Microbial Stematics

The Revision of Lipomycetaceae*

Yuzo Yamada,[1,4,]** Huong Thi Lan Vu,[2] Pattaraporn Yukphan,[1] Somboon Tanasupawat,[3]

[1]BIOTEC Culture Collection (BCC), National Center for Genetic Engineering and Biotechnology (BIOTEC), National Science and Technology Development Agency (NSTDA), 113 Thailand Science Park, Phaholyothin Road, Klong 1, Klong Luang, Pathumthani 12120, Thailand
[2]Department of Microbiology, Faculty of Biology and Biotechnology, University of Science, Vietnam National University-HCM City, 227 Nguyen Van Cu Street, Ward 4, District 5, Hochiminh City, Vietnam
[3]Department of Biochemistry and Microbiology, Faculty of Pharmaceutical Sciences, Chulalongkorn University, 254 Phayathai Road, Wangmai, Pathumwan, Bangkok 10330, Thailand
[4]Laboratory of Applied Microbiology (Professor Emeritus), Department of Agricultural Chemistry, Faculty of Agriculture, Shizuoka University, 836 Ohya, Suruga-ku, Shizuoka 422-8529, Japan

*This article is dedicated to Professor Dr. J. P. van der Walt, South Africa for his excellent taxonomic study on the Lipomycetaceous yeasts, especially in the findings of *Zygozyma oligophaga* and its related species.
*This work was presented at the 27th annual meeting of Japan Society for Microbial Resources and Systematics (JSMRS) on June 23-30, 2021 (Vu *et al*. 2021).

**Corresponding author:
Yuzo Yamada
E-mail: ymdy333@kdt.biglobe.ne.jp
ORCID, 0000-0002-2799-7045
Telephone: +81-54-635-2316

Keywords: *Waltomyces*; *Zygozyma*; *Babjevia*; *Smithiozyma*; *Kockiozyma*

ABSTRACT

In the family Lipomycetaceae, the seven genera *Waltomyces*, *Zygozyma*, *Babjevia*, *Smithiozyma*, *Kawasakia*, *Limtongia*, and *Kockiozyma* were introduced. However, all of them were neither accepted nor recognized. This paper described the historical surveys in the systematics of the Lipomycetaceous yeasts and confirmed the total of ten genera within the family, i.e., the genus *Lipomyces* sensu stricto (the type genus), the above-

mentioned seven genera, the monotypic genus *Dipodascopsis*, and the new genus *Neeoaidaea* from the phylogenetic and the phenotypic points of view.

GRAPHICAL ABSTRACT

The family Lipomycetaceae Novak et Zolt

Genus	Species
1. *Lipomyces* Lodder et Kreger-van Rij (1952) sensu stricto	*L. starkeyi* (the type species), *L. kononenkoae*, *L. tetrasporus*, *L. mesenbrius*, *L. spencermartinsiae*, *L. dorenjongii*, *L. kockii*, *L. yamadae*, *L. yarrowii*, *L. orientalis*, *L. chichibuensis*, *L. kalimanthanensis*, *L. tropicalis*, *L. okinawaensis*
2. *Dipodascopsis* Batra et Millner (1978)	*D. uninucleata*
3. *Waltomyces* Yamada et Nakase (1985)	*W. lipofer*
4. *Zygozyma* van der Walt et von Arx (1987)	*Z. oligophaga*
5. *Babjevia* van der Walt et Smith (1995)	*B. anomala* (the type species), *B. hyphoforaminiformans*, *B. hyphasca*
6. *Smithiozyma* Kock, van der Walt et Yamada (1995)	*S. japonica*
7. *Kawasakia* Yamada et Nogawa (1995)	*K. arxii*
8. *Limtongia* Jindamorakot, Am-in, Yukphan et Yamada (2011)	*L. smithiae*
9. *Kockiozyma* Jindamorakot, Yukphan et Yamada (2012)	*K. suomiensis*
10. *Neoaidaea* Vu, Yukphan, Tanasupawat et Yamada (202/)	*N. tothii*

The family Lipomycetaceae Novak et Zolt

Genus	Species
1. *Lipomyces* Lodder et Kreger-van Rij (1952) sensu Kurtzman, Albertyn et Basehoar-Powers (2007)	*L. starkeyi* (the type species), *L. kononenkoae*, *L. tetrasporus*, *L. mesenbrius*, *L. spencermartinsiae*, *L. dorenjongii, L. kockii*, *L. yamadae*, *L. yarrowii*, *L. orientalis*, *L. chichibuensis*, *L. kalimanthanensis*, *L. tropicalis*, *L. okinawaensis* (= the genus *Lipomyces* sensu stricto); *L. lipofer*, *L. oligophagus*, *L. japonicus*, *L. arxii*, *L. smithiae*, *L. suomiensis*
2. *Dipodascopsis* Batra et Millner (1978) emend. Kurtzman, Albertyn et Basehoar-Powers (2007)	*D. uninucleata* (the type species), *D. tothii*, *D. anomala*

In the family Lipomycetaceae Novak et Zsolt, the seven genera *Waltomyces*, *Zygozyma*, *Babjevia*, *Smithiozyma*, *Kawasakia*, *Limtongia*, and *Kockiozyma* were once introduced (Yamada and Nakase 1985; van der Walt *et al*. 1987; Smith *et al.* 1995; Kock *et al*. 1995; Yamada and Nogawa 1995b; Jindamorakot *et al*. 2011, 2012). All of them were respectively taxonomic-homogeneous natured, i.e., morphologically, physiologically, chemotaxonomically, genetically, and phylogenetically. However, Kurtzman *et al*. (2007) divided the family into two, i.e., the monophyletic genus *Lipomyces* sensu and the paraphyletic genus *Dipodascopsis* emend. instead (Smith and de Hoog 2011; Smith and Kurtzman 2011).

This paper describes the historical surveys in the systematics of the Lipomycetaceous yeasts and covers the seven genera mentioned above as taxonomic criteria, in addition to the genus *Lipomyces* sensu stricto, the monotypic genus *Dipodascopsis* (Jindamorakot *et al*. 2011, 2012), and the new genus *Neoaidaea* (Vu *et al*. 2021) from the phylogenetic and the phenotypic points of view. Accordingly, the family is comprised of ten genera in total as follows.

The family Lipomycetaceae Novak et Zsolt
The type genus is *Lipomyces* Lodder et Kreger van-Rij.
Ten genera are included.

Genus I. *Lipomyces* Lodder et Kreger-van Rij sensu stricto
The type species is *Lipomyces starkeyi* Lodder et Kreger-van Rij.
Fourteen species are included.
1. *Lipomyces starkeyi* Lodder et Kreger-van Rij (1952)
2. *Lipomyces kononenkoae* Nieuwdorp, Bos et Slooff (1974)
3. *Lipomyces tetrasporus* Nieuwdorp, Bos et Slooff (1974)
4. *Lipomyces mesembrius* Botha, van der Walt et Smith (1997)
5. *Lipomyces spencermartinsiae* (van der Walt et Smith) van der Walt et Smith (1997)
Basionym: *Lipomyces kononenkoae* Nieuwdorp, Bos et Slooff subsp. *spencermartinsiae* van der Walt et Smith (1995)
6. *Lipomyces doorenjongii* van der Walt et Smith (1999)
7. *Lipomyces kockii* Smith et van der Walt (1999)
8. *Lipomyces yamadae* van der Walt et Smith (1999)
9. *Lipomyces yarrowii* Smith et van der Walt (1999)
10. *Lipomyces orientalis* Thanh (2006)
11. *Lipomyces chichibuensis* Yamazaki et Kawasaki (2014)
12. *Lipomyces kalimantanensis* Kanti, Yamazaki et Kawasaki (2017)
13. *Lipomyces tropicalis* Kanti, Yamazaki et Kawasaki (2017)
14. *Lipomyces okinawensis* Yamazaki, Yanagiba et Naganuma (2017)

The species classified in the genus *Lipomyces* sensu stricto were tightly coupled with one another in all the three phylogenetic trees based on the concatenated four-gene sequences of 18S rRNA, 26S rRNA, mitochondrial small subunit rRNA, and *EF1-α* derived from the neighbour-joining, the maximum parsimony, and the maximum likelihood methods (Jindamorakot *et al*. 2012). On the other hand, the phylogenetic positions of the *Lipomyces* species newly designated by Kurtzman *et al*. (2007) were quite changeable in the monophyletic genus *Lipomyces* sensu (Jindamorakot *et al*. 2012). In fact, the resulting genus has an extremely wide range of DNA G+C contents (14.2 mol%, from 41.5 - 55.7 mol% G+C; Jindamorakot *et al*., 2012) and three kinds of ubiquinone isoprenologues (Q-8, Q-9, and Q-10: Yamada 1986; Yamada *et al*. 1986). According to Nakase and Komagata (1970) and Yamada *et al.* (1973), such a genus was a taxonomically heterogeneous-natured taxon, just as found in the genus *Pichia* Hansen once designated.

Genus II. *Dipodascopsis* Batra et Millner

Dipodascopsis uninucleata (Biggs) Batra et Millner (1978)

Basionym: *Dipodascus uninucleatus* Biggs (1937).

Two varieties are described.

1. *Dipodascopsis uninucleata* var. *uninucleata*
2. *Dipodascopsis uninucleata* var. *wickerhamii* Kreger-van Rij (1974)

When the phylogenetic tree based on the 26S rRNA gene D1/D2 domain sequences was constructed by the neighbour-joining method, the paraphyletic genus *Dipodascopsis* emend. Kurtzman et al. was split into two and produced a monotypic genus (Fig. 1), as reported previously (Jindamorakot *et al*. 2011, 2012), indicating that *D. uninucleata*, *D. tothii* and *D. anomala* were not tightly coupled within the genus *Dipodascopsis* emend.

Such a phylogenetic data was also given by Kurtzman (2011), i.e., the phylogenetic tree based on the concatenated three-gene sequences of 26S rRNA, 18S rRNA, and *EF1-α* derived from the neighbour-joining method represented that *D. uninucleata* was connected first to *L. starkeyi* but not to *D. anomala* (= *B. anomala*) and then the resulting cluster was done to *D. anomala*. In fact, the calculated sequence similarity (95.7%) between *D. uninucleta* and *L. starkeyi* was much higher than that (90.4%) between *D. uninucleara* and *B. anomala* (Table 1).

Genus III. *Waltomyces* Yamada et Nakase (MB 25779)

Waltomyces lipofer (Lodder et Kreger-van Rij ex Slooff) Yamada et Nakase (1985) (MB 103899)

Basionym: *Lipomyces lipofer* Lodder et Kreger-van Rij (1952) ex Slooff (1970).

The three partial base sequencings in positions 468-622, 155 bases (designated as region *a*) and in positions 1611-1835, 225 bases (designated as region *b*) of 26S rRNA and in positions 1451-1618, 168 bases (designated as region *c*) of 18S rRNA showed that the Q10-equipped species, *W. lipofer* had 88% maximum homology in region *a*, along with *B.*

anomala (= *D. anomala*), to *L. starkeyi*, *L. tetrasporus* and *L. kononenkoae* in the genus *Lipomyces* sensu stricto (Yamada and Nogawa 1995a). In contrast, the above-mentioned three *Lipomyces* species constituted a cluster with 97% or more maximum homologies within the genus, indicating that the species is accommodated to a different genus from the genus *Lipomyces* sensu stricto (Table 1). Such similar experimental data were shown, since the species was used as outgroup in the phylogenetic trees concerned (Kurtzman *et al*. 2007; Yamazaki and Kawasaki 2014).

Genus IV. *Zygozyma* van der Walt et von Arx (MB 25149)

Zygozyma oligophaga van der Walt et von Arx (1987) (MB 131108)

Synonym: *Lipomyces oligophagus* (van der Walt et von Arx) Kurtzman, Albertyn et Basehoar-Powers (2007).

Four *Zygozyma* species were reported (van der Walt *et al*. 1987, 1989b, 1990; Smith *et al*. 1989). However, the four species were not tightly coupled with one another in the phylogenetic trees based on the concatenated four-gene sequences derived from the three methods, i.e., the neighbour-joining, the maximum parsimony, and the maximum likelihood methods (Jindamorakot *et al*. 2012) and chemotaxonomically grouped into two based on the ubiquinone isoprenologues, i.e., Q-8 and Q-9 (Fig. 1) (Yamada and Nogawa 1995a; Jindamorakot *et al*. 2011, 2012). Especially, the Q8-equipped species, *Z. oligophaga* had extremely long branches (Fig. 1) (Jindamorakot *et al*. 2012) and quite low sequence similarities (81.6-86.6%) (Table 1).

Genus V. *Babjevia* van der Walt et Smith (MB 27435)

The type species is *Babjevia anomala* (Babjeva et Gorin) van der Walt et Smith.

Three species are included.

1. *Babjevia anomala* (Babjeva et Gorin) van der Walt et Smith (1995) (MB 363215)

Basionym: *Lipomyces anomalus* Babjeva et Gorin (1975).

Synonym: *Dipodascopsis anomala* (Babjeva et Gorin) Kurtzman, Albertyn et Basehoar-Powers (2007).

2. *Babjevia hyphoforaminiformans* Yamazaki, Lorliam et Kawasaki (2020) (MB 829051)
3. *Babjevia hyphasca* Yamazaki, Lorliam et Kawasaki (2020) (MB 829053)

Kurtzman *et al*. (2007) accommodated *B. anomala* to the paraphyletic genus *Dipodascopsis* emend. as *D. anomala*. However, Jinamorakot *et al*. (2012) insisted that the species, *D. anomala* should be transferred again to the genus *Babjevia* as *B. anomala*, since the species was not tightly coupled with the type species, *D. uninucleata* (Fig. 1). In fact, Yamazaki *et al*. (2020) classified two new species to the genus *Babjevia* but not to the genus *Dipodascopsis*, as already suggested by Jindamorakot *et al*. (2012).

In the phylognetic tree based on the concatenated four-gene sequences derived from the maximum likelihood method (Yamazaki *et al*. 2020), it is reasonable that the names of species, *L. lipofer*, *L. smithiae*, *Zygozyma arxii* (= *L. arxii*), *L. japonicus*, *L. oligophaga* [sic], and *Zygozyma suomiensis* (= *L. suomiensis*) should be changed to *Waltomyces lipofer*, *Limtongia smithiae*, *Kawasakia arxii*, *Smithiozyma japonica*, *Zigozyma oligophaga*, and *Kockiozyma suomiensis* respectively since the generic name of *Babjevia* was revived.

Genus VI. *Smithiozyma* Kock, van der Walt et Yamada (MB 27638)

Smithiozyma japonica (van der Walt, Smith, Yamada et Nakase) Kock, van der Walt et Yamada (1995) (MB 414161)

Basionym: *Lipomyces japonicus* van der Walt, Smith, Yamada et Nakase (1989).

In the three partial base sequencings mentioned above, the Q9-equipped species, *S. japonica* (= *L. japonicus*; van der Walt *et al*. 1989a) represented 89% maximum homology in region *a*, two base differences in region *b* and five base differences in region *c* to *L. starkeyi*, *L. tetrasporus* and *L. kononenkoae* in the genus *Lipomyces* sensu stricto. In contrast, the above-mentioned three *Lipomyces* species constituted clusters with 97% or more maximum homologies (region *a*) and no base differences (regions *b* and *c*) within the genus (Yamada and Nogawa 1995a), indicating that the species is accommodated taxonomically to a different genus from the genus *Lipomyces* sensu stricto (Table 1). In the phylogenetic trees based on the concatenated four-gene sequences, *S. japonica* was not tightly coupled, i.e., the species was connected to the cluster comprised of the Q9-equipped species including *L. starkeyi*, *D. uninucleata* and so on, when constructed by the neighbour-joining method, but to the cluster of Q8-equipped species including *Z. oligophaga* and *Kockiozyma suomiensis*, when constructed by the maximum parsimony method (Jindamorakot *et al*. 2012).

Genus VII. *Kawasakia* Yamada et Nogawa (MB 27831)

Kawasakia arxii (van der Walt, Smith et Yamada) Yamada et Nogawa (1995) (MB 442988)

Basionym: *Zygozyma arxii* van der Walt, Smith et Yamada (1989).

Synonym: *Lipomyces arxii* (van der Walt, Smith et Yamada) Kurtzman, Albertyn et Basehoar-Powers (2007).

The Q9-equipped species, *Kawasakia arxii* was very unique in representing considerably large base differences (six) to the above-mentioned three *Lipomyces* species in the partial base sequencing of 18S rRNA (region *c*), in contrast to *W. lipofer*, which had only one base difference in the same region (Yamada and Nogawa 1995a, b). In the remaining regions *a* and *b*, the maximum homology and the base differences of the species were 93% and only one. The calculated 26S rRNA gene D1/D2 domain sequence similarities of *Kawasakia arxii* were 85.7 - 97.5% (Table 1). In the phylogenetic trees based on the concatenated four-gene sequences, the phylogenetic positions of *Kawasakia arxii* were considerably changeable, indicating that the species was not tightly coupled to any of other species (Jindamorakot *et al*. 2012).

Genus VIII. *Limtongia* Jindamorakot, Am-in, Yukphan et Yamada (MB 582716)

Limtongia smithiae (van der Walt, Wingfield et Yamada) Jindamorakot, Am-in, Yukphan et Yamada (2011) (MB 582717)

Basionym: *Zygozyma smithiae* van der Walt, Wingfield et Yamada (1990).

Synonym: *Lipomyces smithiae* (van der Walt, Wingfield et Yamada) Kurtzman, Albertyn et Basehoar-Powers (2007).

In the three partial base sequencings mentioned above, the Q9-equipped species, *Limtongia smithiae* represented 89% maximum homology, four base differences and three base differences respectively to *L. starkeyi*, *L. tetrasporus* and *L. kononenkoae* in the genus *Lipomyces* sensu stricto (Yamada and Nogawa 1995a). The calculated 26S rRNA gene D1/D2 domain sequence similarities of the species were 82.9 - 92.4%, indicating that the species is accommodated to an independent genus (Table 1).

Genus IX. *Kockiozyma* Jindamorakot, Yukphan et Yamada (MB 587737)

1. *Kockiozyma suomiensis* (Smith, van der Walt et Yamada) Jindamorakot, Yukphan et Yamada (2012) (MB 587754)

Basionym: *Zygozyma suomiensis* Smith, van der Walt et Yamada (1990).

Synonym: *Lipomyces suomiensis* (Smith, van der Walt et Yamada) Kurtzman, Albertyn et Basehoar-Powers (2007).

2. *Kockiozyma yamanashiensis* f.a. (Yamazaki, Yanagiba et Naganuma) comb. nov.

Basionym: *Lipomyces yamanashiensis* f.a. Yamazaki, Yanagiba et Naganuma, Int. J. Syst. Evol. Microbiol. 67, 2945, 2017.

The type strain is NBRC 110621^T = CBS 14748 ^{T}.

In the three partial base sequencings mentioned above, the Q8-equipped species, *Kockiozyma suomiensis* represented 83% maximum homology, 12 base differences and four base differences respectively to *L. starkeyi*, *L. tetrasporus* and *L. kononenkoae* in the genus *Lipomyces* sensu stricto (Yamada and Nogawa 1995a). The calculated 26S rRNA gene D1/D2 domain sequence similarities of the species were 85.9 - 90.6%, indicating that the species is accommodated to an independent genus (Table 1).

Dipodascopsis tothii and *B. anomala* (= *D. anomala*) were tightly coupled in the three phylogenetic trees (Jindamorakot *et al*. 2012), so that the two species appeared to be classified in a single genus (Fig. 1). Due to the priority of *B. anomala*, the single genus was to be named *Babjevia*. However, the distance between the two species, *D. tothii* and *B. anomala* was not so short, when compared with *Kluyveromyces polysporus* (=

Vanderwaltozyma polyspora) and *Saccharomyces cerevisiae* (Jindamorakot *et al*. 2012). In fact, the calculated pair-wise sequence similarity (95.6%) between the two species was interestingly almost the same as that (95.7%) between *D. uninucleata* and *L. starkeyi* and that (95.2%) between *W. lipofer* and *L. starkeyi* and not so high to accommodate the two species to the single genus *Babjevia* (Table 1), indicating that an additional genus can be phylogenetically introduced for *D. tothii*. Phenotypically, the species was quite different from *B. anomala*, e.g., in the morphology of asci and ascospores and the mode of asexual reproduction (Smith and de Hoog 2011).

Yamazaki *et al*. (2017a, b) constructed the phylogenetic trees based on the translation elongation factor 1-alpha (*EF1-α*) gene sequences derived from the neighbour-joining method. In the phylogenetic trees, it is of interest that *D. tothii* was found inside and distantly separated from *B. anomala* as well as *D. uninucleata*. In contrast, the cluster including *L. starkeyi* and its relatives and the cluster including *Kockiozyma suomiensis* and its related *Myxozyma* species were tightly coupled without any exception. In this respect, *D. tothii* was quite different phylogenetically from the remaining two species of the paraphyletic genus *Dipodascopsis* emend., and thus the introduction of a separate new genus was confirmed (Vu *et al*. 2021).

Genus X. *Neoaidaea* Vu, Yukphan, Tanasupawat et Yamada gen. nov.

Neoaidaea (Ne.o.a.i'da.e.a. N. L. fem. n. *Neoaidaea*, new Aida, in honour of Dr. Ko Aida, Professor Emeritus, The Institute of Applied Microbiology, The University of Tokyo, Tokyo, Japan, who introduced the isoprenoid quinone analyses into the microbial systematics.

The colonies are cream-coloured, moist and creamy after 10 d (Smith and de Hoog 2011). Budding cells are absent. Hyphae are firm with inflated cells and intensely amyloid. Arthroconidia are absent. Gametangia are formed laterally on hyphae as curved branches. Asci arise after fusion of a terminal cell with its penultimate cell. Asci are acicular, 50 - 100 μm long and contain 30 - 100 ascospores. Asci open by rupturing at the apex. Ascospores are subhyaline to hyaline, broadly ellipsoidal, occasionally bean-shaped, 1×1.5 - 2 μm and without slime. Fermentation is absent. Grows on glucose, inulin, sucrose, raffinose, galactose, lactose, trehalose, maltose, methyl-α-glucoside, starch, cellobiose, salicin, L-sorbose, xylose, arabinose, L-arabinose, ethanol, glycerol, ribitol, mannitol, glucitol, *myo*-inositol, succinate (w), and gluconate (v), but not on melibiose, L-rhamnose, ribose, methanol, erythritol, galactitol, and DL-lactate. No growth on vitamin-free medium (Smith and de Hoog 2011). Ubiquinone-9 (Q-9) is present (Cottrell and Kock 1989).

Mycobank number is MB/////////.

Neoaidaea tothii (Zolt 1963) Vu, Yukphan, Somboon et Yamada comb. nov.

Basionym: *Dipodascus tothii* Zolt (1963).

Synonym: *Dipodascopsis tothii* (Zolt 1963) Batra et Millner (1978).

The characteristics of the species are the same as those described in the genus (Smith and de Hoog 2011).

The holotype is CBS 759.85^T = NBRC 10813^T.

MycoBank number is MB/////////.

For the detailed characteristics of the taxa mentioned above and the type strains concerned, refer to the related monographs and/or articles.

Kurtzman (2003) introduced 'clade' or 'phylogenetic circumscribed genus' as generic concept. However, it was not yet perfect to get the taxonomic homogeneous-natured taxon for the genus. Namely, the branch lengths should be additionally considered in the phylogenetic trees.

In the seven ranks used for the systematics of plants and animals, the homogeneous-natured taxa can be available only when the lower-ranked two taxa, i.e., species and genus are dealt with taxonomically. Therefore, the present authors naturally selected the homogeneous-natured taxon in the generic designation, since the longer the phylogenetic distances are the more taxonomic heterogeneities will be increased.

Thus, the monophyletic genus *Lipomyces* Lodder et Kreger-van Rij sensu Kurtzman et al. (2007) contained the phylogenetic-distant and the phenotypic-different species such as *Waltomyces lipofer*, *Zygozyma oligophaga*, *Smithiozyma japonica*, *Kawasakia arxii*, *Limtongia smithiae*, and *Kockiozyma suomiensis*, all of which were classified as junior subjective synonyms of *L. lipofer*, *L. oligophagus*, *L. japonicus*, *L. arxii*, *L. smithiae*, and *L. suomiensis* respectively, in addition to *L. starkeyi*, the type species and its closely related *Lipomyces* species, which constituted the genus *Lipomyces* sensu stricto, and so corresponded exactly to the so-called family Lipomycetaceae (Jindamorakot *et al.* 2011, 2012). On the other hand, the paraphyletic genus *Dipodascopsis* Batra et Millner emend. Kurtzman et al. (2007) was a monotypic genus, which included only *D. uninucleata* (Jindamorakot *et al*. 2012). For the remaining two species, one was transferred again to the genus *Babjevia* as *B. anomala* (Jindamorakot *et al*. 2012; Yamazaki *et al*. 2020) and the other was classified in the new genus *Neoaidaea* as *Neoaidaea tothii* gen. nov., comb. nov. (Vu *et al*. 2021).

Acknowledgements

The present authors express their sincere thanks for citing a number of articles for detailed discussions. Thanks are also due to Dr. M. Smith, The Netherlands for her valuable suggestions.

Funding information

The authors received no specific grant from any funding agency.

Conflicts of interest

The authors declare that there are no conflicts of interest.

Author contributions

Y.Y., H.T.L.V., P.Y., and S.T. designed the study. H.T.L.V. performed the main experiments. P.Y. instructed how to make the experiments. Y.Y. prepared the manuscript. The detailed discussion was made among Y.Y., H.T.L.V., P.Y., and S.T.

REFERENCES

Cottrell M, Kock JLF. The yeast family Liopmycetaceae Novak et Zolt emend. van der Walt et al. and the genus *Myxozyma* van der Walt et al. 1. A historical account of its delimitation and 2. The taxonomic relevance of cellular long chain fatty acid composition and other phenotypic characters. *Syst Appl Microbiol* 1989; **12**: 291-305.

Jindamorakot S, Am-in S, Yukphan P, Yamada Y. *Limtongia* gen. nov. for *Zygozyma smithiae* (Lipomycetaceae). *Ann Microbiol* 2011; **61**: 689-693.

Jindamorakot S, Yukphan P, Yamada Y. *Kockiozyma* gen. nov., for *Zygozyma suomiensis*: The phylogeny of the Lipomycetaceous yeasts. *Ann Microbiol* 2012; **62**: 1831-1840.

Kock JLF, van der Walt JP, Yamada Y. *Smithiozyma* gen. nov. (Lipomycetaceae). *South Afr J Bot* 1995; **61**: 232-233.

Kurtzman CP. Phylogenetic circumscription of *Saccharomyces* and *Kluyveromyces* and other members of the Saccharomycetaceae, and the proposal of the new genera *Lachancea*, *Nakaseomyces*, *Naumovia*, *Vanderwaltozyma* and *Zygotorulaspora*. *FEMS Yeast Res* 2003; **4**: 233-245.

Kurtzman CP, Albertyn J, Basehoar-Powers E. Multigene phylogenetic analysis of the Lipomycetaceae and the proposed transfer of *Zygozyma* species to *Lipomyces* and *Babjevia anomala* to *Dipodascopsis*. *FEMS Yeast Res* 2007; **7**: 1027-1034.

Kurtzman CP. Discussion of teleomorphic and anamorphic ascomycetous yeasts and yeast-like taxa. In: Kurtzman CP Fell JW Boekhout T (ed). The Yeasts, A Taxonomic Study, 5th edition. vol. 2. London: Elsevier, 2011, p. 293-307.

Nakase T, Komagata K. Significance of DNA base composition in the classification of the yeast genus *Pichia*. *J Gen Appl Microbiol* 1970; **16**: 511–521.

Smith MTh, van der Walt JP, Yamada Y, Batenburg-van der Vegte WH. *Zygozyma suomiensis* sp. nov. (Lipomycetaceae), a new species from Finland. *Antonie van Leeuwenhoek* 1989; **56**: 283-288.

Smith MTh, van der Walt JP, Batenburg-van der Vegte WH. *Babjevia* gen. nov. - a new genus of the Lipomycetaceae. *Antonie van Leeuwenhoek* 1995; **67**: 177-179.

Smith MTh, de Hoog GS. *Dipodascopsis* Batra & P. Millner emend. Kurtzman, Albertyn & Bosehoar-Powers (2007). In: Kurtzman CP Fell JW Boekhout T (ed). The Yeasts, A Taxonomic Study, 5th edition. vol. 2. London: Elsevier, 2011, p. 379-384.

Smith MTh, Kurtzman CP. *Lipomyces* Lodder & Kreger-van Rij (1952). In: Kurtzman CP Fell JW Boekhout T (ed). The Yeasts, A Taxonomic Study, 5th edition. vol. 2. London: Elsevier, 2011, p. 545-560.

van der Walt JP, von Arx JA, Ferreira NP, Richard PDG. *Zygozyma* gen. nov., a new genus of the Lipomycetaceae. *Syst Appl Microbiol* 1987; **9**: 115-120.

van der Walt JP, Smith MTh, Yamada Y. Nakase T, Richard PDG. *Lipomyces japonicus* sp. nov. from Japanese soil. *Syst App. Microbiol* 1989a; **11**: 302-304.

van der Walt JP, Smith MTh, Yamada Y, Richard PDG. *Zygozyma arxii* sp. n. (Lipomycetaceae), a new species from Southern Africa. *Syst Appl Microbiol* 1989b: **12**, 288-290.

van der Walt JP, Wingfield MJ, Yamada Y. *Zygozyma smithiae* sp. n. (Lipomycetaceae), a new ambrosia yeast from Southern Africa. *Antonie van Leeuwenhoek* 1990; **58**: 95-98.

Vu HTL, Yukphan P, Tanasupawat S, Yamada Y. The revision of the family Lipomycetaceae. *27th Ann Meet JSMRS* 2021; *Gen Lect* O-7: p. 15; on line presentation, p. 1-10.

Yamada Y, Okada T, Ueshima O, Kondo K. Coenzyme Q system in the classification of the ascosporogenous yeast genera *Hansenula* and *Pichia*. *J Gen Appl Microbiol* 1973; **19**: 189–208.

Yamada Y, Nakase T. *Waltomyces*, a new ascosporogenous yeast genus for the Q10-equipped species, slime-producing organisms whose asexual reproduction is by multilateral budding and whose ascospores have smooth surfaces. *J Gen Appl Microbiol* 1985; **31**: 491-492.

Yamada Y. The coenzyme Q system in strains of species of anamorphic yeast genus *Myxozyma*. *J Gen Appl Microbiol* 1986; **32**: 259-261.

Yamada Y, Nakase T, van der Walt JP. The coenzyme Q system in strains of species in the ascosporogenous yeast genera *Lipomyces* and *Waltomyces*. *Trans Mycol Soc Jpn* 1986; **27**: 313-319.

Yamada Y, Nogawa C. The phylogeny of the Lipomycetaceous yeasts based on the partial sequences of 18S and 26S ribosomal RNAs. *Bull Fac Agric Shizuoka Univ* 1995a **45**: 13–23.

Yamada, Y. and Nogawa, C. *Kawasakia* gen. nov., for *Zygozyma arxii*, the Q9- equipped species in the genus *Zygozyma* (Lipomycetaceae). *Bull Fac Agric Shizuoka Univ* 1995b; **45**: 31–34.

Yamazaki A, Kawasaki H. *Lipomyces chichibuensis* sp. nov., isolated in Japan, and reidentification of the type strains of *Lipomyces kononenkoae* and *Lipomyces spencermartinsiae*. *Int J Syst Evol Microbiol* 2014; **64**: 2566–2572.

Yamazaki A, Kanti A, Kawasaki H. Three novel lipomycetaceous yeasts, *Lipomyces maratuensis* sp. nov., *Lipomyces tropicalis* sp. nov. and *Lipomyces kalimantanensis* f.a. sp. nov. isolated from soil from the Maratua and Kalimantan islands, Indonesia. *Mycoscience* 2017a; **58**: 413-423.

Yamazaki A, Yanagiba M, Naganuma T. Two novel Lipomycetaceous yeast species, *Lipomyces okinawensis* sp. nov. and *Lipomyces yamanashiensis* f.a., sp. nov., isolated from soil in the Okinawa and Yamanashi prefectures, Japan. *Int J Syst Evol Microbiol* 2017b; **67**: 2941-2946.

Yamazaki A, Lorliam W, Kawasaki H, Uchino M, Suzuki K. Fourteen novel lipomycetaceous yeast species isolated from soil in Japan and transfer of *Dipodascopsis anomala* to the genus *Babjevia* based on ascospore production phenotype. *Int J Syst Evol Microbiol* 2020; **70**: 1372-1397.

Table 1. The pair-wise 26S rRNA gene D1/D2 domain sequence similarity.

Species	Sequence similarity (%)										
	1	2	3	4	5	6	7	8	9	10	11
1. *Lipomyces starkeyi*											
2. *Waltomyces lipofer*	95.2										
3. *Zygozyma oligophaga*	85.5	83.0									
4. *Babjevia anomala*	91.7	91.0	81.6								
5. *Smithiozyma japonica*	96.4	93.6	85.5	89.9							
6. *Kawasakia arxii*	97.5	94.1	85.7	92.2	95.7						
7. *Limtongia smithiae*	92.4	89.9	82.9	86.8	90.6	91.0					
8. *Kockiozyma suomiensis*	90.6	88.9	85.9	86.2	90.3	90.6	86.4				
9. *Myxozyma geophila*	90.4	89.0	86.6	85.9	90.4	90.3	85.7	98.0			
10. *D. uninucleata var. uninucleata*	95.7	94.0	85.5	90.4	95.0	95.4	91.2	90.2	90.2		
11. *D. uninucleata var. wickerhamii*	95.6	93.8	85.4	90.3	94.9	95.2	91.0	90.1	90.1	99.8	
12. *Neoaidaea tothii*	92.6	90.5	83.4	95.6	90.1	95.2	87.8	87.8	86.7	90.6	90.5

D. uninucleata; *Dipodascopsis uninucleata*: The type strains were used of the respective species.

The pair-wise 26S rRNA gene D1/D2 domain sequence similarities were calculated for 555-568 bases with the program BioEdit (version 7.2.5) (Hall, *GERF Bull Biosci* 2011; **2**: 60,).

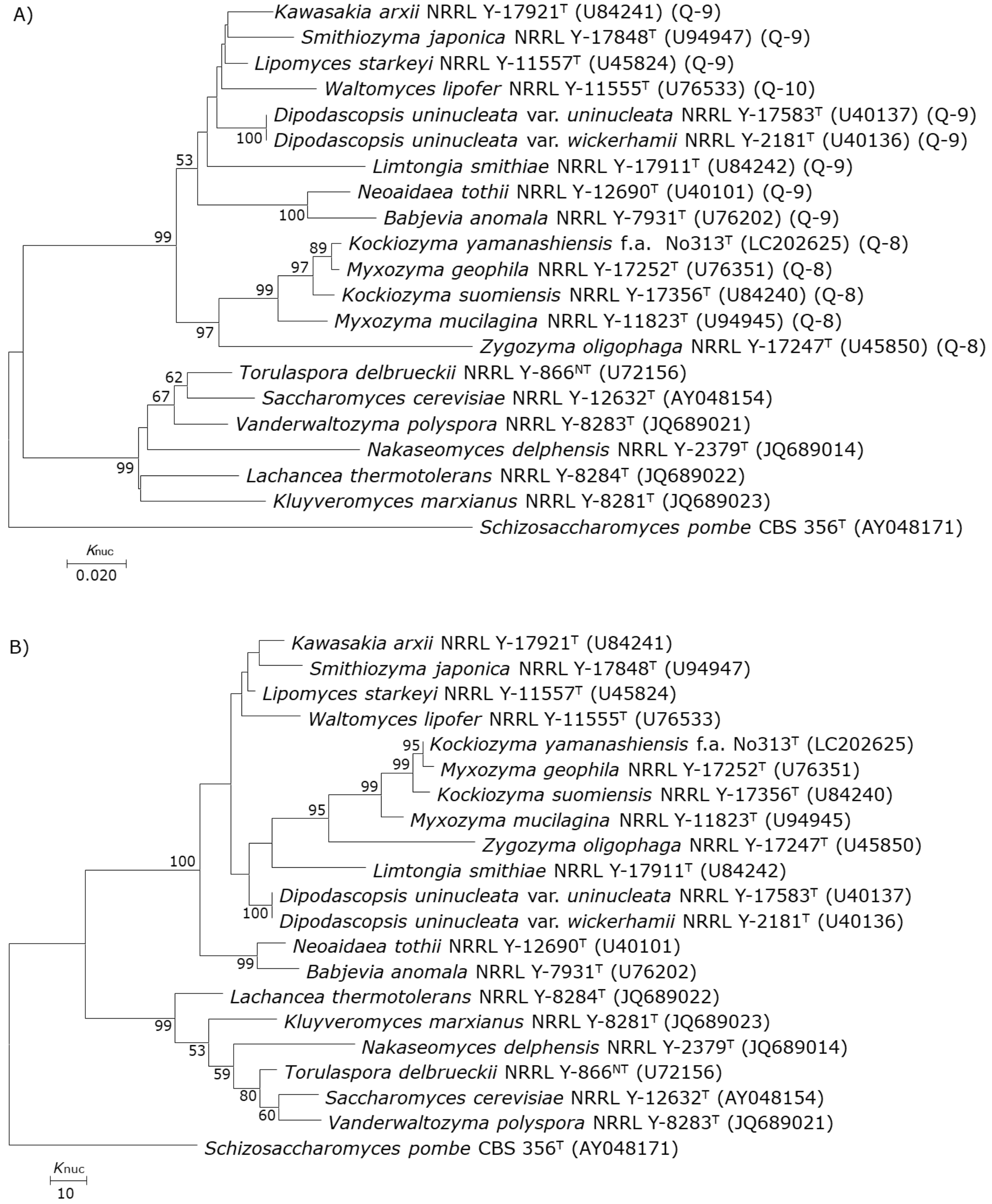

Fig. 1. The phylogenetic relationships of the Lipomycetaceous yeast species. The phylogenetic trees based on the 26S rRNA gene D1/D2 domain sequences (526 bases) were constructed for the Lipomycetaceous yeast species by the neighbour-joining method (A) and by the maximum parsimony method (B). S*accharomyces cerevisiae* and its related species were utilized for reference standards. *Schizosaccharomyces*

pombe was used as outgroup. The evolutionary distances were computed using the Kimura 2-parameter method (Kimura, *J Mol Evol* 1980; **16**: 111). The numerals at the nodes of the respective branches indicate bootstrap values (%) deduced from 1000 replications (Felsenstein, *Evolution* 1985; **39**: 783). The bootstrap values below 50% were deleted. For the additional phylogenetic trees based on the concatenated four-gene sequences, i.e., 18S rRNA, 26S rRNA, mitochondrial small subunit rRNA, and *EF1-α*, derived from the three methods, refer to Jindamorakot *et al*. (2012). According to the theory of Kurtzman *et al*. (2007), the Lipomycetaceous yeast species are designated as *Lipomyces lipofer*, *L. oligophagus*, *L. japonicus*, *L. smithiae*, *L. arxii*, *L. suomiensis*, *Dipodascopsis uninucleata*, *D. anomala*, and *D. tothii* instead.