REVIEW / SYNTHÈSE

Classification of heterobasidiomycetous yeasts: characteristics and affiliation of genera to higher taxa of Heterobasidiomycetes

T. Boekhout[1]
Centraalbureau voor Schimmelcultures, Yeast Division, Julianalaan 67, 2628 BC Delft, the Netherlands
A. Fonseca and J.-P. Sampaio
Instituto Gulbenkian de Ciência, Rua da Quinta Grande, Apartado 14, 2781 Oeiras, Portugal
and
W. I. Golubev
Institute of Biochemistry and Physiology of Microorganisms, Academy of Sciences, Puschino on the Oka, Moscow, Russia

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Introduction

During the last decades the study of heterobasidiomycetous yeasts has flourished. Many new species and genera, both anamorphic and teleomorphic, have been described. Morphological characteristics were among the first to indicate a polyphyletic origin of the yeasts. The presence of ballistoconidia in *Sporobolomyces* led Kluyver and van Niel (1924, 1927) to conclude that these organisms represented basidiomycetous yeasts. The basidiomycetous nature of part of the yeasts was clearly demonstrated by their complicated dimorphic life cycles, similar to those occurring in Heterobasidiomycetes (Banno 1967). This similarity is acknowledged in several classifications. Moore (1972, 1980) referred the Ustilaginales to a separate division Ustomycota, to which the teliospore-forming basidiomycetous yeast genera *Rhodosporidium* and *Leucosporidium* were assigned. This view is not supported by Oberwinkler (1987), who considered the establishment of a separate division Ustomycota to be artificial, because they have many heterobasidiomycetous characteristics. Moreover, teliospores are not confined to ustilaginaceous yeasts but occur also in tremellaceous or filobasidiaceous yeasts.

The classification of heterobasidiomycetous yeasts at higher taxonomic ranks has been hampered by several factors. The available data on the systematics of this group of organisms are scattered and have not been subject to an integrated analysis, and a clear delimitation of orders within the Heterobasidiomycetes has not been fully accomplished (e.g., Bandoni 1984; Oberwinkler 1987). The affiliation of basidiomycetous yeasts to orders of Heterobasidiomycetes has been accepted as it reflects most accurately their phylogenetic position. This conclusion is based on morphological, biochemical, and molecular characteristics, and also on the fact that several representatives of Heterobasidiomycetes possess ontogenetic yeast stages. Teleomorphic heterobasidiomycetous yeast genera with Tremellales affinity are generally grouped in the Filobasidiaceae (Olive 1968; Kwon-Chung 1987) of the Filobasidiales (Jülich 1981). In turn, genera like *Rhodosporidium*, *Leucosporidium*, and *Sporidiobolus* are considered closely related to members of the Ustilaginales that are parasitic on dicotyledonous plants (Blanz and Gottschalk 1984; Deml 1987). The classification of anamorphic heterobasidiomycetous yeasts in two families, Cryptococcaceae and Sporobolomycetaceae (Walt 1987), is parallel with this subdivision of teleomorphic heterobasidiomycetous yeasts. Owing to developments in molecular biology, new characteristics were introduced in fungal taxonomy. However, each character analysis has its limitations. Some characters are applicable at or around the species level, e.g., DNA–DNA reassociation experiments and somatic hybridizations. Others are indicative of main patterns in the evolution of the heterobasidiomycetous yeasts, e.g., septal ultrastructure and rRNA sequencing. In this review recent developments in the systematics of heterobasidiomycetous

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[1] Author for correspondence.

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yeasts are discussed and compared with traditionally studied features. Finally, an arrangement of genera is given according to their most likely phylogenetic affiliations.

Morphology

Morphological characteristics indicative of a basidiomycetous nature are ballistoconidia, enteroblastic budding, dikaryotic hyphae, clamp connections, teliospores, phragmo- or holo-basidia, and haustorioid branches.

Ballistoconidia occur in a limited, but expanding, number of genera (Derx 1948; Nakase and Boekhout 1988; Nakase *et al.* 1989, 1991; Boekhout 1991*a*). The family Sporobolomycetaceae was characterized by this character (Derx 1948). More recently it has become clear that this family in its original sense is polyphyletic (Weijman and Rodrigues de Miranda 1983; Blanz and Gottschalk 1984; Nakase 1989; Boekhout *et al.* 1992*a*) and comprises representatives of Ustilaginales, Tremellales, and Tilletiales (Boekhout *et al.* 1992*a*). Nucleotide sequencing of rRNA suggests a close relationship between ballistoconidia-forming genera and some genera that do not form ballistoconidia, e.g., *Sporobolomyces* and *Rhodotorula* (Takematsu *et al.* 1990; Fell *et al.* 1992), *Sporidiobolus* and *Rhodosporidium* (Fell and Kurtzman 1990), and *Bullera* and *Cryptococcus* (Fell *et al.* 1992).

Conidiogenesis on stalks occurs in a few genera, such as *Sterigmatomyces*, *Sterigmatosporidium*, *Fellomyces*, *Kurtzmanomyces*, and *Tsuchiyaea* (Barnett *et al.* 1990). Recent studies have shown that these genera are closely related to either Tremellales or Ustilaginales (see below). Moreover, stalked conidia also occur in ballistoconidia-forming genera. These facts cast doubts on the use of this criterion to delimitate genera.

Arthroconidia occur in *Trichosporon* (Barnett *et al.* 1990; Guého *et al.* 1992). This genus appears to be heterogeneous, as demonstrated by rRNA sequencing studies (Fell *et al.* 1992; Guého *et al.* 1992).

Transversely septate phragmobasidia commonly occur in ustilaginaceous yeasts, e.g., *Leucosporidium* and *Rhodosporidium* (Fell 1984). However, some species of ustilaginaceous yeasts, e.g., *Sporidiobolus johnsonii*, have holometabasidia (Nyland 1949; Bandoni *et al.* 1971; Fell and Statzell Tallman 1981). Cruciately septate metabasidia are characteristic for Tremellales (Bandoni 1987; Oberwinkler 1987) and occur in *Bulleromyces*, the teleomorph of *Bullera* (Boekhout *et al.* 1991*a*). Holometabasidia occur in genera belonging to Filobasidiales (Kwon-Chung 1987), e.g., *Filobasidiella* (Kwon-Chung 1975, 1987), *Filobasidium* (Olive 1968; Rodrigues de Miranda 1972; Kwon-Chung 1977; Bandoni *et al.* 1991), and *Cystofilobasidium* (Oberwinkler *et al.* 1983; Hamamoto *et al.* 1988*b*).

Teliospores are slightly thick-walled to thick-walled probasidia. They commonly occur in ustilaginaceous yeasts (*Leucosporidium*, *Rhodosporidium*, and *Sporidiobolus*), but also in some tilletiaceous (*Tilletiaria*) and tremellaceous fungi (*Cystofilobasidium* and *Mrakia*) (Oberwinkler *et al.* 1983; Kwon-Chung 1987; Yamada and Komagata 1987; Boekhout 1991*a*).

Haustorioid branches indicate an affinity with the Tremellales–Filobasidiales (Bandoni 1987; Oberwinkler 1987). However, their absence does not necessarily exclude affinity with Tremellales (Bandoni 1987).

Because of their occurrence in both tremellaceous and ustilaginaceous yeasts, the presence or absence of phragmo- or holo-basidia, clamp connections, and (or) teliospores cannot be used to assign genera to taxonomic categories of higher order.

Life cycles and genetics

The most convincing evidence demonstrating the (hetero)basidiomycetous nature of part of the yeasts is their basidiomycetous life cycle (Banno 1963, 1967; Olive 1968; Fell 1970, 1974; Fell and Statzell Tallman 1980, 1981, 1982; Fell *et al.* 1969, 1973; Rodrigues de Miranda 1972; Kwon-Chung 1975, 1976, 1977; Kraepelin and Schulze 1982; Boekhout *et al.* 1991*a*). The general heterobasidiomycetous life cycle comprises haploid yeast stages of different mating types. After conjugation, dikaryotic hyphae are formed containing haploid nuclei. Karyogamy occurs in either thin walled or thick-walled probasidia. After or simultaneously with meiosis, holo- or phragmo-basidia are formed, on which haploid basidiospores are formed. Gene exchange has only been demonstrated to occur in *Filobasidiella neoformans* (Kwon-Chung 1980) and *Rhodosporidium toruloides* (Banno 1963, 1967).

The incompatibility system can be bipolar (biallelic or multiple allelic) or tetrapolar (Fell 1974; Fell and Statzell Tallman 1980, 1981; Fell *et al.* 1969, 1973; Kwon-Chung 1975). In homothallic strains, dikaryotic hyphae with clamp connections are formed without conjugation (Nyland 1948, 1949; Laffin and Cutter 1959; Erke 1976; Fell and Statzell Tallman 1981; Holzschu *et al.* 1981). Some species have both heterothallic and homothallic strains, e.g., *Sporidiobolus johnsonii* (Boekhout 1991*a*), *Sterigmatosporidium polymorphum* (Kraepelin and Schulze 1982), and *Filobasidiella neoformans* (Kwon-Chung 1987; Schmeding *et al.* 1981). Monokaryotic fruiting, i.e., apomictic formation of tentatively generative cells by monokaryotic hyphae without clamp connections or with incomplete clamp connections, occurs as well (Fell *et al.* 1969; Fell 1974). Some species have both heterothallic and apomictic parts in their life cycle, e.g., *Leucosporidium scottii* (Fell *et al.* 1969), *Rhodosporidium dacryoidum* (Fell and Statzell Tallman 1984), and *Itersonilia perplexans* (Boekhout 1991*b*). Sometimes, transitions from an apparently monokaryotic mycelial stage to a dikaryotic one have been observed within one strain (A. Fonseca and J.-P. Sampaio, unpublished observations).

Only limited information is available on the genetics of the life cycles. Most tetrapolar yeast species seem to have a modified tetrapolar mating system with biallelic A factors and multiple allelic B factors (Bandoni 1963; Flegel 1976; Summerbell 1983; Wong 1987).

Little is known about the ploidy levels of different parts of the life cycles. Banno (1967) demonstrated the presence of haploid nuclei in mating yeast strains and in basidiospores of *Rhodosporidium toruloides*. However, yeast cells originating from basidiospores and developing into dikaryotic hyphae were in some cases found to be diploid. In these cases somatic reduction of the diploid nucleus was assumed to occur during the transition from monokaryotic yeast cell into dikaryotic hyphae. Such a mechanism may occur in the life cycles of *Sporidiobolus johnsonii* (Laffin and Cutter 1959) and *Sterigmatosporidium polymorphum* (Kraepelin and Schulze 1982) as well.

Differences in ploidy occur among yeast strains of *Cryptococcus albidus* (Walt and de Leeuw 1970), *Bullera* *dendrophila* (Walt 1973), *Sporobolomyces salmonicolor* (Walt and Pitout 1969), and *Itersonilia perplexans* (Boekhout and Jille 1991). These data and the frequent occurrence of sexually aberrant strains suggest that differences in ploidy among heterobasidiomycetous yeasts, whether euploid or aneuploid, do occur.

Separation of chromosomal DNA by pulsed-field gel electrophoresis (PFGE) has been applied to some basidiomycetous yeasts. Jonge *et al.* (1986) studied patterns from strains belonging to *Cryptococcus laurentii*, *Filobasidiella neoformans*, *Rhodosporidium toruloides*, and *Rhodotorula mucilaginosa*. Chromosomal DNAs of *Filobasidiella neoformans* were studied by Polacheck and Lebens (1989) and Perfect *et al.* (1989). Polacheck and Lebens (1989), using orthogonal-field-alternation gel electrophoresis (OFAGE), observed three distinct patterns of chromosomal DNA, which correlated, according to these authors, with the differentiation into serotypes. On the contrary, Perfect *et al.* (1989), using another system of electrophoresis (contour-clamped homogeneous electric field electrophoresis, CHEF), only observed strain-specific patterns. An extensive study of the karyotypes of *Tilletiopsis* and related fungi (Tilletiales) suggests the presence of species-specific banding patterns (Boekhout *et al.* 1992*b*). However, within the main patterns, strain-specific variation is obvious. Species of *Malassezia* reveal uniform banding patterns. Strains of *Malassezia pachydermatis* have nearly identical patterns, whereas in *Malessezia furfur* three distinct patterns are present (T. Boekhout and R. Bosboom, unpublished results). It has been suggested that chromosomal diversification may be an important factor leading to species formation in anamorphic yeasts (Rustchenko-Bulgac *et al.* 1990; Rustchenko-Bulgac 1991; Wickes *et al.* 1991).

Comparative investigations on mating, life cycles, gene exchange, ploidy, and chromosomal organization will contribute to a better understanding of the dynamics and evolutionary strategies of species, which in many basidiomycetous yeasts comprise different sexual and (or) asexual cycles.

Ultrastructure

Basidiomycetous yeasts are characterized by an electron-dense and lamellate cell wall (Kreger-van Rij and Veenhuis 1971; Simmons and Ahearn 1987; Boekhout *et al.* 1992*a*).

Structural and temporal features of the mitotic apparatus of basidiomycetous yeasts reveal the following sequential characteristics: (*i*) during interphase the nucleus-associated organelle (NAO) is electron dense, diglobular, and extranuclear, (*ii*) the NAO migrates into the bud, (*iii*) the nuclear envelope partly opens to permit entry of the NAO into the nucleus, (*iv*) spindle formation takes place in the bud, and (*v*) the spindle elongates during anaphase–telophase (McCully and Robinow 1972*a*, 1972*b*; Taylor and Wells 1979; Boekhout and Linnemans 1982; Heath *et al.* 1982, 1987).

Basidiomycetes have a wide variety of septal pores (Khan and Kimbrough 1980), which seem indicative of their systematic affiliation. Tremellaceous yeasts (Tremellales–Filobasidiales) have dolipores (Kreger-van Rij and Veenhuis 1971; Moore and Kreger-van Rij 1972; Kwon-Chung and Popkin 1976; Moore 1979, 1987; Khan and Kimbrough 1980; Rhodes *et al.* 1981; Oberwinkler *et al.* 1983; Boekhout *et al.* 1992*a*; Guého *et al.* 1992). Parenthesomes may be present or absent (Moore 1987). Among heterobasidiomycetous yeasts parenthesomes are made up of U-shaped vesicles or tubuli (Tremellales type). Ustilaginaceous yeasts usually have tapering diaphragmlike pores without parenthesomes (Kreger-van Rij and Veenhuis 1971; Johnson-Reid and Moore 1972; Hoog and Boekhout 1982; Boekhout *et al.* 1992*a*). Microporelike structures occur in *Tilletiopsis*, *Tilletiaria*, and anamorphs of *Entyloma* (Boekhout *et al.* 1992*a*), but are also encountered in *Ustilago* species (Bauer *et al.* 1989; Ramberg and McLaughlin 1980), *Trichosporon pullulans*, and *Trichosporon brassicae* (Guého *et al.* 1992). Lenticular bodies are thus far encountered only in ustilaginaceous yeasts (Boekhout *et al.* 1992*a*).

There is a striking correlation between septal pore ultrastructure and 5S rRNA nucleotide sequences (Walker and Doolittle 1982; Templeton 1983; Blanz and Unseld 1987), which is further sustained by the extracellular polysaccharide composition and partial nucleotide sequences of large-subunit rRNA (Fell *et al.* 1992).

Extracellular polysaccharides

The architecture and chemical composition of the fungal cell wall are diverse and specific for different taxa (e.g., Bartnicki-Garcia 1968; Kreger-van Rij and Veenhuis 1971; Fleet 1985, 1991). The qualitative monomer composition of capsular polysaccharides parallels the phylogenetic affiliation of heterobasidiomycetous yeasts. Quantitative differences in the monomer composition can be very significant (Dörfler 1990).

Comparative studies of carbohydrate composition of whole yeast cells (Sugiyama *et al.* 1985; Weijman and Golubev 1987; Weijman and Rodrigues de Miranda 1988; Suzuki and Nakase 1988) reveal two main groups of monosaccharides. The first group includes glucose, mannose, *N*-acetylglucosamine, and usually galactose, which are of cell-wall (glucans, mannans, chitin, galactomannans) or intracellular origin (glycogen) (Fleet 1985). The second group includes xylose, fucose, and rhamnose and originates from capsules (Golubev 1991). These latter monomers are present in whole-cell hydrolyzates of heterobasidiomycetous yeasts, but are absent in yeasts of ascomycetous affinity. Xylose is released from capsular glucuronoxylomannans, which have been investigated in *Filobasidiella neoformans* (Battacharejee *et al.* 1984) and species of *Cryptococcus* and *Bulleromyces* (Vitovskaya *et al.* 1988; Elinov *et al.* 1990). The heteropolysaccharides of these species have the same α-1,3-mannan backbone, but differ in the number and location of side chains of xylosyl and glucuronic acid residues, which are attached to the main chain by β-1,2 and β-1,4 linkages. Xylose occurs in tremellaceous yeasts, e.g., species of the genera *Bulleromyces–Bullera*, *Cryptococcus*, *Cystofilobasidium*, *Filobasidium*, *Mrakia*, *Phaffia*, and *Trichosporon*, and also in representatives of the orders Atractiellales, Cryptobasidiales, and Uredinales (Table 1). The presence of xylose in the latter order is surprising, because members of this order lack dolipores (Littlefield and Bracker 1971). Fucose-containing polysaccharides (Fukagawa *et al.* 1975; Lee *et al.* 1981) occur among ustilaginaceous yeasts, e.g., *Rhodosporidium*, *Rhodotorula*, *Sporidiobolus*, and *Sporobolomyces*. Fucose also occurs in exopolysaccharides produced by members of *Septobasidiales*, *Ustilaginales*, and *Auriculariales* (Table 1). Fucose and xylose rarely are present in the same species, while fucose and rhamnose do frequently coincide, e.g., in species of

TABLE 1. Distribution of xylose, rhamnose, and fucose among some orders of Heterobasidiomycetes

	Order	Species
Xylose present	Atractiellales	*Atractogloea stillata*
	Auriculariales	*Sebacina penetrans*
	Cryptobasidiales	*Microstroma juglandis*
	Filobasidiales	*Filobasidium capsuligenum*
		Filobasidium uniguttulatum
	Tremellales	*Tremella mycophaga*
		Tremella simplex
		Trimorphomyces syzygius
	Uredinales	*Endophyllum sempervii*
		Gymnosporangium clavarieforme
Fucose present	Auriculariales	*Agaricostilbum palmicolum*
		Sebacina penetrans
	Septobasidiales	*Septobasidium carestianum*
	Ustilaginales	*Leucosporidium antarcticum*
		Leucosporidium scottii
		Microbotryum cordae
		Microbotryum scabiosae
Rhamnose present	Cystobasidiales	*Platygloea peniophorae*
Xylose, fucose, and rhamnose absent	Ustilaginales	*Farysia thuemenii*
		Sphacelotheca polygonipersicariae
		Sorisorium transfissum
		Ustilago hordei
		Ustilago longissima
		Ustilago maydis
		Ustilago vinosa

Rhodotorula. The taxonomic significance of rhamnose remains unclear.

In conclusion, tremellaceous or ustilaginaceous affinity is supported by the presence of xylose or fucose, respectively.

Killer phenomenon

Many yeasts excrete into the medium (glyco)proteins (mycocins) that are fungistatic or fungicidal. The growth inhibitory effect of these toxins on sensitive cultures is known as the killer phenomenon. Killer strains are known in about 80 yeast species belonging to ca. 20 genera (W.I. Golubev, unpublished results). The genetics of mycocin production and their physiological conditions, molecular characteristics, and modes of action vary widely in ascomycetous yeasts (Young 1987). However, the principal characteristic of mycocins is their specific toxicity. They are often active against organisms that are taxonomically related to the strain producing the killer toxin. This specificity is caused by the first step of the interaction of mycocin with sensitive cells, namely its binding to cell-wall components (Hutchins and Bussey 1983; Schmitt and Radler 1988; Nakajima *et al.* 1989). This degree of relatedness varies from strains of the same species to representatives of other genera or even higher taxa. The killing patterns of mycocins produced by *Rhodotorula* (Golubev 1989*a*) and *Sporidiobolus* include only species of the order Ustilaginales (Golubev and Tsiomenko 1985; Golubev *et al.* 1988), while mycocins produced by *Cryptococcus* (Golubev and Kuznetsova 1989), *Filobasidium* (Golubev and Kuznetsova 1991), and *Cystofilobasidium* (Golubev 1990) act mainly against members of Tremellales, and also against some members of Atractiellales, Cryptobasidiales, and Auriculariales (Table 2). Ustilaginaceous yeasts generally are insensitive to mycocins formed by tremellaceous yeasts, and vice versa. The only exception known is the mycocin produced by *Rhodotorula fujisanensis*, which acts mainly against ustilaginaceous yeasts but also shows a weak activity against some tremellaceous yeasts (Golubev 1992).

TABLE 2. Genera with species sensitive to mycocins of *Rhodotorula glutinis* and *Cryptococcus laurentii*

Sensitivity to *Rh. glutinis*	Sensitivity to *Cr. laurentii*
Bensingtonia	*Atractogloea*
Kondoa	*Bulleromyces*
Microbotryum	*Cryptococcus*
Rhodosporidium	*Cystofilobasidium*
Rhodotorula	*Fibulobasidium*
Sphacelotheca	*Filobasidiella*
Sporidiobolus	*Filobasidium*
Sporobolomyces	*Itersonilia*
Ustilago	*Microstroma*
	Mrakia
	Sebacina
	Sirobasidium
	Sterigmatosporidium
	Tremella
	Trichosporon
	Trimorphomyces

The division of basidiomycetous yeasts on the basis of the sensitivity and killing patterns of mycocins correlates well with other taxonomic and phylogenetic characteristics, e.g., septal pore ultrastructure (Moore 1987), capsular polysaccharides (Weijman and Golubev 1987), and sequences of the

5S rRNA (Gottschalk and Blanz 1985) and small- or large-subunit rRNA (Guého *et al.* 1989; Fell *et al.* 1992).

However, the taxonomic use of killing patterns has to be done with care as mycocins sometimes show rather wide action spectra. Killer toxins of the ascomycetous yeast *Williopsis pratensis* have been found to inhibit growth of species of *Rhodotorula*, *Rhodosporidium*, *Sporobolomyces*, and *Tilletiopsis*, whereas species of *Bullera*, *Cryptococcus*, *Cystofilobasidium*, *Leucosporidium*, and *Phaffia* have been found not to be inhibited (Vustin *et al.* 1991). Occasionally, mycocins of *Cryptococcus humicolus* antagonize some ascomycetous yeasts (W.I. Golubev, unpublished results).

m-Inositol and D-glucuronate assimilation

Many basidiomycetous yeasts utilize *m*-inositol as their sole carbon and energy source (Barnett *et al.* 1990). The ability to assimilate *m*-inositol correlates well with that of D-glucuronate, which is the first intermediate of the glucuronate–gulonate pathway of *m*-inositol (Golubev 1989*b*). The number of D-glucuronate-assimilating yeasts is much higher than the number of *m*-inositol-assimilating yeasts. Obviously, D-glucuronate-positive but *m*-inositol-negative organisms lost the ability to transport this cyclitol into the cell or to perform oxidative cleavage of *m*-inositol into D-glucuronic acid. A few species are known that assimilate *m*-inositol but are unable to grow on D-glucuronate as the sole carbon source, such as *Rhodotorula hinnulea*, *Rhodotorula phylloplana* (Barnett *et al.* 1990), and most strains of *Tilletiopsis pallescens* (Boekhout 1991a). One has to consider the possibility of alternative metabolic pathways in these species. Recent reclassifications have resulted in an increasing number of genera with consistent patterns of D-glucuronate assimilation. Almost all D-glucuronate-positive species of *Rhodosporidium* were transferred to *Cystofilobasidium* (Hamamoto *et al.* 1988*a*), and *Mrakia* consists of D-glucuronate-positive species formerly classified in *Leucosporidium* (Yamada and Komagata 1987). However, *Rhodosporidium dacryoidum*, *Leucosporidium fellii*, and *Leucosporidium scottii* do grow with D-glucuronate as the sole carbon source. Some genera consist of both D-glucuronate-assimilating and -nonassimilating species, e.g., *Bensingtonia*, *Sporobolomyces*, *Tilletiopsis* (Boekhout 1991*a*), and *Rhodotorula* (Weijman *et al.* 1988; Barnett *et al.* 1990). Most D-glucuronate-negative yeasts belong to the ustilaginaceous yeasts, e.g., *Rhodosporidium* and *Sporidiobolus*, and most of the D-glucuronate-positive organisms are related to *Tremellales*, e.g., *Cystofilobasidium*, *Filobasidiella*, *Filobasidium*, *Mrakia*, and *Sterigmatosporidium* (Golubev 1989*b*). This latter affiliation is strongly supported by the assimilation of D-glucuronate by members of the genera *Fibulobasidium*, *Holtermania*, *Sirobasidium*, and *Tremella* (W.I. Golubev, unpublished results), and corresponds well with their grouping based on sensitivity patterns to mycocins (Table 2), capsular polysaccharide composition (Table 1), septal ultrastructure, and rRNA nucleotide sequences. However, like any single criterion, D-glucuronate assimilation does not provide conclusive evidence by itself.

Pigments

The presence of carotenoid pigments has been used as a criterion for delimitating basidiomycetous yeast genera. The genera *Rhodotorula*, *Rhodosporidium*, *Sporidiobolus*, and *Sporobolomyces* are, amongst others, characterized by red colonies, owing to the presence of carotenoid pigments (Nakayama *et al.* 1954; Valadon 1966, 1976; Fiasson 1967; 1972; Fiasson *et al.* 1973; Eijk *et al.* 1982; Simpson *et al.* 1971). The main carotenoid pigments occurring in these fungi are β- and τ-carotenes, torulene, and torularhodin. *Rhodotorula* species, e.g., *Rhodotorula glutinis* and *Rhodotorula rubra*, contain torularhodin (Nakayama *et al.* 1954; Valadon 1966, 1976; Eijk *et al.* 1982), but this pigment was reported to be absent in strains of *Rhodosporidium* (Eijk *et al.* 1982) as well as in some *Rhodotorula* species, viz. *Rhodotorula aurantiaca*, *Rhodotorula gracilis*, and *Rhodotorula pallida* (Valadon 1976). The taxonomic usefulness of carotenoid composition is questioned because of the presence of β- and τ-carotene and torulene in *Bullera alba* (Fiasson 1972), the influence of growth conditions on pigment production (Nakayama *et al.* 1954), the induction of mutants that do not produce carotenoid pigments of wild type strains that do form these pigments (Villoutreix 1960; Joo *et al.* 1988), and the discovery of nonpigmented species of *Sporobolomyces* and *Rhodotorula*, and pigmented species of *Bullera* and *Cryptococcus* (see, e.g., Buhagiar *et al.* 1983; Weijman *et al.* 1988; Nakase 1989; Barnett *et al.* 1990; Boekhout 1991*a*). Red yeasts seem to be polyphyletic, judging from sequence data of small- and large-subunit rRNA (Fell *et al.* 1992).

Cryptococcus contains mainly β-carotene and minor amounts of τ-carotene (Nakayama *et al.* 1954; Valadon 1976). This is in agreement with the carotenoid composition of *Tremella* (Lederer 1938), which supports the close relationship between these genera. Astaxanthin is found in *Phaffia rhodozyma* (Andrewes *et al.* 1976).

Fatty acids, whole-cell proteins, and enzymes

Qualitative fatty acid composition seems to be fairly constant within species of basidiomycetous yeasts when grown under standard conditions (Smit *et al.* 1987*a*, 1988), although there is a considerable influence of the growth phase on the quantitative fatty acid composition (Smit *et al.* 1987*b*). The occurrence of different fatty acid patterns within currently recognized species e.g., *Cryptococcus albidus*, *Cryptococcus laurentii*, *Cryptococcus luteolus*, *Cryptococcus gastricus* (Smit et al. 1988), and *Rhodotorula aurantiaca* (Westhuizen *et al.* 1991) suggests taxonomic heterogeneity of these species. This is further acknowledged by the recent recognition of several species within the *Cryptococcus albidus* complex (Vaughan-Martini 1991). Different species can have similar fatty acid patterns and this makes the technique not very useful for species identification (Westhuizen *et al.* 1987*a*, 1987*b*). Moreover, different fatty acid profiles have been observed in mating strains of, e.g., *Rhodosporidium malvinellum* (Westhuizen *et al.* 1991). Results on fatty acid composition and enzyme profiles obtained from the same strains do not always correlate.

Electrophoretic isozyme patterns are useful to differentiate species (Yamada *et al.* 1986; Yamada and Nakagawa 1988; Yamazaki and Komagata 1981, 1983) and have been used to analyse teleomorph–anamorph relationships. Dissimilarities of up to approximately 60% have been demonstrated to occur within species (Yamada *et al.* 1986; Yamada and Nakagawa 1988; Nakase *et al.* 1990). Two groups have been recognized within *Mrakia* (Yamada and

Matsumoto 1988). *Mrakia nivalis* and *Mrakia stokesii* show a high degree of similarity of isoenzyme patterns with *Mrakia frigida* and *Mrakia gelida*, respectively. These results are somewhat in conflict with results on whole-cell protein patterns and rRNA sequencing (see below). Taxonomic heterogeneity is suggested for currently recognized species of *Rhodotorula* (Yamazaki and Komagata 1981) and *Tilletiopsis* (Yamazaki *et al.* 1985). *Rhodotorula glutinis* contains six groups with different enzyme patterns (Yamazaki and Komagata 1981).

The presumed closely taxonomic relationships between ustilaginaceous yeasts on the one hand, such as *Sporobolomyces*, *Sporidiobolus*, *Rhodotorula*, and *Rhodosporidium*, and between tremellaceous yeasts on the other, such as *Bullera alba* and *Cryptococcus albidus*, have been supported by isozyme patterns (Yamazaki and Komagata 1983).

Whole-cell protein patterns seem to be species specific (Vancanneyt *et al.* 1992). Four currently recognized species of *Mrakia*, viz. *Mrakia frigida*, *Mrakia gelida*, *Mrakia nivalis*, and *Mrakia stokesii* have identical patterns. This suggests their conspecifity, which is also supported by rRNA sequence data (Yamada and Kawasaki 1989; Fell and Kurtzman 1990; Fell *et al.* 1992). The two varieties of *Filobasidiella neoformans* (= *Cryptococcus neoformans*) have similar protein and fatty acid profiles (Vancanneyt *et al.* 1992; Smit *et al.* 1987*a*). These observations support earlier taxonomic conclusions on the conspecificity of these varieties (Kwon-Chung *et al.* 1982). Mating types of *Rhodosporidium toruloides* with a reported low DNA relatedness (Hamamoto *et al.* 1987) revealed similar protein patterns as well (Vancanneyt *et al.* 1992).

Ubiquinones

The number of isoprene units of coenzyme Q (CoQ), which is part of the mitochondrial electron transfer system, is considered to be an important character in yeast systematics (e.g., Yamada and Kondo 1973; Yamada *et al.* 1983; Billon-Grand 1988). Among heterobasidiomycetous yeasts, 8, 9, or 10 isoprene units occur, which are usually designated as CoQ 8, 9, or 10, respectively. Hydrogenated ubiquinones occur as well, e.g., CoQ 10 (H_2) in *Sporobolomyces elongatus* (Nakase and Suzuki 1986) and *Rhodotorula hasegawae* (Yamada and Komagata 1983). A widely used taxonomic paradigm states that heterogeneity in CoQ composition does not occur within genera. In recent years several genera have been described or split on the basis of CoQ composition. The one genus – one CoQ concept needs critical consideration as CoQ composition is a quantitative, rather than a qualitative, character. In addition to a major CoQ fraction several minor CoQ fractions are usually present (Kuraishi *et al.* 1985; Billon-Grand 1988; Sugiyama *et al.* 1988). The relative proportions of these fractions may be influenced by environmental conditions (Billon-Grand 1989) and several species are found to have two major CoQ fractions (Kuraishi *et al.* 1985; Billon-Grand 1989). Moreover, strains of *Leucosporodium scottii* with different ubiquinones were shown to be closely related on the basis of their rRNA sequences (Yamada and Nakagawa 1990).

Some recently described basidiomycetous yeast genera characterized by their ubiquinone system and carbohydrate composition are *Mrakia* (Yamada and Komagata 1987), *Fellomyces* (Yamada and Banno 1984*b*), *Kurtzmanomyces* (Yamada *et al.* 1988*a*), and *Tsuchiyaea* (Yamada *et al.* 1988*b*). Other genera have been emended, e.g., *Bensingtonia* (Nakase and Boekhout 1988; Boekhout 1991*a*), and species transferred, e.g., *Cystofilobasidium infirmominiatum* (Hamamoto *et al.* 1988*b*). Some of these recently introduced generic concepts are supported by partial rRNA sequencing and (or) extracellular carbohydrate composition, viz. the distinction of *Mrakia* (Fell *et al.* 1992), *Sterigmatomyces*, *Fellomyces*, *Tsuchiyaea*, and *Kurtzmanomyces* (Guého *et al.* 1990).

Bensingtonia and *Sporobolomyces*, characterized by CoQ 9, and CoQ 10 or 10 (H_2), respectively, seem phylogenetically heterogeneous (Fell *et al.* 1992). Among the basidiomycetous yeasts CoQ 8 has been found only among tremellaceous yeasts (Sugiyama *et al.* 1985; Yamada and Komagata 1987).

Ubiquinone composition seems not to be a very reliable phylogenetic marker, as CoQ 9 and 10 occur among both ustilaginaceous and tremellaceous yeasts (Boekhout *et al.* 1992*a*) and fungi (Sugiyama *et al.* 1985; Kuraishi *et al.* 1985; Yamada *et al.* 1987), and clusters of species with similar partial rRNA sequences are found to contain species with different CoQ molecules (Fell *et al.* 1992). However, the presence of different major CoQ molecules within taxa may indicate taxonomic heterogeneity.

DNA

The determination of nDNA base composition (guanine + cytosine content = mol% G + C) has become a routine tool for yeast taxonomists. The taxonomic relevance of mol% G + C values is mainly exclusionary. A difference of about 2–3 mol% usually precludes conspecificity (Kurtzman 1985; Kurtzman and Phaff 1987; Phaff 1989). Values for basidiomycetous yeasts have been published by several authors (for recent compilations see Barnett *et al.* 1990; Boekhout 1991*a*) and range between approximately 35 and 75%. Most basidiomycetous yeasts have a mol% G + C of 50–65. Some currently accepted species have been shown to have different mol% G + C, e.g., *Rhodosporidium toruloides*, *Rhodotorula glutinis*, *Rhodotorula graminis*, and *Rhodotorula araucariae* (Hamamoto *et al.* 1986).

DNA–DNA hybridization studies are primarily employed to determine DNA complementarity among presumedly related species with similar DNA base composition or other phenotypic similarities. The method largely contributes to the delimitation of species (e.g., Kurtzman 1987). Several studies concerning basidiomycetous yeasts have been published in recent years. Anamorph–teleomorph relationships have been demonstrated, e.g., *Rhodotorula sinensis* – *Cystofilobasidium infirmominiatum* (Hamamoto *et al.* 1987); *Rhodotorula glutinis* – *Rhodosporidium kratochvilovae* (Hamamoto *et al.* 1988*a*), and *Sporobolomyces holsaticus* – *Sporidiobolus johnsonii* (Boekhout 1991*a*). Phenotypically distinct species have been found to be conspecific in many cases, e.g., *Rhodotorula pilimanae* – *Rhodotorula (rubra) mucilaginosa* and *Rhodotorula glutinis* (Hamamoto *et al.* 1987); *Sterigmatomyces indicus* – *Sterigmatomyces halophilus* (Kurtzman 1990); *Bullera derxii*, *Bullera alba* var. *lactis*, and *Bullera sinensis* (Nakase *et al.* 1990); *Itersonilia pyriformis*, *Itersonilia pastinacae*, and *Itersonilia perplexans* (Boekhout *et al.* 1991*b*), and *Sporidiobolus salmonicolor* and *Sporidiobolus johnsonii*

TABLE 3. Characteristics of genera of basidiomycetous yeasts,

	Morphology			
	Teliospores	Basidia	Ballistoconidia	Stalks
Ustilaginales				
Teleomorphic genera				
Leucosporidium except *L. larimarinii*	+	Phragmo	−	−
Rhodosporidium (inclusive *Kondoa*)	+	Phragmo	−	−
Sporidiobolus	+	Phragmo/holo	+	−
Anamorphic genera				
Bensingtonia	−	−	+	−(+)
Kurtzmanomyces	−	−	−	+
Rhodotorula (including *Erythrobasidium*)	−	−	−	−
Sporobolomyces (including *Ballistosporomyces*)	−	−	+	−
Sterigmatomyces	−	−	−	+
Tilletiales				
Teleomorphic genus				
Tilletiaria	+	Phragmo	+	−
Anamorphic genus				
Tilletiopsis	−	−	+	−
Tremellales				
Teleomorphic genera				
Bulleromyces	−	Phragmo	+	−
Cystofilobasidium	+	Holo	−	−
Filobasidiella	−	Holo	−	−
Filobasidium	−	Holo	−	−
Mrakia	+	Holo	−	−
Sterigmatosporidium	+	'Holo'	−	+
Tremella	−	Phragmo	−	−
Anamorphic genera				
Bullera	−	−	+	−(+)
Cryptococcus (including *Apiotrichum*)	−	−	−	−
Fellomyces	−	−	−	+
Itersonilia	−	−	+	−
Kockovaella	−	−	+	+
Phaffia	−	−	−	−
Sympodiomycopsis	−	−	−	+
Trichosporon	−	−	−	−
Tsuchiyaea	−	−	−	+
Affiliation uncertain				
Malassezia	−	−	−	−

NOTE: Data are taken from the following sources: Arx and Weijman 1979; Barnett *et al.* 1990; Boekhout 1991*a*; Boekhout *et al.* 1991*a*, 1992*a*; Gorin and Spencer 1970; Goto 1979; Goto *et al.* 1987; Guého *et al.* 1992; Hoog and Boekhout 1982; Johnson-Reid and Moore 1972; Kreger-van Rij and Veenhuis 1971; Kwon-Chung 1987; Kwon-Chung and Popkin 1976; Nakase and Boekhout 1988; Nakase and Suzuki 1986; Nakase *et al.* 1989, 1991; Oberwinkler *et al.* 1983; Rhodes *et al.* 1981; Sugiyama *et al.* 1985; Sugiyama *et al.* 1991; Suzuki and Nakase 1988; Weijman 1979 and Rodrigues de Miranda 1988; Yamada and Banno 1984*a*; Yamada and Komagata 1983, 1987; Yamada and Kondo 1972, 1973; Yamada and Nakagawa 1990; Yamada *et al.* 1982, 1987, 1988*a*, 1988*b*.

(Boekhout 1991*a*). Conversely strains showing similar phenotypic characteristics and currently classified as one species were shown to represent distinct taxa, e.g., species of the *Trichosporon beigelii – cutaneum* complex (Guého *et al.* 1984, 1992), *Rhodotorula glutinis* and *Rhodotorula minuta* (Hamamoto *et al.* 1987), and strains of *Cryptococcus albidus* (Vaughan Martini 1991).

The interpretation of DNA–DNA hybridization studies is not always straightforward. Intermediate values ranging between approximately 30 and 60% DNA–DNA similarity have been observed within the following species complexes: *Filobasidiella neoformans* (Kwon-Chung and Fell 1984); *Rhodosporidium toruloides* (Hamamoto *et al.* 1987); *Malassezia sympodialis* and *Malassezia furfur* (Simmons and Guého 1990); *Rhodotorula graminis* and *Rhodotorula glutinis*; and *Sporobolomyces coprophilus* and *Sporidiobolus ruinenii* (Kurtzman and Fell 1991). These results may indicate ongoing divergence at the DNA level.

The analysis of mitochondrial and ribosomal DNA for taxonomic purposes has been used for ascomycetous yeasts (Clark-Walker *et al.* 1987; Lachance *et al.* 1985). So far, few studies have been performed with basidiomycetous yeasts (Jahnke 1987). Results of restriction fragment length polymorphism (rflp) analyses of the rDNA unit of selected basidiomycetous yeasts have been recently published (Laaser *et al.* 1989; Vilgalys and Hester 1990). These studies have and their affiliation to orders of Heterobasidiomycetes

Biochemistry		Ultrastructure		Physiology		
CoQ	Xylose	Pore	Parenthesome	*m*-Inositol	D-Glucuronic acid	Starch formation
(7),9,10	–	Simple	–	–	Variable	–
10	–	Simple	–	–	–(+)	–
10	–	Simple	–	–	–	–
9	–	Simple	–	–	Variable	–
10	–	?	?	–	–	–
9,10,10(H_2)	–	?	?	–(+)	Variable	–
10,10,(Hg)	–	?	?	–(+)	Variable	–
9	–	?	?	–	Variable	–
10	–	Micro	–	–	+	–
10	–	Micro	–	Variable	Variable	–
10	+	Doli	U-shaped	+	+	+
8	+	Doli	–	+	+	+
10	+	Doli	U-shaped	+	+	+
9,10	+	Doli	–	+	+	+
8	+	?	?	+(–)	+	+
10	+	?	?	+	+	+
10	+	Doli	U-shaped	Variable	Variable	+
10	+	Doli	U-shaped	Variable	+	Variable
8,9,10	+	Doli	–	Variable	+	Variable
10	+	?	?	+	+	+
9	+	Doli	–	Variable	+	–
10	+	?	?	+	+	–
10	+	?	?	–	–	+
10	+	?	?	+	+	+
9,10	+	Doli/micro	U-shaped	+(–)	+	Variable
10	+	?	?	+	?	–
?	–	?	?	?	?	?

demonstrated the potential value of this technique in the systematics of basidiomycetous yeasts.

Ribosomal RNA

The sequencing of rRNA for phylogenetic purposes has attracted the attention of taxonomists, mainly owing to the pioneering work of C. Woese (e.g., Woese 1987).

Eight basidiomycetes studied by Walker and Doolittle (1982) were shown to belong to two different groups on the basis of their 5S rRNA nucleotide sequences. This grouping correlated well with the presence or absence of dolipores (Templeton 1983). After studying more species, five clusters have been distinguished (Walker and Doolittle 1983). The yeast species *Rhodosporidium toruloides* and *Sporobolomyces salmonicolor* were assigned to cluster 1, and *Filobasidium floriforme* and *Filobasidium capsuligenum* were assigned to cluster 5. This last cluster exclusively contains doliporous species. This pattern has been confirmed by Gottschalk and Blanz (1985).

Sequencing of 5.8S rRNA is considered not to offer much additional information in comparison with the 5S rRNA, and therefore has been little studied.

Recently, the larger rRNA molecules, namely the 16S–18S (small subunit (SSU)) rRNA and the 25S–28S (large subunit (LSU)) rRNA, have been studied extensively. Different methods to calculate evolutionary distances are in use. Guého *et al.* (1989, 1990) constructed phylogenetic trees on the basis of combined results of three regions from both the SSU and LSU rRNA. Different dendrograms for each of these regions were constructed by Yamada *et al.* (1989*a*, 1989*b*, 1990*a*, 1990*b*, 1991), Yamada and Kawasaki (1989), and Yamada and Nakagawa (1990).

Results from these sequencing studies are useful at different taxonomic levels. A short nucleotide sequence in a

TABLE 4. Discriminatory levels of characteristics discussed

	Strain	Species	Genus	Family	Order	Class
Morphology						
Vegetative morphology		├──	────	────	──┤	
Sexual morphology			├──	────	──┤	
Cell wall						├──┤
Mitosis					├──	──┤
Septa				├──	──┤	
Biochemistry						
Polysaccharides				├──	────	──┤
Mycocins		├──	────	────	────	──┤
Pigments		├──	──┤			
Fatty acids	├──	──┤				
Proteins	├──	──┤				
Isozymes	├──	──┤				
Ubiquinones		├──	──┤			
Physiology						
Inositol - D-glucuronate			├──	────	──┤	
Molecular						
Karyotypes	├──	──┤				
Mol% G+C		├──┤				
DNA/DNA reassociation		├──┤				
5S rRNA					├──	──┤
18S/26S rRNA		├──	────	────	──┤	
RFLPs	├──	──┤				

conserved region of the SSU rRNA, the so-called fingerprint segment, is claimed to discriminate genera (Yamada *et al.* 1989*a*), and Fell and Kurtzman (1990) suggest that nucleotide sequences in a variable region of the LSU rRNA allow taxonomic discrimination at the species level.

Genera forming conidia on stalks have recently been divided into two phylogenetic groups (Guého *et al.* 1990; Yamada *et al.* 1989*a*, 1991). The genera *Fellomyces*, *Sterigmatosporidium*, and *Tsuchiyaea* were found to be phylogenetically related to the genus *Filobasidiella*, with which they share the presence of xylose, the formation of extracellular starchlike compounds, and the utilization of D-glucuronate (Table 3). In contrast, *Kurtzmanomyces* and *Sterigmatomyces* were found to be more closely related to the teliospore-forming genus *Leucosporidium*. These last two genera lack xylose and do not form extracellular starchlike compounds (Table 3). The rather few heterobasidiomycetous yeasts studied so far can be divided into four groups on the basis of their partial 18S and 26S rRNA sequences (Guého *et al.* 1989): the first group consists of the teliospore-forming species *Rhodosporidium toruloides*, *Sporidiobolus johnsonii*, and *Leucosporidium scottii*, the second cluster comprises the genus *Malassezia*, the third group includes the species *Cystofilobasidium capitatum*, *Phaffia rhodozyma*, and *Trichosporon pullulans*, and the fourth group contains *Trichosporon beigelii*, *Trichosporon cutaneum*, *Filobasidium floriforme*, *Filobasidiella neoformans*, and *Sterigmatosporidium polymorphum*. This clustering correlates well with the distribution of other characters like capsular polysaccharide composition, septal ultrastructure, assimilation of *m*-inositol and (or) D-glucuronate, and production of starchlike compounds (Table 3), and is not in conflict with earlier sequence data of the 5S rRNA (Walker and Doolittle 1982; Gottschalk and Blanz 1985). Groups 1 and 4 can also be recognized on the basis of the entire sequences of small subunit rRNA (Van De Peer *et al.* 1992). *Mrakia gelida*, *Mrakia nivalis*, and *Mrakia frigida* have similar sequences of a single variable region of the LSU rRNA, and may be conspecific (Fell and Kurtzman 1990). These authors also suggested that the pigmented *Rhodotorula* species, *Rhodotorula glutinis*, *Rhodotorula graminis*, and *Rhodotorula mucilaginosa*, are closely related to species of the genus *Rhodosporidium*, as has also been suggested by other authors (Banno 1967; Hamamoto *et al.* 1987; Yamada *et al.* 1990*a*). A close phylogenetic relationship is further suggested for the teliospore-forming genera *Rhodosporidium* and *Sporidiobolus*, and for *Leucosporidium larimarini* with the genus *Cystofilobasidium* (Fell and Kurtzman 1990). The differentiation between the genera *Mrakia*, *Cystofilobasidium*, *Rhodosporidium*, *Leucosporidium*, *Phaffia*, and *Cryptococcus* was supported by 18S and 26S rRNA sequences (Yamada and Kawasaki 1989; Yamada and Nakagawa 1990; Yamada *et al.* 1990*a*, 1990b). However, some genera were still found to be phylogenetically heterogeneous, e.g., *Rhodosporidium* (Yamada *et al.* 1990*a*), *Cryptococcus* (Yamada *et al.* 1990*b*), and *Sporobolomyces* (Takematsu *et al.* 1990; Fell *et al.* 1992).

The degree of infrageneric divergence observed in some currently recognized genera is claimed to be sufficient to replace *Rhodosporidium malvinellum* (Yamada *et al.* 1989*b*), *Leucosporidium scottii* IFO 9474 (Yamada *et al.*

1990*a*), and *Rhodosporidium dacryoidum* (Yamada and Nakagawa 1990). However, it is the present authors' opinion that reclassification on the basis of nucleotide sequences only needs further evaluation, because the number of taxa studied is limited, the comparisons are mainly based on partial sequences of one type of molecule, and the constancy of the evolution of rRNA is questioned (Kurtzman 1992). These considerations make the proposal of new taxa based only on nucleotide sequences premature.

Concluding remarks

The numerous studies on morphological, physiological, biochemical, and molecular characteristics of heterobasidiomycetous yeasts discussed in this paper have changed our taxonomic understanding of these fungi. It is clear that yeasts and yeastlike growth forms can be accommodated in at least three orders of Heterobasidiomycetes, viz. Ustilaginales, Tilletiales, and Tremellales (Table 3). The possibility that other heterobasidiomycetous orders contain yeast and yeastlike growth forms cannot yet be excluded. Molecular studies have demonstrated the need for splitting or merging traditionally recognized genera. Our discussion of currently used taxonomic methods demonstrates the need for an integrated approach in the systematics of these yeasts. Table 4 summarizes the taxonomic resolution of the discussed methodologies.

Because of the intense activity taking place in the taxonomy of basidiomycetous yeasts, many dramatic changes are expected to take place in their classification. These could result in excessive nomenclatural changes that would have a negative impact on the progress of taxonomy, unless proposals are first subjected to the close scrutiny of the international community of researchers in open forums, to be finalized only when a maximum consensus has been reached.

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