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Molecular Phylogenetic Study on Stalked Conidium-Forming Yeasts and Related Basidiomycetous Yeast Taxa Based on 18S rDNA Sequences

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The 18S ribosomal RNA gene (rDNA) sequences of seven species of stalked conidium-forming yeasts, *Fellomyces polyborus, Kockovaella thailandica, Kurtzmanomyces nectairei, Sporobolomyces xanthus, Sterigmatomyces halophilus, Sterigmatosporidium polymorphum,* and *Tsuchiyaea wingfieldii,* and *Fibulobasidium inconspicuum* were determined and analyzed phylogenetically. The xylose-lacking species, *K. nectairei, S. xanthus,* and *S. halophilus,* were located at closely related positions in the phylogenetic tree, and showed a close relationship with some *Bensingtonia* species. The xylose-containing species, *F. polyborus, K. thailandica, S. polymorphum,* and *T. wingfieldii,* made a branch with the species of *Bullera* and *Tremella. Fibulobasidium inconspicuum,* a species of Sirobasidiaceae (Tremellales), was also included in this branch. The molecular phylogeny deduced from 18S rDNA sequences showed that the ability to produce stalked conidia was not a rational taxonomic criterion, and supported the taxonomic importance of cellular xylose in basidiomycetous yeasts.

Key words : stalked conidium-forming yeasts, molecular phylogeny

INTRODUCTION

Since the description of the anamorphic yeast genus *Sterigmatomyces* by Fell(3) which undergoes vegetative reproduction by forming new conidia on the tips of sterigmata (stalked conidia=sterigmatoconidia), several species have been assigned to the genus. Later, the genus was divided into four genera, *Fellomyces, Kurtzmanomyces, Sterigmatomyces*, and *Tsuchiyaea*, based on the mode of the liberation of conidium, ubiquinone system, and monosaccharide composition of whole cell hydrolysate (25~27). On the other hand, Nakase et al. (11,12) described two new anamorphic genera, *Ballistosporomyces* and *Kockovaella*, which reproduce by stalked conidia and ballistoconidia. The species of *Kockovaella* also reproduce by budding yeast cells. Later, Boekhout (2) insisted that the species of *Ballistosporomyces* should be transferred to *Sporobolomyces*, because stalked conidia were also observed in some species of *Sporobolomyces*.

Kraepelin and Schulze (9) described a teleomorphic yeast genus *Sterigmatosporidium polymorphum* which reproduces by stalked conidia. Yamada et al.

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Table 1. Oligonucleotide primers used for sequencing of 18S rDNA

Primer sequences 5′-3′	Approximate position (*Saccharomyces cerevisiae* numbering)
TGGAATTACCGCGGCTGCTGGCACC	585-561
CCGTCAATTCCTTTAAGTTTCAGCC	1147-1123
GACGGGCGGTGTGTACAAAGGGCAG	1642-1618
TCTGGGCCGCACGCGCGCTACACTG	1448-1472

(26, 27) regarded this genus as a teleomorph of *Fellomyces* based on the similarity in the mode of the liberation of stalked conidia, major ubiquinone of Q-10, and the presence of cellular xylose.

The phylogeny of these stalked conidium forming yeasts has been discussed mainly by the comparisons of the partial sequences of 18S and/or 26S ribosomal RNA (4, 7, 11, 28). Apparently, however, those reports are insufficient to show clearly the phylogenetic positions of these yeasts, because the sequence data were compared with only few selected species of related taxa. Recently, the complete or almost complete 18S rDNA sequences of several taxa were reported in basidiomycetes (1, 16～21, 23, 24). In this paper, the 18S rDNA from eight yeast species, seven species of the stalked conidium-forming yeasts and *Fibulobasidium inconspicuum,* were sequenced in order to clarify their phylogenetic position in the basidiomycetes.

MATERIALS AND METHODS

Yeast strains, media, and growth conditions. The following yeast strains were used for sequencing : *Fellomyces polyborus* (Scott et van der Walt) Yamada et Banno 1984 JCM 6908^T, *Fibulobasidium inconspicuum* Badoni 1979 JCM 6898, *Kockovaella thailandica* Nakase, Banno et Yamada 1991 JCM 7824^T, *Kurtzmanomyces nectairei* (Rodrigues de Miranda) Yamada, Itoh, Kawasaki, Banno et Nakase 1988 JCM 6906^T, *Sporobolomyces xanthus* (Nakase, Okada et Sugiyama) Boekhout 1991 JCM 6885^T, *Sterigmatomyces halophilus* Fell 1966 JCM 6905^T, *Sterigmatosporidium polymorphum* Kraepelin et Sculze 1982 JCM 6902^T, and *Tsuchiyaea wingfieldii* (van der Walt, Yamada et Ferreira) Yamada, Kawasaki, Itoh, Banno et Nakase 1988 JCM 7368^T. Strains with a superscript T are derived from the type. The yeasts were grown in YM broth (Difco) at 17 or 25°C for 3 days with shaking.

PCR, cloning, and sequencing of 18S rDNA. The gene of 18S rRNA coding region was amplified by the polymerase chain reaction (PCR) as described in Suh and Nakase (16). The PCR products were cloned directly in the plasmid pT7Blue T-Vector (Novagen), and the single or double strand DNA templates for sequencing were prepared according to the directions of the manufacturer. Sequencing reactions were performed by using the Autocycle Sequencing Kit (Taq DNA polymerase, Pharmacia) or Autoread Sequencing Kit (T7 DNA polymerase, Pharmacia). Four primers for coding conserved areas of 18S rDNA were used (Table 1). Automated electrophoresis and analysis of DNA sequence reactions were performed with a ALFred DNA sequencer (Pharmacia).

Phylogenetic analysis. The 18S rDNA sequences were aligned by using the multialignment program CLUSTAL W (22) with the sequences of following sequence data obtained from the nucleotide sequence libraries (EMBL, GenBank, and DDBJ) : *Bensingtonia ciliata* (D38233), *B. ingoldii* (D38234), *B. intermedia* (D38235), *B. miscanthi* (D38236), *B. musae* (D43946), *B. naganoensis* (D38366), *B. phylladus* (D38237), *B. subrosea* (D38238), *B. yamatoana* (D38239), *B. yuccicola* (D38367) ; *Bullera crosea* (D31648), *B. dendrophila* (D31649), *B. globispora* (D31650), *B. miyagiaga* (D31651), *B. oryzae* (D31652), *B. pseudoalba* (D31660), *B. variabilis* (D31654) ; *Bulleromyces albus* (X60179), *Cryptococcus albidus* (D31655), *Cystofilobasidium capitatum* (D12801), *Erythrobasidium hasegawianum* (D12803), *Filobasidiella neoformans* (X60183),

Filobasidium floriforme (D13460), *Kondoa malvinella* (D13776), *Leucosporidium scottii* (X53499), *Mrakia frigida* (D12802), *Phaffia rhodozyma* (D31656); *Rhodosporidium dacryoidum* (D13459), *R. toruloides* (D12806); *Rhodotorula glutinis* (X69853), *Sporidiobolus johnsonii* (L22261), *Sporobolomyces roseus* (X60181), *Sympodiomycopsis paphiopedili* (D14006), *Tilletia caries* (U00972); *Tremella moriformis* (U00977), *T. globospora* (U00976), *T. foliacea* (L22262); *Trichosporon cutaneum* (X60182); *Udeniomyces megalosporus* (D31657), *U. piricola* (D31659), *U. puniceus* (D31658); *Ustilago hordei* (U00973), and *U. maydis* (X62396).

Ascomycetous yeasts, *Candida albicans* (X53497), *Kluyveromyces lactis* (X51830), and *Saccharomyces cerevisiae* (J01353), and a filamentous fungus *Neurospora crassa* (X04971) were used as outgroup species. For the analysis by the neighbour-joining method (15), distances between the sequences were calculated using Kimura's two-parameter model (8). Sites where gaps existed in any of the sequences were excluded. Bootstrap analysis (5) was performed from 1,000 random resamplings.

RESULTS AND DISCUSSION

About 1,750 bases from PCR product of 18S rDNA, excluding the PCR primer regions for the respective strains, were determined. The nucleotide sequence data reported in this paper will appear in the DDBJ, EMBL, and GenBank nucleotide sequence databases with the following accession numbers: *Fellomyces polyborus* (D64117), *Fibulobasidium inconspicuum* (D64123), *Kockovaella thailandica* (D64133), *Kurtzmanomyces nectairei* (D64122), *Sporobolomyces xanthus* (D64118), *Sterigmatomyces halophilus* (D64119), *Sterigmatosporidium polymorphum* (D64120), and *Tsuchiyaea wingfieldii* (D64121).

The sequence data were well aligned for all 55 fungi, including 47 published data, and a phylogenetic tree was constructed by the neighbour-joining method (Fig. 1). The ascomycetous yeasts, *Saccharomyces cerevisiae, Kluyveromyces lactis,* and *Candida albicans*, and the filamentous fungus, *Neurospora crassa*, were used as an outgroup. As shown in Fig. 1, the basidiomycetes were divided into three major lineages, groups I, II, and III, as reported in several recent papers (16~21). These lineages were well supported statistically as high bootstrap levels about 85 to 100%. Firstly, the species of the smut fungi (Ustilaginales), *Ustilago* and *Tilletia*, and the anamorphic yeast, *Sympodiomycopsis paphiopedili*, were diverged as a major lineage in basidiomycetes. The remaining species of basidiomycetous yeasts were separated into two phylogenetic groups which were correlated well with the presence or absence of xylose in the cells (Fig. 1).

Phylogenetic relationships among the xylose-lacking, stalked conidium-forming yeasts and related yeast taxa. The basidiomycetous yeasts, which have no xylose in the cells, formed a major lineage (group II) with 100% bootstrap confidence level as shown in Fig. 1. The yeasts of group II were also divided into three subgroups. This result well matched the phylogenetic trees written by Takashima et al. (20). *Leucosporidium scottii, Sporidiobolus johnsonii*, and *Rhodosporidium toruloides* made a branch with anamorphic yeasts, *Rhodotorula glutinis, Sporobolomyces roseus, Bensingtonia intermedia*, and *B. yamatoana*. On the other hand, the remaining eight species of *Bensingtonia* and *Kondoa malvinella* also made a branch with the stalked conidium-forming yeasts, *S. halophilus, K. nectairei*, and *S. xanthus*. *Rhodosporidium dacryoidum* and *Erythrobasidium hasegawianum* were distinctly located in the xylose-lacking basidiomycetous cluster the same as the tree of Suh and Sugiyama (18). The three species of stalked conidium-forming yeasts, which lack xylose, were located at comparatively close positions to each other in Fig. 1. *Kurtzmanomyces nectairei* and *S. xanthus* made a branch with 99.9% bootstrap confidence level, while *S. halophilus* showed a close phylogenetic relationship with *B. ingoldii* and *B. musae*.

Sporobolomyces xanthus was described in a new anamorphic genus *Ballistosporomyces* with *S. ruber* by Nakase et al. (12). Later, Boekhout (2) transferred these species to *Sporobolomyces* because he

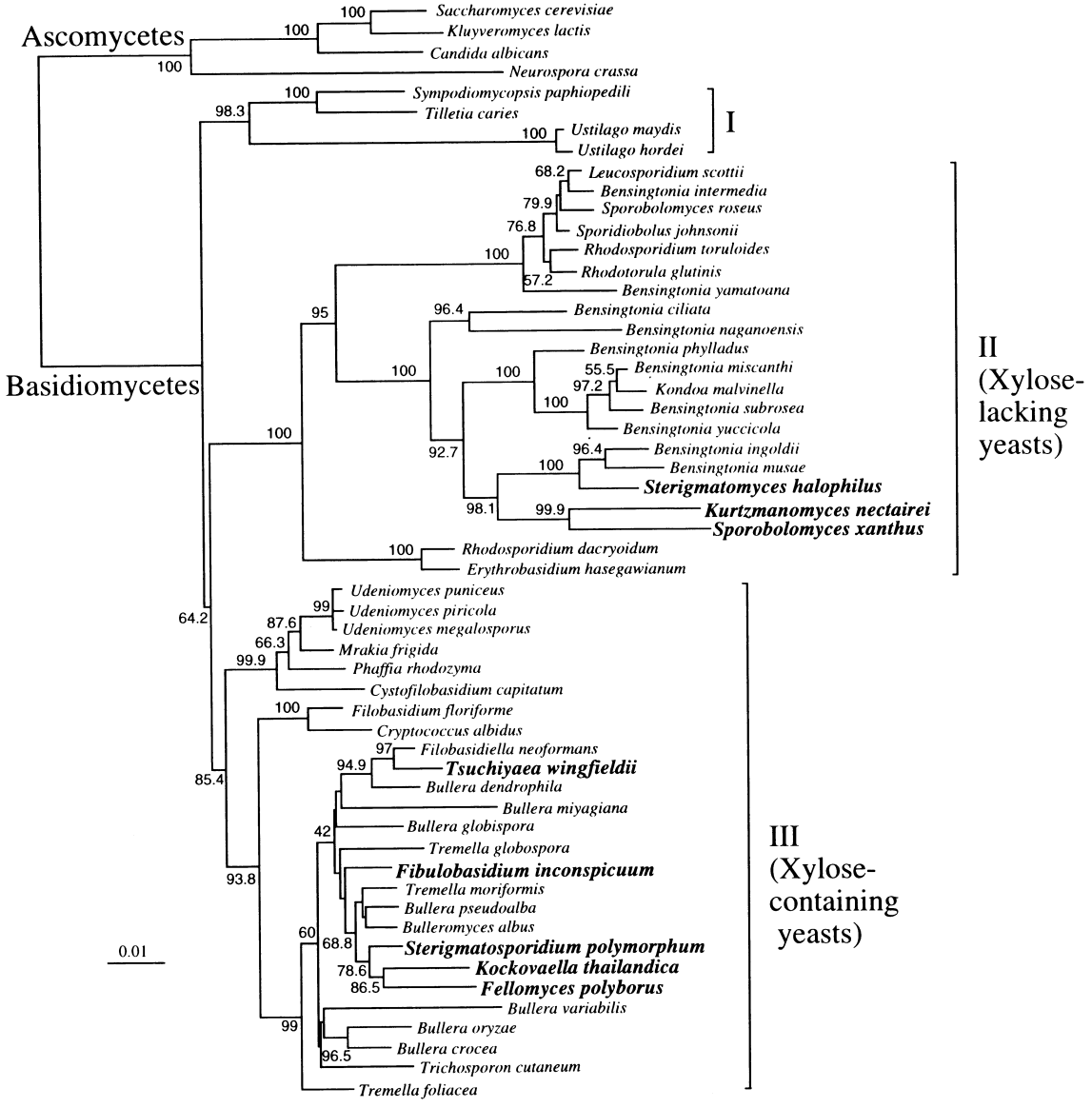

Fig. 1. Phylogenetic tree of 55 fungal species based on 18S rDNA sequence

The tree was constructed by the neighbour-joining method (14). As sites where gaps existed in any of the sequences were excluded, 1,520 nucleotides were used in this analysis. Each number indicates the percentage of bootstrap samplings, derived from 1,000 samples, supporting the internal branches. The frequency less than 50% was not indicated. The distance corresponding to one base change per hundred nucleotide positions is indicated by a bar

had observed stalked conidia in some species of *Sporobolomyces*. The heterogeneity of *Sporobolomyces* has been pointed out based on 18S and 26S rRNA partial sequence comparisons (4, 14). In the present study, *S. xanthus* was located at a position far from the position where *S. roseus*, the type species of the genus, was located (Fig. 1). This fact clearly suggested the phylogenetic heterogeneity of *Sporobolomyces*. *Sporobolomyces xanthus* resembles *Kurtzmanomyces nectairei* in chemotaxonomic and morphological characteristics, except for the ability of ballistoconidium production (Table 2). Although the present phylogenetic analysis suggested a close relationship between *S. xanthus* and *K. nectairei*

Table 2. Taxonomic characteristics of basidiomycetous anamorphic yeasts compared in this study

Genus	Xylose in the cell	Stalked conidium	Ballisto-conidium	Budding yeast cell	Major Ubiquinone
Bensingtonia	−	−	+	+	Q-9
Kurtzmanomyces	−	+	−	−	Q-10
Rhodotorula	−	−	−	+	Q-9/Q-10
*Sporobolomyces**	−	+/−	+	+/−	Q-10/Q-10(H_2)
Sterigmatomyces	−	+	−	−	Q-9
Bullera	+	−	+	+	Q-10
Cryptococcus	+	−	−	+	Q-8/Q-9/Q-10
Fellomyces	+	+	−	−	Q-10
Kockovaella	+	+	+	+	Q-10
Phaffia	+	−	−	+	Q-10
Tsuchiyaea	+	+	−	+	Q-9
Udeniomyces	+	−	+	+	Q-10

All the data are from the literature

* The species of *Ballistosporomyces* were included in this genus

(Fig. 1), further sequencing study, including all of the species of basidiomycetous yeast species, is required for clarifying the correct phylogenetic position of *S. xanthus*.

The stalked conidium-forming yeast *S. halophilus* showed a close relationship with some *Bensingtonia* species in the phylogenetic tree constructed from 18S or 26S rRNA partial sequences (16, 19). The present study supported the close relationship with *S. halophilus* and the ballistoconidium-forming yeast *Bensingtonia*.

Phylogenetic relationships among the xylose-containing, stalked conidium-forming yeasts and related yeast taxa. The basidiomycetous yeasts which contain xylose in the cells also made a major lineage, group III, in the phylogenetic tree (Fig. 1). The lineage could be divided into two groups which were a branch of *Udeniomyces, Mrakia, Phaffia*, and *Cystofilobasidium* and a branch of *Tremella*-like yeasts. These agreed well with the tree of Suh and Nakase (16). The genus *Phaffia* is now considered a synonym of *Rhodomyces*, an anamorph of *Xanthophyllomyces* (6). The species of stalked conidium-forming yeasts, *F. polyborus, K. thailandica, S. polymorphum*, and *T. wingfieldii*, showed close relationships with the species of *Tremella, Bullera*, and the related yeasts. *Fibulobasidium inconspicuum*, a species of Sirobasidiaceae (Tremellales), was also included in this lineage.

Tsuchiyaea wingfieldii made a branch with *Filobasidiella neoformans* with 97% bootstrap confidence level in the tree (Fig. 1). Some phylogenetic trees from partial rRNA sequences supported a close relationship between these two species (4, 7). *Sterigmatosporidium polymorphum, K. thailandica*, and *F. polyborus* were located at positions closely related, and *K. thailandica* and *F. polyborus* composed a branch (Fig. 1). *Kockovaella thailandica* and *F. polyborus* were similar to each other in taxonomic characteristics presently employed (Table 2) though they are distinguished by the formation of ballistospores and budding yeast cells. It is well-known that ballistospore formation is unstable and tends to be lost during culture maintenance, especially by frequent subculturing on agar media, and certain clones of *Kockovaella thailandica* were reported to have no budding yeast cells (13). When *Kockovaella* strains lose the ability to produce ballistoconidia and budding yeast cells, they cannot be distinguished from *Fellomyces* strains.

A teleomorphic genus *Sterigmatosporidium* was described as the teleomorphic state of some species of *Sterigmatomyces sensu* Fell (9). As mentioned above, however, the genus *Sterigmatomyces* was divided into four genera, *Fellomyces, Kurtzmanomyces, Sterigmatomyces*, and *Tsuchiyaea* (25～27). *Sterigmatosporidium* is now regarded as a teleomorph of *Fellomyces* on the basis of the mode of conidium liberation and chemotaxonomic characteristics (26). *Sterigmatosporidium polymorphum* and *F. polyborus* were located at positions closely related showing a close phylogenetic relationship (Fig. 1).

Certain species in Sirobasidiaceae and Tremellaceae in Tremellales produced yeast phases so that they were included in "The Yeasts, a Taxonomic Study, 3 rd ed." (10). *Fibulobasidium inconspicuum*, a species of Sirobasidiaceae, was located at a position closely related with *Tremella globospora, T. moriformis*, and related anamorphs. On the other hand, *T. foliacea* was located at a different position on the phylogenetic tree. This result suggested that the separation of the families Sirobasidiaceae and Tremellaceae may not reflect the phylogenetic relationship.

In conclusion, the results of present study indicated that stalked conidium-forming yeasts are separated into two phylogenetic groups which correlate well with the presence or absence of cellular xylose. The mode of vegetative reproduction, such as budding yeast cells, stalked conidia, and ballistoconidia, does not reflect the phylogenetic relationship among basidiomycetous species though it has long been considered as an important taxonomic criterion in basidiomycetous yeasts. The cellular xylose is considered to be an important taxonomic criterion in the basidiomycetous yeasts as discussed in a previous paper (16).

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18S rDNA 塩基配列に基づく有柄分生子形成酵母および関連担子菌系酵母の分子系統学的研究

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担子菌系酵母のうち，有柄分生子を形成する *Fellomyces polyborus, Kockovaella thailandica, Kurtzmanomyces nectairei, Sporobolomyces xanthus, Sterigmatomyces halophilus, Sterigmatosporidium polymorphum, Tsuchiyaea wingfieldii* の7種と *Fibulobasidium inconspicuum* の 18S rDNA の塩基配列を決定し，系統学的検討を行った．菌体にキシロースを含まない有柄分生子形成酵母の *K. nectairei, S. xanthus* および *S. halophilus* は *Bensingtonia* 属の種と系統枝を形成した．一方，菌体にキシロースを含む有柄分生子形成酵母の *F. polyborus, K. thailandica, S. polymorphum* および *T. wingfieldii* は *Bullera* 属および *Tremella* 属などと系統枝を形成した．ジュズタンシキン科 (Sirobasidiaceae) に属する *F. inconspicuum* もこの系統枝に位置していた．菌体中のキシロースの有無は系統をよく反映していたが、有柄分生子の形成は必ずしも系統樹と一致してはいなかった．