

Review: Diversty of Microorganisms in Global Fermented Foods and Beverages

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Abstract

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Majority of global fermented foods is naturally fermented by both cultivable and uncultivable microorganisms. Food fermentations represent an extremely valuable cultural heritage in most regions, and harbour a huge genetic potential of valuable but hitherto undiscovered strains. Holistic approaches for identification and complete profiling of both culturalable and unculturable microorganisms in global fermented foods are interest to food microbiologists. The application of molecular and modern identification tools through culture-independent techniques has thrown new light on the diversity of a number of hitherto unknown and uncultivable microorganisms in naturally fermented foods. Functional bacterial groups ("phylotypes") may be reflected by their mRNA expression in a particular substrate and not by mere DNA-level detection. An attempt is made here to review the microbiology of some global fermented foods and alcoholic beverages.

Ethics statement

(Authors are required to state the ethical considerations of their study in the manuscript including for cases where the study was exempt from ethical approval procedures.)

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21 Abstract

22 Majority of global fermented foods is naturally fermented by both cultivable and uncultivable 23 microorganisms. Food fermentations represent an extremely valuable cultural heritage in most 24 regions, and harbour a huge genetic potential of valuable but hitherto undiscovered strains. 25 Holistic approaches for identification and complete profiling of both culturalable and 26 unculturable microorganisms in global fermented foods are interest to food microbiologists. 27 The application of molecular and modern identification tools through culture-independent 28 techniques has thrown new light on the diversity of a number of hitherto unknown and uncultivable microorganisms in naturally fermented foods. Functional bacterial groups 29 30 ("phylotypes") may be reflected by their mRNA expression in a particular substrate and not 31 by mere DNA-level detection. An attempt is made here to review the microbiology of some 32 global fermented foods and alcoholic beverages.

34 Introduction

35 Traditionally, boiled rice is a staple diet with fermented and non-fermented legume (mostly 36 soybeans) products, vegetables, pickles, fish and meat as side-dish in Far East Asia, South 37 Asia, North Asia and the Indian subcontinent excluding Western and Northern India; 38 wheat/barley-based breads/loaves comprise a staple diet followed by milk and fermented milk 39 products, meat and fermented meats (sausages) in the Western and Northern part of India to 40 West Asian continent, Europe, North America and even in Australia and New Zealand 41 (Tamang and Samuel, 2010). Sorghum/maize porridges, on the other hand, are main courses of diets with many fermented and non-fermented sorghum/maize/millets, cassava, wild 42 legume seeds, meat, and milk products in Africa and South America. Many food researchers 43 44 have defined fermented foods by their own interpretation, e.g., Hesseltine (1965, 1979) who 45 defined traditional fermented foods as those that have been used for centuries even predating 46 written historical records and are essential for well-being of many people throughout the 47 world. Steinkraus (1994, 1996, 2002) defined indigenous fermented foods as foods where 48 microorganisms bring about some biochemical changes in the substrates during fermentation 49 such as enrichment of human diet through development of a wide diversity of flavours, 50 aromas and texture in foods, by preservation through lactic acid, alcoholic, acetic acid and 51 alkaline fermentation, by biological enrichment of food substrates with protein, essential 52 amino acids, essential fatty acids and vitamins, and also by detoxification of undesirable 53 compounds and decrease in cooking times and fuel requirements. Campbell-Platt (1987, 54 1994) defined fermented foods as foods that have been subjected to the action of 55 microorganisms or enzymes so that desirable biochemical changes cause significant 56 modification to the food. Holzapfel (1997) described fermented foods as palatable and 57 wholesome foods, prepared from raw or heated raw materials by microbial fermentation. 58 Tamang (2010b) defined ethnic fermented foods as foods produced by the ethnic people (of 59 specific culture and using their native knowledge) from locally available raw materials of plant or animal sources either naturally or by adding starter culture(s) containing functional 60 61 microorganisms, which modify the substrates biochemically, and organoleptically into edible products that are culturally and socially acceptable to the consumers. Biochemically, 62 fermentation is defined as the process, which does not require O2, but by using an organic 63 molecule as electron acceptor and performed only by active living cells of microorganisms 64 (Mansi et al., 2003). 65

66 Several researchers have reviewed the microbiology, biochemistry and nutrition of 67 fermented foods and beverages of different countries of Asia (Heseltine, 1979, 1983; Kozaki, 68 1976; Lee, 1997; Nout and Aidoo, 2002; Soni and Dey, 2014; Steinkraus, 1996, 1997; 69 Tamang, 2010a, 2012); Africa (Odunfa and Oyewole, 1997; Olasupo et al., 2010; Franz et al., 70 2014); Europe (Pederson, 1979; Wood, 1998); South America (Chavez-Lopez et al., 2014), 71 and North America (Doyle and Beuchat, 2013; Fleming, 1984). Many genera/species of 72 microorganisms have been reported for various fermented foods and beverages across the 73 world; using molecular tools in recent years has helped to clarify, at least in part, the

nomenclatural confusion and generalisations caused by conventional (phenotypic) taxonomic
 methods. The present paper is an attempt to collate and review the updated information on
 microbiology of some global fermented foods and beverages.

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78 Microorganisms in fermented foods

79 Fermented foods are the hubs of consortia of microorganisms which may be present as natural 80 indigenous microbiota in uncooked plant or animal substrates, utensils, containers, earthen 81 pots, and the environment (Franz et al. 2014; Hesseltine and Wang, 1967; Steinkraus, 1996), 82 or as a result of addition of the microorganisms as starter cultures (Stevens and Nabors, 2009). Microorganisms convert the chemical composition of raw materials during 83 84 fermentation, which enrich the nutritional value in some fermented foods, and impart healthbenefits to conusmers (Farhad et al., 2010; Steinkraus, 2002; Tamang, 2015a). 85 86 Lactic acid bacteria (LAB) are widely present in many fermented foods and beverages 87 (Stiles and Holzapfel, 1997; Tamang, 2010b). Major genera of the LAB isolated from various 88 global fermented foods and beverages Alkalibacterium, Carnobacterium, Enterococcus, 89 Lactobacillus, Lactococcus, Leuconostoc, Oenococcus, Pediococcus, Streptococcus,

90 Tetragenococcus, Vagococcus and Weissella (Axelsson et al., 2012; Holzapfel and Wood,

91 2014; Salminen et al., 2004).

Bacillus is present in alkaline-fermented foods of Asia and Africa (Parkouda et al.,
2009; Tamang, 2015). Species of *Bacillus* present, mostly in legume-based fermented foods,

94	are B. amyloliquefaciens, B. circulans, B. coagulans, B. firmus, B. licheniformis, B.
95	megaterium, B. pumilus, B. subtilis, B. subtilis variety natto, and B. thuringiensis (Kiers et al.,
96	2000; Kubo et al., 2011), while, in addition, strains of <i>B. cereus</i> have been isolated from the
97	fermentation of Prosopis africana seeds for the production of okpehe in Nigeria
98	(Oguntoyinbo et al., 2007). Some strains of <i>B. subtilis</i> produce λ -polyglutamic acid (PGA)
99	which is an amino acid polymer commonly present in Asian fermented soybean foods giving
100	the characteristic sticky texture to the product (Nishito et al., 2010; Urushibata et al., 2002).
101	The association of several species of Kocuria, Micrococcus (members of the
102	Actinobacteria) and Staphylococcus (belonging to the Firmicutes) have been reported for
103	fermented milk products, fermented sausages and meat and fish products (Coton et al., 2010;
104	Martin et al., 2006). Species of Bifidobacterium, Brachybacterium, Brevibacterium, and
105	Propionibacterium are isolated from cheese and species of Arthrobacter and Hafnia from
106	fermented meat products (Bourdichon et al., 2012). Enterobacter cloacae, Klebsiella
107	pneumoniae, K. pneumoniae subsp. ozaenae, Haloanaerobium, Halobacterium, Halococcus,
108	Propionibacterium, Pseudomonas, and various others are also present in many global
109	fermented foods (Tamang, 2010b).
110	Genera of yeasts reported for fermented foods, alcoholic beverages and non-food
111	mixed amylolytic starters are Brettanomyces, Candida, Cryptococcus, Debaryomyces,
112	Dekkera, Galactomyces, Geotrichum, Hansenula, Hanseniaspora, Hyphopichia, Issatchenkia,

113 Kazachstania, Kluyveromyces, Metschnikowia, Pichia, Rhodotorula, Rhodosporidium,

114 Saccharomyces, Saccharomycodes, Saccharomycopsis, Schizosaccharomyces, 115 Sporobolomyces, Torulaspora, Torulopsis, Trichosporon, Yarrowia and Zygosaccharomyces 116 (Kurtzman et al., 2011; Lv et al., 2013; Tamang and Fleet, 2009; Watanabe et al., 2008). Major roles of filamentous moulds in fermented foods and alcoholic beverages are 117 118 mainly production of enzymes and also degradation of anti-nutritive factors (Aidoo and Nout, 119 2010). Species of Actinomucor, Amylomyces, Aspergillus, Monascus, Mucor, Neurospora, 120 Parcilomyces, Penicillium, Rhizopus and Ustilago are reported for many fermented foods, 121 Asian non-food amylolytic starters and alcoholic beverages (Chen et al., 2014; Nout and 122 Aidoo, 2002).

123

124 Taxonomic tools for identification of microorganisms from fermented foods

Use of culture media may ignore several unknown uncultivable microorganisms that may play 125 major or minor functional roles in production of fermented foods. Direct DNA extraction 126 from samples of fermented foods, commonly called culture-independent methods, is 127 128 nowadays frequently used in food microbiology to profile both cultivable and uncultivable 129 microbial populations from fermented foods (Cocolin and Ercolini, 2008; Alegría et al., 2011; 130 Cocolin et al., 2013; Dolci et al. 2015), provided that the amplification efficiency is high 131 enough. PCR-DGGE analysis is the most popular culture-independent technique used for 132 detecting microorganisms in fermented foods and thereby profiling both bacterial populations 133 (Cocolin et al., 2011; Tamang, 2014) and yeast populations in fermented foods (Cocolin et al.,

134	2002; Jianzhonga et al., 2009). Both cultivable and uncultivable microorganisms from any
135	fermented food and beverage may be identified using culture-dependent and -independent
136	methods to document a complete profile of microorganisms, and also to study both inter- and
137	intra-species diversity within a particular genus or among genera (Greppi et al. 2013a,b;
138	Ramos et al., 2010; Yan et al., 2013). The method uses a combination of intercalating dye,
139	propidium monoazide (PMA) which selectively penetrates dead cells through their
140	compromised cell membranes, and both quantitative PCR (qPCR) (Fujimoto and Watanabe,
141	2013) and pyrosequencing (Desfossés-Foucault et al., 2012) have been developed. Combining
142	PMA treatment of samples before DNA exraction and the molecular quantifying methods can
143	be used to accurately enumerate the viable microorganisms in fermented foods.
144	Molecular identification is emerging as an accurate and reliable identification tool, and
145	is widely used in identification of both culture-dependent and culture-independent
146	microorganisms from fermented foods (Dolci et al., 2015; Giraffa and Carminati, 2008).
147	Species-specific PCR primers are used for species level identification (Tamang et al., 2005);
148	this technique is widely applied in the identification of LAB isolated from fermented foods
149	(Robert et al., 2009). The application of real-time quantitative PCR (qPCR) with specific
150	primers enables the specific detection and quantification of LAB species in fermented foods
151	(Park et al., 2009).

Random amplification of polymorphic DNA (RAPD) is a typing method based on thegenomic DNA fragment profiles amplified by PCR and is commonly used for discrimination

154 of LAB strains from fermented foods (Chao et al., 2008; Coppola et al., 2006). The repetitive 155 extragenic palindromic sequence-based PCR (rep-PCR) technique permits typing at 156 subspecies level and reveals significant genotypic differences between strains of the same 157 bacterial species from fermented foods samples (Tamang et al., 2008). Amplified fragment 158 length polymorphism (AFLP) is a technique based on the selective amplification and 159 separation of genomic restriction fragments, and its applicability in identification and to 160 discriminate has been demonstrated for various LAB strains (Tanigawa and Watanabe, 2011). 161 Techniques of denaturing gradient gel electrophoresis (DGGE) and temperature gradient gel electrophoresis (TGGE) have been developed to profile microbial communities 162 163 directly from fermented foods, and are based on sequence-specific distinctions of 16S rDNA 164 or 26S rDNA amplicons produced by PCR (Alegría et al., 2011; Ercolini, 2004; Flórez and 165 Mayo, 2006). However, use of DGGE has also some disadvantages such as being time 166 consuming, unable to determine the relative abundance of dominant species, or to distinguish 167 between viable and non-viable cells, and difficulties in interpretation of multi-bands (Dolci et 168 al., 2015). DGGE can only reveal some of the major bacterial species such as B. licheniformis 169 and B. thermoamylovorans in chungkokjang (sticky fermented soybean food of Korea) and 170 could not detect a large number of predominant or diverse rare bacterial species identified in 171 pyrosequencing analysis (Nam et al., 2011).

The amplified ribosomal DNA restriction analysis (ARDRA) technique using
restriction enzymes is also useful in identification of microorganisms from fermented foods
(Jeyaram et al., 2010).

Multilocus sequence analysis (MLSA), using housekeeping genes as molecular markers alternative to the 16S rRNA genes, is used for LAB species identification: *rpoA* and *pheS* genes for *Enterococcus* and *Lactobacillus, atpA* and *pepN* for *Lactococcus* species, and *dnaA*, *gyrB*, and *rpoC* for species of *Leuconostoc, Oenococcus*, and *Weissella* (de Bruyne et al., 2007, 2008b, 2010; Diancourt et al., 2009; Picozzi et al., 2010; Tanigawa and Watanabe, 2011).

181 Effective tools of next generation sequencing (NGS) such as metagenomics, 182 phylobiomics, and metatranscriptomics are nowadays applied for documentation of cultures 183 in traditional fermented products (Mozzi et al., 2013; van Hijum et al., 2013). However, NGS as a sophisticated tool needs well-trained hands and a well equipped molecular laboratory, 184 185 which may not always be available. Application of metagenomic approaches by using parallel 186 pyrosequencing of tagged 16S rRNA gene amplicons provide information on microbial 187 communities as profiled in kimchi, a naturally fermented vegetable product of Korea (Jung et 188 al., 2011; Park et al., 2012), nukadoko, a fermented rice bran of Japan (Sakamoto et al., 2011), 189 narezushi, a fermented salted fish and cooked rice of Japan (Kiyohara et al., 2012), and ben-190 saalga, a traditional gruel of pearl millet of Burkina Faso (Humblot and Guyot, 2009). 191 Pyrosequencing has revealed the presence of numerous and even minor bacterial groups in

192	fermented foods, but DNA-level detection does not distinguish between metabolically active
193	and "passive" organisms. "Functionally relevant phylotypes" in an ecosystem may be
194	specifically detected by, e.g., weighted UniFrac principal coordinate analysis based on 454
195	pyrosequencing of 16S rRNA genes, as applied in studies on gut microbiota (Wang et al.,
196	2015). The 16S rRNA gene sequence based pyrosequencing method enables a comprehensive
197	and high-throughput analysis of microbial ecology (Sakamoto et al., 2011), and this method
198	has been applied to various traditional fermented foods (Oki et al., 2014).
199	A proteomics identification method based on protein profiling using matrix-assisted
200	laser desorption ionizing-time of flight mass spectrometry (MALDI-TOF MS) is used to
201	identify species of Bacillus in fermented foods of Africa (Savadogo et al., 2011), and species
202	of LAB isolated from global fermented foods (Dušková et al., 2012; Kuda et al., 2014;
203	Nguyen et al., 2013a; Sato et al., 2012; Tanigawa et al., 2010).

204

205 Global fermented foods

Campbell-Platt (1987) reported around 3500 global fermented foods and beverages with some 207 250 groups. We presume that there may be more than 5000 varieties of common and 208 uncommon fermented foods and alcoholic beverages being consumed in the world by billions 209 of people as staple and other food components (Tamang, 2010b). Global fermented foods are 210 classified into nine major groups on the basis of substrates (raw materials) used from 211 plant/animal sources: (1) fermented cereals, (2) fermented vegetables and bamboo shoots, (3) fermented legumes, (4) fermented roots/tubers, (5) fermented milk products, (6) fermented and preserved meat products, (7) fermented, dried and smoked fish products, (8) miscellaneous fermented products, and (9) alcoholic beverages (Steinkraus, 1997; Tamang 215 2010b,c).

216

217 Fermented milk products

218 Fermented milks (Table 1) are classified into two major groups on the basis of dominant 219 microorganisms: (A) lactic fermentation, dominated by species of LAB, comprising the "thermophilic" type (e.g., yogurt, Bulgarian buttermilk), probiotic type (e.g., acidophilus 220 221 milk, bifidus milk), and the mesophilic type (e.g., natural fermented milk, cultured milk, 222 cultured cream, cultured buttermilk); and (B) fungal-lactic fermentations, where LAB and 223 yeasts cooperate to generate the final product. Typical examples include alcoholic milks (e.g., 224 acidophilus-yeast milk, kefir, koumiss), and mouldy milks (e.g., viili) (Mayo et al., 2010). 225 Yogurt is widely consumed highly nutritious fermented milk, and is defined by the Codex 226 Alimentarius (Donovan and Shamir, 2014). Natural fermentation is one of the oldest methods 227 of milk processing using raw or boiled milk to ferment spontaneously or by using the backslopping method, where a part of a previous batch of a fermented product is used to inoculate 228 229 the new batch (Holzapfel, 2002; Josephsen and Jespersen, 2004).

230 Fermented cereal foods

Cereal fermentation is mainly represented by species of LAB and yeasts (Corsetti and 231 232 Settanni, 2007). Enterococcus, Lactococcus, Lactobacillus, Leuconostoc, Pediococcus, 233 Streptococcus and Weissella are common bacteria associated with cereal fermentations (Table 234 2) (de Vuyst et al., 2009; Guyot, 2010; Moroni et al., 2011). Native strains of Saccharomyces 235 cerevisiae are the principal yeast of most bread fermentations (Hammes et al., 2005), but 236 other non-Saccharomyces yeasts are also significant in many cereal fermentations, including 237 Candida, Debaryomyces, Hansenula, Kazachstania, Pichia, Trichosporon and Yarrowia 238 (Iacumin et al., 2009; Johnson and Echavarri-Erasun, 2011; Weckx et al., 2010).

239

240 Fermented vegetable foods

241 Perishable and seasonal leafy vegetables, radish, cucumbers, including young edible bamboo 242 tender shoots, are traditionally fermented into edible products of wide diversity, especially in 243 Asia (Table 3). Fermentation of vegetables is mostly dominated by species of Lactobacillus 244 and Pediococcus, followed by Leuconostoc, Weissella, Tetragenococcus, and Lactococcus 245 (Chang et al., 2008; Watanabe et al., 2009a). A complete microbial profile of LAB in kimchi 246 has been characterised using different molecular identification tools (Jung et al., 2011, 2013a; 247 Nam et al., 2009; Park et al., 2010; Shin et al., 2008;). Natural fermentations during 248 production of *sauerkraut*, a fermented cabbage product of Germany, have studied and species 249 of LAB were reported (Johanningsmeier et al., 2007; Plengvidhya et al., 2007). Species of 250 LAB constitute the native population in the Himalayan fermented vegetable products such as

gundruk, sinki, goyang, khalpi, and *inziangsang* (Karki et al., 1983; Tamang and Tamang,
2007, 2010; Tamang et al., 2005; 2009) and several naturally fermented bamboo products of
India and Nepal (Jayaram et al., 2010; Sonar and Halami, 2014; Tamang and Sarkar, 1996;
Tamang and Tamang, 2009; Tamang et al., 2008).

255

256 Fermented soybeans and other legumes

257 Two types of fermented soybean foods are produced: soybean foods fermented by Bacillus spp. (mostly B. subtilis) with characteristic stickiness, and soybean foods fermented by 258 filamentous moulds, mostly Aspergillus, Mucor, Rhizopus (Tamang, 2010b). Bacillus-259 260 fermented, non-salty and sticky soybean foods are concentrated in an imaginary triangle with 261 three vertices on Japan (natto), east Nepal and North East India (kinema and its similar 262 products) and northern Thailand (thua-nao) named as 'natto triangle' (Nakao, 1972) and 263 renamed as 'kinema-natto-thuanao (KNT)-triangle' (Tamang, 2015b). Within the KNT-264 triangle-bound countries, Bacillus-fermented sticky non-salty soybean foods are consumed 265 such as natto of Japan, chungkokjang of Korea, kinema of India, Nepal and Bhutan, aakhune, 266 bekang, hawaijar, peruyaan and tungrymbai of India, thua nao of Thailand, pepok of 267 Myanmar, and sieng of Cambodia and Laos (Nagai and Tamang, 2010; Tamang 2015 b) 268 (Table 4). Although the method of production and culinary practices vary from product to 269 product, plasmids and phylogenetic analysis of *B. subtilis* showed the similarity among strains 270 of B. subtilis isolated from common sticky fermented soybean foods of Asia (Hara et al., 1986,

271	1995; Meerak et al., 2007; Tamang et al., 2002) suggesting origination from the same stock.
272	Mould-fermented soybean products are miso and shoyu of Japan, tempe of Indonesia, douchi
273	and sufu of China, doenjang of Korea (Sugawara, 2010). Some common non-soybean
274	fermented legumes (e.g., locust beans) of Africa are bikalga, dawadawa, iru, okpehe,
275	soumbala and dugba (Ahaotu et al., 2013; Amoa-Awua et al., 2006; Azokpota et al., 2006;
276	Meerak et al., 2008; Oguntoyinbo et al., 2007, 2010; Ouoba et al., 2004, 2008, 2010;
277	Parkouda et al., 2009), fermented black-grams products such as <i>dhokla, papad</i> and <i>wari</i> of
278	India (Nagai and Tamang, 2010), and maseura of India and Nepal (Chettri and Tamang,
279	2008).

280 Species of Bacillus have been reported for several Asian fermented soybean foods 281 Sarkar et al., 2002; Tamang et al., 2002; Park et al., 2005; Inatsu et al., 2006; Choi et al., 2007; Kimura and Itoh, 2007; Shon et al., 2007; Jeyaram et al., 2008b; Dajanta et al., 2009; 282 Kwon et al., 2009; Kubo et al., 2011; Singh et al., 2014; Tamang, 2003; Wongputtisin et al., 283 2014; Chettri and Tamang, 2015). However, B. subtilis is the dominant functional bacterium 284 285 in Asian fermented soybean foods (Sarkar and Tamang, 1994; Tamang and Nikkuni, 1996; 286 Dajanta et al., 2011). Japanese natto is the only Bacillus-fermented soybean food now 287 produced by commercial mono-culture starter *B. natto*, first isolated from naturally fermented natto by Sawamura (Sawamura, 1906). Ent. Faecium, as minor population group, is also 288 289 present in kinema (Sarkar et al., 1994), in okpehe (Oguntoyinbo et al., 2007), and in 290 chungkukjang (Yoon et al., 2008).

291

292 Fermented root and tuber products

293 Cassava (Manihot esculenta) root is traditionally fermented into staple foods such as gari in 294 Nigeria, *fufu* in Togo, Burkina Faso, Benin and Nigeria, *agbelima* in Ghana, *chikawgue* in 295 Zaire, kivunde in Tanzania, kocho in Ethiopia, foo foo in Nigeria, Benin, Togo and Ghana, 296 respectively (Franz et al., 2014) (Table 5). The initial stage of cassava fermentation is 297 dominated by Corynebacterium manihot (Oyewole et al., 2004) with LAB succession (Lb. 298 acidophilus, Lb. casei, Lb. fermentum, Lb. pentosus, Lb. plantarum (Oguntoyinbo and Dodd, 2010). Cassava root is also traditionally fermented into sweet dessert known as tapé in 299 300 Indonesia (Tamang, 2010b).

301

302 Fermented meat products

Information on microbiota of some traditionally preserved and fermented meat products of the world is summarised in Table 6. LAB predominate in most fermented meat products (Albano et al., 2009; Cocolin et al., 2011; Khanh et al., 2011; Nguyen et al., 2013b), followed by coagulase-negative staphylococci, micrococci and *Enterobacteriaceae* (Cocolin et al., 2011; Marty et al., 2011) and yeasts such as *Debaryomyces hansenii* (Encinas et al., 2000; Tamang and Fleet, 2009). Selection of non-toxinogenic moulds for meat ripening has resulted in the commercialisation of strains of *Penicillium nalgiovense* (Lücke, 2015).

311 Fermented fish products

Preservation of fish through fermentation, sun/smoke drying and salting (Table 7) is traditionally practiced by people living nearby coastal regions, lakes and rivers and is consumed as seasoning, condiments and side dish (Salampessy et al., 2010). Several species of bacteria and yeasts have been reported from fermented and preserved fish products of the world (Hwanhlem et al., 2011; Kobayashi et al., 2000a,b,c; Saithong et al., 2010; Thapa et al., 2004, 2006, 2007; Wu et al., 2000).

318

319 Miscellaneous fermented products

320 Vinegar is one of the most popular condiments in the world and is prepared from sugar or 321 ethanol containing substrates and hydrolyzed starchy materials by aerobic conversion to acetic 322 acid (Solieri and Giudici, 2008). Acetobacter aceti subsp. aceti, A. oryzae, A. pasteurianus, A. 323 polyxygenes, A. xylinum, A. malorum, A. Pomorum dominate during vinegar production 324 (Haruta et al., 2006), while yeast species such as Candida lactis-condensi, C. stellata, 325 Hanseniaspora valbyensis, H. osmophila, Saccharomycodes ludwigii, Sacch.cerevisiae, 326 Zygosaccharomyces bailii, Z. bisporus, Z. lentus, Z. mellis, Z. Pseudorouxii and Z. Rouxii 327 have also been reported (Sengum and Karabiyikli, 2011).

Though normal black tea is consumed everywhere, some ethnic Asian communities enjoy special fermented teas such as *miang* of Thailand (Tanasupawat et al., 2007), *puer* tea and *fuzhuan brick*, and *kombucha* of China (Mo et al., 2008). *Aspergillus niger* is the 331 predominant fungus in *puer* tea while *Blastobotrys adeninivorans*, Asp. glaucus, species of Penicillium, Rhizopus and Saccharomyces and the bacterial species Actinoplanes and 332 333 Streptomyces were also isolated (Abe et al., 2008; Jeng et al., 2007). Brettanomyces 334 bruxellensis, Candida stellata, Rhodotorula mucilaginosa, *Saccharomyces* spp., 335 Schizosaccharomyces pombe, Torulaspora delbrueckii, Zygosaccharomyces bailii, Z. bisporus, Z. kombuchaensis and Z. microellipsoides were isolated from kombucha 336 337 (Kurtzuman et al., 2001; Teoh et al., 2004). Major bacterial genera present in kombucha 338 were Gluconacetobacter. However, Marsh et al. (2014) reported the predomination of 339 Lactobacillus, Acetobacter, and Zygosaccharomyces. Lb. thailandensis, Lb. camelliae, Lb. 340 plantarum, Lb. pentosus, Lb. vaccinostercus, Lb. pantheris, Lb. fermentum, Lb. suebicus, Ped. 341 siamensis, Ent. casseliflavus and Ent. camelliae are involved in the fermentation of miang 342 production (Sukontasing et al., 2007; Tanasupawat et al., 2007). Species of Aspergillus, 343 Penicillium and Eurotium are major fungi for fermentation of fuzhuan brick tea (Mo et al., 2008). 344

Nata or bacterial cellulose produced by *Acetobacter xylinum* is a delicacy of the Philippines, eaten as candy (Adams, 2014; Chinte-Sanchez, 2008; Jagannath et al., 2010). Two types of *nata* are well known: *nata de piña*, produced on the juice from pineapple trimmings, and *nata de coco*, produced on coconut water or coconut skim milk (Adams, 2014). Bacterial cellulose has significant potential as a food ingredient in view of its high

purity, *in situ* change of flavour and colour, and having the ability to form various shapes and
textures (Shi et al., 2014).

352 Chocolate is a product of cocoa bean fermentation where Lb. fermentum and 353 Acetobacter pasteurianus were reported as the predominating bacterial species (Lefeber et al., 354 2010; Papalezandratou et al., 2011). Diverse LAB species appear to be typically associated 355 with the fermentation of cocoa beans in Ghana, which included Lb. ghanensis (Nielsen et al., 356 2007), Weissella ghanensis (de Bruyne et al., 2008), Lb. cacaonum and Lb. fabifermentans (de Bruyne et al., 2009) and Weissella fabaria (de Bruyne et al., 2010). Fructobacillus 357 pseudoficulneus, Lb. plantarum, Acetobacter senegalensis and the enterobacteria Tatumella 358 359 ptyseos and Tatumella citrea were among the prevailing species during the initial phase of 360 cocoa fermentations (Papalezandratou et al., 2011). Yeasts involved during spontaneous 361 cocoa fermentation are Hanseniaspora uvarum, H. quilliermundii, Issatchenkia orientalis 362 (Candida krusei), Pichia membranifaciens, Sacch. cerevisiae and Kluyveromyces species for 363 flavour development (Schillinger et al., 2010).

Pidan is a preserved egg prepared from alkali-treated fresh duck eggs is consumed by
the Chinese, and has a strong hydrogen sulfide and ammonia smell (Ganasen and Bejakul,
2010). The main alkaline chemical reagent used for making *pidan* is sodium hydroxide, which
is produced by the reaction of sodium carbonate, water, and calcium oxide of pickle or
coating mud. *B. cereus, B. macerans, Staph. cohnii, Staph. epidermidis, Staph. haemolyticus*and *Staph. warneri* are predominant in *pidan* (Wang and Fung, 1996).

370

371 Alcoholic beverages

- Tamang (2010c) classified alcoholic beverages of the world into 10 types:
- 1) Non-distilled and unfiltered alcoholic beverages produced by amylolytic starters e.g.,
- 374 *kodo ko jaanr* (fermented finger millets) (Thapa and Tamang, 2004), and *bhaati jaanr*
- 375 (fermented rice) of India and Nepal (Tamang and Thapa, 2006), makgeolli (fermented
- 376 rice) of Korea (Jung et al., 2012).
- 377 2) Non-distilled and filtered alcoholic beverages produced by amylolytic starters e.g.,
 378 *saké* of Japan (Kotaka et al., 2008).
- 379 3) Distilled alcoholic beverages produced by amylolytic starter e.g., *shochu* of Japan, and
 380 *soju* of Korea (Steinkraus, 1996).
- 381 4) Alcoholic beverages produced by involvement of amylase in human saliva e.g., *chicha*382 of Peru (Vallejo et al., (2013).
- 383 5) Alcoholic beverages produced by mono- (single-strain) fermentation e.g., beer
 384 (Kurtzman and Robnet, 2003).
- 385 6) Alcoholic beverages produced from honey e.g., *tej* of Ethiopia (Bahiru et al., 2006).
- 386 7) Alcoholic beverages produced from plant parts e.g., *pulque* of Mexico (Lappe-
- 387 Oliveras et al., 2008), *toddy* of India (Shamala and Sreekantiah, 1988) and *kanji* of
- 388 India (Kingston et al., 2010).

8) Alcoholic beverages produced by malting (germination) e.g., *sorghum ("Bantu")* beer
of South Africa (Kutyauripo et al., 2009), *pito* of Nigeria and Ghana (Kolawole et al.,
2013) and *tchoukoutou* of Benin (Greppi et al., 2013a).
9) Alcoholic beverages prepared from fruits without distillation (e.g., wine, cider).

393 10) Distilled alcoholic beverages prepared from fruits and cereals e.g., whisky and brandy.

394

395 Amylolytic starters

Traditional way of sub-cultuing of essential microorganisms (consortia of filamentous 396 moulds, amylolytic and alcohol-producing yeasts and LAB) with rice or wheat as the base in 397 398 the form of dry, flattened or round balls, for production of alcoholic beverages is a remarkable 399 discovery in the food history of Asian people, which is exclusively practiced in South East 400 Asia including the Himalayan regions of India, Nepal, Bhutan, and China (Tibet) (Hesseltine, 401 1983; Tamang, 2010a). Around 1-2% of previously prepared amylolytic starters are 402 inoculated into the dough, and mixed cultures allowed to develop for a short time, then dried, 403 and used to make either alcohol or fermented foods from starchy materials (Tamang et al., 404 2006). Asian amylolytic starters have different vernacular names such as marcha in India and 405 Nepal, hamei, humao, phab in India, mana and manapu of Nepal, men in Vietnam, ragi in 406 Indonesia, bubod in Philippines, chiu/chu in China and Taiwan, loogpang in Thailand, mae/dombae /buh/puh in Cambodia and nuruk in Korea (Hesseltine and Kurtzman, 1990; 407

408 Nikkuni et al., 1996; Sujaya et al., 2004; Thanh et al., 2008; Tamang et al., 2012; Yamamoto
409 and Matsumoto, 2011).

410	Microbial profiles of amylolytic starters of India, Nepal and Bhutan are filamentous
411	moulds (Mucor circinelloides forma circinelloides, Mucor hiemalis, Rhi. chinensis, and Rhi.
412	stolonifer variety lyococcus (Tamang et al., 1988), yeasts (Sacch. cerevisiae, Sacch. bayanus,
413	Saccharomycopsis (Sm.) fibuligera, Sm. capsularis, Pichia anomala, Pic. burtonii, and
414	Candida glabrata) (Tamang and Sarkar, 1995; Shrestha et al., 2002; Tsuyoshi et al., 2005;
415	Tamang et al., 2007; Jeyaram et al., 2008a, 2011; Chakrabarty et al., 2014), and LAB-Ped.
416	pentosaceus, Lb. bifermentans and Lb. brevis (Hesseltine and Ray, 1988; Tamang and Sarkar,
417	1995; Tamang et al., 2007; Chakrabarty et al., 2014). In ethnic starter culture of Vietnam
418	locally called men contains a diversity of yeasts (Candida tropicalis, Clavispora lusitaniae,
419	Pichia anomala, P. ranongensis, Saccharomycopsis fibuligera, Sacch. cerevisiae,
420	Issatchenkia sp.), filamentous moulds (Absidia corymbifera, Amylomyces rouxii,
421	Botryobasidium subcoronatum, Rhizopus oryzae, Rhi. microsporus, Xeromyces bisporus);
422	LAB (Ped. pentosaceus, Lb. plantarum, Lb. brevis, Weissella confusa, W.
423	paramesenteroides), amylase-producing bacilli (Bacillus subtilis, B. circulans, B.
424	amyloliquefaciens, B. sporothermodurans), acetic acid bacteria (Acetobacter orientalis, A.
425	pasteurianus) (Dung et al., 2006, 2007; Thanh et al., 2008).
426	A combination of Asp. oryzae and Asp. sojae is used in koji in Japan to produce

427 alcoholic beverages including *saké* (Zhu and Trampe, 2013). *Koji* (Chinese *chu, shi* or *qu*)

??

also produces amylases that convert starch to fermentable sugars, which are then used for
the second stage yeast fermentation to make non-alcoholic fermented soybean *miso* and *shoyu* (Sugawara, 2010). *Asp. awamori, Asp. kawachii, Asp. oryzae, Asp. shirousamii,*and *Asp. sojae* have been widely used as the starter in preparation of *koji* for production
of *miso, saké, shoyu, shochu* (Suganuma et al., 2007).

433

434 Non-distilled mild-alcoholic food beverages produced by amylolytic starters

435 The biological process of liquefaction and saccharification of cereal starch by filamentous 436 moulds and yeasts, supplemented by amylolytic starters, under solid-state fermentation is one 437 of the two major stages of production of alcoholic beverages in Asia (Tamang, 2010c). These 438 alcoholic beverages are mostly considered as food beverage and eaten as staple food with high calorie in many parts of Asia, e.g., kodo ko jaanr of the Himalayan regions in India, 439 Nepal, Bhutan and China (Tibet) with 5% alcohol content (Thapa and Tamang, 2004). 440 441 Saccharifying activities are mostly shown by *Rhizopus* spp. and *Sm. fibuligera* whereas 442 liquefying activities are shown by Sm. fibuligera and Sacch. cerevisiae (Thapa and Tamang, 443 2006). Rhizopus, Amylomyces, Torulopsis, and Hansenula are present in lao-chao, a popular 444 ethnic fermented rice beverage of China (Wei and Jong, 1983). During fermentation of 445 Korean *makgeolli* (prepared from rice by amylolytic starter *nuruk*) the proportion of the 446 family Saccharomycetaceae increased significantly, and the major bacterial phylum of the 447 samples shifted from γ -Proteobacteria to Firmicutes (Jung et al., 2012).

448

449 Non-distilled and filtered alcoholic beverages produced by amylolytic starters

- Alcoholic beverages produced by amylolytic starter (*koji*) is not distilled but the extract of fermented cereals is filtered into clarified high alcohol-content liquor, eg *saké* which is a national drink of Japan containing 15 to 20% alcohol (Tamang, 2010c). Improved strains of *Asp. oryzae* are used for *saké* production in industrial scale (Hirasawa et al., 2009; Kotaka et al., 2008).
- 455

456 Distilled alcoholic beverages produced by amylolytic starters

This category of alcoholic drinks is the clear distillate of high alcohol content prepared as drink from fermented cereal beverages by using amylolytic starters. *Raksi* is an ethnic alcoholic (22-27% v/v) drink of the Himalayas with characteristic aroma, and distilled from the traditional fermented cereal beverages (Kozaki et al., 2000).

461

462 Alcoholic beverages produced by human saliva

Chicha is a unique ethnic fermented alcoholic (2-12% v/v) beverage of Andes Indian races of
South America mostly in Peru, prepared from maize by human salivation process (Hayashida,
2008). *Sacch. cerevisiae, Sacch. apiculata, Sacch. pastorianus*, species of *Lactobacillus* and *Acetobacter* are present in *chicha* (Escobar et al., 1996). *Sacch. cerevisiae* was isolated from *chicha* and identified using MALDI-TOF (Vallejo et al., 2013). Species of *Lactobacillus*,

Bacillus, Leuconostoc, Enterococcus, Streptomyces, Enterobacter, Acinetobacter,
Escherichia, Cronobacter, Klebsiella, Bifidobacterium and Propioniobacterium were reported
from chicha of Brazil (Puerari et al., 2015).

471

472 Alcoholic beverages produced from honey

473 Some alcoholic beverages are produced from honey e.g., *tej* of Ethiopia. It is a yellow, sweet,
474 effervescent and cloudy alcoholic (7-14% v/v) beverage (Steinkraus, 1996). *Sacch. cerevisiae,*475 *Kluyvermyces bulgaricus, Debaromyces phaffi*, and *Kl. veronae*, and LAB species of
476 *Lactobacillus, Streptococcus, Leuconostoc* and *Pediococcus* are responsible for *tej*477 fermentation (Bahiru et al., 2006).

478

479 Alcoholic beverages produced from plant parts

480 *Pulque* is one of the oldest alcoholic beverages prepared from juices of the cactus (*Agave*) 481 plant of Mexico (Steinkraus, 2002). Bacteria present during the fermentation of *pulque* were 482 LAB (Lc. lactis subsp. lactis, Lb. acetotolerans, Lb. acidophilus, Lb. hilgardii, Lb. kefir, Lb. 483 plantarum, Leuc. citreum, Leuc. kimchi, Leuc. mesenteroides, Leuc. pseudomesenteroides), 484 the γ -Proteobacteria (*Erwinia rhapontici*, *Enterobacter* spp. and *Acinetobacter radioresistens*, 485 several *a*-Proteobacteria), Zymomonas mobilis, Acetobacter malorum, A. pomorium, Microbacterium arborescens, Flavobacterium johnsoniae, Gluconobacter oxydans, and 486 487 Hafnia alvei (Escalante et al., 2004, 2008). Yeasts isolated from pulque include

488 Saccharomyces (Sacch. bayanus, Sacch. cerevisiae, Sacch. paradoxus) and non489 Saccharomyces (Candida spp., C. parapsilosis, Clavispora lusitaniae, Hanseniaspora
490 uvarum, Kl. lactis, Kl. marxianus, Pichia membranifaciens, Pichia spp., Torulaspora
491 delbrueckii) (Lappe-Oliveras et al., 2008).

Depending on the region, traditional alcoholic drinks prepared from palm juice called
"palm wine" are known by various names, e.g., *toddy* or *tari* in India, *mu, bandji, ogogoro, nsafufuo, nsamba, mnazi, yongo, taberna, tua* or *tubak* in West Africa and South America
(Ouoba et al., 2012). Microorganisms that are responsible for *toddy* fermentation are *Sacch. cerevisiae, Schizosaccharomyces pombe, Acetobacter aceti, A. rancens, A. suboxydans, Leuc.*Dextranicum (mesenteroides), Micrococcus sp., Pediococcus sp., Bacillus sp. and Sarcina sp.
(Shamala and Sreekantiah, 1988).

Kanji is an ethnic Indian strong-flavoured mild alcoholic beverage prepared from beetroot and carrot by natural fermentation (Batra and Millner, 1974). *Hansenlu anomala, Candida guilliermondii, C. tropicalis, Geotrichium candidum, Leuc. mesenteroides, Pediococcus* sp., *Lb. paraplantarum* and *Lb. pentosus* are present in *kanji* (Batra and Millner,
1976; Kingston et al., 2010).

504

505 Alcoholic beverages produced by malting or germination

Bantu beer or sorghum beer of Bantu tribes of South Africa is an alcoholic beverage produced
by malting or germination process (Taylor, 2003). Malted beer is common in Africa with

different names e.g., as *bushera* or *muramba* in Uganda, *chibuku* in Zimbabwe, *dolo, burkutu*and *pito* in West Africa and *ikigage* in Rwanda (Lyumugabe et al., 2012; Muyanja et al.,
2003; Sawadogo-Lingani et al., 2007). Sorghum (*Sorghum caffrorum* or *S. vulgare*) is
malted and used for brewing the beer (Kutyauripo et al., 2009), characterised by a two-stage
(lactic followed by alcoholic) fermentation, with *Lb. fermentum* as the dominating LAB
species (Sawadogo-Lingani et al., 2007).

514

515 Alcoholic beverages produced from fruits without distillation

516 Common example of alcoholic beverages produced from fruits without distillation is wine 517 which is initiated by the growth of various species of *Saccharomyces* and non-*Saccharomyces* 518 (so-called "wild") yeasts (e.g. Candida colliculosa, C. stellata, Hanseniaspora uvarum, Kl. thermotolerans, 519 Torulaspora delbrueckii, Kloeckera apiculata, Metschnikowia 520 pulcherrima) (Moreira et al., 2005; Pretorius, 2000; Sun et al., 2014; Walker, 2014). 521 Candida sp. and Cladosporium sp. were isolated from fermenting white wine using mCOLD-522 PCR-DGGE, but were not detected by conventional PCR (Takahashi et al., 2014). Sacch. 523 cerevisiae strains develop during wine fermentations play an active role in the characteristics 524 wine (Capece 2013). Saccharomyces Genome Database (SGD; of et al., 525 www.yeastgenome.org) provides fee of charge access or links to comprehensive datasets 526 comprising genomic, transcriptomic, proteomic and metabolomic information (Pretorius et527 al., 2015).

528 Conclusions

529 Every community in the world has distinct food culture including fermented foods and 530 alcoholic beverages, symbolising the heritage and socio-cultural aspects of the ethnicity. The 531 word 'culture' denotes food habits of ethnicity; another meaning for the same expression 532 'culture' is a cluster of microbial cells or inoculum, an essential biota for fermentation, 533 fequstly used in the microbiology. The diversity of functional microorganisms ranges from filamentous moulds to enzyme-producing and alcohol-producing yeasts, and from Gram-534 positive to a few Gram-negative bacteria, while even Archaea has been ascribed a role in 535 536 some fermented foods and alcoholic beverages. The relationship between human life and 537 microorganisms benefits both in the natural process. However, consumption of some less 538 known and uncommon ethnic fermented foods is declining due to change in life style, shifting 539 from cultural food habits to commercial foodstuffs and fast foods, drastically effecting 540 traditional culinary practices, and also due to climate change in some environments such as 541 the Sahel region in Africa and vast areas adjacent to the Gobi desert in Asia.

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