The Revision of Lipomycetaceae

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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 Lipomycetaceae, i.e., the genus Lipomyces sensu stricto (the type genus), the above-mentioned seven genera, the monotypic genus Dipodascopsis and the new genus Neoaidaea from the phylogenetic and the phenotypic points of view.

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Supplementary 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.					
10 NO	kononenkoae, L. tetrasporus, L.					
	mesenbrius, L. spencermartinsiae, L.					
	dorenjongii, L. kockii, L. yama-dae,					
	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					
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	L. smithiae					
(2011)						
9. Kockiozyma Jindamorakot, Yukphan et Yamada (2012)	K. suomiensis; K. geophila f.a., K.					
	yamanashiensis f.a.					
10. Neoaidaea Vu, Yukphan, Tanasupawat et Yamada gen.	N. tothii					
nov.						
The family Lipomycetaceae Novak et Zolt						
Genus	Species					
1. Lipomyces Lodder et Kreger-van Rij (1952) sensu	L. starkeyi (the type species), L.					
Kurtzman, Albertyn et Basehoar-Powers (2007)	kononenkoae, L. tetrasporus, L.					
Ratizatian, Albertyn et Dasenbar-1 owers (2007)	mesenbrius, L. spencermartinsiae, L.					
	dorenjongii, L. kockii, L. yama-dae,					
	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,	D. uninucleata (the type species), D.					
Albertyn et Basehoar-Powers (2007)	tothii, D. anomala					

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In the family Lipomycetaceae Novak Zsolt, the seven genera Waltomyces, Zygozyma, Babjevia, Smithiozyma, Kawasakia, Limtongia and Kockiozyma were once introduced [2-8]. All of them were respectively taxonomic-homogeneous natured, i.e., morphologically, physiologically, chemotaxonomically, genetically and phylogenetically. However, Kurtzman et al. divided the family into two, i.e., the monophyletic genus Lipomyces sensu and the paraphyletic genus Dipodascopsis emend instead [9, 10].

This paper describes the historical surveys in the systematics of the Lipomycetaceous yeasts and recovers the seven genera mentioned above as taxonomic criteria, in addition to the genus Lipomyces sensu stricto, the monotypic genus Dipodascopsis and the new genus Neoaidaea from the phylogenetic and the phenotypic points of view [1, 7, 8]. 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 [11]
- 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 (1997) Basionym: Lipomyces kononenkoae Nieuwdorp, Bos et Slooff subsp. spencermartinsiae van der Walt et Smith [5]
- 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 [12]
- 12. Lipomyces kalimantanensis Kanti, Yamazaki et Kawasaki [13]
- 13. Lipomyces tropicalis Kanti, Yamazaki et Kawasaki [13]
- Lipomyces okinawensis Yamazaki, Yanagiba et Naganuma
 [14]

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-a derived from the neighbour-joining, the maximum parsimony and the maximum likelihood methods [8]. On the other hand, the phylogenetic positions of the Lipomyces species newly designated by Kurtzman et al. were quite changeable in the monophyletic genus Lipomyces sensu [8, 9]. 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 [15, 16]. According to Nakase and Komagata and Yamada et al., such a genus was a taxonomically heterogeneous-natured taxon, just as found in the genus Pichia Hansen once designated [17, 18].

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, indicating that D. uninucleata, D. tothii and D. anomala were not tightly coupled within the genus Dipodascopsis emend [7-9].

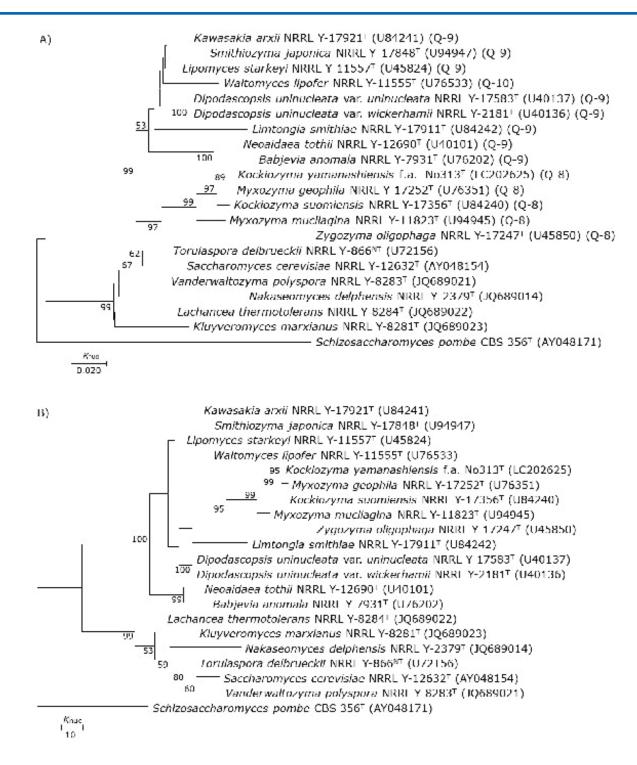


Figure. 1: The phylogenetic relationships of the Lipomycetaceous yeast species. The phylogenetic trees based on the 26S rRNA gene D1/D2 domain sequences (526 bases) were constructed for the Lipomycetaceous yeast species by the neighbour-joining method (A) and by the maximum parsimony method (B). Saccharomyces 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 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-a, derived from the three methods, refer to Jindamorakot et al. [7]. According to the theory of Kurtzman et al., the Lipomycetaceous yeast species are designated as L. starkeyi and its relatives, Lipomyces lipofer, L. oligophagus, L. japonicus, L. smithiae, L. arxii, L. suomiensis, Dipodascopsis uninucleata, D. anomala and D. tothii instead [9].

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Such a phylogenetic data was also given by Kurtzman, i.e., the phylogenetic tree based on the concatenated three-gene sequences of 26S rRNA, 18S rRNA, and EF1-a derived from the neighbour-joining method represented that D [19]. 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).

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

	Sequence similarity (%)										
Species											
	1	2	3	4	5	6	7	8	9	10	11
1. Lipomyces starkeyi											
2. Waltomyc es 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. Kocki ozyma suomiensi s	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			
0. D. unimucleata var. unimucleata	95.7	94.0	85.5	90.4	95.0	95.4	91.2	90.2	90.2		
1. D. unimuc leat a var. wicker hamii	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

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,).

Genus III. Waltomyces Yamada et Nakase (MB 25779) Waltomyces lipofer (Lodder et Kreger-van Rij ex Slooff) Yamada et Nakase (MB 103899)

Basionym: Lipomyces lipofer Lodder et Kreger-van Rij ex Slooff [2, 11, 17].

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. 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 [9, 12].

Genus IV. Zygozyma van der Walt et von Arx (MB 25149) Zygozyma oligophaga van der Walt et von Arx (MB 131108) Synonym: Lipomyces oligophagus (van der Walt et von Arx) Kurtzman, Albertyn et Basehoar-Powers [3, 9].

Four Zygozyma species were reported [3, 20-22]. However, the four 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 and chemotaxonomically grouped into two based on the ubiquinone isoprenologues, i.e., Q-8 and Q-9 (Fig. 1) [7, 8, 16]. Especially, the Q8-equipped species, Z. oligophaga had extremely long branches (Fig. 1) and quite low sequence similarities (81.6-86.6%) (Table 1) [8].

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 (MB 363215)

Basionym: Lipomyces anomalus Babjeva et Gorin (1975) [4]. Synonym: Dipodascopsis anomala (Babjeva et Gorin) Kurtzman, Albertyn et Basehoar-Powers [9].

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

Kurtzman et al. accommodated B [9]. anomala to the paraphyletic genus Dipod-ascopsis emend. as D. anomala. However, Jindamorakot et al. insisted that the species, D [8]. 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. did not classified two new species to the genus Dipodascopsis emend. but the genus Babjevia as already suggested by Jindamorakot et al., indicating that the generic concept of Kurtzman et al. completely lost its validity [8, 9, 23].

In the phylognetic tree based on the concatenated four-gene sequences derived from the maximum likelihood method, L. lipofer, L. smithiae, Zygozyma arxii (= L. arxii), L. japonicus, L. oligophaga [sic] and Zygozyma suomiensis (= L. suomiensis) were preferable to be improved to Waltomyces lipofer, Limtongia smithiae, Kawasakia arxii, Smithiozyma japonica, Zigozyma oligophaga and Kockiozyma suomiensis [7, 8, 23].

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 (MB 414161) Basionym: Lipomyces japonicus van der Walt, Smith, Yamada et Nakase [5, 22].

In the three partial base sequencings mentioned above, the Q9-equipped species, S. japonica represented 89% maximum homology in region a, two base differences in region b and five base differences in region c to L. starkeyi, L [24]. 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, indicating that the species is accommodated taxonomically to a different genus from the genus Lipomyces sensu stricto (Table 1) [16]. 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 Q9equipped 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 [8].

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 [12]. Synonym: Lipomyces arxii (van der Walt, Smith et Yamada) Kurtzman, Albertyn et Basehoar-Powers [9].

The Q9-equipped species, Kawasakia arxii was very unique in representing considerably large base differences (six) from 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 [6, 16]. 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 [8].

Yamada [25].

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 [7] (MB 582717) Basionym: Zygozyma smithiae van der Walt, Wingfield et

Synonym: Lipomyces smithiae (van der Walt, Wingfield et Yamada) Kurtzman, Albertyn et Basehoar-Powers [9].

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 [16]. 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 [8] (MB 587754)

Basionym: Zygozyma suomiensis Smith, van der Walt et Yamada [21].

Synonym: Lipomyces suomiensis (Smith, van der Walt et Yamada) Kurtzman, Albertyn et Basehoar-Powers [8].

2. Kockiozyma geophila f.a comb. Nov [24].

Basionym: Myxozyma geophila van der Walt, Yamada et Nakase, Syst. Appl. Microbiol. 9: 122, 1987.

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

3. Kockiozyma sirexii f.a. comb. nov.

Basionym: Myxozyma sirexii Spaaij et Weber, Syst. Appl. Microbiol. 15: 429, 1992.

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

4. Kockiozyma yamanashiensis f.a. comb. Nov [14].

Basionym: Lipomyces yamanashiensis f.a. Yamazaki, Yanagiba et Naganuma, Int. J. Syst. Evol. Microbiol. 67: 2945, 2017. The type strain is NBRC 110621 = CBS 14748.

In the three partial base sequencings mentioned above, the Q8equipped species, Kockiozyma suomiensis represented 83% maximum homology in region a, 12 base differences in region b, and four base differences in region c respectively to L. starkeyi, L. tetrasporus, and L. kononenkoae in the genus Lipomyces sensu stricto [16]. 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). On the other hand, Myxozyma geophila, the Q8-equipped anamorphic species showed 92% maximum homology, and one and one base difference to Kockiozyma suomiensis in the three partial base sequencings [16]. In addition, the sequence similarity between Kockiozyma suomiensis and Myxozyma geophila was 98.0%, the value of which was almost identical with that (98.1%) between Octosporomyces octosporus and Octosporomyces osmophilus [26]. From the results obtained above, the generic name of Kockiozyma was able to be given to the anamorphic

species as Kockiozyma geophila f.a. As well as Kockiozyma melibiosi f.a., Kockiozyma mucilagina f.a., Kockiozyma sirexii f.a., Kockiozyma neotropica f.a., Kockiozyma vanderwalti f.a. and Kockiozyma neglecta f.a. [27].

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 and Saccharomyces cerevisiae [8, 28]. In fact, the calculated pairwise 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 [10].

Yamazaki et al. Constructed the phylogenetic trees based on the translation elongation factor 1-alpha (EF1-□) gene sequences derived from the neighbour-joining method [13, 14]. 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. Kurtzman et al., and thus the introduction of a separate new genus was confirmed [1, 8].

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 [10]. 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 arises after fusion of a terminal cell with its penultimate cell. Asci is acicular, 50 - 100 □m long and contain 30 - 100 ascospores. Asci opens by rupturing at the apex. Ascospores are subhyaline to hyaline, broadly ellipsoidal, occasionally bean-shaped, 1×1.5 - 2 □m and without slime. Fermentation is absent. Grows on glucose, inulin, sucrose, raffinose, galactose, lactose, trehalose, maltose, methyl-□-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 [10]. Ubiquinone-9 (Q-9) is present [29].

Mycobank number is 846280.

Neoaidaea tothii (Zolt) Vu, Yukphan, Tanasupawat et Yamada comb. Nov.

Basionym: Dipodascus tothii Zolt, Acta Bot. Hung. 9: 226, 1963. Synonym: Dipodascopsis tothii (Zolt) Batra et Millner (1978).

The characteristics of the species are the same as those described in the genus [10].

The holotype is CBS $759.85^{T} = NBRC 10813^{T}$.

MycoBank number is 846281.

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

Kurtzman introduced 'clade' or 'phylogenetic circumscribed genuses as generic concept [28]. 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. contained the phylogenetic-distant and the phenotypic-different species, i.e., L. lipofer, L. oligophagus, L. japonicus, L. arxii, L. smithiae and L. suomiensis, all of which were re-classified as Waltomyces lipofer, Zygozyma oligophaga, Smithiozyma japonica, Kawasakia arxii, Limtongia smithiae and Kockiozyma suomiensi respectively, in addition to L. starkeyi, the type species and its closely related Lipomyces species that constituted the genus Lipomyces sensu stricto, and so corresponded taxonomically to the so-called family [7-9].

On the other hand, the paraphyletic genus Dipodascopsis Batra et Millner emend. Kurtzman et al was a monotypic genus, which included only D. uninucleata [8, 9]. For the remaining two species, one was transferred again to the genus Babjevia as B. anomala and the other was classified in the new genus Neoaidaea as Neoaidaea tothii gen. Nov., comb. Nov. [1, 8, 23].

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