KVASNÝ PRŮMYSL

Kvasny prumysl (2023) 69: 707–718
https://doi.org/10.18832/kp2023.69.707

Brewers lost in wild yeast nomenclature

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Abstract

In recent decades many changes have been adopted in the fungal nomenclature, including the names of yeasts, to achieve a more natural and uniform systematics. The use of one correct name is essential for communication, the search for new knowledge, research studies or business purposes not only in the brewing branch. Nevertheless, how can such rapid progress be followed? The paper attempted to briefly explain the reasons for immense changes that have occurred in the taxonomic and nomenclatural system mainly as a result of modern molecular findings. The process of reclassification is demonstrated on a group of selected contaminants currently detected in Czech beers or breweries. This article presents several online databases that document the ongoing changes and make it easy for experts from various fields to find valid names.

Keywords: wild yeasts; beer contaminants; brewery; classification; taxonomy; revisions; Candida; Cryptococcus

1 Introduction

The term wild yeast in brewing generally includes saccharomycetous together with non-saccharomycetous yeasts occurring in the brewing environment and not usually desirable for beer production. Wild yeasts herein refer only to non-*Saccharomyces* species currently found in breweries. They are known to be undesirable contaminants, but on the other hand, their importance for the production of unusual beer styles has been recognised. These types of beers are primarily spontaneously fermented, such as famous Belgian lambic beer or gueuze, where a number of different species are involved in the fermentation process. Non-*Saccharomyces* yeasts, typically *Saccharomycodes ludwigii* or *Zygosaccharomyces rouxii*, are used to produce alcohol free beers. In addition, former yeast contaminants have become beer producers due to the recent boom in the search for new and sometimes exotic beer styles such as brett beer in which *Brettanomyces* species are used for its production (Kochlanova et al., 2016a, 2016b; Kyselová, 2020a, 2020b).

Whether wild yeasts found in the brewing environment are considered contaminants or producers, their names have undergone many recent changes. This great nomenclatural instability has accelerated, and it is not only brewers who have begun to get lost in the yeast nomenclature. Figure 1 simply summarises the complexity of the influences that cause this apparent chaos.

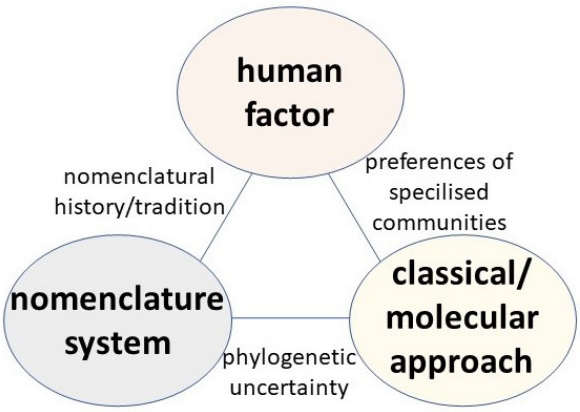

Figure 1 *A diagram illustrating the fundamental interacting factors that introduce instability and apparent chaos into current nomenclature of yeasts/fungi.*

Research Institute of Brewing and Malting
Published online: 15 April 2023

Classical/molecular approach. The comprehensive yeast systematics is based on an established phylogenetic approach that relies on the quality of data obtained at a given time along with the successful reconstruction of evolution branches (Lachance, 2016). Classical identification of yeasts was based on the characterization of selected morphological and physiological properties. However, this identification method could generate erroneous results because individual cultures showed false-negative results or the strains belonging to different species exhibited similar morphological and physiological characteristics (Kurtzman et al., 2011). Rapidly advancing molecular techniques associated with accumulation of a huge amount of new data have radically enriched (and recently even have started to displace) the former knowledge based on morphological and phenotypic features (Matoulkova and Savel, 2007). This new approach obviously shakes up the hierarchical organization of microorganisms (Borman and Johnson, 2021; Lucking et al., 2021). Thus, new phylogenetic relationships and affiliations have been recognized, resulting in an incessant realignment of the existing taxonomy. And therefore, users have to face nomenclatural changes, including name rejection and its reintroduction, shift of species to new genera, etc. (Borman and Johnson, 2021; Lachance, 2016).

Nomenclature system. The nomenclature of Kingdom Fungi, which also includes the nomenclature of yeasts is regulated by the *International Code of Nomenclature for algae, fungi, and plants* (https://www.iapt-taxon.org/nomen/main.php). Nomenclature matters are discussed and approved through special committees and congresses. A brief description supplemented by a clear timeline of important events in the fungal taxonomy and nomenclature can be found for instance in Lucking et al. (2021). To give an idea of the approximate time period for the introduction of the necessary official changes, consider the example of the International Mycological Congress, which is held every 4 years. This means that the process of proposals, discussions, voting, etc. takes several years. At the same time, new data and knowledge are increasing at an astronomical rate and it is challenging to keep pace with the quick progress.

Sometimes radical changes are needed, as in the case of the Amsterdam Declaration in 2011 (Hawksworth et al., 2011), which has introduced new united rules for the nomenclature and thus brought further fundamental changes to the conventional nomenclature system. The use of a single name for all fungi, including the pleomorphic ones, according to the slogan "One fungus=One name" (Hawksworth et al., 2011) was agreed. This means that separate names for the teleomorphic (sexual) and anamorphic (asexual) states of fungi were abandoned (Borman and Johnson, 2021; Hawksworth et al., 2011).

Human factor. The main goal of the taxonomists has been to develop a lexicon describing biodiversity so that not only scientists could communicate among themselves (Hibbett and Taylor, 2013). It is known that there are many inconsistencies in the yeast classification system, mainly due to the fact that scientists followed a different taxonomic way. For example, Hibbett and Taylor (2013) reported that about 100,000 species of fungi were accepted at that time, however, 4 times as many species names such as numerous synonyms were recorded in the literature. Focusing only on yeasts, Boekhout et al. (2022) mentioned about 3,500 yeast species names published, with 2000–2200 species accepted now. Modern data acquisition tools have introduced additional challenges, and thus the scientific world is forced to abandon its habits and adopt a major reorganisation of the classification concept to ensure a stable nomenclature in the near future. In this context, it is important to note that discussions among mycologists about approving new rules and obtaining consensus is a lengthy and demanding task. And when the long-debated rules are finally agreed, many scientists ignore them or interpret them in their own way. Thus the chaos of fungal names in scientific literature continues inertially (Borman and Johnson, 2021; Hawksworth et al., 2011; Lucking et al., 2021), which is a natural process accompanying the effort to cope up with the new era.

The aim of this paper is to offer a practical guide through the taxonomy of several yeast species currently found in brewery environments. We attempted to simplify the way, showing how it is possible to adapt to coming changes, navigate in the apparent chaos and have up to date information.

2 Taxonomy of non-*Saccharomyces* yeast contaminants in brewing

Generally, yeasts are characterised as unicellular eukaryotes classified in the Kingdom Fungi. Yeasts do not form any natural taxonomic group and, therefore, they cannot be uniformly defined. They are conservatively included in two phyla/divisions of Fungi that are Ascomycota and Basidiomycota (Kochlanova et al., 2016a). However, the reality is more complicated due to exceptions such as dimorphic filamentous fungi that form yeast like stages or yeast lineages revealing strictly filamentous growth (Boekhout et al., 2022). The brewing environment offers yeast members from both phyla, and diversity of yeasts contaminating beer is considerable. For the purpose of this paper, a limited group of yeast contaminants was selected, see Table 1. Our laboratory has frequently detected these yeasts in the brewing environment or in beer, and the isolated strains were stored in an internal collection of microorganisms for further study. Now they can serve as a case study.

Table 1 *Current names of beer spoilers commonly known by the synonymous name as reported in 5 selected reputable databases*

Original names widespread in brewing	Current legitimate names according to selected databases				
	ITIS	MycoBank	NCBI	Specie Fungorum	The Yeasts
Candida boidinii	*Candida boidinii*	[Candida] *boidinii*	[Candida] *boidinii*	[Candida] *boidinii*	[Candida] *boidinii*
Candida famata	*Torulopsis candida*	*Atelosaccharomyces hudeloi*	*Debaryomyces hansenii*	*Debaryomyces hansenii*	*Debaryomyces hansenii*
Candida guilliermondii	*Candida guilliermondii*	*Meyerozyma guilliermondii*	*Meyerozyma guilliermondii*	*Meyerozyma guilliermondii*	*Meyerozyma guilliermondii*
Candida krusei	*Candida krusei*	*Pichia kudriavzevii*	*Pichia kudriavzevii*	*Pichia kudriavzevii*	*Pichia kudriavzevii*
Candida lambica	*Candida lambica*	*Pichia fermentans*	*Pichia fermentans*	*Pichia fermentans*	*Pichia fermentans*
Candida lusitaniae	*Candida lusitaniae*	*Clavispora lusitaniae*	*Clavispora lusitaniae*	*Clavispora lusitaniae*	*Clavispora lusitaniae*
Candida norvegica	–	[Candida] *norvegica*	[Candida] *norvegica*	[Candida] *norvegica*	[Candida] *norvegica*
Candida pelliculosa	*Hansenula anomala*	*Wickerhamomyces anomalus*	*Wickerhamomyces anomalus*	*Wickerhamomyces anomalus*	*Wickerhamomyces anomalus*
Candida pulcherrima	*Candida pulcherrima*	*Metschnikowia pulcherrima*	*Metschnikowia pulcherrima*	*Metschnikowia pulcherrima*	*Metschnikowia pulcherrima*
Candida rugosa	*Candida rugosa*	*Diutina rugosa*	*Diutina rugosa*	*Diutina rugosa*	*Diutina rugosa*
Candida sake	*Candida sake*	[Candida] *sake*	[Candida] *sake*	[Candida] *sake*	[Candida] *sake*
Candida valida	–	*Pichia membranifaciens*	*Pichia membranifaciens*	*Pichia membranifaciens*	*Pichia membranifaciens*
Cryptococcus albidus	*Cryptococcus albidus*	*Naganishia albida*	*Naganishia albida*	*Naganishia albida*	*Naganishia albida*
Cryptococcus curvatus	–	*Cutaneotrichosporon curvatum*	*Cutaneotrichosporon curvatum*	*Cutaneotrichosporon curvatum*	*Cutaneotrichosporon curvatum*
Cryptococcus humicola	–	*Vanrija humicola*	*Vanrija humicola*	*Vanrija humicola*	*Vanrija humicola*
Cryptococcus laurentii	*Cryptococcus laurentii*	*Papiliotrema laurentii*	*Papiliotrema laurentii*	*Papiliotrema laurentii*	*Papiliotrema laurentii*

– No records found
Grey cells highlight a name that is different from other databases.
References: ITIS (2022); MycoBank (2023); NCBI (Schoch et al., 2020); Species Fungorum (2023); The Yeasts (2022)

Table 2 *An overview of the selected wild yeasts occurrence in breweries/beers based on scientific papers and unpublished RIBM results*

Yeasts	Location	References
Pichia membranifaciens, Issatchenkia orientalis[a], *Clavispora lusitaniae, Wickerhamomyces anomalus, Candida norvegica*[b]	biofilms in filling halls (conveyors, belts, star wheels, crowners, filling heads)	Suiker et al. (2021)
Pichia membranifaciens, Candida boidinii, Pichia fermentans	draught beer (keg ale, stout, cask ale, lager)	Jevons and Quain (2022)
Candida boidinii	yeast slurry, fermenting wort, filtered beer	Manzano et al. (2011)
Pichia guilliermondii[c]	fermenting wort	
[1]*Candida guilliermondii*[c], *Candida valida*[d], *Issatchenkia orientalis*[a], *Candida pelliculosa*[e], *Candida sake*	several biofilms and swabs from filling plants[1]	Timke et al. (2008)
Wickerhamomyces anomalus	lager, IPA[2]	Bose et al. (2021)
Candida norvegica[b]	EPA[3]	
Cadida sake	IPA[2]	
Candida krusei[a]	membrane filter, beer tank	Turvey et al. (2016)
Candida guilliermondii[c]	wort, yeast tank	
Candida pelliculosa[e]	yeast tank	
[4]*Pichia fermentans (9.7%)* *Pichia membranifaciens (8.1%)* *Pichia guilliermondiic (0.8%)* *Candida boidinii (4.8%)* *Candida sake (1.6 %)*	41 out of 101 samples of young beer after fermentation (collected world-wide) were positive; wild yeasts were identified in 24 lager breweries out of 45 tested	Kuhle and Jespersen (1998)
Wickerhamomyces anomalus	bottling plant of an industrial German brewery	Riedl et al. (2019)
Debaryomyces hansenii, Metschnikowia pulcherrima, Candida boidinii	historical stock ales	Thomas et al. (2021)
Pichia fermentans, Pichia mambranifaciens	conditioning tanks	Pham et al. (2011)
Meyerozyma guilliermondii	sorghum beer tchapalo	Attchelouwa et al. (2018)
Candida boidinii	beer samples from commercial breweries	RIBM (2023)[5]
Candida norvegica	beer samples from commercial breweries	
Candida sake	beer samples from commercial breweries	
Clavispora lusitaniae	beer samples from commercial breweries	
Debaryomyces hansenii	beer samples from commercial breweries + brewing environment	
Diutina rugosa	beer samples from commercial breweries + brewing environment	
Metschnikowia pulcherrima	beer samples from commercial breweries + brewing environment	
Meyerozyma guilliermondii	beer samples from commercial breweries	
Pichia fermentans	beer samples from commercial breweries	
Pichia membranifaciens	beer samples from commercial breweries	
Pichia kudriavzevii	beer samples from commercial breweries	
Wickerhamomyces anomalus	beer samples from commercial breweries + brewing environment	
Cutaneotrichosporon curvatum	brewing environment	
Naganishia albida	beer samples from commercial breweries + brewing environment	
Papiliotrema laurentii	beer samples from commercial breweries + brewing environment	
Vanrija humicola	brewing environment	

current names [a]*Pichia kudriavzevii;* [b]*Pichia novergensis;* [c]*Meyerozyma guilliermondii;* [d]*Pichia membranifaciens;* [e]*Wickerhamomyces anomalus*
[1] *Timke et al. (2008) performed a comprehensive sampling of filling halls in 2 breweries including for example star wheels, filler carousel, infeed and discharge conveyors*
[2] *IPA – Indian Pale Ale* | [3] *EPA – English Pale Ale* | [4] *frequency of the detection in total isolates in that study*
[5] *RIBM – Research Institute of Brewing and Malting*

2.1 *Beer contaminants formerly/currently included in the genus* Candida

The original genus *Candida* Berkhout was a highly heterogenous group of yeasts containing plant endophytes, insect symbionts or opportunistic human pathogens (Lucking et al., 2021; Shin et al., 1996; Tsui et al., 2008). Despite numerous revisions (Lucking et al., 2021; Shin et al., 1996; Odds et al., 1990; Wijman et al., 1988) it still contains roughly 300 species, which are spread over more than 3 phylogenetic clades (Boekhout et al., 2022). Numerous anamorphic phylogenetically unrelated species were placed in the artificially clustered genus *Candida* because of the lack of common features which can result in association with a more natural genus. Especially in *Candida* case many species were included into it, based on a single-gene phylogeny. When a multiple gene phylogenesis appeared, the frequent revisions occurred (Tsui et al., 2008).

Three complex relationship trees based on the Internal Transcribed Spacers (ITS), rDNA Large Subunit (LSU) and their combination (polyphasic analysis) are available to see at MycoBank (2023). Looking at these cluster analyses, which were constructed using unweighted pair-group arithmetic average (UPGMA) method, it is not surprising that there are numerous revisions of relatedness as well as reclassifications.

Currently the 300 aforementioned strikingly heterogenous species are associated with several accepted genera and 17 non-affiliated clades. This fact suggests that extensive taxonomic changes can be expected soon (Boekhout et al., 2022).

Fortunately, there are several nucleotide sequence repositories which accumulated extremely large number of records regarding fungi (Boekhout et al., 2022) such as MycoBank (2023), Species Fungorum (2023) (formerly

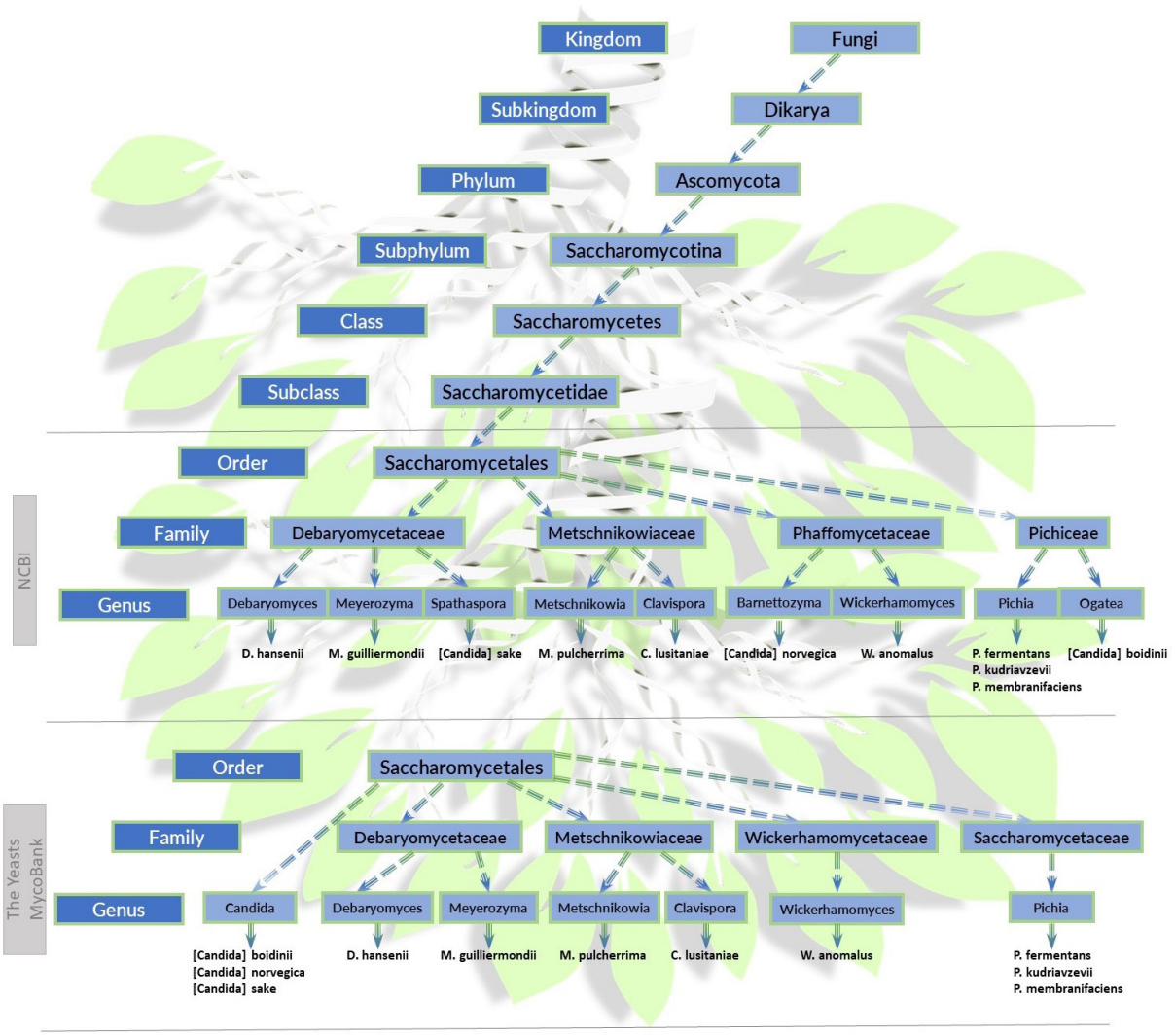

Figure 2 *Current phylogenetic classification of the selected group of beer contaminating yeasts according to NCBI, The Yeasts and MycoBank. Square brackets ([ ]) for* Candida *names indicate that the name is awaiting an appropriate revision by the research community.*

Index Fungorum), NCBI (Schoch et al., 2020) and a new promising platform The Yeasts (2022). However, it is necessary to take into account that they are not infallible. Most of them seriously indicate that the taxonomy may not be 100% up to date. Anyway, such records are very useful, because they provide a sufficient overview of recent changes in the taxonomic classification.

Based on the information from these sources, a mini-phylogenetic tree of the selected spoilage yeasts that were previously grouped into the *Candida* genus, was constructed (Figure 2). The Figure 2 shows that the new findings exhibit relatedness at the order level. This large order was established in 1960 by Kudrjavzev and all the members exhibit the following common features:

- no or only rudimentary hyphae;
- vegetative cells proliferating by budding or fission;
- cell walls without chitin;
- asci occurring singly or in chains (Diezmann et al., 2004).

A single evolutionary origin of *Saccharomycetales* is supported also by the phylogenetic analysis of rDNA and RNA polymerase II (Y. Liu et al., 1999). However, further subdivision into families and genera are controversial in many cases (MycoBank, 2023; The Yeasts, 2022; Schoch et al., 2020; Diezmann et al., 2004), including the small group of brewing contaminants presented in this paper.

Candida boidinii is a widespread methylotrophic yeast first identified by Ramírez (Ramírez, 1953; Camiolo et al., 2017). Many various studies were carried out dealing with the physiological, biochemical and genetic characteristics of *Candida boidinii* (Suzuki and Nakase, 2002; Meyer and Yarrow, 1998; Lin et al., 1996; C. Lee et al., 1994; Kumamoto et al., 1986; J. Lee and Komagata, 1983). It was the analysis of the rRNA gene that suggested its relation to the *Ogatea* clade (The Yeasts, 2022; Camiolo et al., 2017). However, this species is marked by considerable intraspecific diversity, such as high variability of nucleotide compositional patterns and genomic structures (Camiolo et al., 2017), and thus the accurate phylogenetic relationships are still opened.

Candida famata is an anamorphic stage of the ubiquitous highly osmotolerant yeast ***Debaryomyces hansenii*** (teleomorphic stage) (The Yeasts, 2022; Hutzler et al., 2012). From the phylogenetic point of view, *D. hansenii* is a member of a group of closely related species *Debaryomyces fabryi* and *Debaryomyces subglobosus*, whose distribution has been revised many times, e.g. by chemotaxonomic methods including a DNA base composition and DNA-DNA hybridization, etc. (Nakase and Suzuki, 1985a, 1985b), based on a set of phenotypic and genotypic data (Prillinger et al., 1999), using Southern hybridization with various species specific probes (Corredor et al., 2003, 2000), PCR fingerprinting, DNA reassociation and partial ACT1 gene sequence analysis (Groenewald et al., 2008), or intraspecific variability of the nuclear mitochondrial DNA insertions (Jacques et al., 2010). However, even in this case there is no certainty of a definitive correct species classification (The Yeasts, 2022).

Meyerozyma guilliermondii known rather as *Pichia guilliermondii* (teleomorph) or ***Candida guilliermondii*** (anamorph) is a typical beverage-spoiling yeast species (Hutzler et al., 2012). Here again, the distinction of considerable number of species in the *Pichia guilliermondii* clade, which displayed similar phenotypic characteristics, was ambiguous. Among them, some synonyms of the former *Pichia/Candida guilliermondii*. Bai (1996) demonstrated the distinctness of the synonym *Torula fermentati* from *C. guilliermondii* using a DNA base composition and electrophoretic karyotyping. San Millan et al. (1997) confirmed the other synonym *Candida fermentati* as a different species based on isoenzyme and randomly amplified polymorphic DNA profiles. Both synonyms were found to be conspecific and the species *Candida fermentati* became a legitimate species. However, the data also revealed that *Candida guilliermondii* was still too heterogenous species. Therefore, Kurtzman and Suzuki (2010) studied linkages among *Pichia* species producing coenzyme Q-9. The analysis of gene sequences D1/D2 LSU rRNA together with SSU rRNA provided a strong evidence for placement of the CoQ-9 species in several new genera. Due to this research *Pichia guilliermondii* was transferred to the new genus *Meyerozyma*.

Pichia kudriavzevii. Kudryavtsev (1960) originally classified this yeast as *Issatchenkia orientalis*. Over the years, there have been quite frequent changes in the species name, while the yeast was placed in the genus *Pichia* and returned back to *Issatchenkia* (The Yeasts, 2022). ***Candida krusei*** was considered an anamorphic form due to its nuclear DNA affinity (Kurtzman et al., 1980). The present assignment to the genus *Pichia* is based on D1/D2 LSU rRNA gene sequences as well as a multigene analysis (Kurtzman et al., 2008). *Pichia kudriavzevii* is moderately osmotolerant, forming a filamentous coating on liquid surfaces. It survives strongly acidic environments and is highly resistant to pasteurization temperatures (Hutzler et al., 2012).

Pichia fermentans with its anamorph ***Candida lambica*** is ubiquitous and presents a typical beverage-spoiling yeasts (Kochlanova et al., 2016b; Hutzler et al., 2012). Regarding the systematics, it is considered as one of the most basal species of the *Pichia* group, which is supported by the multigene sequence analysis (The Yeasts, 2022).

Clavispora lusitaniae. The genus *Clavispora* was proposed after observations of mating followed by formation of clavate ascospores, which were unknown until then with yeasts (Rodrigues de Miranda, 1979). The physiological characters are very similar to those of the genus *Metschnikowia* and the rRNA gene sequence analysis proved that *Clavispora* is a sister taxon of *Metschnikowia*. Therefore, both are classified in the family *Metschnikowiaceae* (see Figure 2). Nevertheless, the phylogenetic relationships are not yet fully clarified and it is expected that a multigene phylogenetic analysis across taxon could provide a more reliable delineation (The Yeasts, 2022).

Candida norvegica is another widespread yeast, isolated from various material including clinical specimens, food, beverages, insects and plants. The original name was *Torulopsis norvegica*, which can be found as a synonym in the literature. The multi-gene analysis assigns the yeast in the *Barnettozyma* clade (The Yeasts, 2022).

Wickerhamomyces anomalus is a typical microorganism of brewing environment and usually is involved in the formation of various biofilms, where it is frequently detected (Riedl et al., 2019; Hutzler et al., 2012). The yeast was originally described as *Saccharomyces anomalus* by Hansen and since then many synonyms have emerged. This yeast has historically passed through the genera *Hansenula* and *Pichia*. The species of the genus *Hansenula* were separated from those of the genus *Pichia* on the basis of their ability to assimilate nitrate. However, this ability was found being a species variable character and type of spores were considered as a more relevant feature. On the basis of it, all *Hansenula* species producing hat-shaped spores were transferred to the genus *Pichia*. Over the time, several related taxa have been isolated, but their relationship to *Hansenula anomala* has not been fully elucidated. A recent multigene sequence analysis has led to the division of the genus *Pichia* into a number of phylogenetically defined genera. Thus, *Pichia anomala* ended up in *Wickerhamomyces* typified on the validly described *W. canadensis* (Kurtzman, 2011).

Metschnikowia pulcherrima, or formerly *Torulopsis pulcherrima* or also *Candida pulcherrima* (anamorph), is well known from wine production. However, it is no stranger to the brewing environment (RIBM, 2023; Thomas et al., 2021). The taxonomic affiliation of *M. pulcherrima* is not a simple matter. Up to know, eight species closely related to *M. pulcherrima,* as well as to each other, have been validly described (*M. andauensis, M. fructicola, M. leonuri, M. persimmonesis, M. rubicola, M. shanxiensis, M. sinensis* and *M. ziziphicola*) (Sipiczki, 2022). However, several type strains could not be distinguished due to the considerable intragenomic diversity observed, which was comparable or even higher than the interstrain diversity. This alludes against the basic assumptions that sequence differences in conserved gene segments are smaller within strains than between species (Hebert et al., 2003). Deep taxonomic revision of the closely related *Metschnikowia* species showed that it was not possible to distinguish between them by any of the phenotypic, phylogenetic, and biological species concepts. Therefore, the term *M. pulcherrima* clade is used for this group of maroon-red pigment producing species and the strains related to it (Sipiczki, 2022, 2020).

In yeasts, the D1/D2 domain of the LSU rRNA gene and the ITS1 and ITS2 are most commonly parts of rDNA used to elucidate phylogenetic relationships. Nevertheless, also these segments were highly heterogenous in pulcherrimin-producing *Metschnikowia* strains. It can be concluded that the-molecular-gene analysis of very complicated genomic structure sometimes called mosaic structure of the tested individuals, can provide only inconsistent phylogenetic relationships (Sipiczki, 2022). The future will hopefully bring more satisfactory results.

Candida rugosa is now classified as ***Diutina rugosa***. A phylogenetic analysis based on both the small and the large rRNA gene subunits showed a connection of several *Candida* species. This clade formed a well distinguishable lineage from the genus *Candida* and Khunnamwong et al. (2015) proposed to group this clade into the new genus *Diutina*.

The phylogenetic position of ***Candida sake***, that present monotypic lineages, is still open. Many species have been misidentified as *C. sake* in the past. Due to numerous revisions and reclassifications and thus a clearer definition of phenotypic characteristics, physiology-based identification can be used in today's practice (The Yeasts, 2022). A variable association of *C. sake* with the *Spathaspora* clade was found based on the LSU rRNA gene D1/D2 sequence analyses. However, it is considered that despite the weak linkage with *Spathaspora* it is an independent taxon with respect to the long branch distances (Daniel et al., 2014).

The ubiquitous yeasts ***Pichia membranifaciens***, together with its anamorph ***Candida valida***, presents a typical food and beverage spoilage microorganism (The Yeasts, 2022; Kochlanova et al., 2016b). Many new species have been described in the past on the basis of similar phenotypic characteristics (Wu et al., 2006). The complicated situation is also underlined by a large number of synonyms (The Yeasts (2022) and the MycoBank (2023) currently lists 64 of them). It was molecular methods that began to yield a more natural order. The research team of Mikata and Ueda- Nishimura (Ueda-Nishimura and Mikata, 2001; Mikata and Ueda-Nishimura, 2000) started to revise many synonyms and related species of *P. membranifaciens* based on nDNA base composition and nDNA/nDNA reassociation. They reclassified 49 strains tested. Wu et al. (2006)

continued revisions employing a sequence analysis of 26S rDNA D1/D2 LSU and ITS rRNA genes. They assigned 14 of the 20 studied strains to *P. membranifaciens*. At the same time, they revealed 5 separate species.

2.2 *Beer contaminants formerly included in the genus* Cryptococcus

The polyphyletic genus *Cryptococcus* belongs to basidiomycetous yeasts, originating from diverse geographic locations and habitats, which includes many species with different genetic characteristics. Polyphyletic means that the genus comprises species of more than one order. The classical identification of *Cryptococcus* species involved the determination of physiological and morphological characteristics. This approach is currently inadequate both because of the high similarity of the individual species (Fell et al., 2000) and because of the different taxonomic consequences that provided molecular phylogenetic analyses (Okoli et al., 2007).

In principle, *Cryptococcus* represented a more or less artificial genus that had to be properly revised like the genus *Candida* (The Yeasts, 2022). Due to the inconsistency in the type of the species status and the general importance of the pathogenic species *C. neoformans* and *C. gattii*, the genus was neotyped as *C. neoformans* (Kwon-Chung et al., 2010). The modern phylogenetic concept brought many changes and thus the large genus *Cryptococcus* was redefined into smaller monophyletic lineages as can be seen in case of selected species occurring in the brewing environment. The relatedness of our selected contaminants can only be observed at the level of the class *Tremellomycetes* (Figure 3).

The assignment of families and genera to *Tremellomycetes* was given again by morphological and biochemical information in the past. However, due to the discrepancy with classification based on sequence data, the class *Tremellomycetes* was also revised and reassessed following the phylogenetic analyses of a seven-gene dataset combined with phenotypic characteristics (X. Liu et al., 2015). *Tremellomycetes*

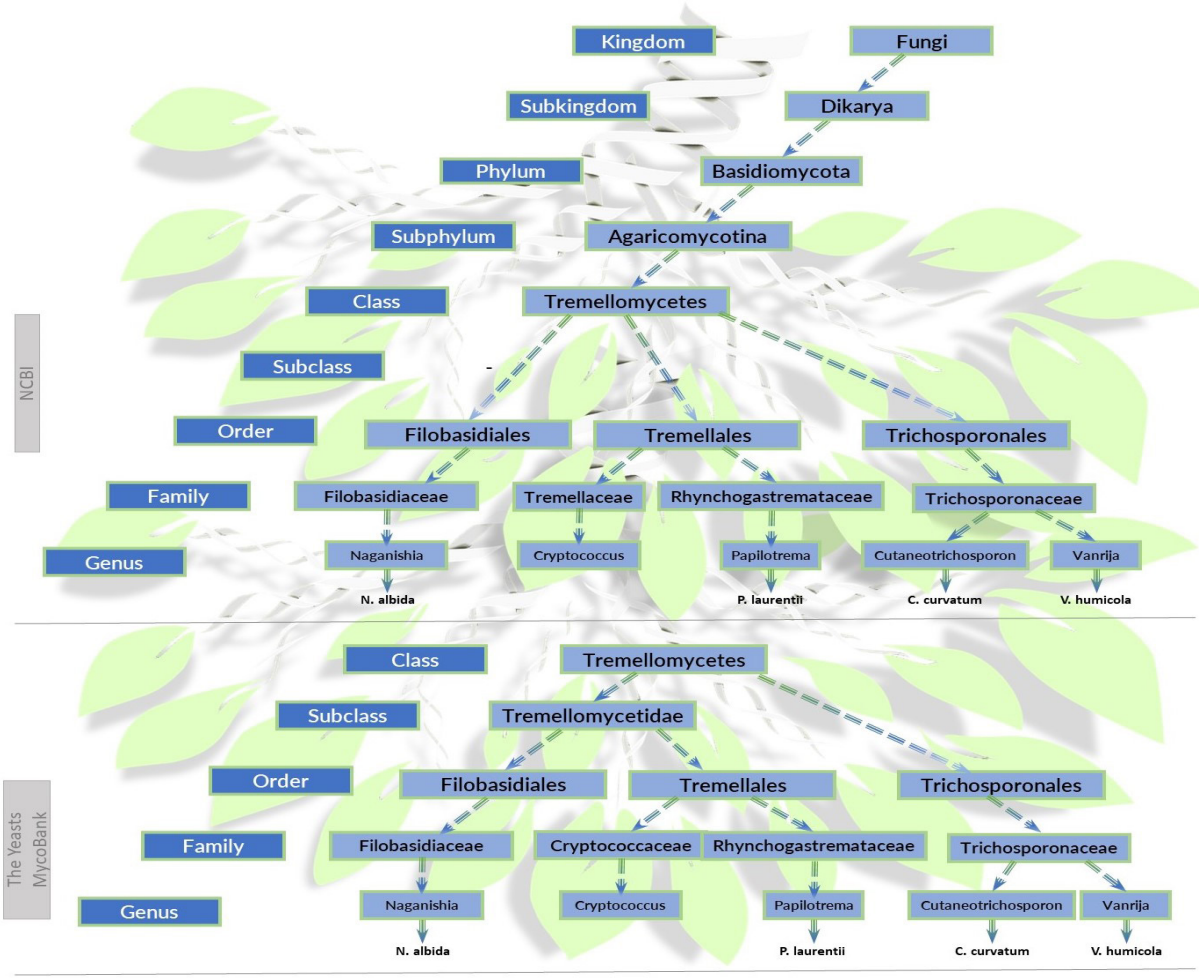

Figure 3 *Current phylogenetic classification of the selected group of beer contaminating yeasts formerly known as* Cryptococcus *according to NCBI, The Yeasts and MycoBank.*

comprises 5 orders including *Filobasidiales*, *Tremellales* and *Trichosporonales*, to which four beer spoilage species formerly known as *Cryptococcus* are nowadays assigned.

Naganishia albida formerly ***Cryptococcus albidus*** is a widespread distributed yeast isolated from natural as well as man-made environments. The original *C. albidus* was considered a heterogenous species, but recent research discovered that it is in fact a complex of species (Fonseca et al., 2000). Fonseca et al. (2000) dealt with diversity of the clade including *C. albidus* along with other phylogenetically related *Cryptococcus* and *Filobasidium* species. Their study was based on a comparative analysis of the sequence data (rDNA sequences of the 26S gene, D1/D2 region and non-coding ITS2 region) as well as on the physiological, biochemical and morphological characteristics. They revealed that the original species *C. albidus* actually includes at least 12 species.

The genus *Naganishia* was later re-established mainly due to the inclusion of 15 species of the albidus clade previously classified as *Cryptococcus*, including *C. albidus* (X. Liu et al., 2015).

Although species of *Bullera* and *Cryptococcus* do not produce arthroconidia, their several members are placed in the order *Trichosporonales* alongside the anthroconidia-producing *Trichosporon*. Based on the evaluation of phenotypic and molecular data, two families were established. The beer spoilage yeasts selected in this paper belong to the family *Trichosporonaceae*. This family is constituted by a monophyletic lineage comprising several clades also including cutaneum and *Vanrija* clade (X. Liu et al., 2015).

Cutaneotrichosporon curvatum formerly ***Cryptococcus curvatus*** presents the type species of the genus *Cutaneotrichosporon* (X. Liu et al., 2015). This is a very common yeast often associated with food or food spoilage. Interestingly, it is an oleaginous yeast with an important industrial potential (The Yeasts, 2022). Phenotypic characteristics are very similar to *Cryptococcus* species belonging to *Trichosporonales*. A comparison of sequences D1/D2 and/or ITS is considered as reliable identification (Scorzetti et al., 2002; Sugita et al., 2000).

Vanrija humicola formerly ***Cryptococcus humicola*** has been isolated from various environments, including extreme environment (The Yeasts, 2022). It is a type species of the genus *Vanrija* (X. Liu et al., 2015).

The strains of ***Papiliotrema laurentii*** formerly ***Cryptococcus laurentii*** were isolated from many different sources, but there can be a problem with their identity. The classification of strains that were not described by molecular characteristics is uncertain. Reliable placement of them to species is again provided only by D1/D2 and/or ITS sequences (The Yeasts, 2022).

P. laurentii is currently classified in the order *Tremellales*, which is the largest order within the *Tremellomycetes*, consisting of 6 families including *Rhynchogastremaceae*. This family covers a monophyletic lineage comprising several clades. The genus *Papiliotrema* was defined as a monophyletic clade, while 16 anamorphic *Cryptococcus* species including *C. laurentii* were also assigned in this genus (X. Liu et al., 2015).

3 How to find the current scientific name

The situation is quite simple if you only need to find or verify an actual name of the yeast. In this case, you can usually simply enter your synonym in one of the databases:

- MycoBank https://www.mycobank.org/page/Basic%20names%20search
- NCBI https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi
- Species Fungorum http://www.speciesfungorum.org/Names/Names.asp
- The Yeasts https://theyeasts.org/

The basis for identifying of an unknown yeast contaminant/producer in a consortium is still driven by morphological and nutritional characteristics along with other biochemical tests. It has been indicated above that such identification can be highly unreliable. Therefore, it is strongly recommended to extend the usual approach to include short gene sequences such as the D1/D2 domain of LSU rRNA and the nuclear ITS region of rDNA operon, which are both barcoding markers of the yeasts (Lucking et al., 2021; Vu et al., 2016; Matoulkova and Savel, 2007). The obtained sequence data can be easily compared to those published in one of the nucleotide sequence databases to find which species it really is:

- GenBank https://www.ncbi.nlm.nih.gov/genbank/
- EMBL-EBI https://www.ebi.ac.uk/
- DDBJ http://getentry.ddbj.nig.ac.jp/top-e.html
- UNITE http://unite.ut.ee

These databases are excellent helpers, however, it must be remembered that the large public repositories are not curated, i.e. anyone can contribute to them, and data checking is minimal and rather superficial. For this reason, interpretation of the obtained results can be complicated. It is certainly advisable to check the results offered in the original publication in which the sequences were published (Crous et al., 2021).

A simpler alternative may be MALDI–TOF MS, which has also proven itself in practice for fast and reliable identification of yeasts (Lau, 2021).

4 Conclusion

The paper attempted to capture the recent nomenclature changes in widespread yeast contaminants of beer. A number of names are now frequently being revised and adopted, while others in common use are being abandoned. This makes communication among experts as well as among general public difficult. Obviously, the general use of new names requires more time, patience and willingness. Due to the expanding knowledge of phylogeny and molecular characteristics of individual genera and species, it is necessary to consider further changes in the nomenclatural system. Here, we have tried to explain the background of the apparently confusing phylogenetic scene and to offer guidance on how the new rapid taxonomic revolution may be pursued. Fortunately, there are several platforms whose curators keep track of the latest studies, events and approval processes. Thanks to this, even the rest of us from marginal disciplines have a chance to stay up to date, as it has been demonstrated in the sample of brewing contaminants. Nevertheless, the best way for brewers to avoid trouble with wild yeast nomenclature is a thorough and careful hygiene of brewing equipment and premises.

5 Acknowledgement

The work was supported by the Ministry of Agriculture of the Czech Republic (institutional support MZE-RO1923) and by the Collection of Brewing Microorganisms RIBM 655.

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