *Zygozyma suomiensis* and the clusters containing *Zygozyma smithiae* and *Zygozyma arxii*, the calculated bootstrap value was 59%. The type strain of *Zygozyma oligophaga* (Q-8), the type species of the genus *Zygozyma*, was located on outermost branch of the phylogenetic tree. The calculated bootstrap values were 100 and 59%. The phylogenetic branches among the resulting clusters of the respective *Zygozyma* species were almost similar in length to that between the type strains of *Kuraishia capsulata* and *Citeromyces matritensis*, and much longer than that between the type strains of *Saccharomyces cerevisiae* and *Kluyveromyces polysporus* (= *Vanderwaltozyma polysporus*). The results obtained suggest that all four *Zygozyma* species can be distinguished from one another phylogenetically at the generic level.

In the phylogenetic tree based on 26S rRNA gene sequences (Fig. 1b), the type strain of *Zygozyma suomiensis* and the type strains of *Myxozyma* species constituted a cluster with a bootstrap value of 100%. The type strain of *Zygozyma oligophaga* was connected to the cluster with a bootstrap value of 83%. However, the phylogenetic branch of *Zygozyma oligophaga* was quite far from the type strain of *Zygozyma suomiensis*. The type strains of *Zygozyma arxii* and *Zygozyma smithiae* were connected to each other with a bootstrap value of 69%. The results obtained suggest that *Zygozyma suomiensis* is phylogenetically independent from *Zygozyma oligophaga* as well as *Zygozyma arxii* and *Zygozyma smithiae*.

Fig. 1 a–e Phylogenetic relationships of *Zygozyma* species. The phylogenetic trees are based on 18S rRNA gene sequences of 1,622 bases (**a**), 26S rRNA gene sequences of 3,013 bases (**b**), mitochondrial small subunit rRNA gene sequences of 147 bases (**c**), EF-1α gene sequences of 654 bases (**d**), and concatenated sequences of 18S rRNA-, 26S rRNA-, EF-1α- and mitochondrial small subunit rRNA-genes of 5,436 bases (**e**), and were constructed by the neighbor-joining method. Numerals at nodes indicate bootstrap values (%) derived from 1,000 replications

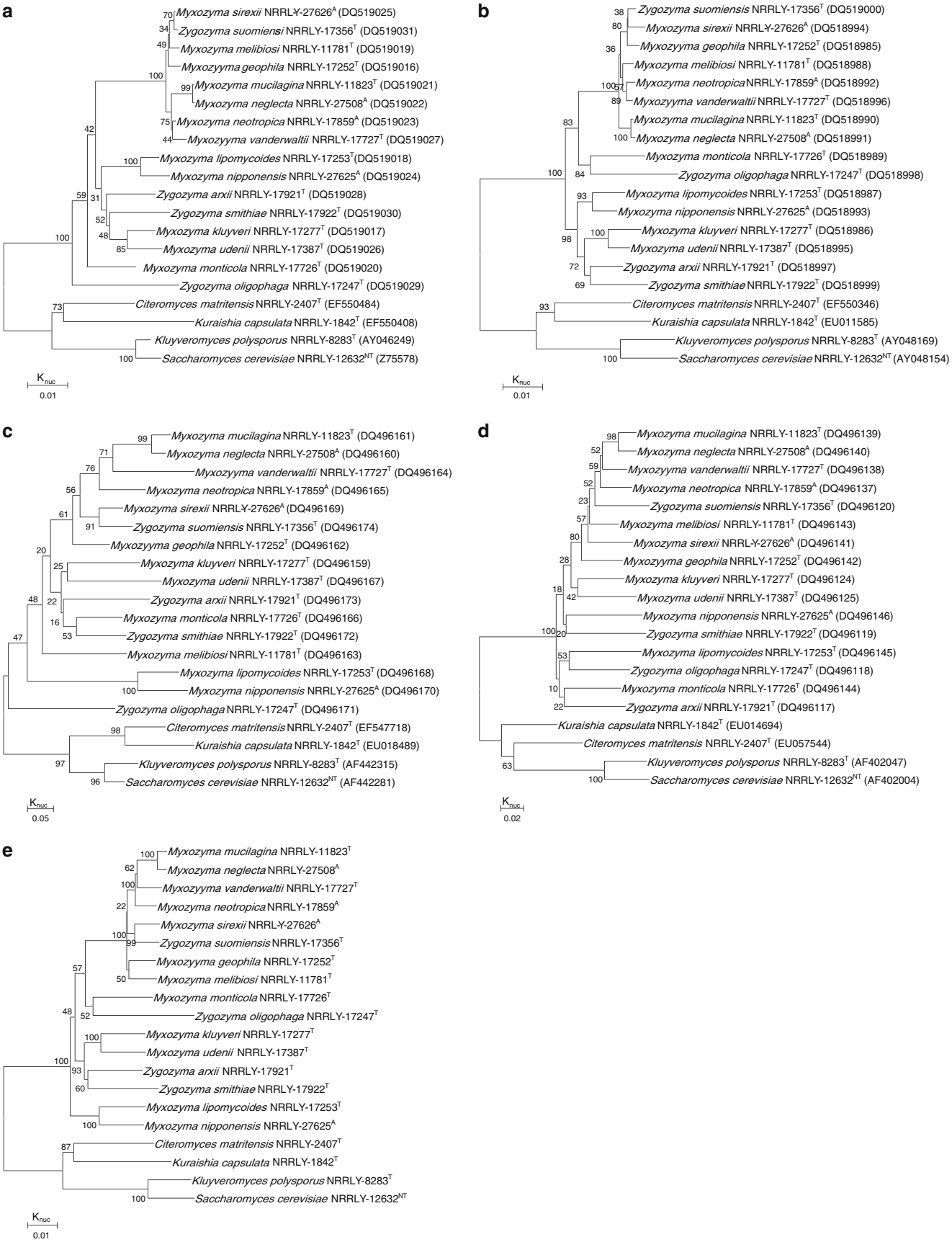
In the phylogenetic tree based on mitochondrial small subunit rRNA gene sequences (Fig. 1c), the type strains of *Zygozyma suomiensis*, *Zygozyma arxii*, *Zygozyma smithiae* and *Zygozyma oligophaga* constituted their respective clusters with quite low bootstrap values of 16, 20, 48, 47% and so on. The phylogenetic branches among the resulting clusters of the respective *Zygozyma* species were almost similar in length to that between the type strains of *Kuraishia capsulata* and *Citeromyces matritensis*, and much longer than that between the type strains of *Saccharomyces cerevisiae* and *Kluyveromyces polysporus*.

In the phylogenetic tree based on EF-1α gene sequences (Fig. 1d), the type strains of the four *Zygozyma* species constituted their respective clusters independently, with calculated bootstrap values of 10, 18 and 100%.

In the phylogenetic tree based on the concatenated sequences of 18S rRNA genes, 26S rRNA genes, the EF-1α genes and mitochondrial small subunit rRNA genes (Fig. 1e), the type strains of *Zygozyma oligophaga* and *Zygozyma suomiensis* were connected with a bootstrap value of 57%. The type strains of *Zygozyma arxii* and *Zygozyma smithiae* were connected to each other with a bootstrap value of 60%.

In all the five kinds of phylogenetic trees constructed, it is obvious that the four species of the genus *Zygozyma* were phylogenetically independent from one another and *Zygozyma smithiae* was distinguished phylogenetically from the remaining three species of the genus *Zygozyma*.

Kurtzman et al. (2007) constructed a phylogenetic tree based on the concatenated sequences from the nearly entire 18S rRNA, 26S rRNA, mitochondrial small subunit rRNA and the EF-1α genes and showed that the family Lipomycetaceae, including the genera *Lipomyces*, *Dipodascopsis*, *Zygozyma* and *Babjevia*, has a monophyletic lineage since the bootstrap value of 100% was calculated between the cluster including *Babjevia anomala* and


a
Myxozyma sirexii NRRLY-27626A (DQ519025)
Zygozyma suomiensi NRRLY-17356T (DQ519031)
Myxozyma melibiosi NRRLY-11781T (DQ519019)
Myxozyyma geophila NRRLY-17252T (DQ519016)
Myxozyma mucilagina NRRLY-11823T (DQ519021)
Myxozyma neglecta NRRLY-27508A (DQ519022)
Myxozyma neotropica NRRLY-17859A (DQ519023)
Myxozyyma vanderwaltii NRRLY-17727T (DQ519027)
Myxozyma lipomycoides NRRLY-17253T(DQ519018)
Myxozyma nipponensis NRRLY-27625A (DQ519024)
Zygozyma arxii NRRLY-17921T (DQ519028)
Zygozyma smithiae NRRLY-17922T (DQ519030)
Myxozyma kluyveri NRRLY-17277T (DQ519017)
Myxozyma udenii NRRLY-17387T (DQ519026)
Myxozyma monticola NRRLY-17726T (DQ519020)
Zygozyma oligophaga NRRLY-17247T (DQ519029)
Citeromyces matritensis NRRLY-2407T (EF550484)
Kuraishia capsulata NRRLY-1842T (EF550408)
Kluyveromyces polysporus NRRLY-8283T (AY046249)
Saccharomyces cerevisiae NRRLY-12632NT (Z75578)
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b
Zygozyma suomiensis NRRLY-17356T (DQ519000)
Myxozyma sirexii NRRLY-27626A (DQ518994)
Myxozyyma geophila NRRLY-17252T (DQ518985)
Myxozyma melibiosi NRRLY-11781T (DQ518988)
Myxozyma neotropica NRRLY-17859A (DQ518992)
Myxozyyma vanderwaltii NRRLY-17727T (DQ518996)
Myxozyma mucilagina NRRLY-11823T (DQ518990)
Myxozyma neglecta NRRLY-27508A (DQ518991)
Myxozyma monticola NRRLY-17726T (DQ518989)
Zygozyma oligophaga NRRLY-17247T (DQ518998)
Myxozyma lipomycoides NRRLY-17253T (DQ518987)
Myxozyma nipponensis NRRLY-27625A (DQ518993)
Myxozyma kluyveri NRRLY-17277T (DQ518986)
Myxozyma udenii NRRLY-17387T (DQ518995)
Zygozyma arxii NRRLY-17921T (DQ518997)
Zygozyma smithiae NRRLY-17922T (DQ518999)
Citeromyces matritensis NRRLY-2407T (EF550346)
Kuraishia capsulata NRRLY-1842T (EU011585)
Kluyveromyces polysporus NRRLY-8283T (AY048169)
Saccharomyces cerevisiae NRRLY-12632NT (AY048154)
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c
Myxozyma mucilagina NRRLY-11823T (DQ496161)
Myxozyma neglecta NRRLY-27508A (DQ496160)
Myxozyyma vanderwaltii NRRLY-17727T (DQ496164)
Myxozyma neotropica NRRLY-17859A (DQ496165)
Myxozyma sirexii NRRLY-27626A (DQ496169)
Zygozyma suomiensis NRRLY-17356T (DQ496174)
Myxozyyma geophila NRRLY-17252T (DQ496162)
Myxozyma kluyveri NRRLY-17277T (DQ496159)
Myxozyma udenii NRRLY-17387T (DQ496167)
Zygozyma arxii NRRLY-17921T (DQ496173)
Myxozyma monticola NRRLY-17726T (DQ496166)
Zygozyma smithiae NRRLY-17922T (DQ496172)
Myxozyma melibiosi NRRLY-11781T (DQ496163)
Myxozyma lipomycoides NRRLY-17253T (DQ496168)
Myxozyma nipponensis NRRLY-27625A (DQ496170)
Zygozyma oligophaga NRRLY-17247T (DQ496171)
Citeromyces matritensis NRRLY-2407T (EF547718)
Kuraishia capsulata NRRLY-1842T (EU018489)
Kluyveromyces polysporus NRRLY-8283T (AF442315)
Saccharomyces cerevisiae NRRLY-12632NT (AF442281)
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Myxozyma mucilagina NRRLY-11823T (DQ496139)
Myxozyma neglecta NRRLY-27508A (DQ496140)
Myxozyyma vanderwaltii NRRLY-17727T (DQ496138)
Myxozyma neotropica NRRLY-17859A (DQ496137)
Zygozyma suomiensis NRRLY-17356T (DQ496120)
Myxozyma melibiosi NRRLY-11781T (DQ496143)
Myxozyma sirexii NRRLY-27626A (DQ496141)
Myxozyyma geophila NRRLY-17252T (DQ496142)
Myxozyma kluyveri NRRLY-17277T (DQ496124)
Myxozyma udenii NRRLY-17387T (DQ496125)
Myxozyma nipponensis NRRLY-27625A (DQ496146)
Zygozyma smithiae NRRLY-17922T (DQ496119)
Myxozyma lipomycoides NRRLY-17253T (DQ496145)
Zygozyma oligophaga NRRLY-17247T (DQ496118)
Myxozyma monticola NRRLY-17726T (DQ496144)
Zygozyma arxii NRRLY-17921T (DQ496117)
Kuraishia capsulata NRRLY-1842T (EU014694)
Citeromyces matritensis NRRLY-2407T (EU057544)
Kluyveromyces polysporus NRRLY-8283T (AF402047)
Saccharomyces cerevisiae NRRLY-12632NT (AF402004)
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Myxozyma mucilagina NRRLY-11823T
Myxozyma neglecta NRRLY-27508A
Myxozyyma vanderwaltii NRRLY-17727T
Myxozyma neotropica NRRLY-17859A
Myxozyma sirexii NRRLY-27626A
Zygozyma suomiensis NRRLY-17356T
Myxozyyma geophila NRRLY-17252T
Myxozyma melibiosi NRRLY-11781T
Myxozyma monticola NRRLY-17726T
Zygozyma oligophaga NRRLY-17247T
Myxozyma kluyveri NRRLY-17277T
Myxozyma udenii NRRLY-17387T
Zygozyma arxii NRRLY-17921T
Zygozyma smithiae NRRLY-17922T
Myxozyma lipomycoides NRRLY-17253T
Myxozyma nipponensis NRRLY-27625A
Citeromyces matritensis NRRLY-2407T
Kuraishia capsulata NRRLY-1842T
Kluyveromyces polysporus NRRLY-8283T
Saccharomyces cerevisiae NRRLY-12632NT
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Dipodascopsis tothii and the cluster including *Dipodascopsis uninucleata* and *Lipomyces* and *Zygozyma* species. On the basis of these findings, the family Lipomycetaceae was monophyletic, and thus the genus *Zygozyma* was transferred to the genus *Lipomyces* to construct the genus *Lipomyces* Lodder et Kreger van-Rij emend. Kurtzman et al. However, the emended genus *Lipomyces* was in fact not monophyletic but polyphyletic, since the calculated bootstrap values at the branching points in the phylogenetic tree were quite low within the emended genus. For example, the type strain of *Zygozyma arxii* (= *Kawasakia arxii*) showed an independent cluster, and the calculated bootstrap value at the branching point was quite low, since there was no indication of any numeral for the bootstrap value, and the type strain of *Zygozyma smithiae* was quite distant phylogenetically from the type strain of *Zygozyma arxii*. These facts suggested that the taxonomic subdivision of the emended genus would be possible from the phylogenic point of view.

The teleomorphic genus *Lipomyces* Lodder et Kreger-van Rij emend. Kurtzman et al. has an extremely wide range of DNA base composition. The calculated DNA G+C contents of the emended genus were estimated to be from 41.5 to 55.7 mol%, with a range of 14.2 mol% (Smith 1998a, b). According to Nakase and Komagata (1970), such an emended genus that is genetically diverse has a heterogeneous nature taxonomically. Chemotaxonomically, the emended genus has three kinds of isoprenoid quinone homologs (Smith 1998a, b; Yamada 1986; Yamada et al. 1986), suggesting that the emended genus is also taxonomically heterogeneous, as found in the genus *Pichia* Hansen emend. Kurtzman (Kurtzman 1984; Yamada and Kondo 1972; Yamada et al. 1973). These genetic and chemotaxonomic data indicated that the emended genus *Lipomyces* is subject to be divided into several genera that have smaller generic circumscriptions, as already performed in the genus *Pichia* Hansen emend. Kurtzman (Billon-Grand 1989; Kurtzman and Suzuki 2010; Kurtzman et al. 2008).

Upon subdivision of the genus *Lipomyces* Lodder et Kreger-van Rij emend. Kurtzman et al., the genera *Waltomyces* Yamada et Nakase (Yamada and Nakase 1985), *Babjevia* van der Walt et Smith (Smith et al. 1995), *Smithiozyma* van der Walt, Kock et Yamada (Kock et al. 1995) and *Kawasakia* Yamada et Nogawa (Yamada and Nogawa 1995b)—all names that were not accepted by Kurtzman et al. (2007)—should be retained. And additional new genera can be proposed.

The four species of the genus *Zygozyma* that were proved to have long phylogenetic distances and low bootstrap values at the branching points, respectively, in the phylogenetic trees are enough to constitute respective genera, as suggested previously (Yamada and Nogawa 1995a) (Fig. 1).

Genetically, the range of DNA G+C content of the genus *Zygozyma* was 14.0 mol% from 41.7 to 55.7 mol% for the only four species, and *Zygozyma smithiae* is unique, which was 55.7 mol% G+C in the type strain and much higher than those (41.7–47.4 mol% G+C) of the type strains of the remaining three species (Smith 1998b). Chemotaxonomically, *Zygozyma smithiae* is characterized by Q-9, which was able to discriminate the species from the Q-8-equipped species, *Zygozyma oligophaga* and *Zygozyma suomiensis*. Morphologically, the Q-9-equipped *Zygozyma smithiae* is able to be discriminated from the Q-9-equipped *Zygozyma arxii* by the presence of plasmodesmal cannals in cells (van der Walt et al. 1991). These genetic, chemotaxonomic and morphological characteristics are enough to distinguish *Zygozyma smithiae* at the generic level, and the species can appropriately be classified in a separate new genus. The name of the genus is *Limtongia* gen. nov.

Limtongia Jindamorakot, Am-in, Yukphan et Yamada gen. nov.

Genus ad Lipomycetaceae pertinens. Cellulae incapsulatae, globosae, ellipsoideae vel ovoideae, singularae vel binae, gemmantes multilateraliter. Asci non juncti, affixi, globosi, allantoideae amoeboidei, multispori, evanescentes, oriundi intercalaritaer vel terminariter per transformationem directas cellularum singularum vegetativarum aggregatarum. Ascosporae allantoideae vel cymbiformes, glabrae, succinae, conglutinantes ubi liberatae. Fermentatio abest. D-Glucosum, D-xylosum, D-xylitolum, glycerolum, acidum 2-keto-D-gluconicum, acidum 5-keto-D-gluconicum et sucrosum assimilantur. D-Galactosum, L-sorbosum, D-arabinosum, L-arabinosum, D-mannitolum, D-sorbitolum, L-arabitolum, D-ribitolum, maltosum, lactosum, melibiosum, trehalosum et raffinosum non assimilantur. Nitras kali non assimilatur. Systema coenzymatis Q-9 adest. Proportio guanini+cytosini deoxiribonucleati 55.3–55.7 mol%.

Species typica: *Limtongia smithiae* (van der Walt, Wingfield et Yamada) Jindamorakot, Am-in, Yukphan et Yamada comb. nov.

Genus belongs to Lipomycetaceae. Cells are encapsulated, globose, ellipsoid or ovoid, occurring singly or in pairs, budding multilaterally. Asci are unconjugated, attached, globose, allantoid or amoeboid, multispored, evanescent, arising by direct transformation of single vegetative cells aggregated. Ascospores are allantoid to cymbiform, glabrous, amber-coloured and conjugated when liberated. Fermentation is absent. D-Glucose, D-xylose, D-xylitol, glycerol, 2-keto-D-gluconic acid, 5-keto-D-gluconic acid and sucrosum are assimilated. D-Galactose, L-sorbose, D-arabinose, L-arabinose, D-mannitol, D-sorbitol, L-arabitol, D-ribitol, maltose, lactose, melibiose, trehalose and raffinose

are not assimilated. Potassium nitrate is not assimilated. Coenzyme Q-9 system is present. Guanine+cytosine contents of DNA are 55.3–55.7 mol%.

Type species: *Limtongia smithiae* (van der Walt, Wingfield et Yamada) Jindamorakot, Am-in, Yukphan et Yamada comb. nov.

Basionym: *Zygozyma smithiae* van der Walt, Wingfield et Yamada, Antonie van Leeuwenhoek 58: 96, 1990.

Typus: CBS 7407.

Etymology: the genus is named in honor of Dr. Savitree Limtong, Professor, Department of Microbiology, Kasaetsart University, Bangkok, Thailand for her contributions to yeast systematics.

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