Recent Progress in the Systematics of Basidiomycetous Yeasts

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Basidiosporogenous yeasts and basidiomycetous anamorphic yeasts have been classified based on the morphological, physiological and biochemical characteristics. Higher taxonomic ranks such as genus, family etc. are classified based on the mode of vegetative reproduction, morphological characteristics found during sexual reproduction and certain physiological characteristics such as the assimilability of inositol. Recent chemosystematic studies suggest the unreasonableness of the taxonomic system based on these characteristics. Monosaccharide compositions of the cells, especially the presence or absence of xylose, and ubiquinone systems are suggested to be more reliable systematic criteria than the mode of vegetative reproduction and morphological criteria found during the sexual reproduction on the basis of the partial sequencing study of rRNAs. Ultrastructural features well correlate with chemosystematic characteristics and are regarded as reliable systematic criteria in higher taxonomic ranks. Polyphasic approaches are essential for further progress of the systematics of basidiomycetous yeasts.

Key words: Basidiomycetous yeasts, Ballistosporous yeasts, Chemosystematics, Systematics, Mode of conidiogenesis

1. Introduction

The system for the classification of yeasts has been constructed based on morphological, physiological and biochemical characteristics. In recent years, modification of the taxonomic system of basidiomycetous yeasts has been suggested from chemosystematic studies.

The mode of vegetative reproduction, especially the mode of conidiogenesis, and morphological characteristics observed during sexual reproduction still play important roles in the classification of higher taxonomic ranks in basidiomycetous yeasts. However, the unreason-

ableness of a classification system based on such characteristics was pointed out by several investigators on the basis of chemosystematic studies. The taxonomic rank species is now distinguished based on chemosystematic techniques such as DNA-DNA reassociation experiment, zymography, etc., in addition to the interfertility of cells. Reclassification of several genera have been proposed based mainly on chemosystematic criteria.

The progress of systematics of basidiomycetous yeasts since the publication of the 3rd edition of "The Yeasts, a Taxonomic Study"¹⁾ is discussed in this paper in relation to the

evaluation of criteria used for systematics of these yeasts.

2. Basidiomycetous anamorphic yeasts

Basidiomycetous anamorphic yeasts have been classified by their modes of vegetative reproduction and several physiological and biochemical characteristics such as the assimilability of inositol.

In the mentioned volume published in 1984, they were classified into ten genera in two families¹⁾. Sporobolomycetaceae includes two genera of ballistosporous yeasts, *Bullera* and *Sporobolomyces*, in which strains reproduce by budding (enteroblastic budding) in addition to reproduction by ballistospores. Pseudomycelium and true mycelium may be formed in these genera.

The remaining basidiomycetous yeasts were classified into 8 genera in the family Cryptococcaceae which comprises both ascomycetous and basidiomycetous anamorphic yeasts. In addition to budding (enteroblastic budding) yeast cells, pseudomycelia, true mycelia and arthrospores (fission cells) may be produced in these yeasts. The genera *Candida*, *Cryptococcus* and *Rhodotorula* reproduce by multilateral budding. Pseudomycelium and true mycelium may be formed in these genera. *Phaffia* reproduces by budding and may form pseudomycelium. The mode of budding in this genus was reported as monopolar¹⁾, however, it seems to be similar to those found in *Candida*, *Cryptococcus* and *Rhodotorula*. *Trichosporon* is characterized by the reproduction by budding and fission (formation of abundant true mycelium with arthrospores). *Sarcinosporon* produces sarcina-like cross-walled cells and hyphae, arthrospores and budding cells. *Malassezia* reproduces exclusively by monopolar budding and *Sterigmatomyces* reproduces exclusively by the production of buds on stalks (stalked conidia). The genera *Candida* and *Trichosporon* consist of both ascomycetous and basidiomycetous species.

The progress of systematics of several groups of basidiomycetous yeasts is discussed with the systematic evaluation of the mode of

vegetative reproduction mentioned above from a chemosystematic viewpoint. Stalked conidia and ballistospores can be regarded as budding cells as stated in "The Yeasts"¹⁾. In this paper, however, they are dealt with as different from the usual budding cell (blastoconidium) found in basidiomycetous yeasts, because the productivity of these kinds of conidia has been considered as an important taxonomic criterion by which higher taxonomic ranks of yeasts can be distinguished.

A. Expansion of the world of ballistosporous yeasts

In "The Yeasts"¹⁾, 13 species of anamorphic ballistosporous yeasts were listed, 6 in *Bullera* and 7 in *Sporobolomyces*. Extensive isolation studies on these yeasts have been carried out over the past several years and now 47 species are recognized²⁻²⁶⁾. Thirteen of them are included in three new genera, *Bensingtonia*, *Ballistosporomyces* and *Kockovaella*.

The genus *Bensingtonia* was described by Ingold¹⁰⁾ based on a single isolate. The original description so strongly resembles that of *Sporobolomyces* that it can hardly be discriminated from colorless strains of *Sporobolomyces*. Boekhout²⁷⁾, however, reported that it lacks xylose in the cells and has Q-9 as the major ubiquinone and can be discriminated from *Sporobolomyces* in the latter criterion. Nakase and Boekhout²⁸⁾ emended the diagnosis of the genus to permit the inclusion of all the ballistosporous anamorphic yeasts which lack xylose in the cells and have Q-9 as the major ubiquinone.

The genus *Ballistosporomyces* is characterized by reproduction by ballistospores and stalked conidia but not by budding cells²³⁾. Stalked conidia proliferate sympodially, percurrently or in the intermediate mode. Strains of *Ballistosporomyces* lack xylose in the cells and have Q-10 as the major ubiquinone. This corresponds to a ballistosporous state of *Kurtzmanomyces*²⁹⁾, which was proposed for xyloselacking and Q-10 equipped species of the genus *Fellomyces*³⁰⁾.

The genus *Kockovaella* was proposed based

Table 1. Grouping of ballistosporous yeasts

Group	Genus	No. of species	Xylose in cells	Ubi-quinone	Stalked conidia	Ballisto-spores	Carotenoids	2KG	Non-ballistosporous state
1	<i>Sporobolomyces</i>	1	—	Q-10 (H ₂)	—	asy	+	—	(<i>Rhodotorula</i>)
2	2a <i>Sporobolomyces</i>	15*	—	Q-10	—	asy	+/(—)	—	<i>Rhodotorula</i>
	2b <i>Sporobolomyces</i>	5	—	Q-10	—	asy	—	+	<i>Rhodotorula</i>
	2c <i>Sporobolomyces</i>	2	—	Q-10	—	asy	—	—	<i>Rhodotorula</i>
3	<i>Bensingtonia</i>	9	—	Q-9	—	asy/sy	—/+	—/+	<i>Rhodotorula</i>
5	<i>Ballistosporomyces</i>	2	—	Q-10	+	asy	+	—	<i>Kurtzmanomyces</i>
4	4a <i>Bullera</i>	11	+	Q-10	—	sy	—/+	+	<i>Cryptococcus</i>
	4b <i>Bullera</i>	3	+	Q-10	—	asy/sy	(+)	+	<i>Cryptococcus</i>
6	<i>Kockovaella</i>	2	+	Q-10	+	asy/sy	+	+	(<i>Fellomyces</i>)

* *Sporidiobolus* species are included.

on three isolates from plants in Thailand²⁶⁾. It is characterized by the reproduction by ballistospores, stalked conidia and budding cells, and by the presence of xylose in the cells and Q-10 as the major ubiquinone. This genus resembles the ballistosporous state of *Fellomyces* though budding cells are not found in the latter.

Forty-seven species of ballistosporous anamorphic yeasts were tentatively classified into 6 groups based on the presence or absence of xylose in the cells, major ubiquinones, and the modes of vegetative reproduction. Each group corresponds to the taxonomic rank genus (Table 1).

The presence or absence of xylose in the cells should be regarded as a criterion to separate the taxonomic rank family or order. Weijman and Rodrigues de Miranda³¹⁾ investigated the presence of xylose in the genera *Bullera* and *Sporobolomyces* by gas-liquid chromatographic analysis of derivatized whole cell hydrolyzates. They found xylose in the majority of *Bullera* strains but not in most *Sporobolomyces* strains and suggested the transfer of *Sporobolomyces puniceus*, a xylose-containing species, to *Bullera*. However, they obtained insignificant results in *Bullera salicina*, *Bullera tsugae* and *Sporobolomyces gracilis*. Suzuki and Nakase³²⁾ investigated these three strains by an improved technique using high performance liquid chromatography and confirmed the absence of

xylose in their cells. Based on the presence or absence of xylose, *B. tsugae* and *B. salicina* were transferred to *Sporobolomyces*³³⁾ and *S. puniceus* was transferred to *Bullera*⁹⁾.

Weijman and Rodrigues de Miranda³¹⁾ reported that the carbohydrate patterns recorded for the xylose-containing *Bullera* strains closely resemble the patterns of *Cryptococcus*, *Trichosporon*, *Filobasidium* and other basidiomycetous fungi presently classified in Filobasidiaceae.

The type of ubiquinone system is considered to be a criterion to define the taxonomic rank genus¹⁾. Each group in Table 1 has its own major ubiquinone. *Sporobolomyces elongatus* is placed in group 1 and the remaining *Sporobolomyces* species are placed in group 2. The former species has Q-10 (H₂) as the major ubiquinone and differs from the remaining species of *Sporobolomyces* in this respect. A close relationship of this species to *Erythrobasidium hasegawae* is suggested and is discussed later. It might represent a genus different from *Sporobolomyces*.

By the finding of yeasts belonging to the genera *Ballistosporomyces* and *Kockovaella*, the modes of conidiogenesis became complicated as compared with those shown in "The Yeasts"¹⁾. The modes of conidiogenesis found in basidiomycetous anamorphic yeasts are summarized in Fig. 1. Combinations of the modes of conidiogenesis, allow basidiomycetous anamorphic yeasts to be classified into 9

groups. We assume that yeasts belonging to groups 1 to 6 have an ability to carry out these three kinds of conidiogenesis: (multilateral) budding, production of stalked conidium, and production of ballistospores, when suitable conditions are provided. Namely, we assume that ballistosporous yeasts do not comprise a special group of basidiomycetous yeasts but represent a ballistosporous aspect of various of these yeasts.

B. Relationships between ballistosporous and non-ballistosporous yeasts.

It is well known that ballistospore-forming ability is easily lost during maintenance. In fact, type strains of *Bullera singularis*, *Bullera tsugae*, *Sporobolomyces albo-rubescens*, *Sporobolomyces gracilis* and *Sporobolomyces puniceus* were reported to show no ballistosporous

ability¹⁾. Even in freshly isolated strains, ballistosporous ability is often very poor or completely lacking. Nakase and Suzuki⁶⁾ isolated 13 strains of *Bullera crocea* from dead leaves of a rice plant, *Oryza sativa*. Ballistospore-formation was abundant in 3 strains, moderate in 2 strains, and poor in 3 strains. The remaining 5 strains did not produce ballistospores on any media examined. Non-ballistosporous strains showed characteristics identical to ballistosporous strains except for ballistosporous ability therefore must be identified as *B. crocea* in spite of the lack of ballistospores.

When ballistospores cannot be observed in ballistosporous yeasts strains, we cannot discriminate them from non-ballistosporous yeasts. Non-ballistosporous strains are identified as

Type of conidium		Genus	Group
Blastoconidium (Budding cell)		<i>Candida</i> * ¹ <i>Cryptococcus</i> <i>Phaffia</i> <i>Rhodotorula</i>	1
		<i>Sterigmatomyces</i> <i>Kurtzmanomyces</i> <i>Fellomyces</i>	2
Blastoconidium (Budding cell)	Stalked conidium	<i>Tsuchiyaea</i>	3
Blastoconidium (Budding cell)	Ballistospore	<i>Kockovaella</i>	4
		<i>Ballistosporomyces</i>	5
		<i>Bensingtonia</i> <i>Bullera</i> <i>Sporobolomyces</i>	6
Blastoconidium* ³	Arthrospore* ²	<i>Trichosporon</i> * ¹ <i>Sarcinosporon</i>	7 8
		<i>Malassezia</i>	9

*¹ in parte *² Fission *³ Monopolar budding

Fig. 1. The mode of conidiogenesis found in genera of basidiomycetous anamorphic yeasts.

Rhodotorula, *Kurtzmanomyces*, *Cryptococcus* and probably as *Fellomyces* as shown in Table 1. Yamazaki and Komagata³⁴⁾ reported that a strain of *Cryptococcus albidus* var. *albidus*, a non-ballistosporous yeast, showed similar enzyme patterns to *Bullera alba*, a ballistosporous yeast, in slab-gel electrophoresis. We can easily assume a close relationship between ballistosporous taxa and their corresponding non-ballistosporous taxa.

Based on this assumption, Nakase et al.²⁶⁾ compared the sequences of 170 bases in the positions from 1451 to 1618 of 18S rRNA from strains of *Kockovaella* with strains of *Bullera* and xylose-positive, stalked conidium-forming non-ballistosporous yeasts. A dendrogram prepared based on the base difference is shown in Fig. 2. Strains of *Kockovaella*, *Fellomyces* and *Sterigmatosporidium* comprise a single cluster and base differences among these yeasts were found to be two to four. This suggested a close phylogenetic relationship among these three genera and implies that the presence or absence of ballistospores and budding cells is not as important a taxonomic criterion as has long been believed.

It seems more reasonable to combine *Kockovaella* and *Fellomyces* in a single genus than to deal with them as different genera. However, we hesitate to do so yet. When it is once done, the same principle must be applied to the remaining groups of basidiomycetous anamorphic yeasts, for example, we have to combine *Bullera* and *Cryptococcus*, and *Sporobolomyces* and *Rhodotorula*. Apparently, there is little merit to do so because a respective combined genus increases its heterogeneity. Further, the sequence of 170 bases corresponds to just about 10% of the whole molecule. Any great change in the system of classification should be performed only when sufficient chemosystematic and molecular systematic information has been accumulated.

C. Stalked conidium-forming yeasts

A single genus *Sterigmatomyces* was listed in stalked conidium-forming yeasts in "The Yeasts"¹⁾. Yamada and Banno³⁰⁾ excluded spe-

cies having Q-10 as the major ubiquinone and liberating conidium by end-break from *Sterigmatomyces* and proposed a new genus *Fellomyces* for these species. Later, Yamada et al.^{29, 35)} divided stalked conidium-forming yeasts into 4 genera based on the presence or absence of xylose in the cells, ubiquinone types and the position of the liberation of conidium from the stalk.

Sterigmatosporidium, which has been considered a teleomorphic counterpart of *Sterigmatomyces*, was regarded as a teleomorph of *Fellomyces*³⁰⁾. A close relationship of *Sterigmatosporidium* to *Fellomyces* was suggested based on the comparison of the partial base sequences of 18S rRNA as mentioned above (Fig. 2). This classification was supported by recent studies on the partial sequence of 18S and 25S rRNA from stalked conidium-forming yeasts^{36, 37)}.

D. Other basidiomycetous anamorphic genera

Before publication of "The Yeasts"¹⁾, Moore³⁸⁾ proposed a new genus *Vanrija* for basidiomycetous species included in *Candida* and *Torulopsis*. This genus is not adopted in the monograph. Apparently, *Vanrija* includes a variety of basidiomycetous anamorphic yeasts of supposedly diverse phylogenetic origins.

Weijman and Rodrigues de Miranda³⁹⁾ found that species in the genus *Candida* can be separated into 3 groups based on the monosaccharide component of whole cell hydrolyzates. Cells of ascomycetous species are composed mainly of mannose and lack rhamnose, fucose and xylose. Basidiomycetous species are divided into two groups. One group contains xylose and does not contain a large amount of mannose; this pattern is characteristic of Cryptococcales and Tremellales. The other group contains fucose and/or rhamnose and a relatively large amount of mannose; this pattern is characteristic of Sporobolomycetaceae. This caused Weijman et al.⁴⁰⁾ to transfer species of the former group of basidiomycetous yeasts to a redefined genus *Cryptococcus* and those of the latter to a redefined genus *Rhodotorula*.

As shown for ballistosporous yeasts, the

Fig. 2. Dendrogram based on the base difference of sequences of positions 1451 through 1618 of 18S rRNA of strains of *Kockovaella* and supposedly related genera (prepared by unweighted pair-group method).

monosaccharide composition of cells, especially the presence or absence of xylose, seems a better criterion by which to separate the taxonomic rank genus in basidiomycetous yeasts than the assimilation of inositol and the productivity of mycelium and pseudomycelium now employed to separate the three genera mentioned above.

3. Basidiosporogenous yeasts

Basidiosporogenous yeasts were classified into 3 groups, Filobasidiaceae, teliospore-forming yeasts, and Tremellales with a yeast phase. Among them, the genera *Rhodospordium* and *Leucosporidium* in teliospore-forming yeasts show great heterogeneities. Respective genus includes both xylosecontaining and xylose-lacking species, as well as species having 3 different kinds of major ubiquinones, Q-8, Q-9, and Q-10.

Xylose-containing and Q-8-equipped species in *Rhodospordium* are now placed in *Cystofilobasidium*. Oberwinkler et al.⁴¹⁾ transferred *Rhodospordium bisporidiis* and *Rhodospordium capitatum* to a newly established genus

Cystofilobasidium, which was placed in Filobasidiaceae, because yeasts in this genus produce holobasidia, sessile basidiospores and dolipore-like septal pores, in spite of the fact that they can produce teliospores. Later, Hamamoto et al.⁴²⁾ transferred *Rhodospordium infirmuminiatum* to *Cystofilobasidium*.

Rhodospordium malvinellum, a xylose-lacking, Q-9-equipped species, was transferred to a newly proposed genus *Kondoa* based on the difference of base sequences of 18S and 26S rRNAs⁴³⁾. A two-celled basidium is formed in this genus. Very recently, Suh and Sugiyama (unpublished data) found that this species had septal pores as seen in species of *Atractogloea* in the Atractiellales. This finding reinforces this proposal.

Four species of xylose-containing and Q-8-equipped yeasts in *Leucosporidium* were transferred to *Mrakia*, a newly established genus⁴⁴⁾. The basidial form in the genus is holobasidium. *Mrakia* was placed in Filobasidiaceae in spite of its production of teliospores. The septal pore structure of *Mrakia frigida* and *Mrakia*

Table 2. Grouping of teliospore-forming yeasts and related genera

Genus	Xylose in cells	Major ubiquinone	Teliospore	Basidial form	Septal pore structure
Group A *					
<i>Kondoa</i>	—	Q-9	+	phragmo	simple pore
<i>Leucosporidium</i>	—	Q-9/Q-10	+	phragmo	simple pore
<i>Rhodospiridium</i>	—	Q-9/Q-10	+	phragmo	simple pore
<i>Sporidiobolus</i>	—	Q-10	+	holo/phragmo	simple pore
<i>Erythrobasidium</i>	—	Q-10 (H ₂)	—	holo	simple pore
Group B *					
<i>Mrakia</i>	+	Q-8	+	holo	primitive dolipore
<i>Cystofilobasidium</i>	+	Q-8	+	holo	primitive dolipore
<i>Filobasidium</i>	+	Q-9/Q-10	—	holo	primitive dolipore
<i>Filobasidiella</i>	+	Q-10	—	holo	primitive dolipore

*Group A, Ustilaginale affinity; Group B, Filobasidiaceae.

nivalis is primitive dolipore (Suh and Sugiyama, unpublished data).

In 1988, Hamamoto et al.⁴⁵⁾ found a sexual stage of *Rhodotorula hasegawae* and proposed a new genus *Erythrobasidium* for this species. *Erythrobasidium* is characterized by Q-10 (H₂), the absence of xylose in the cells, the lack of teliospores and the production of holobasidia. They tentatively placed it in Filobasidiaceae based on the morphological characteristics which are similar to yeasts in Filobasidiaceae. This genus differs from other yeasts in Filobasidiaceae in its lack of xylose in the cells. The septal pore structure of *Erythrobasidium hasegawae* was found to be simple pore (Suh and Sugiyama, unpublished data).

Monosaturated ubiquinone Q-10 (H₂) is popular in Ascomycotina but rare in Basidiomycotina. In yeasts, it was found in two species, *Erythrobasidium hasegawae* and *Sporobolomyces elongatus*, as the major ubiquinone^{46,47)}. Takematsu et al. (unpublished data) compared the partial sequence of 18S rRNA of these two species in the positions from 1451 to 1618. They found that the RNAs have an identical base sequence in this region, strongly suggesting a close relationship between these two species. *Erythrobasidium* is assumed to be related to xylose-negative teliospore-forming yeasts though it does not produce teliospores. As mentioned above, the septal pore structure

of *Erythrobasidium hasegawae* is of the simple pore type and differs from those of Filobasidiaceae.

The salient characteristics of genera in "teliospore-forming yeasts" and Filobasidiaceae are summarized in Table 2. These yeasts are classified into 2 groups.

Group A comprises five genera. Xylose is not found in the cells and septal pore structure is simple pore. Teliospores are produced in 4 genera but not 1 genus. The basidial form is usually, phragmobasidium but sometimes holobasidium.

Group B comprises four genera. Xylose is found in the cells and septal pore structure is primitive dolipore. Basidial form is holobasidium. This classification is supported by the partial sequencing study of 18S rRNA (Joo, Sugiyama and Komagata, unpublished data).

The presence or absence of xylose in the cells and the septal pore structures are considered to be more reliable taxonomic criteria than the teliospore-forming ability and basidial form in the classification of higher taxonomic ranks such as genus, family, etc.

4. Conclusion

Based on extensive studies on carbohydrate patterns of yeasts and yeast-like fungi, Weijman and Golubev⁴⁸⁾ presented cell wall categories of yeasts and yeast-like fungi which showed the

relationships of carbohydrate patterns to taxonomic ranks, families and classes. They considered that the presence or absence of xylose, fucose or rhamnose is important in basidiomycetous yeasts and yeastlike fungi, together with the amount of mannose and chitin. The carbohydrate pattern of the cells, as a reflection of the cell wall structure, is considered to be an important taxonomic criterion in yeasts.

Recent studies on the sequences of rRNAs revealed the significance of this technique. As with the definition of taxonomic rank species, chemosystematic approaches are essential for the systematics of higher taxonomic ranks such as genus, family, order, etc., of basidiomycetous yeasts.

van der Walt and von Arx⁴⁹⁾ emphasized the use of ultrastructural characters in yeast systematics. They discussed the significance of ultrastructural features of the cell walls, septa and ascospores. As discussed, a good correlation is observed between ultrastructure of septal pores and chemosystematic criteria. Together with chemosystematic studies, ultrastructural studies will provide invaluable information on yeast systematics.

Polyphasic approaches appear to be required for further progress in the systematics of basidiomycetous yeasts. Chemosystematic approaches are believed to be especially important for the establishment of a rational classification system.

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