

Biotechnology of non-*Saccharomyces* yeasts—the basidiomycetes

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Abstract Yeasts are the major producer of biotechnology products worldwide, exceeding production in capacity and economic revenues of other groups of industrial microorganisms. Yeasts have wide-ranging fundamental and industrial importance in scientific, food, medical, and agricultural disciplines (Fig. 1). *Saccharomyces* is the most important genus of yeast from fundamental and applied perspectives and has been expansively studied. Non-*Saccharomyces* yeasts (non-conventional yeasts) including members of the *Ascomycetes* and *Basidiomycetes* also have substantial current utility and potential applicability in biotechnology. In an earlier mini-review, “Biotechnology of non-*Saccharomyces* yeasts—the ascomycetes” (Johnson Appl Microb Biotechnol 97: 503–517, 2013), the extensive biotechnological utility and potential of ascomycetous yeasts are described. Ascomycetous yeasts are particularly important in food and ethanol formation, production of single-cell protein, feeds and fodder, heterologous production of proteins and enzymes, and as model and fundamental organisms for the delineation of genes and their function in mammalian and human metabolism and disease processes. In contrast, the roles of basidiomycetous yeasts in biotechnology have mainly been evaluated only in the past few decades and compared to the ascomycetous yeasts currently have limited industrial utility. From a biotechnology perspective, the basidiomycetous yeasts are known mainly for the production of enzymes used in pharmaceutical and chemical synthesis, for production of certain classes of primary and secondary metabolites such as terpenoids and carotenoids, for aerobic catabolism of complex carbon sources, and for bioremediation of environmental pollutants and xenotoxins. Notwithstanding, the basidiomycetous yeasts appear to have considerable potential in

biotechnology owing to their catabolic utilities, formation of enzymes acting on recalcitrant substrates, and through the production of unique primary and secondary metabolites. This and the earlier mini-review (Johnson Appl Microb Biotechnol 97:503–517, 2013) were motivated during the preparation and publication of the landmark three-volume set of “The yeasts: a taxonomic study, 5th edition” (Kurtzman et al. 2011a, b).

Keywords Yeasts · Basidiomycetes · Yeast biotechnology · Industrial enzymes · Bioremediation · Oxidative catabolism · Pollutant degradation · Terpenoids · Carotenoids

Introduction

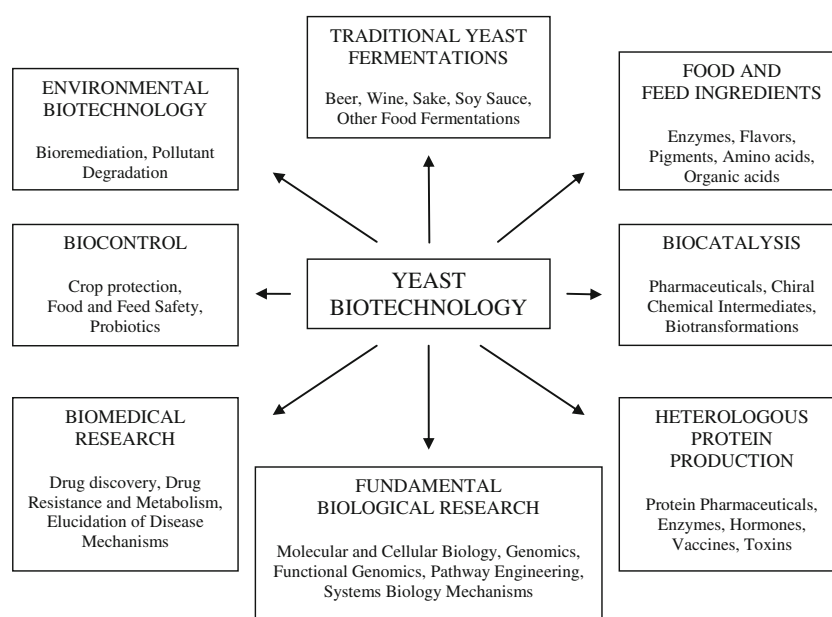
Many of the ascomycetous yeasts are well known in biotechnology and have been utilized for centuries in food production and various biotechnology processes (Johnson 2013) (Fig. 1). In contrast, many of the basidiomycetous yeasts have been relatively under-studied in their importance for biotechnology, agriculture and foods, and environmental processes. The objective of this chapter is to describe the basidiomycetous yeast processes currently used by the industry as well as those in developmental stages and close to commercialization. The unique catabolic and ecological roles of the basidiomycetous yeasts will be emphasized. Importance will be given to new developments and opportunities in industrial applications of prominent basidiomycetous yeast genera and species with applications in biotechnology (Table 1).

Historical importance of yeasts to human societies

As described in an earlier review, the importance of ascomycetous yeasts in biotechnology has been known since ancient times, particularly for the production of fermented beverages

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Fig. 1 Various disciplines in yeast biotechnology (adapted and expanded from Walker (1998))



and foods. *Saccharomyces cerevisiae* has contributed prominently to the worldwide advancement and sustainability of human societies (Legras et al. 2007; Ulber and Soye 2004). The domestication of *S. cerevisiae* is considered a pivotal event in human history and for advances in biotechnology. The production of fermented beverages and foods occurred in parallel with the onset of agriculture and provided nutrition and sustenance to humans (Legras et al. 2007; Ulber and Soye 2004). Historical evidence indicates that the availability of fermented beverages and foods was a motivation for humans to settle in geographic areas and to become agriculturists. Settlement was a successful strategy to provide a reliable and secure food supply compared to nomadic life and provided social, economic, and health attributes for human nourishment and development.

In contrast, the basidiomycetous yeasts have not commonly been recognized to have historical beneficial roles in human evolution and domestication. However, during the past five decades to the present, basidiomycetous yeast species have

been shown to have beneficial attributes, including the formation of secondary metabolites such as carotenoids and fragrances, aerobic catabolism of numerous natural and synthetic compounds, formation of enzymes important in pharmaceutical production and biotransformations, and in important bioremediation processes and degradation of pollutants. Basidiomycetous yeasts are also involved in food spoilage and economic loss, especially the genera *Cryptococcus* and *Rhodotorula* (Boekhout and Robert 2003; Querol and Fleet 2006; Tibor 2008). However, ascomycetous yeasts are much more common spoilage organisms of foods (Boekhout and Robert 2003; Querol and Fleet 2006; Tibor 2008).

Significance of basidiomycetous yeasts in biotechnology

Although most biologists are familiar with the importance of ascomycetous yeasts, particularly *S. cerevisiae*, the *Basidiomycetes* form a unique group of fungi with several key features, including the formation of a distinct sexual state characterized by basidia and basidiospores (Fig. 2), a unique cell wall composition, generally highly oxidative catabolic capabilities with ability to degrade recalcitrant natural substrates and xenobiotics, and the ability of certain species to form brilliant carotenoid pigments and aromas derived from primary metabolites (Boekhout et al. 2011; Kurtzman et al. 2011a, b).

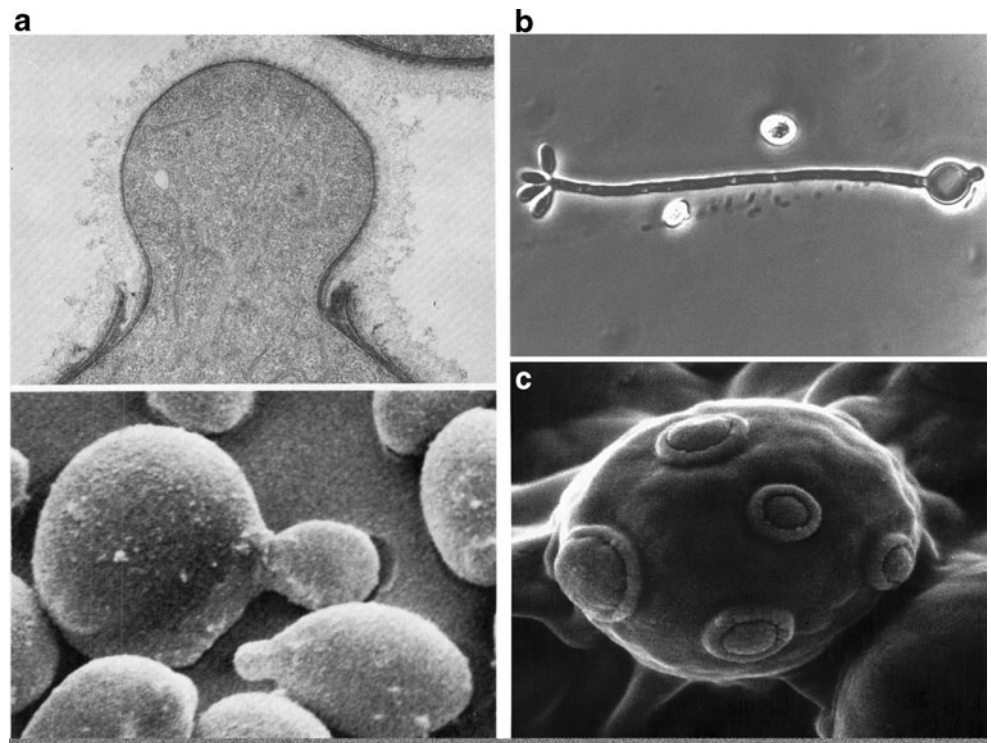
The classification and general characteristics of the basidiomycetous yeasts have been expertly reviewed (Boekhout et al. 2011; Kurtzman et al. 2011b; Scorzett et al. 2002). All yeasts are recognized as fungi that asexually reproduce by budding or fission, resulting in growth that is comprised mainly of single cells. Yeasts do not form their sexual states within or upon a fruiting body. Basidiomycetous yeasts are

Table 1 Principal basidiomycetous yeast genera and species of biotechnological importance

Yeast species
<i>Cryptococcus</i> spp. (non-pathogenic)
<i>Rhodotorula</i> spp.
<i>Rhodospiridium</i> spp.
<i>Trichosporon</i> spp.
<i>Xanthophyllomyces dendrorhous</i>
<i>Phaffia rhodozyma</i>

These yeasts were chosen on the basis of their potential and realized importance in industrial fermentations and biotechnological processes

Fig. 2 Characteristic morphologies of anamorphic and teleomorphic states of basidiomycetous yeasts. Note the unipolar budding in *P. rhodozyma* with multiple bud scars (a), the basidium with multiple basidiospores in *Xanthophyllomyces dendrorhous* (b), and the multipolar budding with numerous bud scars around the thallus in *Saccharomyces cerevisiae* (c). Photographs provided by Kyria Bounds-Mills, UC Davis, CA, USA and Jack Fell, University of Miami



usually phylogenetically separate from the mushrooms and other taxa that form complex fruiting bodies. The life cycle of basidiomycetous yeasts include heterothallic and homothallic systems, and the teleomorphic species form basidia. Molecular phylogenetic studies with the small subunit ribosomal rDNA gene have revealed three main lineages: (1) Class *Urediniomycetes*, (2) Class *Ustilaginomycetes*, and (3) Class *Hymenomycetes*. A detailed description of the classification basidiomycetous yeasts is expertly reviewed (Boekhout et al. 2011; Kurtzman et al. 2011a, b).

The habitat of many basidiomycetous yeasts is the phylloplane, and many species utilize refractory substrates, including pentoses such as xylose and arabinose, sugar alcohols, and to a limited degree tannin and lignin components present in lignocellulose, providing a means of biomass utilization (Table 2). As residents of the phylloplane at high elevations, many of these yeasts tolerate and likely degrade pollutants such as ozone and volatile aromatic compounds, including aromatic substrates. By virtue of their ecology and habitat, many basidiomycetous yeasts produce valuable enzymes and end-products (Tables 3 and 4). Many of these products enable protection against irradiation, reactive oxygen species, and pollutants and allow these yeasts to grow oxidatively on recalcitrant substrates. Basidiomycetous yeasts are important in environmental remediation, including metal absorption and probably radionuclide extraction from the environment. Methods for isolation, characterization, and pathogenic potential of basidiomycetous yeasts have been described (Cooper 2011; Hazen and Howell 2007; Kurtzman et al. 2011a; Phaff 1990; Phaff et al. 1978).

Discovery of basidiomycetous yeasts

Basidiomycetous yeasts were not recognized as such until the twentieth century. The yeast pioneers Albert Jan Kluyver (1888–1956) and Cornelius Bernardus (Kees) Van Niel (a doctoral student of Kluyver) (1897–1985) from the renowned Delft School of yeast biologists (Bennett and Phaff 1995; Lachance 2003; Robertson 2003; Spath 1999; Theunissen 1996; van Niel 1949) initially observed the presence of ballistoconidia in *Sporobolomyces*, which led to their hypotheses that this yeast is basidiomycetous (Boekhout et al. 2011; Spath 1959; Van Niel and Kluyver 1927). Kluyver (with John Louis Donker) is famous for the classic paper “Die Einheit in der Biochimie” (“Unity in Biochemistry”) (Kluyver and Donker 1926) and for the aphorism “From elephant to butyric acid bacterium—it is all the same” (Kamp et al. 1959). His aphorism was sufficiently widespread that in 1961 François Jacob and Jacques Monod paraphrased it, without mentioning Kluyver, as “as that old axiom ‘what is true for *E. coli* is also true for elephants” to justify the genetic code’s universality (Monod and Jacob 1961). Kluyver devoted much of his work to “Microbiology and Industry” (reviewed in Spath (1959)).

The definitive demonstration of yeasts with basidiomycetous sexual reproduction was shown in *Rhodotorula*, leading to the new teleomorph species *Rhodospiridium* (Banno 1963, 1967) and subsequent discovery of sexual states in other yeast species and strains such as *Leucosporidium*, *Filobasidiella*, and *Xanthophyllomyces* (Fell et al. 1969, 1973, 2011; Kwon-Chung 1975). The teleomorphic states of basidiomycetous yeasts are

Table 2 Select recalcitrant carbon and nitrogen sources utilized by many basidiomycetous yeasts (from Kurtzman et al. (2011))

L-Arabinose	Nitrite
D-Arabinose	Propane-1,2-diolribitol
Cadaverine	Proteocatechuate
Cellobiose	Salicin
Creatinine	Tartaric acid
Ethanol	Urea
Ferulic acid	Vanillic acid
Ethylamine	Veratric acid
Galacticol	Xylitol
Gallic acid	Hydrocarbons
Gentisic acid	Hexadecane
D-Glucuronate	
P-Hydroxybenzoate	
M-Hydroxybenzoate	

fully described in Boekhout et al. (2011). Examples of the basidiomycetous teleomorphic stage (*Xanthophyllomyces*

dendrorhous) are illustrated in Fig. 2. Other than the human pathogenic species, most of the basidiomycetous yeasts are in the early stage of genetic manipulation, metabolic engineering, and other disciplines important for biotechnology purposes.

Prominent basidiomycetous yeast genera and species of medical and biotechnological importance

The primary basidiomycetous yeast genera important in biotechnology are designated in Table 1 and described in the following sections.

X. dendrorhous (anamorph *Phaffia rhodozyma*)

Of the beneficial yeasts in biotechnology, *X. dendrorhous* (anamorph *P. rhodozyma*) (Fell and Johnson 2011; Fell et al. 2011) has been studied by several research groups since it produces the high-value carotenoid astaxanthin (e.g., Johnson and An 1991; Johnson and Schroeder 1995; Marcoleta et al.

Table 3 Select enzymes from basidiomycetous yeasts

Enzyme	Yeast	Industry
Lipase	<i>Pseudozyma antarctica</i>	Flavors
Reetz 2002; Waché et al. 2006	<i>Trichosporon fermentum</i>	Degreasing
		Bioremediation
L-Phenylalanine ammonia lyase	<i>Rhodotorula</i> spp.	Pharmaceutical
Quinn et al. 2011	<i>Rhodospiridium</i> spp.	
Lactamase/racemase	<i>Cryptococcus laurentii</i>	Pharmaceutical
Aldehyde reductase	<i>Sporobolomyces salmonicolor</i>	Pharmaceutical
Psychrophilic hydrolases	<i>Cryptococcus</i> ;	Various
Birgisson et al. 2003	<i>Glaciozyma</i> ;	
Buzzini et al. 2012	<i>Cystofilobasidium</i>	
	<i>Leucosporidium</i>	
Flavoprotein monooxygenases	<i>Trichosporon</i> spp.	Bioremediation
Crozier-Reabe and Moran 2012		
Beta-glucosidase	<i>Trichosporon asahii</i>	Flavors
Cytochrome P450s	Various genera	Chemical syntheses, biodegradations
Xylanase, cold-adapted	<i>Cryptococcus</i> spp.	Biodegradation
Petrescu et al. 2000; Gomez 2000		
Glutaminase, salt stable	<i>Cryptococcus</i> spp.	Fod processing
Satto et al.		
Epoxide hydrolase	<i>Cryptococcus</i> spp.	Pharmaceutical
Botes et al. 2005		
Xylanase, cutinase	<i>Cryptococcus</i> spp.	Biodegradation
Middelhoven 1997		
Galacturonase, cold-adapted	<i>Mrakiella</i>	Biodegradation, food processing
Pfeiffer et al. 2004		
Pectate lyase, cold-adapted	<i>Mrakiella</i>	Biodegradation, food processing
Margesin and Fell 2008		

Table 4 Fermentation products from basidiomycetous yeasts

Yeast	Product	References
<i>Xanthophyllomyces dendrorhous</i> <i>Phaffia rhodozyma</i>	Astaxanthin	Johnson 2003
<i>Xanthophyllomyces dendrorhous</i>	Mucosporine–glutamicol–glucoside	Kogej et al. 2006
<i>Rhodotorula</i> spp.	Torularhodin	Frengova and Beshkova 2009
Various basidiomycetous yeasts	Plectanixanthin	Bae et al. 1971; Madhour et al. 2005
<i>Moniella</i> spp.	Erythritol	Deng et al. 2012
<i>Trichosporon fermentans</i>	Lipids/oils	Huang et al. 2012c
<i>Cryptococcus curvatus</i>	Lipids/oils	Papanikolaou and Aggelis 2011;
<i>Trichosporon fermentans</i>		Ageitos et al. 2011
<i>Rhodospiridium</i>		Ageitos et al. 2011
<i>Rhodospiridium toruloides</i>		Ageitos et al. 2011
<i>Rhodotorula</i>		Ageitos et al. 2011

2011; Schmidt et al. 2011). Astaxanthin is one of the most common carotenoids in the biosphere, particularly in marine environments, and is produced by relatively few species of bacteria, microalgae, and fungi (Aki et al. 2007; Bhosale and Bernstein 2005; Chang et al. 2012; Johnson and Schroeder 1995; Schmidt et al. 2011). These organisms serve as the base of a food chain for various macro-creatures that leads to attractive pigmentation of birds, such as the flamingo and scarlet ibis, marine crustacea, including shrimp and lobsters, and fish, particularly salmonids (Johnson et al. 1977; Johnson 2003; Rajasingh et al. 2007). Since these animals cannot biosynthesize astaxanthin, this pigment or appropriate precursors must be included in the animals' diets to achieve their characteristic pigmentation and associated metabolic functions such as protection against oxidative stress. Astaxanthin also has beneficial health attributes for humans and has been deemed beneficial for the prevention of degenerative syndromes such as cancer and cardiovascular disease (Bertram and Vine 2005; Fasset and Coombes 2012; Goswami et al. 2010; Hussein et al. 2006; Mayne 1996; Miki 1991; Perera and Yen 2007; Takuji et al. 2012; Yuan et al. 2011).

The astaxanthin pathway differs from the carotenoid pathways in other carotenogenic basidiomycetous yeasts such as *Rhodotorula* and *Cryptococcus*. Both groups of yeast produce acyclic and cyclic carotene hydrocarbons and then transform the carotenes to oxygenated derivatives (xanthophylls). *Rhodotorula* produces primarily torularhodin as its end-product, while *Xanthophyllomyces* produces astaxanthin. The mechanism of transformation of beta-carotene to all-*trans* astaxanthin with the 3*R*, 3*R'* optical configuration posed an enigma for several years (An et al. 1989). Based on metabolic properties related to oxidative metabolism, our laboratory first suggested in 1989 that oxidative transformation occurred by cytochrome P450 activity (An et al. 1989). Strong support for this was provided by Hoffmann-La Roche (Hoshino et al. 2000), who transformed a beta-carotene-accumulating mutant from our lab with a gene that

resulted in the formation of astaxanthin (Hoshino et al. 2000; Ojima et al. 2006). Considerable work has supported that the transformation to astaxanthin occurs by a unique cytochrome P450 (e.g., Álvarez et al. 2007; Ojima et al. 2006). Astaxanthin and certain other carotenoids are considered lead industrial compounds for industrial biotechnology (Kaur and Singh 2011). *X. dendrorhous* has also been used as a source of carotenogenic genes for expression in *S. cerevisiae* (Lange and Steinbüchel 2011).

Much effort has been devoted to generating mutant strains of *X. dendrorhous* that produce high quantities of astaxanthin. *X. dendrorhous* is unusual among basidiomycetous yeasts in having the capability of fermenting glucose and certain other sugars, and under these conditions pigmentation is considerably reduced (Johnson and Lewis 1980). Wild strains of *X. dendrorhous dendrorhous* and *P. rhodozyma* strains produce low quantities of astaxanthin (0.05–0.5 mg/g dry yeast). Industrial strains and processes have been reported for *X. dendrorhous* strains that yield values of 4 to 15 mg astaxanthin/g dry cell weight (DCW). The highest levels of carotenoids based on fluorescence analysis have been estimated to be 15–20 mg/g DCW (An et al. 1991, 2000; Wegner 1983). *X. dendrorhous* has also been reported to reach very high cell densities of ≥ 50 g DCW per liter in submerged fermentations with sufficient mass transfer and oxygenation. Due to its lipid nature, astaxanthin is located intracellularly (An et al. 1989, 1991), and methods such as mechanical cracking, enzyme and/or chemical treatment, or autolysis would be needed to increase its industrial feasibility as a pigment source. Therefore, a major challenge in the development of *X. dendrorhous* as an industrial organism is the release of intracellular astaxanthin in order that it can be uptaken by salmonids and other animals and humans (Johnson and An 1991; Seok-Keun et al. 2007).

In addition to the antioxidant astaxanthin, *X. dendrorhous* synthesizes mucosporine–glutaminol–glucoside (MGG). The

compound is unique among yeasts, while similar mycosporines such as mucosporine–glutamicol–glucoside have also been found in a few yeast species (Kogej et al. 2006). Mycosporines and derivatives protect organisms against UV light and have been considered to be “nature's sunscreens” (Bandanranayake 1998). Strains from UV-exposed habitats had higher quantities of MGG, and its synthesis was also increased in media containing complex sources of nutrients by the shikimate pathway (Libkind et al. 2004a,b). MGG and other mycosporines are important in protecting basidiomycetous yeasts from getting killed in strong UV environments such as in high-elevation habitats or in marine and freshwaters (Fell 1976; Fell et al. 1973; Kutty and Philp 2008; Libkind et al. 2004a, b, 2010). In high-elevation environments, source ozone that reacts with plant compounds to form singlet oxygen (Kanofsky and Sima 1995), and carotenoids and other antioxidants thus probably provide for yeast survival in the presence of pollutants such as reactive oxygen species.

Xanthophyllomyces and certain other basidiomycetous yeasts have been shown to produce killer toxins, whose functions are unknown but probably involve competition with related yeasts (Baeza et al. 2012; Magliani et al. 1997). Killer toxins could possibly help maintain mono-cultures in industrial fermentations. The dsRNAs in *X. dendrorhous* strains were recently found to be characteristic of Totiviruses (Baeza et al. 2012), similar to those present in *S. cerevisiae* (Schmitt and Breinig 2006).

The industrial potential for *X. dendrorhous* and other basidiomycetous yeasts could be enhanced by the production of more than one product of value. Methods have been proposed for the production and extraction of astaxanthin and fructofuranosidase from the yeast. The fructofuranosidase has applications for the development of prebiotics for enhancing the colonization of beneficial microbiota in infant humans and animals (Fernandez et al. 2007; Linde et al. 2012; Polo et al. 2010). Other basidiomycetous yeasts also produce oligosaccharides for biotechnology applications (Kritzinger et al. 2003; Torres et al. (2010).

Rhodotorula spp. and *Rhodosporidium* spp.

Rhodotorula spp. and its teleomorph *Rhodosporidium* have long been known to produce the canonical yeast carotenoids, including beta-carotene, torulene, and torularhodin (reviewed in Frengova and Beshkova (2009); Tefft et al. 1970). Moliné et al. (2010) showed that torularhodin and other carotenoids protected *Rhodotorula mucilaginosa* from light exposure. Torularhodin does not appear to have industrial value at this time, and instead the yeast has been extensively studied for total lipid production and for enzymes used in pharmaceutical and chemical syntheses, particularly epoxidases, D-amino acid oxidases, ammonia lyases, and enzymes involved in the formation of lactones for flavorants

(Aguedo et al. 2004; and Hagedorn and Kaphammer 1994) (Tables 4 and 5) (Romero-Guido et al. 2011; Sacchi et al. 2012; Turner 2011). *Rhodotorula* spp. also have potential for degradation of tannins and pectins in industrial waste streams (Taskin 2013). Lignin and related compounds can be used as a carbon source by some *Rhodotorula* spp. (Hainal et al. 2012). These examples illustrate the abilities of basidiomycetous yeasts to oxidatively bioconvert recalcitrant substrates (Table 6).

Considerable attention has been focused on the formation of lipids and polysaccharides in this oleaginous group of yeasts (Frengova et al. 2006; Leman 1997) (Table 5). *Rhodotorula* is a lipid-accumulating yeast that has been considered for the production of single cell oils (Ageitos et al. 2011; Amaretti et al. 2010; Frengova et al. 1994; Louhasakul and Cheirslip 2013). The yeast is able to grow on various waste streams such as distillery wastewater and raw olive oil wastewater for lipid production (Gonzalez-Garcia et al. 2013; Karakaya et al. 2012; Louhasakul and Cheirslip 2013). Sophorolipids and other surfactants have been shown to accumulate in *Rhodotorula* spp. under certain nutritional conditions (Csutak et al. 2012; Ribeiro et al. 2012).

Rhodotorula, *Sporobolomyces*, and other basidiomycetous yeast species have been considered for industrial production of ubiquinone Q (10) (Yurkov et al. 2008). Due to their oxidative ability, *Rhodotorula* spp. are able to hydroxylate monoterpenes, including limonene and piperidine, as well as cyclohexanes in soil (Pohl et al. 2011; Thanh et al. 2004; van Rensburg et al. 1997) (Table 6).

Rhodotorula spp. and certain other prominent basidiomycetous yeasts produce the enzyme phenylalanine ammonia lyase (PAL) (El-Batal 2002; Orndorff et al. 1988; Quinn et al. 2011), which is useful in medicine and pharmacology for the treatment of phenylketonuria. A direct one-step synthesis of L-phenylalanine methyl ester was achieved in an organic–aqueous biphasic system using PAL from *R. glutinis* (Quinn et al. 2011). *Rhodotorula* has also been evaluated as a source of D-amino acid oxidase (Pollegoni et al. 2008).

Rhodotorula spp. have been used for whole-cell-mediated xanthone synthesis by means of oxidative intramolecular cyclization (Fromentin et al. 2012). *Rhodotorula buffonii* was used for this process with a yield of 48 % compared to 19 and 17 % yields in the ascomycetous yeasts *Candida pini* and *Wickerhamomyces anomalus* (*Pichia anomala*), respectively (Rustoy et al. 2008). *Rhodotorula minuta* catalyzed an efficient biotransformation of dialkyl esters of 2-oxoglutaric acid (Rustoy et al. 2008). *Rhodotorula* spp. and other basidiomycetous yeasts used limonene piperidine in soils (Thanh et al. 2004; van Rensburg et al. 1997). These examples provide compelling evidence that enzymes from *Rhodotorula* spp. and oxidative basidiomycetous yeasts have applicability in the chemical and biotechnology industries (Pscheidt and Glieder 2008) (Table 6).

Table 5 Examples of enzymes from basidiomycetous yeasts used in biotransformation/bio-catalytic processes in the pharmaceutical and fine chemicals industries

Yeast enzyme or whole cell	Product	Reference
Lipase (<i>Pseudozyma antarctica</i>)	Ribavirin (antiviral)	Patel 2004, 2007
<i>Rhodotorula</i> spp.	Pharmaceutical intermediate	Patel 2004, 2007
Epoxide hydrolase (<i>Rhodotorula glutinis</i>)	Melatonin receptor agonist	Patel 2004, 2007
Lipase (<i>Pseudozyma antarctica</i>), <i>Hyphozyma</i> sp., <i>Cryptococcus tsukubaensis</i>	Tachykinin receptor agonists	Patel 2004, 2007
Lipase, reductase (<i>Pseudozyma antarctica</i>)	Beta-blockers	Zelaszyk and Kiec-Kononowicz 2007

Rhodotorula and *Rhodospiridium* species have also been evaluated as agents for control of postharvest diseases of fruits and vegetables. In particular, these species showed biocontrol activity against *Botrytis cinerea* rot on apples and *B. cinerea* on the phylloplanes of beans and tomatoes (Buck 2002; Castoria et al. 1997, 2005).

Trichosporon spp.

Trichosporon spp. are anamorphic basidiomycetous yeasts that are widespread in nature and have been isolated from soils, sediments, waste waters, sludge, wood pulp, and clinical specimens (Kurtzman et al. 2011b). Industrial interest has focused on the ability of the species to utilize a range of substrates, particularly aromatic compounds, aliphatic lipids, amines, and complex nitrogenous compounds, as sole sources of carbon and energy, including uric acid, ethylamine, hydroxyproline, tyramine, and L-phenylamine (Godjevargova et al. 2003; Krastonof et al. 2013; Middlehoven et al. 2004) (Table 2). There has been industrial interest in the use of *Trichosporon* cells or enzyme systems to metabolize pollutants and xenobiotics in bioremediation processes (Bergauer et al. 2005; Gdjevargova 2003; Middlehoven 1993). Safety evaluation of *Trichosporon* species for industrial uses is important since certain species have been associated with infections in humans, particularly in patients with underlying immunodeficiencies (Diaz and Fell 2004).

Trichosporon has also been investigated as an oleaginous yeast for lipid accumulation in waste streams such as lignocellulose hydrolysates (Huang et al. 2012a). The

yeast was able to degrade microbial inhibitors such as furans (Huang et al. 2012b). As is currently fashionable, it is one of the many organisms considered for biodiesel formation (Demirbas 2009). The economic utility of microbial systems for biodiesel formation will depend on the molding of many disciplines, including engineering, biochemistry, and microbiology, and is currently only viable for large-scale performance in most developed countries with oil-based energy foundations through government subsidies.

Trichosporon mycotoxinivorans was found to degrade ochratoxin in broiler serum and tissues (Hanif et al. 2012) and also to act as a probiotic in production, possibly through degradation of mycotoxins (García-Hernández et al. 2012). *Trichosporon* also exhibited high tolerance for heavy metals in wastewaters, thus providing a potential method of decontamination by cell absorption (Muñoz et al. 2012).

Pseudozyma (Candida) antarctica

Pseudozyma (Candida) antarctica is an anamorphic yeast of basidiomycetous affinity. The yeast has attracted considerable industrial attention, primarily as a source of lipase enzymes used in a number of industrial processes for food, fine chemical, and pharmaceutical applications (Aehle 2004; Blaser 2003; Houde et al. 2004; Sandoval 2012) (Table 5). *Pseudozyma* has also been evaluated for biodiesel production (Demirbas 2009). *Cryptococcus* and *Pseudozyma* have been shown to degrade plastic films and poly-lactic materials (Masaki et al. 2005; Seo et al. 2007; Shinozaki et al. 2013b). *Pseudozyma* has also been considered for the production of

Table 6 Biotransformation of recalcitrant chemicals, pollutants, and xenobiotics by basidiomycetous yeasts

Yeast	Compound transformed	References
<i>Rhodotorula</i> spp.	Monoterpenes, limonene	Thanh et al. 2004
	piperitine	Van Rensburg et al. 1997
<i>Cryptococcus</i> spp.	Electron-poor alkenes, carvone	Goretti et al. 2009
<i>Rhodotorula</i> , <i>Cryptococcus</i> , <i>Xanthophyllomyces</i> , <i>Trichosporon</i> ; other spp.	Various recalcitrant compounds	Urlacher and Gurhard 2011; Crenar and Petric 2011
<i>Rhodotorula</i> spp.	Cyclohexanes	Pohl et al. 2011
<i>Rhodotorula</i> spp.	Betulin	Mao et al. 2012
<i>Rhodotorula</i> spp.	Patulin	Castoria et al. 2005

native surfactant proteins (Arutchiva and Doble 2011; Cameotra and Makkar 2004; Kaneko et al. 1976; Konishi et al. 2008; Morita et al. 2007, 2012), antimycotics (Shinozaki et al. 2013a; Mimeo et al. 2005), itaconic acid (Levinson et al. 2006), and heterologous proteins (Avis et al. 2005). Strains of *Pseudozyma* have been reported to degrade plastics, polyurethanes, and related substances (Mendes et al. 2012) and for production of biodiesel from waste substrates (Mendes et al. 2012). Isolate NRRL produced 30 g/l of itaconic acid using glucose as a substrate in an aerobic fermentation, while other strains were unable to accumulate this product (Levinson et al. 2006). Finally, several publications indicate biocontrol activity of *Pseudozyma* spp. and strains against rot fungi, possibly due to the synthesis of inhibitory glycolipids (Kitamoto et al. 2009; Marchand et al. 2009; Teichmann et al. 2011). These examples show that *Pseudozyma* has industrial potential for synthetic and catabolic activities in various disciplines.

Sporobolomyces

Sporobolomyces spp. are oleaginous and provide potential sources of microbial oils and biodiesel from carbohydrates (Kaneko et al. 1976; Poli et al. 2010). *Sporobolomyces carnicolor* accumulated intracellular lipids to 50 % of biomass from glucose, pentoses, and polysaccharides (Matsui et al. 2012). The major fatty acids that accumulated were distinct from those produced by *Rhodotorula* and the ascomycetous oleaginous yeasts *Lipomyces* and *Yarrowia*. *Cryptococcus*, *Sporobolomyces*, and *Trichosporon* have also been studied by several investigators for the digestion of aromatics and other recalcitrant compounds (Abbott et al. 2013; Krallish et al. 2006; Middlehoven 1993; Middlehoven et al. 1984, 2004). *Sporobolomyces* and other basidiomycetous yeasts, particularly those residing in the phylloplane, have been recognized for pest resistance and degradation of mycotoxins such as patulin and ochratoxin (Castoria et al. 1997; 2003). *Sporobolomyces* has been proposed for the removal of nitrate from wastewater (Sollai et al. 2012).

Cryptococcus

The genus *Cryptococcus* comprises a diverse species which includes the pathogens *Cryptococcus neoformans* and *Cryptococcus gatii*. Due to their pathogenicity, *Cryptococcus* (and *Malassezia*) are model organisms in the study of basidiomycetous yeasts (Boekhout et al. 2010; Heitman et al. 2011). *Cryptococcus* spp. have also been studied for numerous biotechnological applications, and genetic tools for tailoring this organism for industrial needs are advancing.

Certain species of *Cryptococcus* produce certain unique carotenoids, including plectanixanthin (Bae et al. 1971).

This xanthophyll has also been detected in other basidiomycetous yeasts, including *Dioszegia zsoltsii*, and the pigment alleviates stress to reactive oxygen species (Madhour et al. 2005). *Cryptococcus* spp. are able to transform electron-poor alkenes such as carvone through enoate reductases and oxidative enzymes (Goretti et al. 2009). *Cryptococcus* spp. and certain other basidiomycetous yeasts, including *Mrakii* spp., *Glaciozyma* spp., and *Rhodotorula* spp., produce enzymes which are cold-adapted in marine and Arctic and Antarctic environments (Brizzio et al. 2007; Edwards et al. 2013; Hamada et al. 2010; Nakagawa et al. 2004; Singh and Singh 2012; Singh et al. 2013).

Several cryptococci have lipolytic activity, are oleaginous, and have been proposed for the production of cocoa butter equivalent, single-cell oil, and biodiesel (Davies 1988) (Table 3). Certain species have been reported to utilize glycerol and to accumulate up to 60 % of their biomass as triacylglycerols (Meesters et al. 1996). *Cryptococcus* has also been studied for the production of exopolysaccharides and lipids (Pavlova et al. 2012).

Transgenic basidiomycetous yeasts

Transgenic organisms that possess and express genes from other organisms have become a very important area of biotechnology. The majority of studies on heterologous expression of eukaryotic, including human, genes in yeasts have focused on ascomycetous yeasts (Buzzini et al. 2005), particularly *S. cerevisiae* and *Komagataella (Pichia) pastoris*. Basidiomycetous yeasts may have advantages for the expression of some human genes since basidiomycetes may have greater phylogenetic relationships to humans (Baldauf and Palmer 1993). However, expression systems in basidiomycetous yeasts are just beginning to be developed. In one example, *X. dendrorhous* was transformed with the *Cop6* gene originating from the fungus *Coprinus cinereus*, and *X. dendrorhous* functionally expressed the gene and synthesized alpha-cuprenene and astaxanthin, thus expanding its repertoire of terpenoid products (Melillo et al. 2013). *X. dendrorhous* also expressed pantalenene synthase from *Streptomyces* UC5319, resulting in a shut-down of astaxanthin production and formation of pantalenene by the yeast (Melillo et al. 2012). As genetic tools and systems become developed, more products with biotechnological potential will be expressed in basidiomycetous yeasts.

Degradation of pollutants, xenobiotics, and roles in bioremediation

Basidiomycetous fungi and yeasts have important roles in the biotransformation and degradation of pollutants and xenobiotics, as well as in the bioremediation of minerals,

metals, and radionuclides (Gadd 2007; Gadd and Raven 2010) (Table 6). This activity is thought mostly to be due to the production of solubilizing acids within microbial consortia such as biofilms.

Non-pathogenic species of *Cryptococcus* and *Trichosporon* are capable of degrading polysaccharides, phenolic compounds, complex organic acids, and C2 hydrocarbons (Middelhoven 2006). Strains of *Pseudozyma* have been reported to degrade plastics and related compounds (Osamai et al. 2004). Basidiomycetous yeasts were shown to degrade starch, pullulan, dextran, xylan, polygalacturonate, galactomannan, and tannic acid as sole carbon source. They were unable to grow on cellulose, chitin, arabinogalactan, and xanthan gum. Several basidiomycetous yeasts grow on phenolic compounds. Basidiomycetous yeast diversity varied in 54 different soils varieties under different management regimes, including species of *Cryptococcus*, *Rhodotorula*, and *Trichosporon* (Yurkov et al. 2012). These results indicate that basidiomycetous yeasts are involved in the natural biodegradation of biomass and may have potential for remediation of various industrial waste streams.

Various basidiomycetous yeasts such as *Cryptococcus* are able to withstand and concentrate high quantities of heavy metals such as selenium (Golubev and Golubev 2002). *Cryptococcus luteolus* absorbed significant quantities of copper and lead (Elinov et al. 1999). Magnetically modified *Rhodotorula glutinis* effectively absorbed uranium in cultures and may have utility in decreasing toxicity in uranium wastewaters (Bai et al. 2012; Priest 2001). *R. glutinis* showed high tolerance to aluminum (Tani et al. 2010).

Due to the ability of various yeast species to grow on a wide diversity of substrates, including aromatic molecules, alkanes, compounds, amines, and other recalcitrant compounds, they have the capacity for the transformation of deleterious compounds to innocuous derivatives. Many of the oxidative transformations in yeast and fungi are performed by cytochrome (Urlacher and Girhard 2011), enzymes, and flavoprotein monooxygenases (Crenar and Petric 2011; Crozier-Reabe and Moran 2012; Kita et al. 1999; Lewis 2001; Pompon et al. 2008; Schuler and Werck-Reichert 2003). Since many basidiomycetous yeasts have strong oxidative metabolism, they are able to degrade recalcitrant compounds and other resistant chemicals. Phenolic degradation is carried out by

Table 7 Completed and ongoing genome sequencing projects for basidiomycetous yeasts (February 2013)

Completed projects		
<i>Cryptococcus gattii</i>	R265	Broad Institute
<i>Cryptococcus gattii</i>	WM276	University of British Columbia
<i>Cryptococcus neoformans</i> var. <i>grubii</i>	H99	Broad Institute
<i>Cryptococcus neoformans</i> var. <i>neoformans</i>	B-3501A	Stanford University
<i>Cryptococcus neoformans</i> var. <i>neoformans</i>	JEC21	TIGR
<i>Cryptosporidium parvum</i>	Iowa II	University of Minnesota
<i>Cryptosporidium parvum</i>		MRC Laboratory of Molecular Biology, UK
<i>Malassezia globosa</i>	CBS 7966	Procter & Gamble
<i>Malassezia restricta</i>	CBS 7877	Procter & Gamble
<i>Piriformospora indica</i>	DSM 11827	Institute of Bioinformatics and Systems Biology, Hemholtz Zentrum Munchen, Germany
<i>Rhodosporidium toruloides</i>	MTCC 457	Institute of Microbial Technology (IMTECH)-CSIR, Chandigarh
<i>Rhodosporidium toruloides</i>	NP11	Dalian Institute of Chemical Physics
<i>Rhodotorula glutinis</i>	ATCC 204091	Mississippi State University
<i>Trichosporon asahii</i> var. <i>asahii</i>	CBS 8904	Beijing Military Command General Hospital of PLA, China
<i>Trichosporon asahii</i> var. <i>asahii</i>	CBS 2479	Beijing Military Command General Hospital of PLA, China
Ongoing projects		
<i>Cryptococcus flaveszens</i>	OH182.9_3C	OSU/OARDC
<i>Cryptococcus neoformans</i> var. <i>grubii</i>	125.91	Broad Institute
<i>Cryptococcus neoformans</i> var. <i>grubii</i>	A1-35-8	Broad Institute
<i>Rhodotorula graminis</i>	WP1	DOE Joint Genome Institute
<i>Xanthophyllomyces dendrorhous</i>	MYA131	Universidad de Salamanca, Spain

Data tabulated from NCBI genome database (<http://www.ncbi.nlm.nih.gov/Genomes/>)

several yeasts, particularly basidiomycetous genera such as *Cryptococcus*, *Rhodotorula*, and *Trichosporon* (Bergauer et al. 2005; Mao et al. 2012; Margesin 2007; Middelhoven 2006; Middelhoven et al. 1991; Sampaio 1999). Several species of *Candida* and *Trichosporon* spp. are recognized to efficiently transform halogenated compounds (Kurtz and Crow 1997). Polycyclic aromatic hydrocarbons from coastal sediments were degraded by species of *Candida*, *Cryptococcus*, *Rhodotorula*, and *Trichosporon* (MacGillivray and Shiaris 1993). Recombinant yeasts expressing soybean cytochrome P450 enhanced the metabolism of phenylurea herbicides (Bernhardt 2006; Siminszky et al. 1999). It has been reported that *Pseudozyma jejuensis* is capable of degrading certain plastic wastes (Seo et al. 2007).

X. dendrorhous and *P. rhodozyma* have been reported to degrade ochratoxin, a potent mycotoxin (Péteri et al. 2007). *Trichosporon* spp. are capable of degrading ochratoxin A and zearalenone (Molnar et al. 2004) in laboratory cultures. The ability of yeasts to degrade mycotoxins has important health implications since these toxicants occur in commodities, such as feeds, foods, and beverages, and are considered as serious health hazards.

The presence of basidiomycetous yeasts, including species of *Cryptococcus*, *Glaciozyma*, *Mrakii*, and *Rhodotorula*, on glaciers and other high-altitude and cold environments contributes to the global carbon cycle (Anesio et al. 2009; Margesin 2007; Margesin and Fell 2008; Singh and Singh 2012; Singh et al. 2013). Basidiomycetous yeasts in these habitats likely contribute significantly to the degradation of pollutants such as ozone.

Miscellaneous activities of basidiomycetous yeasts

Many of the potential industrial activities of basidiomycetous yeasts are only beginning to be revealed. *Acaryomyces* isolated from mites has been reported to have biocontrol activity (Boekhout et al. 2003). The species was found to reduce the numbers of the two-spotted spider mite and also reduced the growth of the phytophagous fungi *Sclerotium sclerotiorum* and *Sclerotium rolfsii* (Gerson et al. 2005). Species of *Meira* were isolated from a carmine spider on castor bean and may have fungicidal activity (Boekhout et al. 2003).

Genomics of basidiomycetous yeasts

Genomic approaches in yeasts are increasingly being utilized to elucidate the biological and industrial properties of yeasts. Advances in genomics and systems biology are fundamentally transforming the field of toxicology, and the field of toxicogenomics is under development (Waters and Fostel 2004).

The availability and accessibility of genomes of various yeast species is advancing rapidly and will impact the understanding of eukaryotic biology, human disease, as well as advance the development of yeasts for industrial purposes (Adrio and Demain 2003; Bennett and Arnold 2001; Stewart, 2006). Although many more genomes from ascomycetous yeasts have been studied, momentum is increasing in the sequencing and analysis of genomes of basidiomycetous yeasts (Table 7). Currently, about 20 yeast genome projects have been completed or are in development for basidiomycetous yeasts (Table 7). The increasing availability of genomics has led to the initial stages of metabolic pathways with importance in medicine and biotechnology (Galagan et al. 2008; Kozybowski et al. 2009; Morita et al. 2013). The important focus in yeast genomics supports the high expectations of yeasts for their utility in biotechnology.

Summary and perspectives

Basidiomycetous yeasts are evolutionarily distinct from the ascomycetes and often have different roles in nature. They commonly reside on the phylloplane at high altitudes, in marine and freshwater environments and in cold habitats such as Antarctica and within glaciers. Consequently, the products best known for are cold-adapted enzymes and substances such as carotenoids and mycosporines that protect against reactive oxygen species and intense light. Many species have strong oxidative metabolism that enables the bioremediation and degradation of chemicals, pollutants such as aromatic compounds, plastics, and other recalcitrant compounds and polymers. Since the basidiomycetous yeasts were only definitively recognized and studied in the latter half of the twentieth century, they are a group of organisms that are largely unexplored for their biotechnological potential. As they continue to be characterized, it appears that they provide a unique resource with considerable potential in several areas of biotechnology.

References

- Abbott EP, Inairi G, Castoria R, Idnurm A (2013) Overcoming recalcitrant transformation and gene manipulation in *Pucciniomycotina* yeasts. *Appl Microbiol Biotechnol* 97:283–295
- Aehle W (ed) (2004) *Enzymes in industry. Production and applications*, 2nd edn. Wiley, Weinheim
- Ageitos JM, Vallejo JA, Viega-Crespo P, Villa TG (2011) Oily yeasts as oleaginous cell factories. *Appl Microbiol Biotechnol* 90:1219–1227
- Aguedo MH, Ly I, Belo JA, Teixeira J-M, Belin, Waché (2004) The use of enzymes and microorganisms for the production of aroma compounds from lipids. *Food Technol Biotechnol* 42:327–336
- Aki T, Yamasaki T, Nanko TM, Shionsaki M, Kawawato S, Ono K (2007) Xanthophylls and polyunsaturated acids produced by

- matine thaustochytrids. In: Hou CT, Shaw J-F (eds) Biocatalysis and biotechnology for functional foods and industrial products. CRC, Boca Raton, pp 187–198
- Álvarez V, Rodríguez-Sáiz M, de la Fuente JL, Gudiña EJ, Godio RP, Martín JF, Barredo JL (2007) The *crtS* gene of *Xanthophyllomyces dendrorhous* encodes a novel cytochrome-P450 hydroxylase involved in the conversion of beta-carotene into astaxanthin and other xanthophylls. *Fungal Genet Biol* 43:261–272
- Amaretti A, Raimondi SM, Roncaglia L, De Lucia M, Leonardi A, Rossi M (2010) Single cell oils of the cold-adapted oleaginous yeast *Rhodotorula glacialis* DBVPG 4785. *Microb Cell Fact* 9:73
- An GH, Schuman D, Johnson EA (1989) Isolation of *Phaffia rhodozyma* mutants with increased astaxanthin content. *Appl Environ Microbiol* 55:116–124
- An GH, Bielich J, Auerbach R, Johnson EA (1991) Isolation and characterization of carotenoid hyperproducing mutants of yeast by flow-cytometry and cell sorting. *Bio-Technol* 9:70–73
- An GH, Suh OS, Kwon HC, Kim K, Johnson EA (2000) Quantification of carotenoids in cells of *Phaffia rhodozyma* by autofluorescence. *Biochem Lett* 22:1031–1034
- Anesio AM, Hodson AJ, Fritz A, Psenner R, Sattler B (2009) High microbial activity on glaciers: importance to the global carbon cycle. *Global Change Biol* 15:955–960
- Arutchiva J, Doble M (2011) Mannosylerythritol lipids: microbial production and their applications. *Biosurfactants: from genes to applications*. Microbiol Monographs 20:147–177
- Avis TJ, Cheng YL, Zhao YY, Bolduc S, Neveu B, Anguenot LC, Belzile F, Bélanger RR (2005) The potential of *Pseudozyma* yeast-like epiphytes for the production of heterologous recombinant proteins. *Appl Microbiol Biotechnol* 69:304–311
- Bae M, Lee TH, Yokoyama H, Boettger HG, Chichester CO (1971) The occurrence of plectanixanthin in *Cryptococcus laurentii*. *Phytochem* 10:625–629
- Baeza M, Bravo N, Sanhueza M, Flores O, Villarreal, Cifuentes V (2012) Molecular characterization of totiviruses in *Xanthophyllomyces dendrorhous*. *Virology* 9:140
- Bai J, Wu XL, Fan FL, Tian W, Yin XJ, Zhao L, Fan FY, Li Z, Tian LL, Qin Z, Guo JS (2012) Biosorption of uranium by magnetically modified *Rhodotorula glutinis*. *Enzyme Microb Technol* 51:382–387
- Baldauf SL, Palmer JD (1993) Animals and fungi are other's closest relatives: congruent evidence from multiple proteins. *Proc Natl Acad Sci U S A* 93:7749–7754
- Bandanranayake W (1998) Mycosporines: are they nature's sunscreens? *Nat Prod Rep* 15:159–172
- Banno I (1963) Preliminary report on cell conjugation and mycelial stage in *Rhodotorula* yeasts. *J Gen Appl Microbiol* 9:249
- Banno I (1967) Studies on the sexuality of *Rhodotorula*. *J Gen Appl Microbiol* 13:167–196
- Bennett JW, Phaff HJ (1995) Early biotechnology: the Delft connection. *ASM News* 59:401–404
- Bergauer P, Fonteyne PA, Nold N, Schinner F, Margesin R (2005) Biodegradation of phenol and phenol-related compounds by psychrophilic and cold-tolerant alpine yeasts. *Chemosphere* 59:909–918
- Bernhardt R (2006) Cytochromes P450 as versatile biocatalysts. *J Biotechnol* 124:128–145
- Bertram JS, Vine AL (2005) Cancer prevention by retinoids and carotenoids: independent action on a common target. *Biochim Biophys Acta* 1740:170–178
- Bhosale P, Bernstein PS (2005) Microbial xanthophylls. *Appl Microbiol Biotechnol* 68:445–455
- Blaser H-U (2003) Enantioselective catalysis in fine chemicals production. *Chem Commun* 3:293–296
- Boekhout T, Robert V (eds) (2003) Yeasts in foods. Beneficial and detrimental aspects. Behr's, Hamburg
- Boekhout T, Theelen B, Houben J, Robert V, Scorzetti G, Gafni A, Gerson U, Szejnaberg A (2003) Novel anamorphic mite-associated fungi belonging to the *Ustilaginomycetes*: *Meira geulakonigii* gen. nov. sp. Nov., *Meira argovae* sp. nov. and *Aciaromyces ingoldii* gen. nov. *Int J Syst Evol Microbiol* 53:1655–1664
- Boekhout T, Gueho Kellermann E, Mayser P, Velegraki A (eds) (2010) *Mallessezia* and the skin: science and clinical practice. Springer, New York
- Boekhout T, Fonseca A, Sampaio JP, Bandoni RJ, Fell JW, Kwon-Chung KJ (2011) Discussion of teleomorphic and anamorphic basidiomycetous yeasts. In: Kurtzman CP, Fell JW, Boekhout T (eds) *The yeasts: a taxonomic study*, vol 3, 5th edn. Elsevier, Amsterdam, pp 1339–1372
- Botes AL, Lotter J, Rhode OH, Botha A (2005) Interspecies differences in the enantioselectivity of epoxide hydrolases in *Cryptococcus* (Kufferath) C. E. Skinner and *Cryptococcus podzolicus* (Ba'j'eva & Reshetova) Golubev. *Syst Appl Microbiol* 28:27–33
- Brizzio S, Turchetti B, de Garcia V, Libkind D, Buzzini P, van Broock M (2007) Extracellular enzymatic activities of basidiomycetous yeasts isolated from glacial and subglacial waters of northwest Patagonia (Argentina). *Can J Microbiol* 53:519–525
- Buck JW (2002) In vitro antagonism of *Botrytis cinerea* by phylloplane yeasts. *Can J Bot* 80:885–891
- Buzzini P, Romano SB, Turchetti A, Vaughan UM, Pagnoni, Davoli P (2005) Production of volatile organic sulfur compounds (VOSCs) by basidiomycetous yeasts. *FEMS Yeast Res* 5:379–385
- Buzzini P, Branda E, Goretti M, Turchetti B (2012) Psychrophilic yeasts from worldwide glacial habitats: diversity, adaptation strategies and biotechnological potential. *FEMS Microb Ecol* 82:217–241
- Cameotra SS, Makkar RS (2004) Recent application of biosurfactants as biological and immunological molecules. *Curr Opin Microbiol* 7:262–266
- Castoria R, De Curtis F, Lima G, De Cicco V (1997) Beta-1, 3 glucanase activity of two saprophytic yeasts and possible mode of action involved as biocontrol agents against postharvest disease. *Post-harvest Biol Technol* 12:293–300
- Castoria R, Morena V, Caputo L, Panfili G, De Cicco V (2005) Effect of the yeast *Rhodotorula glutinis* strain LS11 on patulin accumulation in stored apples. *Phytopathol* 95:1271–1278
- Chang KJL, Dunstan GA, Abell GJC, Clementson LA, Blackburn SI, Nichols PD, Koutoulis A (2012) Biodiscovery of Australian thaustochytrids for production of biodiesel and long-chain omega-3 oils. *Appl Microbiol Biotechnol* 93:2215–2231
- Cooper CR Jr (2011) Yeasts pathogenic to humans. In: Kurtzman CP, Fell JW, Boekhout T (eds) *The yeasts: a taxonomic study*, vol 1, 5th edn. Elsevier, Amsterdam, pp 9–19
- Crenar B, Petric S (2011) Cytochrome P450 enzymes in the fungal kingdom. *Biochim Biophys Acta* 1814:29–35
- Crozier-Reabe K, Moran GR (2012) Form follows function: structural and catalytic variation in class A flavoprotein monooxygenases. *Int J Mol Sci* 13:15601–15639
- Csutak O, Stoica I, Vassu T (2012) Evaluation of production, stability and activity of biosurfactants from yeasts with application of bioremediation of oil-polluted environment. *Rev Chim* 63:973–977
- Davies RJ (1988) Yeast oil from chese whey: process development. In: Moreton RS (ed) *Single cell oil*. Longman Scientific & Technical, Harlow, pp 99–145
- Demirbas A (2009) Progress and recent trends in biodiesel fuels. *Energy Conversion Manag* 50:14034
- Deng H, Han Y, Liu Y, Jia W, Zhou Z (2012) Identification of a newly isolated erythritol-producing yeast and cloning of its erythritol reductase genes. *J Ind Microbiol Biotechnol* 39:1663–1672
- Diaz MR, Fell JW (2004) High-throughput detection of pathogenic yeasts of the genus *Trichosporon*. *J Clin Microbiol* 42:3696–3706
- Edwards A, Douglas B, Anesio AM, Rassner SM, Irvine-Flynn TDL, Sattler B, Griffith GW (2013) A distinctive fungal community inhabiting cryconite holes on glaciers in Switzerland. *Fungal Ecol* 6:1680176

- El-Batal AI (2002) Continuous production of L-phenylalanine by *Rhodotorula glutinis* immobilized cells using a column reactor. *Acta Microbiol Pol* 51:153–169
- Elinov NP, Ananeva EP, Yaskovich GA (1999) Activity of exoglycans as sorbents of ions and heavy metals. *Appl Biochem Microbiol* 35:168–171
- Fassett RG, Coombes JS (2012) Astaxanthin in cardiovascular health and disease. *Molecules* 17:2030–2048
- Fell JW (1976) Yeasts in oceanic regions. In: Jones EBG (ed) Recent advances in aquatic mycology. Elek Science, London, pp 93–124
- Fell JW, Johnson EA (2011) *Phaffia* M. W. Miller, Yoneyama & Soneda (1976). In: Kurtzman CP, Fell JW, Boekhour T (eds) The yeasts. A taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1853–1855
- Fell JW, Statzell AC, Hunter IL, Phaff HJ (1969) *Leucosporidium* genus, heterobasidiomycetous stage of several yeasts of genus *Candida*. *Ant J Leeuwen J Microbiol Serol* 35:433
- Fell JW, Hunter IL, Tallman AS (1973) Marine basidiomycetous yeasts (*Rhodospiridium* ss.n.) with tetrapolar and multiple allelic bipolar mating systems. *Can J Microbiol* 19:643–657
- Fell JW, Johnson EA, Scorzett G (2011) *Xanthophyllomyces* Golubev (1995). In: Kurtzman CP, Fell JW, Boekhour T (eds) The yeasts. A taxonomic study, 5th edn. Elsevier, Amsterdam, pp 1595–1599
- Fernandez-Arroyo LD, Marin AG, De Segura D, Linde M, Alcalde P, Gutierrez-Alonso I, Ghazi FJ, Plou M, Fernandez-Lobato M, Ballesteros A (2007) Transformation of maltose into prebiotic isomaltoligosaccharides by a novel alpha-glucosidase from *Xanthophyllomyces dendrorhous*. *Process Biochem* 42:1530–1536
- Frengova GI, Beshkova DM (2009) Carotenoids from *Rhodotorula* and *Phaffia*: yeasts of biotechnological importance. *J Indust Microbiol Biotechnol* 36:163–180
- Frengova G, Simova E, Pavlova K, Beshkova D, Grigorova D (1994) Formation of carotenoids by *Rhodotorula glutinis* in whey ultrafiltrate. *Biotechnol Bioeng* 44:888–894
- Frengova G, Simova E, Pavlova K, Beshkova D, Grigorova D (2006) Beta-carotene-rich carotenoid protein preparation and exopolysaccharide production by *Rhodotorula rubra* GED8 grown with a yogurt starter culture. *Zeitschr Naturforsch- A J Biosci* 61:571–577
- Fromentin Y, Grellier P, Wansi JD, Lallemand MC, Buisson D (2012) Yeast-mediated xanthone synthesis through oxidative intramolecular cyclization. *Org Lett* 14(19):5054–5057
- Gadd GM (2007) Geomycology: biogeochemical transformations of rocks, minerals, metals, and radionuclides by fungi, bioweathering and bioremediation. *Mycol Rec* 111:3–49
- Gadd GM, Raven JA (2010) Geomicrobiology of eukaryotic microorganisms. *Geomicrobiol J* 26:491–519
- Galagan JE, Henn MR, Ma L-J, Cuomo CA, Birren B (2008) Genomics of the fungal kingdom: insights into eukaryotic biology. *Genome Res* 15:1620–1631
- García-Hernández, Rodríguez Z, Brandão LR, Rosa CA, Nicoli JR, Iglesias AE, Pérez-Sánchez T, Salabarría RB, Haliel N (2012) Identification and in vitro screening of avian yeasts for use as a probiotic. *Res Vet Sci* 93:798–802
- Gerson U, Paz Z, Kushnir L, Szejnberg A (2005) New fungi to control phytophagous mites and phytopathogenic fungi. *Org Biol Control IOBC/WPRS Bull* 28:103–106
- Godjevargova T, Ivanova D, Alexieva Z, Dimova N (2003) Biodegradation of toxic organic components from industrial phenol production waste waters by free and immobilized *Trichosporon cutaneum*. *Proc Biochem* 38:9150920
- Golubev VI, Golubev NV (2002) Selenium tolerance of yeasts. *Microbiology* 71(4):386–390
- Gonzalez-García Y, Hernandez R, Zhang G, Escalante FME, Holmes W, French WT (2013) Lipids accumulation in *Rhodotorula glutinis* and *Cryptococcus curvatus* growing on distillery wastewater as culture medium. *Environ Prog Sustainable Energy* 32:69–74
- Goretti M, Ponzoni C, Caselli E, Marchigiani E, Cramarossa MR, Turchetti B, Buzzini P, Forti L (2009) Biotransformation of electron-poor alkenes by yeasts: asymmetric reduction of (4s)-(+)-carvone by yeast enoate reductases. *Enzyme Microb Technol* 45:463–468
- Goswami G, Chaudhuri S, Dutta D (2010) The present perspective of astaxanthin with reference to biosynthesis and pharmacological importance. *World J Microbiol Biotechnol* 26:1925–1939
- Hagedorn S, Kaphammer B (1994) Microbial biocatalysis in the generation of fragrance chemicals. *Annu Rev Microbiol* 48:773–800
- Hainal AR, Caparu AM, Voif I, Popa VI (2012) Lignin as a carbon source for the cultivation of some *Rhodotorula* species. *Cellulose Chem Technol* 46:87–96
- Hamada S, Seike Y, Tanimori S, Sakamoto T, Kishida M (2010) Characterization of D-galacturonate reductase purified from the psychrophilic yeast species *Cryptococcus diffluens*. *J Biosci Bioeng* 111:518–521
- Hanif NQ, Muhammed G, Muhammed K, Tahira I, Raja GK (2012) Reduction of ochratoxin A in broiler serum and tissues by *Trichosporon mycotoxinivorans*. *Res Veterinary Sci* 93:795–797
- Hazen KC, Howell SA (2007) *Candida*, *Cryptococcus*, and other yeasts of medical importance. In: Murray PR, Barron JO, Jorgensen JH, Landry ML, Pfaller MA (eds) Manual of clinical microbiology, vol 2, 9th edn. ASM, Washington, DC, p 1762
- Heitman J, Kozel TR, Kwon Chung KJ, Perfect JR, Casadevall A (eds) (2011) *Cryptococcus*: from human pathogen to model yeast. ASM, Washington, DC
- Hoshino T, Ojima K, Setoguchi Y (2000) Astaxanthin synthase. Hoffmann-LaRoche, European patent no. 1035206-A3
- Houde A, Kademi AD, Leblanc D (2004) Lipases and their industrial applications—an overview. *Appl Biochem Biotechnol* 118:155–170
- Huang C, Wu H, Smith TJ, Liu Z-J, Lou W-Y, Zong M-H (2012a) In vivo detoxification of furfural during lipid production by the oleaginous yeast *Trichosporon fermentans*. *Biotechnol Lett* 34:1637–1642
- Huang C, Wu H, Smith TJ, Liu ZJ, Lou WY, Zong MH (2012b) In vivo detoxification of furfural during lipid production by the oleaginous yeast *Trichosporon fermentans*. *Biotechnol Lett* 34:1637–1642
- Huang C, Wu H, Liu L-P, Lou W-Y, Zong M-H (2012c) Effects of alcohol compounds on growth and lipid accumulation of oleaginous yeast *Trichosporon fermentans*. *PLoS One* 7:e46975
- Hussein G, Sankawa U, Goto H, Matsumoto K, Watanabe H (2006) Astaxanthin, a carotenoid with potential in human health and nutrition. *J Nat Prod* 69:443–449
- Johnson EA (2003) *Phaffia rhodozyma*: a colorful odyssey. *Int Microbiol* 6:169–174
- Johnson EA (2013) Biotechnology of non-*Saccharomyces* yeasts—the ascomycetes. *Appl Microb Biotechnol* 97:503–517
- Johnson EA, An GH (1991) Astaxanthin from microbial sources. *Crit Rev Biotechnol* 11:297–326
- Johnson EA, Lewis MJ (1980) Astaxanthin formation by the yeast *Phaffia rhodozyma*. *J Gen Microbiol* 115:173–183
- Johnson EA, Schroeder (1995) Microbial carotenoids. *Adv Biochem Eng/Biotech* 53:119–178
- Johnson EA, Conklin DE, Lewis MJ (1977) The yeast *Phaffia rhodozyma* as a dietary pigment source in salmonids and crustaceans. *J Fish Res Board Can* 34:2417–2421
- Kamp AF, La Rivière JWM, Verhoeven W (1959) Albert Jan Kluyver: his life and work. Interscience, New York, p 20
- Kaneko H, Hosohara M, Tanaka M, Itoh T (1976) Lipid composition of 30 species of yeast. *Lipids* 11:837–844
- Kanofsky JR, Sima P (1995) Singlet oxygen generation from the reactions of ozone with plant leaves. *J Biol Chem* 270:7850–7852
- Karakaya A, Laieli T, Takac S (2012) Development of process conditions for biodegradation of raw olive mill wastewater by *Rhodotorula glutinis*. *Int J Biotreatment Biodegradation* 75:75–82
- Kaur CG, Singh B (2011) Production and characterization of microbial carotenoids as an alternative to synthetic colors: a review. *Int J Food Prod* 147:503–513

- Kita K, Fukura T, Nakase K-I, Okamoto K, Yanase K, Shimizu S (1999) Cloning, overexpression, and mutagenesis of the *Sporobolomyces salmonicolor* AKU4429 gene encoding a new aldehyde reductase, which catalyzes the stereoselective reduction of ethyl 4-chloro-3-oxobutanoate to ethyl (S)-4-chloro-3-hydroxybutanoate. *Appl Environ Microbiol* 65:5207–5211
- Kitamoto D, Morita T, Fukukoa T, Konishi M, Imura T (2009) Self-assembling properties of glycolipid biosurfactants and their potential applications. *Curr Opin Colloid Interface Sci* 14:315–328
- Kluyver AJ, Donker HJL (1926) Die Einheit der Biochemie. *Chem Zelle Gewebe* 13:134–190
- Kojeh T, Gostincar C, Volkmann M, Gorbushina A, Gunde-Cimeran N (2006) Mycosporines in extremophilic fungi—novel complementary osmolytes? *Environ Chem* 3:105–110
- Konishi M, Morita T, Fukuoka R, Imura T, Kakugawa K, Kitamoto D (2008) Efficient production of mannosylerythritol lipids with high hydrophilicity by *Pseudozyma hubeiensis* KM-59. *Appl Microbiol Biotechnol* 78:37–46
- Krallish I, Gonta S, Savenkova L, Bergauer P, Margesin R (2006) Phenol degradation by immobilized cold-adapted yeast strains of *Cryptococcus terreus* and *Rhodotorula creatinivora*. *Extremophiles* 10:441–449
- Krastonof A, Alexieva Z, Yemendzhiev H (2013) Microbial degradation of phenol and phenolic derivatives. *Eng Life Sci* 13:76–87
- Kritzinger SM, Kilian SG, Potgieter MA, du Preez JC (2003) The effect of production parameters on the synthesis of the prebiotic trisaccharide, neokestose, by *Xanthophyllomyces dendrorhous* (*Phaffia rhodozyma*). *Enz Microb Technol* 32:728–737
- Kurtz AM, Crow SA (1997) Transformation of chlororesorcinol by the hydrocarbonoclastic yeasts *Candida maltosa*, *Candida tropicalis*, and *Trichosporon olivide*. *Curr Microbiol* 35:165–168
- Kurtzman CP, Fell JW, Boekhout T (eds) (2011a) The yeasts: a taxonomic study, vol 1–3, 5th edn. Amsterdam, Elsevier
- Kurtzman CP, Fell JW, Boekhout (2011b) Definition classification and nomenclature of the yeasts. In: Kurtzman CP, Fell JW, Boekhout (eds) The yeasts: a taxonomic study, 5th edn. Elsevier, Amsterdam, p 5
- Kutty SN, Philp R (2008) Marine yeasts—a review. *Yeast* 25:465–483
- Kwon-Chung KJ (1975) A new genus, *Filobasidella*, the perfect state of *Cryptococcus neoformans*. *Mycologia* 67:1197–1200
- Lachance MA (2003) The Phaff school of yeast ecology. *Int Microbiol* 6:163–167
- Lange N, Steinbüchel A (2011) Beta-Carotene production by *Saccharomyces cerevisiae* with regard to plasmid stability and culture media. *Appl Microbiol Biotechnol* 91(6):1611–1622
- Legras HL, Merdinoglu D, Cornuet JM, Karst F (2007) Bread, beer and wine: *Saccharomyces cerevisiae* diversity reflects human history. *Mol Ecol* 16:2091–2102
- Leman J (1997) Oleaginous microorganisms: an assessment of the potential. *Adv Appl Microbiol* 43:195–243
- Levinson WE, Kurtzman CP, Kuo TM (2006) Production of itaconic acid by *Pseudozyma antarctica* NRRL Y-7808 under nitrogen-limited conditions. *Enzyme Microb Technol* 39:824–827
- Lewis DFV (2001) Guide to cytochromes P450: structure and function. Taylor and Francis, London
- Libkind D, Brizzio S, van Broock MR (2004a) *Rhodotorula mucilaginosa*, a carotenoid producing yeast from a Patagonian high altitude lake. *Folia Microbiol* 49:19–25
- Libkind D, Pérez P, Sommaruga R, Diéguez MC, Ferraro M, Brizzio S, Hl Z, van Broock MR (2004b) Constitutive and UV-inducible synthesis of photoprotective compounds (carotenoids and mucosporines) by freshwater yeasts. *Photchem Photobiol Sci* 3:281–286
- Libkind D, Moline M, van Broock M (2010) Production of the UVB-absorbing compound mycosporine-glutaminol-glucoside by *Xanthophyllomyces dendrorhous* (*Phaffia rhodozyma*). *FEMS Yeast Res* 11:52–59
- Linde D, Rodriguez-Colinas B, Estevez M, Poveda A, Piou FJ, Lobata MF (2012) Analysis of neofructooligosaccharides production mediated by the extracellular beta-fructofuranosidase from *Xanthophyllomyces dendrorhous*. *Bioresource Technol* 109:123–130
- Louhasakul Y, Cheirslip B (2013) Industrial waste utilization for low-cost production of raw material oil through microbial fermentation. *Appl Microbiol Biotechnol* 169:1101–1122
- MacGillivray AR, Shiaris MP (1993) Biotransformation of polycyclic aromatic hydrocarbons by yeasts isolated from coastal sediments. *Appl Environ Microbiol* 59:1613–1618
- Madhour A, Anke H, Mucci A, Daboli P, Weber RWS (2005) Biosynthesis of the xanthophyll plectanixanthin as a stress response in the red yeast *Dioszegia* (*Tremellales*, *Heterobasidiomycetes*, *Fungi*). *Phytochem* 66(22):2617–2626
- Magliani W, Conti S, Gerloni M, Bertolotti PL (1997) Yeast killer systems. *Clin Microbiol Rev* 10:369–400
- Mao D-B, Feng Y-Q, Bai Y-H, Xu C-P (2012) Novel biotransformation to produce betulone by *Rhodotorula mucilaginosa*. *J Taiwan Inst Chem Eng* 43:825–829
- Marchand G, Remus W, Chain F, Jammanmi W, Belzile F, Belanger RR (2009) Identification of genes potentially involved in the biocontrol activity of *Pseudozyma flocculosa*. *Phytopathol* 99:1142–1149
- Marcoleta A, Niklitschek M, Wozniak A, Lozano C, Alcáino BM, Cifuentes V (2011) Glucose and ethanol-dependent transcriptional regulation of the astaxanthin biosynthesis pathway in *Xanthophyllomyces dendrorhous*. *BMC Microbiol* 11:190
- Margesin R (2007) Alpine microorganisms: useful tools for low-temperature bioremediation. *J Microbiol* 45:281–285
- Margesin R, Fell JW (2008) *Mrakiella cryoconiti* gen. nov., sp. nov., a psychrophilic, anamorphic, basidiomycetous yeast from alpine and arctic habitats. *Evol Microbiol Microbiol* 58:2977–2982
- Masaki K, Kamini NR, Ikeda H, Iefuji (2005) Cutinase-like enzyme from the yeast *Cryptococcus* sp strain S-2 hydrolyzes polylactic and other biodegradable plastics. *Appl Environ Microbiol* 71:7548–7550
- Matsui T, Otsuka K-Y, Sato (2012) Microbial oil production from carbohydrates using *Sporobolomyces carnicolor* strain O33. *Ann Microbiol* 62:861–864
- Mayne ST (1996) Beta-carotene, carotenoids, and disease prevention in humans. *FASEB J* 10:690–701
- Meesters PAEP, Huijbert GNM, Eggink G (1996) High cell density cultivation of the lipid accumulating yeast *Cryptococcus curvatus* using glycerol as a carbon source. *Appl Microbiol Biotechnol* 45(5):575–579
- Melillo E, Mentendam R, Quax RJ, Kayser O (2012) Heterologous expression of pentalenene synthase (PSS) from *Streptomyces* UC5319 in *Xanthophyllomyces dendrorhous*. *J Biotechnol* 161:302–307
- Melillo E, Sestroikromo QWJ, Kayser O (2013) Production of alpha-cuprene in *Xanthophyllomyces dendrorhous*: a step closer to a potent terpene biofactory. *Microbial Cell Factories* 12:13
- Mendes AA, Oliveira PC, Velez AM, Giordano RC, Giordano Rde L, de Castro HF (2012) Evaluation of immobilized lipases on polyhydroxybutyrate beads to catalyze biodiesel synthesis. *Int J Biol Macromol* 50(3):503–511
- Middelhoven WJ (2006) Polysaccharides and phenolic compounds as substrates for yeasts isolated from rotten wood and description of *Cryptococcus fagi* sp. nov. *Ant Leeuwen Int J Gen Mol Microbiol* 90:57–67
- Middelhoven WJ, Dejong IM, Dewinter M (1991) *Arxula adenivorans*, a yeast assimilating many nitrogenous and aromatic compounds. *Ant Leeuw Int J Gen Mol Microbiol* 59:129–137
- Middelhoven WJ (1993) Catabolism of benzen compounds by ascomycetous and basidiomycetous yeasts and yeast-like fungi—a literature review and an experimental approach. *Ant Leeuw Int J Gen Appl Mol Microbiol* 63:125–144
- Middelhoven WJ, Hoogkamer TE, Niet MC, Krieger van Rij NJW (1984) *Trichosporon adenivorans* sp. nov., a yeast species

- utilizing adenine, xanthine, uric acid, putrescine, and primary *n*-alkylamines as sole source of carbon. Antonie Van Leeuwenhoek 50:369–378
- Middlehoven WJ, Scorzetti G, Fell JW (2004) Systematics of the anamorphic basidiomycetous yeast genus *Trichosporon* Behrend with the description of five novel species: *Trichosporon vadense*, *T. smithiae*, *T. dehoogii*, *T. scarabaeorum*, and *T. gamsii*. Int J Syst Evol Biol 54:975–986
- Miki W (1991) Biological functions and activities of animal carotenoids. Pure Appl Chem 63:141–146
- Mimee B, Labbe B, Pelletier R, Belanger RR (2005) Antifungal activity of flocculosin, a novel glycolipid isolated from *Pseudozyma flocculosa*. Antimicrob Agents Chemother 49:1597–1599
- Moliné M, Flores R, Libkind D, Dieguez MC, Fariás ME, van Broock M (2010) Photoprotection by carotenoid pigments in the yeast *Rhodotorula mucilaginosa*: the role of torularhodin. Photochem Photobiol Sci 9:1145–1151
- Molnar O, Schatzmayr G, Fuchs E, Prillinger H (2004) *Trichosporon mycotoxinivorans* sp. nov., a new yeast species useful in biological detoxification of various mycotoxins. Syst Appl Microbiol 27:661–671
- Monod J, Jacob F (1961) General conclusions: teleonomic mechanisms in cellular metabolism, growth, and differentiation. Cold Spring Harb Symp Quant Biol 26:389–401
- Morita T, Konishi M, Fukuoka T, Imura T, Kitamoto D (2007) Physiological differences in the formation of the glycolipid biosurfactants, mannosylerythritol lipids, between *Pseudozyma antactica* and *Pseudozyma aphidis*. Appl Microbiol Biotechnol 74:307–315
- Morita T, Fukuoka T, Imura T, Kitamoto D (2012) Formation of two novel glycolipid biosurfactants, mannosylribitol lipid and amannosylarabitol lipid, by *Pseudomya parantarctica* JCM 11752(T). Appl Microbiol Biotechnol 96:931–938
- Morita T, Kolke H, Koyama Y, Hagiwara J, Ito E, Fukuoka T, Imura T, Machida M, Kitamoto D (2013) Genome sequence of the basidiomycetous yeast *Pseudozyma antarctica* T-34, a producer of the glycolipid biosurfactants mannosylerythritol lipids. Genome Announc 1(2):e00064-13. doi:10.1128/genomeA00064-13
- Muñoz AJ, Ruiz E, Abriouel H, Gálvez A, Ezzouhri L, Lairini K, Espinola F (2012) Heavy metal tolerance of microorganisms isolated from wastewaters: Identification and evaluation of its potential for biosorption. Chem Eng J 210:325–332
- Nakagawa T, Nagaoka T, Taniguchi S, Miyaji T, Tomizuka N (2004) Isolation and characterization of psychrophilic yeast producing cold-adapted enzymes. Lett Appl Microbiol 38:383–387
- Ojima K, Breitenbach J, Visser H, Setoguchi Y, Tabata K, Hoshino T, van den Berg J, Sandmann G (2006) Cloning of the astaxanthin synthase gene from *Xanthophyllomyces dendrorhous* (*Phaffia rhodozyma*) and its assignment as a beta-carotene 3-hydroxylase/4-ketolase. Mol Genet Genom 275:148–158
- Orndorff SA, Constantino N, Stewart D, Durham DR (1988) Strain improvement of *Rhodotorula graminis* for production of a novel L-phenylalanine ammonia lyase. Appl Environ Microbiol 54:996–1002
- Patel RN (2004) Biocatalytic synthesis of chiral pharmaceutical intermediates. Food Technol Biotechnol 42:305–325
- Patel RN (2007) Biocatalysis: synthesis of chiral intermediates for pharmaceuticals. In: Hou CT, Shaw J-F (eds) Biocatalysis and biotechnology for functional goods and industrial products. CRC, Boca Raton, pp 283–322
- Pavlova K, Ziatanov M, Antova G, Angelova-Romova M, Georgina K (2012) Biosynthesis and characterization of exopolysaccharides and lipids from Antarctic yeasts. Biotechnol Biotechnol Equip 26:3223–3228
- Perera CO, Yen GM (2007) Functional properties of carotenoids in human health. Int J Food Prop 10:201–230
- Péteri Z, Téren J, Vágvolgyi C, Varga J (2007) Ochratoxin degradation and adsorption by astaxanthin-producing yeasts. Food Microbiol 24:205–210
- Petrescu I, Lamotte-Braaseur J, Chessa JP, Ntarima P, Claeysens M, Devreese B, Marino G, Gerday C (2000) Xylanase from psychrophilic yeast *Cryptococcus adeliae*. Extremophiles 4:137–144
- Phaff HJ (1990) Isolation of yeasts from natural sources. In: Labeda DP (ed) Isolation of biotechnological organisms from nature. McGraw-Hill, New York, pp 53–79
- Phaff HJ, Miller MW, Mrak EM (1978) The life of yeasts, 2nd edn. Harvard University Press, Cambridge
- Pohl CH, Smit MS, Albertyn J (2011) *Rhodotorula bloemfonteinensis* sp. Nov., *Rhodotorula eucalyptica* sp. nov., *Rhodotorula orientis* sp. nov. and *Rhodotorula pini* sp. nov., yeasts isolated from monoterpene-rich environments. Int J Syst Evol Microbiol 61:23202327
- Poli A, Anzelmo G, Tommonaro G, Pavlova K, Casburi A, Nicolaus B (2010) Production and chemical characterization of an expolysaccharide synthesized by psychrophilic yeast strain *Sporobolomyces salmonicolor* AL(1) isolated from Livingston Island, Antarctica. Foli Microbiol 55:576–581
- Pollegoni L, Molia G, Sacchi S, Rosini E, Verga R, Pilone MS (2008) Properties and applications of microbial D-amino oxidases: current state and perspectives. Appl Microbiol Biotechnol 78:1–16
- Polo A, Linde D, Estevez M, Fernandez-Lobato M, Sanz-Aparicio J (2010) Crystallization and preliminary X-ray diffraction analysis of the fructofuranosidase from *Xanthophyllomyces dendrorhous*. Acta Crystal Section F—Struct Biol Crystal Commun 66:1441–1444
- Pompon D, Truan G, Urban P (2008) Cytochrome P450 engineering. Biofutur 288:34–38
- Priest ND (2001) Toxicity of depleted uranium. Lancet 357:244–246
- Pscheidt B, Glieder A (2008) Yeast cell factories for fine chemical and API production. Microb Cell Factories 7:25
- Querol A, Fleet G (eds) (2006) Yeasts in foods and beverages. Springer, Berlin
- Quinn AJ, Pickup MJ, D'Cunha GB (2011) Enzyme activity evaluation of organic solvent-treated phenylalanine ammonia lyase. Biotechnol Progr 27:1554–1560
- Rajasisingh H, Vage DI, Pavey SA, Omholt SW (2007) Why are salmonids pink? Can J Fish Aquat Sci 64:1614–1627
- Rensburg V, Moleleki N, van der Walt JP, Botes P, van Dyk MS (1997) Biotransformation of (+) limonene and (–) piperitone by yeasts and yeast like fungi. Biotechnol Lett 19:779–782
- Ribeiro IA, Bronze MR, Castro MF, Ribeiro MHL (2012) Design of selective production of sophorolipids by *Rhodotorula bogoreinsis* through nutritional requirements. J Molec Recog 25:630–640
- Robertson LA (2003) The Delft School of Microbiology, the nineteenth to the twenty-first century. Adv Appl Microbiol 52:357–388
- Romero-Guido C, Belo I, Ta TMN, Cao-Hoang L, Alchihab M, Gomes N, Thonart P, Texeira JA, Destain J, Wache Y (2011) Biochemistry of lactone formation in yeast and fungi and its utilisation for the production of flavour and fragrance compounds. Appl Microbiol Biotechnol 89:535–547
- Rustoy EM, Cerruti P, Galvagno MA, Baldessari A (2008) An efficient biotransformation of dialkyl esters of 2-oxoglutaric acid by *Rhodotorula minuta* whole cells. Biocatal Biotransform 26:204–209
- Sacchi S, Caidnelli, Cappelletti P, Pollegoni L, Molia G (2012) Structure–function relationships in human D-amino acid oxidase. Amino Acids 43:1833–1850
- Sampaio JP (1999) Utilization of low molecular weight aromatic compounds by heterobasidiomycetous yeasts: taxonomic implications. Can J Microbiol 45:491–512
- Sandoval G (ed) (2012) Lipases and phospholipases. Methods and protocols. Humana, New York
- Schmidt I, Schewe H, Gassel S, Jin C, Buckingham J, Hümbelin M, Sandmann G, Schrader J (2011) Biotechnological production of astaxanthin with *Phaffia rhodozyma*/*Xanthophyllomyces dendrorhous*. Appl Microbiol Biotechnol 89:555–571
- Schmitt MJ, Breinig F (2006) Yeast viral killer toxins: lethality and self-protection. Nat Rev Microbiol 4:212–221

- Schuler MA, Werck-Reichert D (2003) Functional genomics of P450s. *Annu Rev Plant Biol* 54:629–667
- Scorzetti G, Fell JW, Fonseca A, Statzell-Tallman A (2002) Systematics of basidiomycetous yeasts: a comparison of large subunit D1/D2 and internal transcribed spacer rDNA. *FEMS Yeast Res* 2:495–517
- Seo H, Um H-J, Min J, Rhee S-K, Cho TJ, Kim Y-H, Lee J (2007) *Pseudozyma jejuensis* sp. nov., a novel cutinolytic yeast species that is able to degrade plastic waste. *FEMS Yeast Res* 7:1035–1045
- Seok-Keun C, Kim J-H, Park Y-S, Kim Y-J, Chang H-H (2007) An efficient method for the extraction of astaxanthin from the red yeast *Xanthophyllomyces dendrorhous*. *J Microbiol Biotechnol* 17:847–852
- Shinozaki Y, Morita T, Cao XH, Yoshida S, Koitabashi M, Watanabe T, Suzuki K, Sameshima-Yamashita Y, Nakajima-Kambe T, Fujii T, Kitamoto HK (2013a) Biodegradable plastic-degrading enzyme from *Pseudozyma antarctica*: cloning, sequencing, and characterization. *Appl Microbiol Biotechnol* 97(7):2951–2959
- Shinozaki Y, Watanabe T, Nakajima-Kambe T, Kitamoto HK (2013b) Rapid and simple colorimetric assay for detecting the enzymatic degradation of biodegradable plastic films. *J Biosci Bioeng* 115:111–114
- Siminsky B, Corbin FT, Ward ER, Fleischmann TJ, Dewey RE (1999) Expression of a soybean cytochrome P450 monooxygenase cDNA in yeast and tobacco enhances the metabolism of phenylurea herbicides. *Proc Natl Acad Sci USA* 96(4): 1750–1755
- Singh P, Singh SM (2012) Characterization of yeasts and filamentous fungi isolated from cryonite holes of Svalbard. *Polar Biol* 35:575–583
- Singh P, Tsuji M, Singh SM, Roy U, Hoshino T (2013) Taxonomic characterization, adaptation strategies and biotechnological potential of cryophilic yeasts from ice cores of Midere Lovénbreen glacier, Svalbard, Arctic. *Cryobiology* 66:167–175
- Sollai FA, Zyca P, Rescigno A, Dumitriu E, Sanjust E (2012) *Sporobolomyces salmonicolor* as a tool for nitrate removal from wastewaters. *Environ Eng Manag J* 11:1455–1460
- Spath SB (1999) C. B. Van Niel and the culture of microbiology, 1920–1965. Ph.D. thesis, University of California, Berkeley
- Stewart JD (2006) Genomes as resources for biocatalysis. *Adv Appl Microbiol* 59:31–52
- Takuji T, Shimizu M, Moriawaki H (2012) Cancer chemoprevention by carotenoids. *Molecules* 17:2030–2048
- Tani A, Kawahara T, Yamamoto Y, Kimbara K, Kawai F (2010) Genes involved in novel adaptive aluminum resistance in *Rhodotrula glutinis*. *J Biosci Bioeng* 109:453–458
- Taskin M (2013) Co-production of tannase and pectinase by free and immobilized cells of the yeast *Rhodotorula glutinis* MP-10 isolated from tannin-rich persimmon (*Diospyros kaki* L.) fruits. *Bioprocess Biosyst Eng* 36:165–172
- Tefft RE, Goodwin TW, Simpson KL (1970) Aspects of the stereochemistry of torularhodin biosynthesis. *Biochem J* 117:921
- Teichmann B, Labbe C, Lefebvre F, Bolker M, Linne BRR (2011) Identification of a biosynthesis gene cluster for flocculosin a cellobiose lipid produced by the biocontrol agent *Pseudozyma flocculosa*. *Mol Microbiol* 79:148301495
- Thanh VN, Smit MS, Moleleki N, Fell JW (2004) *Rhodotorula cycloclastica* sp. nov., *Rhodotorula retinophila* sp. nov. and *Rhodotorula terpenoidalis* sp. nov., three limonene-utilizing yeasts isolated from soil. *FEMS Yeast Res* 4:857–863
- Theunissen B (1996) The beginnings of the Delft tradition revisited: Beijerinck and the genetics of microorganisms. *J Hist Biol* 29:197–228
- Tibor D (ed) (2008) Handbook of food spoilage yeasts, 2nd edn. Boca Raton, CRC
- Torres DPM, Goncalves MP, Texiera JA, Rodrigues LR (2010) Galactooligosaccharides: production, properties, and significance as prebiotics. *Comprehen Rev Food Sci Food Safety* 9:438–454
- Turner NJ (2011) Ammonia lyases and aminomutases as biocatalysts for the synthesis of alpha-amino acids. *Curr Opin Chem Biol* 15:234–240
- Ulber R, Soye K (2004) From wine to penicillin—5000 years of biotechnology *Chemie Unserer Zeit* 38: 172–180
- Urlacher VB, Girhard M (2011) Cytochrome P450 monooxygenases: an updated on perspectives for synthetic applications. *Trends Biotechnol* 30:26–35
- van Niel CB (1949) The “Delft School” and the rise of general microbiology. *Bacteriol Rev* 13:161–174
- Van Niel CB, Kluyver AJ (1927) *Sporobolomyces*—ein Basidiomycet? *Ann Mycol Notitiam Sci Mycol Univ* 25:389
- Waché Y, Husson G, Feron GJ, Belin J-M (2006) Yeast as an efficient biocatalyst for the production of lipid-derived flavours and fragrances. *Antonie van Leeuwenhoek* 89:405–416
- Walker GM (1998) *Yeast Physiology and Biotechnology*. Chichester, New York
- Wegner GH (1983) Biochemical conversions by yeast fermentation at high cell densities. United States Patent, 4,329,414
- Yuan J-P, Peng J, Yin K, Wang J-H (2011) Potential health-promoting effects of astaxanthin: a high-value carotenoid mostly from microalgae. *Mol Nutr Food Res* 55(1):150–165
- Yurkov AM, Vustin MM, Tyaglov BV, Maksimova IA, Sineokly SP (2008) Pigmented basidiomycetous yeasts are a promising source of carotenoids and ubiquinone Q (10). *Microbiol* 77:1–6
- Yurkov AM, Kemler M, Begerow D (2012) Assessment of yeast diversity in soils under different management regimes. *Fungal Ecol* 5(1):24–35