

1 Microbial Systematics

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3 **The Revision of Lipomycetaceae***

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21 *This article is dedicated to Professor Dr. J. P. van der Walt, South Africa for his excellent
22 taxonomic study on the Lipomycetaceous yeasts, especially in the findings of *Zygozoma*
23 *oligophaga* and its related species.

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36 **ABSTRACT**

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

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

44

45

46 GRAPHICAL ABSTRACT

47

The family Lipomycetaceae Novak et Zolt

Genus

1. *Lipomyces* Lodder et Kreger-van Rij (1952) sensu stricto

2. *Dipodascopsis* Batra et Millner (1978)

3. *Waltomyces* Yamada et Nakase (1985)

4. *Zygozoma* van der Walt et von Arx (1987)

5. *Babjevia* van der Walt et Smith (1995)

6. *Smithiozoma* Kock, van der Walt et Yamada (1995)

7. *Kawasakia* Yamada et Nogawa (1995)

8. *Limtongia* Jindamorakot, Am-in, Yukphan et Yamada (2011)

9. *Kockiozoma* Jindamorakot, Yukphan et Yamada (2012)

10. *Neoaidaea* Vu, Yukphan, Tanasupawat et Yamada (2022)

Species

L. starkeyi (the type species), *L. kononenkoeae*, *L. tetrasporus*, *L. mesenbrius*, *L. spencermartinsiae*, *L. dorenjongii*, *L. kockii*, *L. yamadae*, *L. yarrowii*, *L. orientalis*, *L. chichibuensis*, *L. kalimantanensis*, *L. tropicalis*, *L. okinawaensis*

D. uninucleata

W. lipofer

Z. oligophaga

B. anomala (the type species), *B. hyphoforaminiformans*, *B. hyphasca*

S. japonica

K. arxii

L. smithiae

K. suomiensis

N. tothii

48

The family Lipomycetaceae Novak et Zolt

Genus

1. *Lipomyces* Lodder et Kreger-van Rij (1952) sensu Kurtzman, Albertyn et Basehoar-Powers (2007)

2. *Dipodascopsis* Batra et Millner (1978) emend. Kurtzman, Albertyn et Basehoar-Powers (2007)

Species

L. starkeyi (the type species), *L. kononenkoeae*, *L. tetrasporus*, *L. mesenbrius*, *L. spencermartinsiae*, *L. dorenjongii*, *L. kockii*, *L. yamadae*, *L. yarrowii*, *L. orientalis*, *L. chichibuensis*, *L. kalimantanensis*, *L. tropicalis*, *L. okinawaensis* (= the genus *Lipomyces* sensu stricto); *L. lipofer*, *L. oligophagus*, *L. japonicus*, *L. arxii*, *L. smithiae*, *L. suomiensis*

D. uninucleata (the type species), *D. tothii*, *D. anomala*

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52

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

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

68
69 The family Lipomycetaceae Novak et Zsolt
70 The type genus is *Lipomyces* Lodder et Kreger van-Rij.
71 Ten genera are included.

72
73 Genus I. *Lipomyces* Lodder et Kreger-van Rij sensu stricto
74 The type species is *Lipomyces starkeyi* Lodder et Kreger-van Rij.
75 Fourteen species are included.

- 76 1. *Lipomyces starkeyi* Lodder et Kreger-van Rij (1952)
- 77 2. *Lipomyces kononenkoeae* Nieuwdorp, Bos et Slooff (1974)
- 78 3. *Lipomyces tetrasporus* Nieuwdorp, Bos et Slooff (1974)
- 79 4. *Lipomyces mesembrius* Botha, van der Walt et Smith (1997)
- 80 5. *Lipomyces spencermartinsiae* (van der Walt et Smith) van der Walt et Smith (1997)
81 Basionym: *Lipomyces kononenkoeae* Nieuwdorp, Bos et Slooff subsp. *spencermartinsiae*
82 van der Walt et Smith (1995)
- 83 6. *Lipomyces doorenjongii* van der Walt et Smith (1999)
- 84 7. *Lipomyces kockii* Smith et van der Walt (1999)
- 85 8. *Lipomyces yamadae* van der Walt et Smith (1999)
- 86 9. *Lipomyces yarrowii* Smith et van der Walt (1999)
- 87 10. *Lipomyces orientalis* Thanh (2006)
- 88 11. *Lipomyces chichibuensis* Yamazaki et Kawasaki (2014)
- 89 12. *Lipomyces kalimantanensis* Kanti, Yamazaki et Kawasaki (2017)
- 90 13. *Lipomyces tropicalis* Kanti, Yamazaki et Kawasaki (2017)
- 91 14. *Lipomyces okinawensis* Yamazaki, Yanagiba et Naganuma (2017)

92
93 The species classified in the genus *Lipomyces* sensu stricto were tightly coupled with

94 one another in all the three phylogenetic trees based on the concatenated four-gene
95 sequences of 18S rRNA, 26S rRNA, mitochondrial small subunit rRNA, and *EFI- α*
96 derived from the neighbour-joining, the maximum parsimony, and the maximum
97 likelihood methods (Jindamorakot *et al.* 2012). On the other hand, the phylogenetic
98 positions of the *Lipomyces* species newly designated by Kurtzman *et al.* (2007) were quite
99 changeable in the monophyletic genus *Lipomyces* sensu (Jindamorakot *et al.* 2012). In
100 fact, the resulting genus has an extremely wide range of DNA G+C contents (14.2 mol%,
101 from 41.5 - 55.7 mol% G+C; Jindamorakot *et al.*, 2012) and three kinds of ubiquinone
102 isoprenologues (Q-8, Q-9, and Q-10: Yamada 1986; Yamada *et al.* 1986). According to
103 Nakase and Komagata (1970) and Yamada *et al.* (1973), such a genus was a taxonomically
104 heterogeneous-natured taxon, just as found in the genus *Pichia* Hansen once designated.
105

106 Genus II. *Dipodascopsis* Batra et Millner

107 *Dipodascopsis uninucleata* (Biggs) Batra et Millner (1978)

108 Basionym: *Dipodascus uninucleatus* Biggs (1937).

109 Two varieties are described.

110 1. *Dipodascopsis uninucleata* var. *uninucleata*

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

112
113 When the phylogenetic tree based on the 26S rRNA gene D1/D2 domain sequences was
114 constructed by the neighbour-joining method, the paraphyletic genus *Dipodascopsis*
115 emend. Kurtzman *et al.* was split into two and produced a monotypic genus (Fig. 1), as
116 reported previously (Jindamorakot *et al.* 2011, 2012), indicating that *D. uninucleata*, *D.*
117 *tothii* and *D. anomala* were not tightly coupled within the genus *Dipodascopsis* emend.

118 Such a phylogenetic data was also given by Kurtzman (2011), i.e., the phylogenetic tree
119 based on the concatenated three-gene sequences of 26S rRNA, 18S rRNA, and *EFI- α*
120 derived from the neighbour-joining method represented that *D. uninucleata* was connected
121 first to *L. starkeyi* but not to *D. anomala* (= *B. anomala*) and then the resulting cluster was
122 done to *D. anomala*. In fact, the calculated sequence similarity (95.7%) between *D.*
123 *uninucleata* and *L. starkeyi* was much higher than that (90.4%) between *D. uninucleata* and
124 *B. anomala* (Table 1).
125

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

127 *Waltomyces lipofer* (Lodder et Kreger-van Rij ex Slooff) Yamada et Nakase (1985) (MB
128 103899)

129 Basionym: *Lipomyces lipofer* Lodder et Kreger-van Rij (1952) ex Slooff (1970).
130

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

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

142

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

144 *Zygozoma oligophaga* van der Walt et von Arx (1987) (MB 131108)

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

147

148 Four *Zygozoma* species were reported (van der Walt *et al.* 1987, 1989b, 1990; Smith *et*
149 *al.* 1989). However, the four species were not tightly coupled with one another in the
150 phylogenetic trees based on the concatenated four-gene sequences derived from the three
151 methods, i.e., the neighbour-joining, the maximum parsimony, and the maximum
152 likelihood methods (Jindamorakot *et al.* 2012) and chemotaxonomically grouped into two
153 based on the ubiquinone isoprenologues, i.e., Q-8 and Q-9 (Fig. 1) (Yamada and Nogawa
154 1995a; Jindamorakot *et al.* 2011, 2012). Especially, the Q8-equipped species, *Z.*
155 *oligophaga* had extremely long branches (Fig. 1) (Jindamorakot *et al.* 2012) and quite low
156 sequence similarities (81.6-86.6%) (Table 1).

157

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

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

160 Three species are included.

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

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

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

165 2. *Babjevia hyphoforaminiiformans* Yamazaki, Lorliam et Kawasaki (2020) (MB
166 829051)

167 3. *Babjevia hyphasca* Yamazaki, Lorliam et Kawasaki (2020) (MB 829053)

168

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

175 In the phylogenetic tree based on the concatenated four-gene sequences derived from the

176 maximum likelihood method (Yamazaki *et al.* 2020), it is reasonable that the names of
177 species, *L. lipofer*, *L. smithiae*, *Zygozoma arxii* (= *L. arxii*), *L. japonicus*, *L. oligophaga*
178 [sic], and *Zygozoma suomiensis* (= *L. suomiensis*) are changed to *Waltomyces lipofer*,
179 *Limtongia smithiae*, *Kawasakia arxii*, *Smithiozoma japonica*, *Zigozoma oligophaga*, and
180 *Kockiozoma suomiensis* respectively since the generic name of *Babjevia* was revived.

181

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

183 *Smithiozoma japonica* (van der Walt, Smith, Yamada et Nakase) Kock, van der Walt et
184 Yamada (1995) (MB 414161)

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

186

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

201

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

203 *Kawasakia arxii* (van der Walt, Smith et Yamada) Yamada et Nogawa (1995) (MB
204 442988)

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

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

208

209 The Q9-equipped species, *Kawasakia arxii* was very unique in representing
210 considerably large base differences (six) to the above-mentioned three *Lipomyces* species
211 in the partial base sequencing of 18S rRNA (region *c*), in contrast to *W. lipofer*, which had
212 only one base difference in the same region (Yamada and Nogawa 1995a, b). In the
213 remaining regions *a* and *b*, the maximum homology and the base differences of the species
214 were 93% and only one. The calculated 26S rRNA gene D1/D2 domain sequence
215 similarities of *Kawasakia arxii* were 85.7 - 97.5% (Table 1). In the phylogenetic trees
216 based on the concatenated four-gene sequences, the phylogenetic positions of *Kawasakia*

217 *arxii* were considerably changeable, indicating that the species was not tightly coupled to
218 any of other species (Jindamorakot *et al.* 2012).

219

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

221 *Limtongia smithiae* (van der Walt, Wingfield et Yamada) Jindamorakot, Am-in,

222 Yukphan et Yamada (2011) (MB 582717)

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

224 Synonym: *Lipomyces smithiae* (van der Walt, Wingfield et Yamada) Kurtzman,

225 Albertyn et Basehoar-Powers (2007).

226

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

233

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

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

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

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

240 2. *Kockiozoma geophila* f.a. (van der Walt, Yamada et Nakase) comb. nov.

241 Basionym: *Myxozoma geophila* van der Walt, Yamada et Nakase, Syst. Appl.
242 Microbiol. 9: 122, 1987.

243 The type strain is CBS 7219 = NRRL Y-17252.

244 3. *Kockiozoma sirexii* f.a. (Spaaij et Weber) comb. nov.

245 Basionym: *Myxozoma sirexii* Spaaij et Weber, Syst. Appl. Microbiol. 15: 429, 1992.

246 The type strain is UOFS Y-2054 = NRRL Y-27626

247 4. *Kockiozoma yamanashiensis* f.a. (Yamazaki, Yanagiba et Naganuma) comb. nov.

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

250 The type strain is NBRC 110621 = CBS 14748.

251

252 In the three partial base sequencings mentioned above, the Q8-equipped species,
253 *Kockiozoma suomiensis* represented 83% maximum homology in region *a*, 12 base
254 differences in region *b*, and four base differences in region *c* respectively to *L. starkeyi*, *L.*
255 *tetrasporus*, and *L. kononenkoe* in the genus *Lipomyces* sensu stricto (Yamada and
256 Nogawa, 1995a). The calculated 26S rRNA gene D1/D2 domain sequence similarities of
257 the species were 85.9 - 90.6%, indicating that the species is accommodated to an

258 independent genus (Table 1). On the other hand, *Myxozyma geophila*, the Q8-equipped
259 anamorphic species showed 92% maximum homology, and one and one base difference to
260 *Kockiozyma suomiensis* in the three partial base sequencings (Yamada and Nogawa,
261 1995a). In addition, the sequence similarity between *Kockiozyma suomiensis* and
262 *Myxozyma geophila* was 98.0%, the value of which was almost identical with that
263 (98.1%) between *Octosporomyces octosporus* and *Octosporomyces osmophilus* (Yamada
264 *et al.*, 2022). From the results obtained above, the generic name of *Kockiozyma* was able
265 to be given to the anamorphic species as *Kockiozyma geophila* f.a. (Lachance, 2012).
266

267 In the three partial base sequencings mentioned above, the Q8-equipped species,
268 *Kockiozyma suomiensis* represented 83% maximum homology, 12 base differences and
269 four base differences respectively to *L. starkeyi*, *L. tetrasporus* and *L. kononenkoeae* in the
270 genus *Lipomyces* sensu stricto (Yamada and Nogawa 1995a). The calculated 26S rRNA
271 gene D1/D2 domain sequence similarities of the species were 85.9 - 90.6%, indicating that
272 the species is accommodated to an independent genus (Table 1).
273

274 *Dipodascopsis tothii* and *B. anomala* (= *D. anomala*) were tightly coupled in the three
275 phylogenetic trees (Jindamorakot *et al.* 2012), so that the two species appeared to be
276 classified in a single genus (Fig. 1). Due to the priority of *B. anomala*, the single genus
277 was to be named *Babjevia*. However, the distance between the two species, *D. tothii* and
278 *B. anomala* was not so short, when compared with *Kluyveromyces polysporus* (=
279 *Vanderwaltozyma polyspora*) and *Saccharomyces cerevisiae* (Jindamorakot *et al.* 2012). In
280 fact, the calculated pair-wise sequence similarity (95.6%) between the two species was
281 interestingly almost the same as that (95.7%) between *D. uninucleata* and *L. starkeyi* and
282 that (95.2%) between *W. lipofer* and *L. starkeyi*, and not so high to accommodate the two
283 species to the single genus *Babjevia* (Table 1), indicating that an additional genus can be
284 phylogenetically introduced for *D. tothii*. Phenotypically, the species was quite different
285 from *B. anomala*, e.g., in the morphology of asci and ascospores and the mode of asexual
286 reproduction (Smith and de Hoog 2011).

287 Yamazaki *et al.* (2017a, b) constructed the phylogenetic trees based on the translation
288 elongation factor 1-alpha (*EF1- α*) gene sequences derived from the neighbour-joining
289 method. In the phylogenetic trees, it is of interest that *D. tothii* was found inside and
290 distantly separated from *B. anomala* as well as *D. uninucleata*. In contrast, the cluster
291 including *L. starkeyi* and its relatives and the cluster including *Kockiozyma suomiensis* and
292 its related *Myxozyma* species were tightly coupled without any exception. In this respect,
293 *D. tothii* was quite different phylogenetically from the remaining two species of the
294 paraphyletic genus *Dipodascopsis* emend., and thus the introduction of a separate new
295 genus was confirmed (Vu *et al.* 2021).
296

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

298 *Neoaidaea* (Ne.o.a.i'da.e.a. N. L. fem. n. *Neoaidaea*, new Aida, in honour of Dr. Ko

299 Aida, Professor Emeritus, The Institute of Applied Microbiology, The University of
300 Tokyo, Tokyo, Japan, who introduced the isoprenoid quinone analyses into the microbial
301 systematics.

302 The colonies are cream-coloured, moist and creamy after 10 d (Smith and de Hoog
303 2011). Budding cells are absent. Hyphae are firm with inflated cells and intensely
304 amyloid. Arthroconidia are absent. Gametangia are formed laterally on hyphae as curved
305 branches. Asci arise after fusion of a terminal cell with its penultimate cell. Asci are
306 acicular, 50 - 100 µm long and contain 30 - 100 ascospores. Asci open by rupturing at the
307 apex. Ascospores are subhyaline to hyaline, broadly ellipsoidal, occasionally bean-shaped,
308 1×1.5 - 2 µm and without slime. Fermentation is absent. Grows on glucose, inulin,
309 sucrose, raffinose, galactose, lactose, trehalose, maltose, methyl-α-glucoside, starch,
310 cellobiose, salicin, L-sorbose, xylose, arabinose, L-arabinose, ethanol, glycerol, ribitol,
311 mannitol, glucitol, *myo*-inositol, succinate (w), and gluconate (v), but not on melibiose, L-
312 rhamnose, ribose, methanol, erythritol, galactitol, and DL-lactate. No growth on vitamin-
313 free medium (Smith and de Hoog 2011). Ubiquinone-9 (Q-9) is present (Cottrell and Kock
314 1989).

315 Mycobank number is 846280.

316 *Neoaidaea tothii* (Zolt) Vu, Yukphan, Tanasupawat et Yamada comb. nov.

317 Basionym: *Dipodascus tothii* Zolt, Acta Bot. Hung. 9: 226, 1963.

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

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

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

322 MycoBank number is 846281.

323

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

326

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

331

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

337

338 Thus, the monophyletic genus *Lipomyces* Lodder et Kreger-van Rij sensu Kurtzman et
339 al. (2007) contained the phylogenetic-distant and the phenotypic-different species such as

340 *Waltomyces lipofer*, *Zygozoma oligophaga*, *Smithiozoma japonica*, *Kawasakia arxii*,
341 *Limtongia smithiae*, and *Kockiozoma suomiensis*, all of which were re-classified as junior
342 subjective synonyms of *L. lipofer*, *L. oligophagus*, *L. japonicus*, *L. arxii*, *L. smithiae*, and
343 *L. suomiensis* respectively, in addition to *L. starkeyi*, the type species and its closely
344 related *Lipomyces* species, which constituted the genus *Lipomyces* sensu stricto, and so
345 corresponded exactly to the so-called family Lipomycetaceae (Jindamorakot *et al.* 2011,
346 2012). On the other hand, the paraphyletic genus *Dipodascopsis* Batra et Millner emend.
347 Kurtzman *et al.* (2007) was a monotypic genus, which included only *D. uninucleata*
348 (Jindamorakot *et al.* 2012). For the remaining two species, one was transferred again to
349 the genus *Babjevia* as *B. anomala* (Jindamorakot *et al.* 2012; Yamazaki *et al.* 2020) and
350 the other was classified in the new genus *Neoaidea* as *Neoaidea tothii* gen. nov., comb.
351 nov. (Vu *et al.* 2021).

352

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357

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360

361 Conflicts of interest

362 The authors declare that there are no conflicts of interest.

363

364 Author contributions

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

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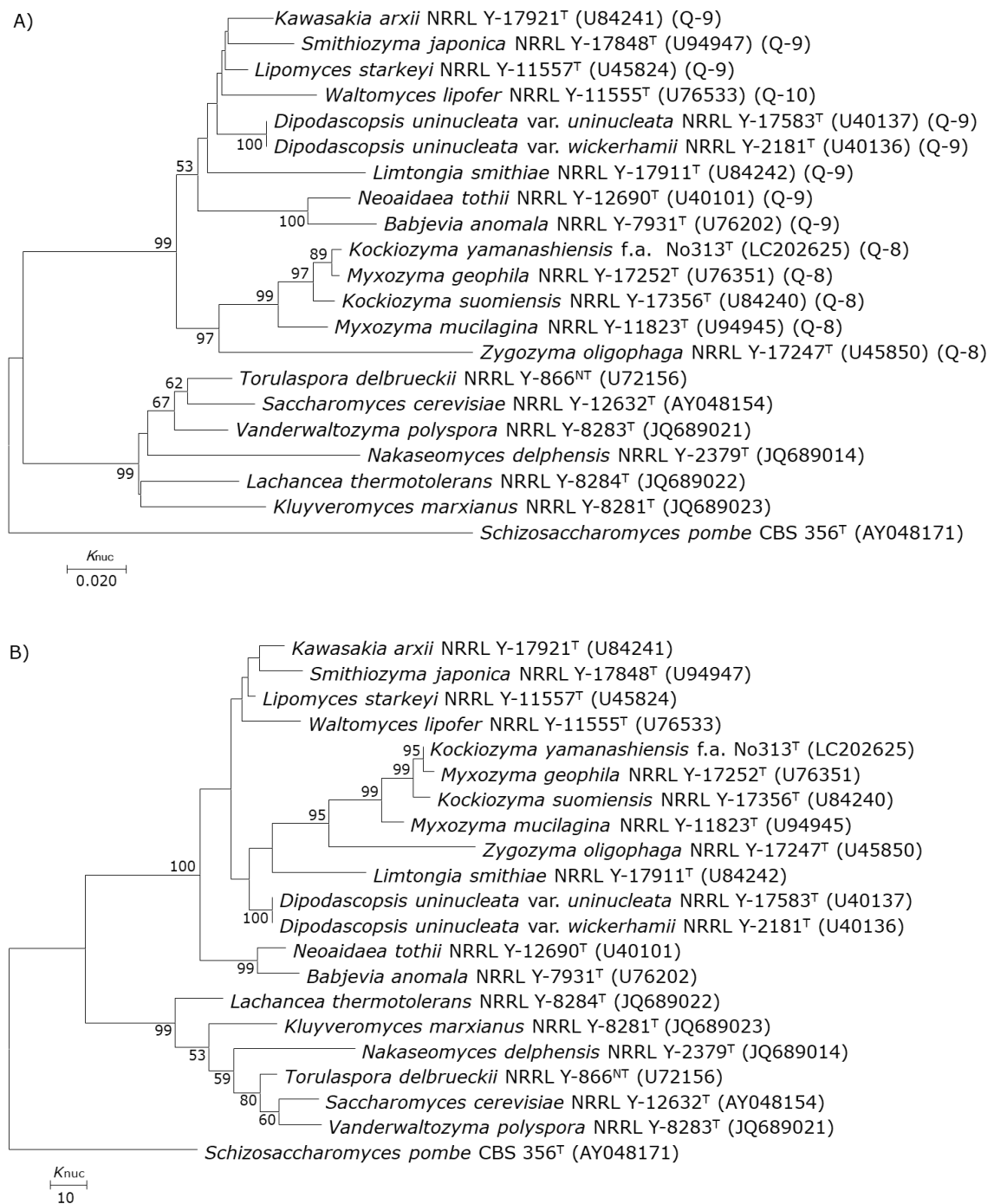
Table 1. The pair-wise 26S rRNA gene D1/D2 domain sequence similarity.

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

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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).

Saccharomyces 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

474 values below 50% were deleted. For the additional phylogenetic trees based on the concatenated four-gene
475 sequences, i.e., 18S rRNA, 26S rRNA, mitochondrial small subunit rRNA, and *EF1- α* , derived from the
476 three methods, refer to Jindamorakot *et al.* (2012). According to the theory of Kurtzman *et al.* (2007), the
477 Lipomycetaceous yeast species are designated as *Lipomyces lipofer*, *L. oligophagus*, *L. japonicus*, *L.*
478 *smithiae*, *L. arxii*, *L. suomiensis*, *Dipodascopsis uninucleata*, *D. anomala*, and *D. tothii* instead.
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