



Review

Food fermentations: Microorganisms with technological beneficial use

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ABSTRACT

Microbial food cultures have directly or indirectly come under various regulatory frameworks in the course of the last decades. Several of those regulatory frameworks put emphasis on “the history of use”, “traditional food”, or “general recognition of safety”. Authoritative lists of microorganisms with a documented use in food have therefore come into high demand. One such list was published in 2002 as a result of a joint project between the International Dairy Federation (IDF) and the European Food and Feed Cultures Association (EFFCA). The “2002 IDF inventory” has become a de facto reference for food cultures in practical use. However, as the focus mainly was on commercially available dairy cultures, there was an unmet need for a list with a wider scope. We present an updated inventory of microorganisms used in food fermentations covering a wide range of food matrices (dairy, meat, fish, vegetables, legumes, cereals, beverages, and vinegar). We have also reviewed and updated the taxonomy of the microorganisms used in food fermentations in order to bring the taxonomy in agreement with the current standing in nomenclature.

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1. Introduction

Preservation of food including the use of fermentation of otherwise perishable raw materials has been used by man since the Neolithic period (around 10000 years BC) (Prajapati and Nair, 2003). The scientific rationale behind fermentation started with the identification of microorganisms in 1665 by Van Leeuwenhoek and Hooke (Gest, 2004). Pasteur revoked the “spontaneous generation theory” around 1859 by elegantly designed experimentation (Wyman, 1862; Farley and Geison, 1974). The role of a sole bacterium, “*Bacterium*” *lactis* (*Lactococcus lactis*), in fermented milk was shown around 1877 by Sir John Lister (Santer, 2010). Fermentation, from the Latin word *fervere*, was defined by Louis Pasteur as “La vie sans l’air” (life without air). From a biochemical point of view, fermentation is a metabolic process of deriving energy from organic compounds without the involvement of an exogenous oxidizing agent. Fermentation plays different roles in food processing. Major roles considered are:

- (1) Preservation of food through formation of inhibitory metabolites such as organic acid (lactic acid, acetic acid, formic acid, propionic acid), ethanol, bacteriocins, etc., often in combination with decrease of water activity (by drying or use of salt) (Ross et al., 2002; Gaggia et al., 2011).
- (2) Improving food safety through inhibition of pathogens (Adams and Mitchell, 2002; Adams and Nicolaidis, 2008) or removal of toxic compounds (Hammes and Tichaczek, 1994).
- (3) Improving the nutritional value (van Boekel et al., 2010; Poutanen et al., 2009).
- (4) Organoleptic quality of the food (Marilley and Casey, 2004; Smit et al., 2005; Lacroix et al., 2010; Sicard and Legras, 2011).

An authoritative list of microorganisms with a documented use in food was established as a result of a joint project between the International Dairy Federation (IDF) and the European Food and Feed Cultures Association (EFFCA). This list was published in 2002 by Mogensen et al. (2002a, 2002b). With the current review, we have undertaken the task to establish a revised and updated inventory of microorganisms with a history of use in fermented foods. We have chosen a pragmatic approach for updating the inventory by creating a “gross list” consisting of the 2002 inventory supplemented with additions suggested by the National Committees of IDF and members of EFFCA, as well as additions found by searching the scientific literature for documentation of food fermentations with emphasis on microbial associations and food matrices not initially covered. From this greatly expanded list we then critically reviewed the literature for each species in order to maintain only microbial species making desirable

contributions to the food fermentation. This final step is not without ambiguity as taste and flavor preferences can be quite different, and what some would consider spoilage can be regarded as desirable by others. We intend to be conservative, and the current list is therefore less than exhaustive and it cannot be considered definitive. An updating process following the scientific rationale detailed in the present article will be established and hosted by IDF. The criteria chosen for including species on the list are:

- Inclusion
 - Microbial species with a documented presence in fermented foods
- Exclusion
 - Lack of documentation for any desirable function in the fermentation process
 - The species is a contaminant and/or does not harbor any relevant metabolic activity
 - The species is undesirable in food for scientifically documented reasons.

Microorganisms conferring a health benefit to the host (FAO and WHO, 2002) are thus included if they are part of a culture used in a food fermentation process, whereas we have decided not to include microbial species of probiotic strains only used in supplements or over the counter (OTC) products.

As part of the process of reviewing the microbial species used in food fermentations, we also review the regulatory systems, some of the legal terms, and scientific criteria relevant for microbial food cultures (MFC). Accordingly, we have structured the review to cover:

- Regulatory systems and legal terms
- Scientific criteria
- Inventory of microbial species in food fermentations.

2. Regulatory systems and legal terms

2.1. Definition of MFC

It is remarkable that MFC have not been defined legally. To alleviate this, EFFCA has proposed the following definition: “Microbial food cultures are live bacteria, yeasts or molds used in food production”. MFC preparations are formulations, consisting of one or more microbial species and/or strains, including media components carried over from the fermentation and components which are necessary for their survival, storage, standardization, and to facilitate their application in the food production process.

2.2. Definition of “history of use”

The concept of “history of safe use” has appeared recently in regulations and in safety assessment guidance. One definition of “history of safe use” proposes “significant human consumption of food over several generations and in a large, genetically diverse population for which there exist adequate toxicological and allergenicity data to provide reasonable certainty that no harm will result from consumption of the food” (Health Canada, 2003). In order to evaluate the history of safe use of a microorganism, it is necessary to document not just the occurrence of a microorganism in a fermented food product, but also to provide evidence whether the presence of the microorganism is beneficial, fortuitous, or undesired.

2.3. US regulatory environment

In the United States, food and substances used in food are regulated according to the Food Drug and Cosmetic Act (1958), in which the status of Generally Recognized As Safe (GRAS) was introduced (FDA, 2010). Accordingly, a GRAS substance is generally recognized, among qualified experts, as having been adequately shown to be safe under the conditions of its intended use. A substance recognized for such use prior to 1958 is by default GRAS (like food used in the EU prior to May 15, 1997, not being Novel Food) (Anon, 1997, ILSI Europe Novel Food Task Force, 2003). MFC are an integral part of traditional fermented foods. As a significant number of people have consumed these foods for many centuries before 1958, the fermenting microorganisms of these products can be said to be GRAS. If a substance (microorganism) is GRAS for one food usage, it is not necessarily GRAS for all food uses. It is the use of a substance rather than the substance itself that is GRAS, as the safety determination is always limited to its intended conditions of usage. When microorganisms with a safe history in food are employed for a different use or at a significantly higher dosage, a GRAS determination for these new usages is needed.

There are three ways to obtain GRAS status for an MFC:

1. A GRAS notification where a person/company informs FDA of a determination that the usage of a substance is GRAS and followed by the receipt of a no-objection letter from FDA
2. A GRAS determination made by qualified experts outside of the US government and the result is kept by the person/company behind the determination
3. GRAS due to a general recognition of safety, based on experience from common use in food by a significant number of people before 1958.

Lists of microorganisms and microbial derived ingredients used in foods can be found at the FDA web site (FDA, 2001). As a result of the different ways to obtain GRAS, the FDA lists of GRAS substances are not expected to include all substances, nor all pre-1958 natural, nutritional substances. For a more comprehensive US regulatory update on MFC, we refer to a recent review by Stevens and O'Brien Nabors (2009).

2.4. European regulatory environment

In the European Union, the MFCs are considered ingredients and must satisfy the legal requirements of regulation EC no. 178/2002. Consequently, the responsibility for the safe use of microorganisms in food should be ensured by food manufacturers.

In 2007, the European Food Safety Authority (EFSA) introduced “Qualified Presumption of Safety” (QPS) for a premarket safety assessment of microorganisms used in food and feed production. QPS is applicable to food and feed additives, food enzymes and plant protection products (Anon, 2005). The QPS system was proposed to harmonize approaches to the safety assessment of microorganisms across the various EFSA scientific panels. The QPS approach is meant

to be a fast track for species for which there is a sufficient body of knowledge that all strains within a species are assumed to be safe. This presumption may be qualified by some restrictions such as the absence of specific characteristics (for example the absence of transmissible antibiotic resistance, absence of food poisoning toxins, absence of surfactant activity, and absence of enterotoxic activity). The QPS list covers only selected groups of microorganisms which have been referred to EFSA for a formal assessment of safety (Anon, 2005; Leuschner et al., 2010). Seventy-nine species of microorganisms have so far been submitted to EFSA for a safety assessment; the list is updated annually (EFSA, 2007, 2008, 2009, 2010). The absence of a particular organism from the QPS list does not necessarily imply a risk associated with its use. Individual strains may be safe, but this cannot be ascertained from the existing knowledge of the taxonomic unit to which it belongs. Another reason for a species not being on the list could be that EFSA has not been asked to assess the safety of any strains of the species. A recent review (Herody et al., 2010) gives a thorough description of the European regulatory environment for microbial food cultures.

Denmark is the nation with the first national legislation (since 1974) that specifically requires safety approval of MFC. More than 80 species used in 14 different food categories have been approved and published at the Danish Veterinary and Food Administration web site (Anon, 2009). In 2010, the regulation was changed. Approval is no longer needed, but a notification of a new species or a new application is still required before it can be marketed in Denmark. This topic has also recently been investigated by Germany (Vogel et al., 2011).

3. Scientific criteria for evaluation of MFC

3.1. Taxonomy

Taxonomy and systematics constitute the basis for the regulatory frameworks for MFCs. It is thus somewhat unfortunate that the definition of microbial species as a taxonomic unit lacks a theoretical basis (Stackebrandt, 2007). For this reason, we briefly outline the current status of bacterial and fungal taxonomy.

In the third edition of Prokaryotes (Stackebrandt, 2006), Stackebrandt proposes a prokaryotic species to be defined by:

- a phylogenetic component given as “the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descendents” (Cracraft, 1983),

and

- a taxonomic component given as “a group of related organisms that is distinguished from similar groups by a constellation of significant genotypic, phenotypic, and ecological characteristics.” (Colwell, 1970).

In general, a polyphasic approach to taxonomy is recommended in bacteriology (Vandamme et al., 1996). In practice, this means that a bacterial species is represented by a type strain with strains showing a high degree of phenotypic and/or genotypic similarity to the type strain regarded as belonging to the same species. Whilst objective measures of relatedness have been proposed (such as percentage genome hybridization or sequence similarity), there is no simple definition of the species as a taxonomical unit.

As a basis for the current taxonomy of prokaryotes we have used the classification of the International Committee on Systematics of Prokaryotes (ICSP—<http://www.the-icsp.org/>) and available publications in International Journal of Systematic and Evolutionary Microbiology (IJSEM—<http://ijs.sgmjournals.org/>). The Taxonomic Outline of the Bacteria and Archea (TOBA—<http://www.taxonomicoutline.org/>) in its release 7.7 of March 6, 2007, and the amended lists of bacterial names (Skerman et al., 1989) were used as reference.

In fungal taxonomy different concepts to define microbial species are used without reaching a final consensus between the numerous relationships observed between phenotypic and molecular methods (Guarro et al., 1999; Hawksworth, 2006). Several definitions have been used to describe the yeast domain. Yeasts may be defined as being ascomycetous or basidiomycetous fungi that reproduce vegetatively by budding or fission, with or without pseudohyphae and hyphae, and forming sexual states that are not enclosed in fruiting bodies (Boekhout and Robert, 2003). Phylogenetic studies have now clearly shown the clustering of the hemiascomycetous yeasts forming a single clade within the ascomycota, the other yeasts belonging to the basidiomycetes (Hibbett et al., 2007).

Yeasts used to be commonly identified phenotypically, but they are now identified from diagnostic sequences (Daniel and Meyer, 2003). Techniques using molecular biology are seen as an alternative to traditional methods since they analyze the genome independently of the physiological characteristics, which may vary within the species (Boekhout and Robert, 2003; Fernández-Espinar et al., 2006; Kurtzman et al., 2011). Molecular techniques are more reproducible and faster than the conventional methods based on physiological and morphological characteristics. Furthermore, these techniques prevent misclassification of species on the basis of their sexuality. In some cases, ribosomal D1/D2 sequence comparison cannot discriminate between species, and more discriminating sequences have to be used in parallel (Jacques and Casaregola, 2008). Overall, a combination of proven loci such as *ACT1*, *RPB1* and *RPB2*, and Elongation Factor genes are suitable, if they are included in a multilocus analysis. Genomic studies have greatly helped the search for yeast identification markers (Casaregola et al., 2011; Aguilera et al., 2008).

The variability in the fungal kingdom is even wider considering molds: estimations are currently rated around 100000 species. It is thought that there are between 700000 to 1.5 million species that are yet to be identified and classified (McLaughlin et al., 2009). Recently, a comprehensive monograph on all the genera of anamorphic fungi (hyphomycetes, fungi imperfecti, deuteromycetes, asexual fungi) was published (Seifert et al., 2011). This book, together with the Dictionary of the Fungi (Kirk et al., 2008), gives an overview of the taxonomic status of all genera of filamentous fungi.

As for the current taxonomy of fungi, we have used the references and documentation provided by the International Commission on the Taxonomy of Fungi (ICTF) on their website (<http://www.fungaltaxonomy.org/>) and the Mycobank initiative (Crous et al., 2004), as well as expert groups on invasive fungal infections and taxonomic issues (Mycoses Study Group—<http://www.doctorfungus.org/>).

3.2. Undesirable properties of MFC

Although they have been used since ancient times in fermentation processes without any identified major concern, recent discovery of rare events of adverse effects caused by microorganisms in fermented foods raise uncertainty about the level of risk, depending either on the food matrix or the susceptibility of the host (Gasser, 1994; Miceli et al., 2011).

3.2.1. Opportunistic infections

Commensal bacteria have been described to cause infections in patients with underlying disease (Berg and Garlington, 1979; Berg, 1985, 1995). Owing to its natural presence in different sites of the human body and in fermented food products, the genus *Lactobacillus* has gained particular attention. *Lactobacillus* infections occur at a very low rate in the generally healthy population—estimated 0.5/1 million per year (Borriello et al., 2003; Bernardeau et al., 2006). As stated in two reviews of *Lactobacillus* infections: “Underlying disease or immunosuppression are common features in these cases, whereas infection in previously healthy humans is extremely rare” (Aguirre and Collins, 1993). “*Lactobacillus* bacteraemia is rarely fatal *per se* but serves as an

important marker of serious underlying disease” (Husni et al., 1997). Sporadic infections have been reported in immuno-compromised patients. The underlying problems have mainly been central venous catheter (CVC) in place, metabolic disorders, organ failure, or invasive procedures such as dental work (Axelrod et al., 1973; Liang, 2008). Infections by other bacterial species used as MFC are also extremely rare (Horowitz et al., 1987; Barton et al., 2001; Mofredj et al., 2007; Leuschner et al., 2010).

Infections with the commonly used yeast and mold species are rare events as well (Enache-Angoulvant and Hennequin, 2005). Most of the infections are due to opportunistic pathogens not recognized as MFC and affect immuno-compromised patients and hospitalized patients (Winer-Muram, 1988; Jacques and Casaregola, 2008; Miceli et al., 2011).

3.2.2. Toxic metabolites and virulence factors

Biogenic amine formation in fermented foods by lactic acid bacteria (LAB) has recently been reviewed (Spano et al., 2010). Following food poisoning outbreaks (Sumner et al., 1985), metabolic pathways have been elucidated (Straub et al., 1995) and screening procedures proposed to limit the level of production (Bover-Cid and Holzapfel, 1999; Bover-Cid et al., 2000).

The presence of mycotoxin genes also raises safety concerns, although the level of expression within fermented food is very unlikely to cause any health hazard (Barbesgaard et al., 1992). Within fungi, the potential for antibiotic production is also an undesired property.

The occurrence of virulence traits should not be present in microorganisms used in food fermentation. A specific risk assessment should be conducted on strains presenting these undesirable properties, even if they belong to a species with a long history of use (Semedo et al., 2003a, 2003b).

3.2.3. Antibiotic resistance

The emergence and spread of antibiotic resistance is a major global health concern. The on-going Codex ad hoc intergovernmental task force on antimicrobial resistance is focused on the non-human use of antimicrobials. Microorganisms intentionally added to food and feed for technological purposes have not been shown to aggravate the problem of spreading antibiotic resistant pathogens (Anon, 2001).

Intrinsic resistance or resistance that is caused by mutation in an indigenous gene not associated with mobile elements would represent a very low risk of dissemination (Saarela et al., 2007). Acquired antibiotic resistance genes, especially when associated with mobile genetic elements (plasmids, transposons), can be transferred to pathogens or other commensals along the food chain, from within the product until consumption (FEEDAP, 2005, 2008; Nawaz et al., 2011).

The role of MFC in the spread of antibiotic resistance has been assessed in fermented foods (Nawaz et al., 2011) as well as more specifically for probiotic food products (Saarela et al., 2007; Mater et al., 2008; Vankerckhoven et al., 2008). Results of such studies confirm the role of a reservoir of antibiotic resistance genes from the food microbiota, without identifying any major health concerns to date.

It is considered that strains carrying acquired antibiotic resistance genes might act as a reservoir of transmissible antimicrobial resistance determinants (FEEDAP, 2005, 2008). Gene transfer of antibiotic resistance between microorganisms in the food and feed chain is thus considered to be a topic of surveillance for the safety demonstration of microorganisms (FAO and WHO, 2001, 2002; Borriello et al., 2003; Gueimonde et al., 2005).

4. Inventory of microbial species used in food fermentations

The “2002 IDF Inventory” listed 82 bacterial species and 31 species of yeast and molds whereas the present “Inventory of MFC” contains 195 bacterial species and 69 species of yeasts and molds. The overview of the distribution of species over the relevant taxonomic units

is given in Table 1 for bacteria and Tables 2 and 3 for fungi. We publish the complete current “Inventory of Microbial Food Cultures” as accompanying material to the present paper.

4.1. Bacteria

4.1.1. Actinobacteriaceae

The genus *Brachybacterium* enters the list with two species, *B. alimenterium* and *B. tyrofermentans*. Both species have been characterized as important and beneficial components of the surface microbiota of Gruyère and Beaufort cheese (Schubert et al., 1996).

Microbacterium enters the list with one species, *M. gubbeenense*. *M. gubbeenense* is a component of the traditional red smear surface culture of surface ripened cheeses (Bockelmann et al., 2005). The species was first proposed by Brennan and colleagues in 2001 (Brennan et al., 2001), and before this, *M. gubbeenense* isolates would have been considered members of *Arthrobacter nicotinae*, a species included in the “2002 IDF Inventory”.

Bifidobacterium was represented with eight species in the 2002 IDF inventory. On the one hand, the species *B. infantis* disappears, as this taxon is now transferred to *B. longum* as *B. longum* subsp. *infantis*. On the other hand, the species *B. thermophilum* is included on the list as this species is reported to have food applications (Xiao et al., 2010).

The species *Brevibacterium aurantiacum*, established in 2005, has entered the list. This species is like the two other *Brevibacterium* species, *B. linens* and *B. casei*, a component of the red smear ripening microbiota for surface ripened cheeses (Leclercq-Perlat et al., 2007).

Corynebacterium casei and *Corynebacterium variabile* are added to the list as both are components of the surface ripening microbiota. *C. casei* is a relatively “new” species (Bockelmann et al., 2005).

Micrococcus was represented with one species on the 2002 IDF inventory, *M. varians*. The species was renamed and attributed to the genus *Kocuria* (Stackebrandt et al., 1995). On the current list, *Micrococcus* is represented with the two species, *M. luteus* and *M. lygae*,

Table 1

Bacterial diversity in the 2011 update of microorganisms with beneficial use.

Phylum	Family	Genus	Species	
Actinobacteria	<i>Bifidobacteriaceae</i>	<i>Bifidobacterium</i>	8	
	<i>Brevibacteriaceae</i>	<i>Brevibacterium</i>	3	
	<i>Corynebacteriaceae</i>	<i>Corynebacterium</i>	4	
	<i>Dermabacteraceae</i>	<i>Brachybacterium</i>	2	
	<i>Microbacteriaceae</i>	<i>Microbacterium</i>	1	
	<i>Micrococcaceae</i>	<i>Arthrobacter</i>	4	
		<i>Kocuria</i>	2	
		<i>Micrococcus</i>	2	
		<i>Propionibacterium</i>	5	
		<i>Streptomyces</i>	1	
	Actinobacteria—species			32
	Firmicutes	<i>Bacillaceae</i>	<i>Bacillus</i>	3
		<i>Carnobacteriaceae</i>	<i>Carnobacterium</i>	3
<i>Enterococcaceae</i>		<i>Enterococcus</i>	3	
		<i>Tetragenococcus</i>	2	
<i>Lactobacillaceae</i>		<i>Lactobacillus</i>	84	
		<i>Pediococcus</i>	3	
<i>Leuconostocaceae</i>		<i>Leuconostoc</i>	12	
		<i>Oenococcus</i>	1	
		<i>Weissella</i>	9	
<i>Staphylococcaceae</i>		<i>Macroccoccus</i>	1	
		<i>Staphylococcus</i>	15	
<i>Streptococcaceae</i>	<i>Lactococcus</i>	3		
	<i>Streptococcus</i>	3		
Firmicutes—species			142	
Proteobacteria	<i>Acetobacteraceae</i>	<i>Acetobacter</i>	9	
		<i>Gluconacetobacter</i>	9	
	<i>Enterobacteriaceae</i>	<i>Hafnia</i>	1	
		<i>Halomonas</i>	1	
	<i>Sphingomonadaceae</i>	<i>Zymomonas</i>	1	
Proteobacteria—species			21	
Total number of species			195	

Table 2

Fungal diversity in the 2011 update of microorganisms with beneficial use.

Phylum	Family	Genus	Species
Ascomycota	<i>Cordycipitaceae</i>	<i>Lecanicillium</i>	1
	<i>Dipodascaceae</i>	<i>Geotrichum</i>	1
		<i>Yarrowia</i>	1
		<i>Galactomyces</i>	1
	<i>Microascaceae</i>	<i>Scopulariopsis</i>	1
	<i>Nectriaceae</i>	<i>Fusarium</i>	2
	<i>Saccharomycetaceae</i>	<i>Candida</i>	10
		<i>Cyberlindnera</i>	2
		<i>Debaryomyces</i>	1
		<i>Dekkera</i>	1
		<i>Hanseniaspora</i>	3
		<i>Kazachstania</i>	2
		<i>Kluyveromyces</i>	1
		<i>Lachancea</i>	2
		<i>Metschnikowia</i>	1
		<i>Pichia</i>	4
		<i>Saccharomyces</i>	4
		<i>Schwanniomyces</i>	1
		<i>Starmerella</i>	1
		<i>Trigonopsis</i>	1
		<i>Wickerhamomyces</i>	1
		<i>Zygosaccharomyces</i>	1
		<i>Zygorulasporea</i>	1
		<i>Kluyveromyces</i>	1
	<i>Sarcosomataceae</i>	<i>Torulasporea</i>	1
	<i>Schizosaccharomycetaceae</i>	<i>Schizosaccharomyces</i>	1
	<i>Sordariaceae</i>	<i>Neurospora</i>	1
	<i>Trichocomaceae</i>	<i>Aspergillus</i>	4
		<i>Penicillium</i>	7
Ascomycota—species			59
Basidiomycota	<i>Cystofilobasidiaceae</i>	<i>Cystofilobasidium</i>	1
		<i>Guehomyces</i>	1
Basidiomycota—species			2
Zygomycota	<i>Mucoraceae</i>	<i>Mucor</i>	4
		<i>Rhizopus</i>	4
Zygomycota—species			8
Total number of species			69

used for cheese ripening and meat fermentation, respectively (Bonnarme et al., 2001; Garcia Fontan et al., 2007).

Propionibacterium includes one new subspecies of *P. freudenreichii* subsp. *globosum*, and the newly added species *P. jensenii*. The species *P. arabinosum* is considered synonymous with *P. acidipropionici* and is thus no longer on the list as a separate entity.

4.1.2. Firmicutes

The genus *Carnobacterium* is new on the list and is now represented by three species, *C. divergens*, *C. maltaromaticum*, and *C. piscicola*. The inclusion of *Carnobacterium* commonly used in meat fermentations stems from widening the scope of the list from dairy to food fermentations (Hammes et al., 1992).

The genus *Tetragenococcus* was proposed in 1990 and validated in 1993 for newly identified species and some species previously belonging to *Pediococcus* and *Enterococcus*.

The genus *Weissella* was introduced in 1993 for some species previously belonging to the *Leuconostoc mesenteroides* species group. *Weissella* would have been in the 2002 IDF inventory if meat cultures had been included at the time. *Weissella* species are used for fermentation of meat, fish, cabbage (Kimchi), cassava, and cocoa (Collins et al., 1993).

Among the enterococci, *Enterococcus faecalis* has entered the list owing to its use in dairy, meat, vegetables and probiotics (Foulquie Moreno et al., 2006).

The genus *Lactobacillus* was already widely present in the initial inventory. Owing to its wide use in other food matrices and the new scope of the inventory, this is the genus with the largest number of changes and now represented by 82 species.

Table 3
Filamentous fungi and yeasts for beneficial use and their teleomorphs, anamorphs and most important synonyms.

Current name	Teleomorphic state	Anamorphic state	Important synonyms
<i>Aspergillus acidus</i>	–	<i>Aspergillus acidus</i>	<i>Aspergillus foetidus</i>
<i>Aspergillus niger</i>		<i>Aspergillus niger</i>	
<i>Aspergillus oryzae</i>		<i>Aspergillus oryzae</i>	
<i>Aspergillus sojae</i>		<i>Aspergillus sojae</i>	
<i>Candida etchellsii</i>		<i>Candida etchellsii</i>	<i>Torulopsis etchellsii</i>
<i>Candida milleri</i>		<i>Candida milleri</i>	<i>Candida humilis</i>
<i>Candida oleophila</i>		<i>Candida oleophila</i>	<i>Candida deformans</i>
<i>Candida rugosa</i>		<i>Candida rugosa</i>	<i>Mycoderma rugosum</i>
<i>Candida tropicalis</i>		<i>Candida tropicalis</i>	<i>Odium tropicale</i> , <i>Candida kefyri</i>
<i>Candida versatilis</i>		<i>Candida versatilis</i>	<i>Torulopsis versatilis</i>
<i>Candida zemplinina</i>		<i>Candida zemplinina</i>	
<i>Candida zeylanoides</i>		<i>Candida zeylanoides</i>	<i>Monilia zeylanoides</i>
<i>Cyberlindnera jadinii</i>	<i>Cyberlindnera jadinii</i>	<i>Candida guillemondii</i>	<i>Candida utilis</i>
<i>Cyberlindnera mrakii</i>	<i>Cyberlindnera mrakii</i>		<i>Hanseluna jadinii</i> , <i>Williopsis mrakii</i> , <i>Hanseluna mrakii</i>
<i>Cystofilobasidium infirmominiatum</i>	<i>Cystofilobasidium infirmominiatum</i>	<i>Cryptococcus infirmominiatus</i>	<i>Rhodospodium infirmominatum</i>
<i>Debaryomyces hansenii</i>	<i>Debaryomyces hansenii</i>	<i>Atelosaccharomyces hudeloi</i>	<i>Pichia hansenii</i>
<i>Dekkera bruxellensis</i>	<i>Dekkera bruxellensis</i>	<i>Brettanomyces abstinens</i>	
<i>Fusarium domesticum</i>		<i>Fusarium domesticum</i>	<i>Trichothecium domesticum</i>
<i>Fusarium venenatum</i>		<i>Fusarium venenatum</i>	
<i>Galactomyces candidum</i>	<i>Galactomyces candidum</i>		
<i>Geotrichum candidum</i>		<i>Geotrichum candidum</i>	<i>Acrosporium candidum</i>
<i>Guehomyces pullulans</i>		<i>Guehomyces pullulans</i>	<i>Trichosporon fuscans</i>
<i>Hanseniaspora guilliermondii</i>	<i>Hanseniaspora guilliermondii</i>	<i>Kloeckera apiculata</i>	<i>Hanseniaspora apuliensis</i>
<i>Hanseniaspora osmophila</i>	<i>Hanseniaspora osmophila</i>	<i>Kloeckera corticis</i>	
<i>Hanseniaspora uvarum</i>	<i>Hanseniaspora uvarum</i>	<i>Kloeckera uvarum</i>	<i>Hanseniaspora apiculata</i>
<i>Kazachstania exigua</i>	<i>Kazachstania exigua</i>	<i>Candida holmii</i>	
<i>Kazachstania unispora</i>	<i>Kazachstania unispora</i>		<i>Saccharomyces unisporus</i>
<i>Kluyveromyces lactis</i>	<i>Kluyveromyces lactis</i>		<i>Saccharomyces lactis</i>
<i>Kluyveromyces marxianus</i>	<i>Kluyveromyces marxianus</i>	<i>Atelosaccharomyces pseudotropicalis</i>	<i>Saccharomyces marxianus</i>
<i>Lachancea fermentati</i>	<i>Lachancea fermentati</i>		<i>Zygosaccharomyces fermentati</i>
<i>Lachancea thermotolerans</i>	<i>Lachancea thermotolerans</i>		<i>Kluyveromyces thermotolerans</i>
<i>Lecanicillium lecanii</i>	<i>Cordyceps confragosa</i>	<i>Lecanicillium lecanii</i>	<i>Verticillium lecanii</i>
<i>Metschnikowia pulcherrima</i>	<i>Metschnikowia pulcherrima</i>	<i>Asporomyces uvae</i>	<i>Candida pulcherrima</i>
<i>Mucor hiemalis</i>			
<i>Mucor mucedo</i>			
<i>Mucor plumbeus</i>			
<i>Mucor racemosus</i>			
<i>Neurospora sitophila</i>	<i>Neurospora sitophila</i>	<i>Chrysonilia sitophila</i>	
<i>Penicillium camemberti</i>		<i>Penicillium camemberti</i>	<i>Penicillium album</i> , <i>Penicillium candidum</i> , <i>Penicillium caseicola</i> , <i>Penicillium rogeri</i>
<i>Penicillium caseifulvum</i>		<i>Penicillium caseifulvum</i>	
<i>Penicillium chrysogenum</i>		<i>Penicillium chrysogenum</i>	<i>Penicillium notatum</i>
<i>Penicillium commune</i>		<i>Penicillium commune</i>	<i>Penicillium cyclopium</i>
<i>Penicillium nalgiovense</i>		<i>Penicillium nalgiovense</i>	
<i>Penicillium roqueforti</i>		<i>Penicillium roqueforti</i>	<i>Penicillium aromaticum</i> , <i>Penicillium gorgonzolae</i> , <i>Penicillium stilton</i>
<i>Penicillium solitum</i>		<i>Penicillium solitum</i>	<i>Penicillium casei</i> , <i>Penicillium mali</i>
<i>Pichia fermentans</i>	<i>Pichia fermentans</i>		<i>Zymopichia fermentans</i>
<i>Pichia kluyveri</i>	<i>Pichia kluyveri</i>		<i>Hanseluna kluyveri</i>
<i>Pichia kudriavzevii</i>	<i>Pichia kudriavzevii</i>	<i>Candida acidothermophilum</i>	<i>Issatchenkia orientalis</i>
<i>Pichia membranifaciens</i>	<i>Pichia membranifaciens</i>		<i>Saccharomyces membranifaciens</i>
<i>Pichia occidentalis</i>	<i>Pichia occidentalis</i>	<i>Candida soli</i>	
<i>Pichia pijperi</i>	<i>Pichia pijperi</i>		<i>Wickerhamomyces pijperi</i> , <i>Hanseniaspora pijperi</i>
<i>Rhizopus microsporus</i>			<i>Mucor microsporus</i>
<i>Rhizopus oligosporus</i>			
<i>Rhizopus oryzae</i>			<i>Rhizopus arrhizus</i> , <i>Mucor arrhizus</i>
<i>Rhizopus stolonifer</i>			<i>Mucor stolonifer</i>
<i>Saccharomyces bayanus</i>	<i>Saccharomyces bayanus</i>		<i>Saccharomyces uvarum</i>
<i>Saccharomyces cerevisiae</i>	<i>Saccharomyces cerevisiae</i>		
<i>Schizosaccharomyces pombe</i>	<i>Schizosaccharomyces pombe</i>		<i>Saccharomyces pombe</i>
<i>Schwanniomyces vanrijiae</i>	<i>Schwanniomyces vanrijiae</i>		<i>Pichia vanrijiae</i>
<i>Scopulariopsis flava</i>		<i>Scopulariopsis flava</i>	<i>Acaulium flavum</i>
<i>Starmerella bombicola</i>	<i>Starmerella bombicola</i>		
<i>Torulasporea delbrueckii</i>	<i>Torulasporea delbrueckii</i>	<i>Candida colliculosa</i>	<i>Zymodebaryomyces delbrueckii</i>
<i>Torulopsis candida</i>		<i>Torulopsis candida</i>	<i>Cryptococcus candidus</i>
<i>Torulopsis holmii</i>		<i>Torulopsis holmii</i>	<i>Candida holmii</i>

Table 3 (continued)

Current name	Teleomorphic state	Anamorphic state	Important synonyms
<i>Trigonopsis cantarellii</i>	<i>Trigonopsis cantarellii</i>		<i>Candida cantarellii</i> , <i>Torulopsis vinacea</i>
<i>Wickerhamomyces anomalus</i> <i>Yarrowia lipolytica</i> <i>Zygosaccharomyces rouxii</i>	<i>Wickerhamomyces anomalus</i> <i>Yarrowia lipolytica</i>	<i>Candida beverwijkiae</i> <i>Candida deformans</i> <i>Zygosaccharomyces rouxii</i>	<i>Saccharomyces anomalus</i> <i>Saccharomycopsis lipolytica</i> <i>Zygosaccharomyces japonicas</i> , <i>Torulasporea rouxii</i>
<i>Zygorulasporea florentina</i>	<i>Zygorulasporea florentina</i>		<i>Saccharomyces florentinus</i> , <i>Torulapora florentinus</i>

Leuconostoc is also a genus having expanded considerably from the two species present in the 2002 IDF inventory. This is mainly due to the inclusion of species useful for coffee and vegetable fermentations, among which are also several species being proposed recently as *L. holzapfelii*, *L. inhae*, *L. kimchii*, and *L. palmae*.

Staphylococcus is now represented by 13 species. The growth in number is caused by the consideration of mostly meat fermentation processes and the role in numerous other food matrices (Nychas and Arkoudelos, 1990).

Lactococcus has only been expanded with a single species *L. raffi-nolactis*, a species occasionally involved in the ripening of cheese (Ouadghiri et al., 2005).

Also *Streptococcus* has increased with a single species, due to the use of *S. gallolyticus* subsp. *macedonicus* in ripening cultures for cheese (Georgalaki et al., 2000).

Bacillus species have been included in the inventory due to the widening of scope by incorporation of new food matrices such as cocoa beans (Schwan and Wheals, 2010) and soy beans (Kubo et al., 2011).

4.1.3. Proteobacteriaceae

Acetobacter and *Gluconacetobacter* are represented by nine and eight species, respectively. They are mainly utilized in the production of vinegar, but also of importance in the fermentation of cocoa and coffee (Sengun and Karabiyikli, 2011).

Halomonas elongata, a new species of the family *Enterobacteriaceae*, was added to the list because of its relevance in meat fermentation (Hinrichsen et al., 1994).

As a consequence of the widened scope of the inventory, the genus *Zymomonas* has been added to the list. It is represented by the species *Z. mobilis*, which is widely used for the fermentation of alcoholic beverages in many tropical areas of America, Africa, and Asia (Rogers et al., 1984; Escalante et al., 2008).

Klebsiella mobilis, formerly *Enterobacter aerogenes* in the 2002 IDF inventory, was rejected as the reference of food usage (Gassem, 1999) indicated the species as part of the spoilage microbiota.

4.2. Fungi

The number of recognized species with beneficial use for foods has grown considerably. Contributions to the expansion come from changes in taxonomy and description of species to be important in natural fermentations or used as inoculants (Table 3). We have added 24 eukaryotic genera: *Aspergillus*, *Cyberlindnera*, *Cystofilobasidium*, *Dekkera*, *Guehomyces*, *Hanseniaspora*, *Kazachstania*, *Lachancea*, *Lecanicillium*, *Metschnikowia*, *Mucor*, *Neurospora*, *Rhizopus*, *Schizosaccharomyces*, *Schwanniomyces*, *Scopulariopsis*, *Sporendonema*, *Starmerella*, *Torulasporea*, *Trigonopsis*, *Wickerhamomyces*, *Yarrowia*, *Zygosaccharomyces*, and *Zygorulasporea*. Widening the scope of food matrices covers a large number of the additions. The inclusion of wine and beverages leads to the addition of the following yeast species: *Cyberlindnera*, *Dekkera*, *Hanseniaspora*, *Lachancea*, *Metschnikowia*, *Schizosaccharomyces*, *Schwanniomyces*, *Starmerella*, *Trigonopsis*, and *Wickerhamomyces*; and the inclusion of soy and vegetable fermentations leads to the addition of the following yeast and

filamentous fungi: *Aspergillus*, *Guehomyces*, *Mucor*, *Neurospora*, *Rhizopus*, and *Zygosaccharomyces*.

The changes in taxonomy have, however, also contributed to changing the appearances in the inventory. Most of the species recorded as *Candida* in the former list have been transferred to other genera or included under the teleomorphic name (Table 3). Recently, it has been suggested by many mycologists that only one name should be given to any fungus, as is already done in Zygomycota. Thus it would be preferred to refer to the most well-known species as *Saccharomyces cerevisiae* (the teleomorphic and holomorphic name), rather than the anamorphic name *Candida robusta*. According to present rules as guided by the International Code of Botanical Nomenclature Article 59, fungi in Ascomycota and Basidiomycota can have two names; one for the teleomorph and holomorph, which is recommended, and one for the anamorphic state.

4.2.1. Yeasts

Candida famata is the anamorph of *Debaryomyces hansenii*. *Candida utilis*, used for single cell protein production, should be called *Cyberlindnera jadinii*. *Williopsis mrakii* (= *Hansenula mrakii*) is now also included in the genus *Cyberlindnera* as *C. mrakii*. *Saccharomyces unisporus* has been transferred to *Kazachstania unispora*, and *Candida holmii* has also been transferred to *Kazachstania* as *K. exigua*. *Candida krusei* is now called *Pichia kudriavzevii*. *Candida kefir* (= *Candida pseudotropicalis*) is placed in *Kluyveromyces marxianus*. *Candida valida* is now called *Pichia membranefaciens* and finally *Saccharomyces florentinus* is now called *Zygorulasporea florentina* (Table 3; Boekhout and Robert, 2003; Kurtzman et al., 2011). Regarding *Candida*, many additional species have been suggested for beneficial use in foods, including *C. etchellsii*, *C. intermedia*, *C. maltosa*, *C. versatilis* and *C. zeylanoides*. Teleomorphic states are not known for these species. Other species recently suggested include *Clavispora lusitanae*, *Cystofilobasidium infirmominatum*, *Dekkera bruxellensis*, *Hanseniaspora uvarum*, *Kazachstania turicensis*, *Metschnikowia pulcherrima*, *Pichia occidentalis*, *Rhodospiridium* sp., *Saccharomyces pastorianus*, *Saccharomycopsis fibuligera*, *Saturnisporus saitoi*, *Sporobolomyces roseus*, *Torulasporea delbrueckii*, *Trichosporon cutaneum*, *Wickerhamomyces anomalus*, *Yarrowia lipolytica*, *Zygosaccharomyces bailii*, and *Z. rouxii*. In the current update of the inventory of microorganisms, we tend to be conservative and only include species with a well-documented technological benefit. One example is *Dekkera bruxellensis* (anamorph *Brettanomyces bruxellensis*), which was formerly regarded as a spoiler of beer (and wine). However, it is used for production of Belgian Lambic-Geuze beer. *D. bruxellensis* produces acetic acid that in moderate amounts gives a unique taste to those beers (Boekhout and Roberts, 2003). Other examples are *Debaryomyces hansenii* and *Yarrowia lipolytica* which are very important for aroma formation in Munster and Parmesan cheeses. *Saccharomyces cerevisiae*, *Hanseniaspora uvarum*, *Kluyveromyces marxianus* and *Pichia fermentans* are extremely important for the development of the fine aroma of cocoa beans (Boekhout and Roberts, 2003).

4.2.2. Filamentous fungi

Relatively few filamentous fungi have been added to the list since the last compilation. However, several fungal starter cultures

commonly used in Asia could potentially be used in Europe, as fungi can add fiber, vitamins, proteins etc. to fermented foods, or be consumed as single cell protein (SCP) (Nout, 2000, 2007). *Aspergillus* species and other fungi found in Asian traditional fermented foods were not mentioned in the first 2002 IDF inventory list as they are not commonly used in fermented dairy products. For instance *Aspergillus oryzae* and *A. sojae* are used in the production of miso and soya sauce fermentations. *Aspergillus oryzae* and *A. niger* are also used for production of sake and awamori liquors, respectively (Nout, 2000, 2007). *Aspergillus acidus* is used for fermenting Puerh tea (Mogensen et al., 2009).

Rhizopus oligosporus is used in the fermentation process of Tempeh (Hachmeister and Fung, 1993).

Fusarium domesticum was first identified as *Trichothecium domesticum*, but was later allocated to *Fusarium* (Bachmann et al., 2005; Schroers et al., 2009; Gräfenham et al., 2011). This species has been used for cheese fermentations (cheese smear). *Fusarium solani* DSM 62416 was isolated from a Vacherin cheese, but has not been examined taxonomically in detail yet. *Fusarium venenatum* A 3/5 (first identified as *F. graminearum*) is being used extensively for mycoprotein production in Europe (Thrane, 2007). This strain is capable of producing trichothecene mycotoxins in pure culture, but does not produce them under industrial conditions (Thrane, 2007).

Penicillium camemberti is the correct name for the mold use for all white-mold cheeses (Frisvad and Samson, 2004). Even though *P. commune*, *P. bifforme*, *P. fuscoglaucum*, and *P. palitans* are found on cheese, either as contaminants or “green cheese mold”, they are not necessarily suitable for fermenting cheeses. *P. commune* is the wild-type “ancestor” of *P. camemberti* however (Pitt et al., 1986; Polonelli et al., 1987; Giraud et al., 2010).

A species closely related to *P. camemberti*, *P. caseifulvum* has an advantage in not producing cyclopiazonic acid, a mycotoxin often found in *P. camemberti* (Lund et al., 1998; Frisvad and Samson, 2004). *P. caseifulvum* grows naturally on the surface of blue mold cheeses and has a valuable aroma (Larsen, 1998). Important mycotoxins identified in these species include cyclopiazonic acid and rugulovasine A and B (Frisvad and Samson, 2004), and cyclopiazonic acid can be detected in white-mold cheeses (Le Bars, 1979; Teuber and Engel, 1983; Le Bars et al., 1988).

Blue-mold cheeses are always fermented with *Penicillium roqueforti*, and not with the closely related species *P. carneum*, *P. paneum* or *P. psychrosexualis*. The latter three species produce several mycotoxins (Frisvad and Samson, 2004; Houburaken et al., 2010) and have often been referred to as *P. roqueforti* (Engel and von Milczewski, 1977; von Krusch et al., 1977; Olivigni and Bullerman, 1978; Engel and Prokopek, 1980; Teuber and Engel, 1983; Erdogan and Sert, 2004). However, *P. roqueforti* itself can produce the secondary metabolites PR-toxin, roquefortine C, mycophenolic acid and andrastin A in pure culture (Frisvad et al., 2004; Nielsen et al., 2005). One of these secondary metabolites is regarded as a mycotoxin, PR-toxin. This mycotoxin is unstable in cheese and is converted to PR-imine (Engel and Prokopek, 1979; Siemens and Zawistowski, 1993). Mycophenolic acid (Lafont et al., 1979; López-Díaz et al., 1996), roquefortine C (López-Díaz et al., 1996; Finoli et al., 2001) and andrastin A (Nielsen et al., 2005; Fernández-Bodega et al., 2009) have been found in blue cheese, but the consequences to human health are probably minor (Larsen et al., 2002). Yet another species, *Penicillium solitum* is found on naturally fermented lamb meat on the Faroe Islands, and may be used as a starter culture. This species does not produce any known mycotoxins (Frisvad et al., 2004). On other meat products, *Penicillium nalgiovense* and few strains of *Penicillium chrysogenum* are used (Nout, 2000; Frisvad and Samson, 2004), especially for mold-fermented salami. However, *P. nalgiovense* was originally found on cheeses from Nalzozy, and may be used for fermenting cheeses too.

Verticillium lecanii has changed to *Lecanicillium lecanii* (Zare and Gams, 2001), and this strain has been listed as potentially useful for cheese ripening (see Tables 2 and 3).

Finally, some fungi can be used to produce food colorants, including *Epicoccum nigrum* and *Penicillium purpurogenum*, but these fungi are not used directly for food fermentation (Stricker et al., 1981; Mapari et al., 2010).

5. Conclusion

The list of microorganisms with a history of use in food originally included 31 genera in the 2002 IDF inventory, and was essentially limited to the microbial use in dairy matrices. By also considering other food matrices, we consider 62 genera in the 2011 update. One was rejected as its usage in food has not been documented and the initial reference in the 2002 IDF inventory was inadequate. The evolution in taxonomy, the extension of varied usages in other matrices, yeast fermentations and fungal foods have also resulted in a growing number of species; from 113 to 264 species with demonstration of food usage. There are many new possibilities, however, and these should be explored to a much greater extent.

Either in traditional fermented foods or as new opportunities, the rationalized use of microorganisms in our diet opens new perspectives. In recent years, microorganisms have been used in fields other than the traditional food industry: *Lactococcus spp.* is used for its potential role in vaccination, and microorganisms are also used for the specific production of biogenic compounds. As we did not consider fermentation in liquid tailor-made media, species used in an industrial microbiology process were not considered if no reference to food usage could be provided.

Microbiological research mostly focuses on the pathogenic potential of microorganisms, while neglecting their positive role. Recent scientific advances have revealed the preponderant role of our own microbiota, our “other genome”, from the skin, gut, and other mucosa. Though this remains undoubtedly promising, one should not forget that man has not yet finished characterizing traditional fermented foods consumed for centuries, with often numerous isolates belonging to species with undefined roles.

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Appendix A. Supplementary

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