



## Review

## African fermented dairy products – Overview of predominant technologically important microorganisms focusing on African *Streptococcus infantarius* variants and potential future applications for enhanced food safety and security



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## ABSTRACT

Milk is a major source of nutrients, but can also be a vehicle for zoonotic foodborne diseases, especially when raw milk is consumed. In Africa, poor processing and storage conditions contribute to contamination, outgrowth and transmission of pathogens, which lead to spoilage, reduced food safety and security. Fermentation helps mitigate the impact of poor handling and storage conditions by enhancing shelf life and food safety. Traditionally-fermented sour milk products are culturally accepted and widely distributed in Africa, and rely on product-specific microbiota responsible for aroma, flavor and texture. Knowledge of microbiota and predominant, technologically important microorganisms is critical in developing products with enhanced quality and safety, as well as sustainable interventions for these products, including Africa-specific starter culture development.

This narrative review summarizes current knowledge of technologically-important microorganisms of African fermented dairy products (FDP) and raw milk, taking into consideration novel findings and taxonomy when re-analyzing data of 29 publications covering 25 products from 17 African countries. Technologically-important lactic acid bacteria such as *Lactococcus lactis* and *Streptococcus infantarius* subsp. *infantarius* (*Sii*), *Lactobacillus* spp. and yeasts predominated in raw milk and FDP across Africa. Re-analysis of data also suggests a much wider distribution of *Sii* and thus a potentially longer history of use than previously expected. Therefore, evaluating the role and safety of African *Sii* lineages is important when developing interventions and starter cultures for FDP in Africa to enhance food safety and food security. In-depth functional genomics, epidemiologic investigations and latest identification approaches coupled with stakeholder involvement will be required to evaluate the possibility of African *Sii* lineages as novel food-grade *Streptococcus* lineage.

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Abbreviations: FDP, fermented dairy products; GRAS, Generally Recognized as Safe; LAB, lactic acid bacteria; MLST, multi locus sequence typing; QPS, qualified presumption of safety; SBSEC, *Streptococcus bovis*/*Streptococcus equinus* complex; Sgg, *Streptococcus gallolyticus* subsp. *gallolyticus*; Sgm, *Streptococcus gallolyticus* subsp. *macedonicus*; Sgp, *Streptococcus gallolyticus* subsp. *pasteurianus*; Sii, *Streptococcus infantarius* subsp. *infantarius*.

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## 1. Introduction

Milk is a very important source of nutrients. Historically, milk was mainly a key component in the diets of pastoral communities in Africa and particularly in sub-Saharan Africa, but increasingly milk also plays an important role in the diets of the growing population of sedentarized pastoralists as well as urban communities (Dirar, 1993; Fratkin et al., 2004; Wurzinger et al., 2009). Milk delivers high quality proteins, micronutrients, vitamins and energy-containing fat (Schönfeldt and Gibson Hall, 2012; Wuehler et al., 2011). The total annual consumption and demand for milk and animal products is increasing across sub-Saharan Africa due to population growth and changes in lifestyle such as urbanization (The World Bank, 2015). Products are often consumed raw, as well as in the form of traditional fermented dairy products (FDP) for extended shelf life. The microbiota of FDP greatly influences spoilage, food safety, food security and product characteristics. However, despite the long tradition of FDP in Africa (Franz et al., 2014), general knowledge of the unique aspects of the fermentative microbiota of these products has only recently been obtained. While the knowledge on zoonotic and foodborne diseases and hygiene aspects of dairy production in Africa is profound, a comprehensive overview of the fermentative and technologically important microorganisms of the microbiota of milk and FDP in Africa is lacking. This knowledge is pivotal to designing local, adapted starter cultures that could assist in enhancing food safety, food quality and eventually food security through FDP. Thus, this review is intended to provide the current status of knowledge of fermentative and technologically important microorganisms in African milk products, with a focus on the most recent developments and novel emerging *Streptococcus infantarius* subsp. *infantarius* (*Sii*) variants in sub-Saharan Africa. The review also envisages steps to evaluate the role and safety of the novel (*Sii*) variants in food fermentation. These findings are discussed within the context of recent changes in taxonomy, advances in microbiological tools, and laboratory technologies to provide recommendations for future work on microbiota analysis of novel fermented products in other settings based on the lessons learnt from *Sii* in African FDP. The findings are also embedded in the context of foodborne infectious diseases and the socioeconomic aspects of dairy production systems in Africa that are the basis of livelihoods for a large number of communities.

## 2. The various roles of livestock milk in Africa

Milk in Africa has a strong connection to pastoralists, who have a long tradition in dairy production (Ranciaro et al., 2014). An estimated 20 million pastoralists and 240 million agro-pastoralists live in sub-Saharan Africa (FAO, 2001); such pastoralists often have a mobile way of life to make new pastures available to their livestock. For pastoralists, milk is an important source of micronutrients, vitamins and energy-containing fat. Milk contributes 10% of the energy and more than 50% of the micronutrients, including vitamins A, B12 and C, to their diets (Iannotti and Lesorogol, 2014). In Chadian mobile pastoralists, milk was identified as the primary source for vitamin A (Bechir et al., 2012; Zinsstag et al., 2002). Milk further serves as a source of animal fat and

thus provides energy to consumers (Schönfeldt and Gibson Hall, 2012), which highlights the importance of dairy livestock and their primary products to human nutrition in Africa.

In 2013, Africa was home to an estimated 304 million cattle, 333 million sheep, 364 million goats and 23 million camels of which an estimated 294 million cattle, 262 million sheep, 328 million goats and 22 million camels were located in sub-Saharan Africa (FAOSTAT, 2015). This visualizes the important contribution of sub-Saharan Africa to the African livestock sector. Livestock production is dominated (70–90%) by small scale and extensive livestock production systems (Bosire et al., 2015) in arid and semi-arid land areas (Bosire et al., 2015; Ndambi et al., 2008). Approximately 80–90% of the milk volume is produced and marketed through informal channels by smallholder dairy units and pastoral communities (Grimaud et al., 2009; Kamana et al., 2014; Noor et al., 2013). Total milk production in Africa was 49 million tons in 2013 and nearly doubled in sub-Saharan Africa during the last two decades to 33 million tons in 2013, with the majority being produced in East Africa (FAOSTAT, 2015). However, productivity per animal is significantly lower compared to industrialized countries; the increased production volume was mainly due to larger animal populations (Cardoso, 2012). In parallel, approximately 25–30% of the milk produced in sub-Saharan Africa is lost because of spillage and spoilage prior to reaching the consumer (Gustavsson et al., 2011). Local production is not sufficient to provide adequate milk for all consumers, and thus does not sufficiently contribute to food security or to meet the increasing demand. Thus, many sub-Saharan countries depend on imported milk or powdered milk, which account for 24–60% of the milk quantity consumed (Ayenew et al., 2009; Bayemi and Webb, 2009; Bosire et al., 2015; Kamana et al., 2014; Mapekula et al., 2009; Sanogo et al., 2013). This highlights the need to optimize local milk production and decrease losses along the milk value chain.

Milk is prone to microbial spoilage and can harbor a wide variety of foodborne and zoonotic agents (Quigley et al., 2013b). Sub-Saharan Africa and other less developed regions share a significantly higher burden of diseases by zoonotic agents than industrialized countries (Kirk et al., 2015). Key zoonotic and foodborne pathogens in milk such as *Staphylococcus aureus*, *Campylobacter* spp., *Clostridium perfringens*, *Clostridium botulinum*, *Bacillus cereus*, *Brucella* spp., *Listeria monocytogenes*, *Mycobacterium bovis*, *Salmonella* spp. and Shiga-toxin producing *Escherichia coli* are important contributors to the high foodborne disease burden in sub-Saharan Africa (Havelaar et al., 2015; Jans et al., 2017; Kirk et al., 2015).

Raw milk is a major contributor to humans contracting bovine tuberculosis and brucellosis (Dean et al., 2012; Müller et al., 2013). Bovine tuberculosis caused by *M. bovis* is estimated to yield seven cases per 100,000 population/year in developing countries. This is significantly higher compared to 1 case per 100,000 population/year in developed countries (Müller et al., 2013). Similarly, brucellosis caused by *Brucella* spp. has an estimated 34 cases per 100,000 person years among mobile pastoralists vs. 0.02–0.09/100,000 in developed countries (Dean et al., 2012; Dean et al., 2013). *Streptococcus agalactiae*, a pathogen less recognized for its zoonotic potential, was detected in Kenyan camel milk at  $10^7$  CFU/mL at the consumer level, which might pose additional health

**Table 1**  
Overview of predominant LAB and yeasts in African raw and fermented dairy products (FDP).

Name	Country	Description	pH (range)	Agar media <sup>a</sup> and log <sub>10</sub> CFU/mL	LAB and yeast species <sup>b</sup>	Methodology of identification	Reference
Amabere amaruranu	Kenya	Fermented cow milk	4.5	M17 7.1–7.9 MRS 7.3–8.1 PDA 4.7–6.1	<b>Predominant:</b> <i>Lb. plantarum</i> , <i>Leuc. mesenteroides</i> , <i>S. thermophilus</i> <sup>c,e</sup> ; <i>Saccharomyces cerevisiae</i> , <i>Trichosporon mucoides</i> , <i>Candida famata</i> , <i>Candida albicans</i> <b>Others:</b> <i>Lb. bulgaricus</i> , <i>Lb. helveticus</i> , <i>Lb. fermentum</i>	API 50 CH, API 20C AUX	(Nyambane et al., 2014)
Amasi	South Africa	Fermented cow milk	n/a	n/a	<b>Predominant:</b> <i>Lc. lactis</i> <b>Others:</b> <i>E. faecalis</i> , <i>Lb. casei</i> , <i>Lb. paracasei</i> , <i>Lb. plantarum</i> , <i>Leuc. pseudomesenteroides</i>	16S clone library and DGGE	(Osvik et al., 2013)
Ergo	Ethiopia	Fermented cow milk	4.5–4.8	PCA 11.0 Rogosa Agar 9.1 Azide blood agar + Slanetz/Berteley 9.8 PDA 16.0	<b>Predominant:</b> <i>Lb. mesenteroides</i> <sup>g</sup> , <i>Lc. lactis</i> subsp. <i>cremoris</i> , <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>Leuc. cremoris</i> , <i>S. thermophilus</i> <sup>c</sup> <b>Others:</b> <i>Lb. delbrueckii</i> , <i>Lb. homi</i> , <i>Micrococcus</i> spp.	Basic phenotypic characterization	(Gonfa et al., 1999)
Fènè	Mali	Fermented cow milk	4.4–4.8	MRS 7.9–9.2 M17 8.2–9.2	<b>Predominant:</b> <i>Enterococcus</i> spp., <i>Sii</i> <b>Others:</b> <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>P. pentosaceus</i> , <i>W. confusa</i>	Rep-PCR for clustering, species-specific PCR assay	(Wullschleger et al., 2013)
Fermented cow milk	Côte d'Ivoire	Fermented cow milk	4.5–5.5	M17 7.9–9	<b>Predominant:</b> <i>Sii</i> <b>Others:</b> <i>Sgm</i> , other species not investigated	Rep-PCR for clustering, species-specific PCR assay, 16S rRNA gene sequencing	(Jans et al., 2013b)
Gariss	Sudan	Fermented camel milk	3.8–4.4	MRS 7.76–8.66 PDA 6.05–7.79	<b>Predominant:</b> <i>Lb. fermentum</i> , <i>Sii</i> ; <i>Kluyveromyces marxianus</i> <b>Others:</b> <i>E. faecium</i> , <i>Lb. helveticus</i> ; <i>Issatchenkia orientalis</i>	rep-PCR for clustering, 16S rRNA gene, <i>rpoB</i> , <i>sodA</i> , <i>gtf</i> sequencing, API 50 CHL, API ID 32C and 26S rRNA gene for yeasts	(Abdelgadir et al., 2008)
Kefir	South Africa	Fermented milk (likely cow)	n/a	MRS 6.0–7.6 KCA 4.8–7.8 KCA + V 5.4–7.7 MEA/YEC (yeast) 5.2–8.6	<b>Predominant:</b> <i>Lb. delbrueckii</i> subsp. <i>delbrueckii/lactis</i> , <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>Lb. fermentum</i> , <i>Leuc. lactis</i> , <i>Leuc. mesenteroides</i> subsp. <i>mesenteroides/dextranicum</i> <i>Candida kefir</i> , <i>Candida holmii</i> , <i>Candida lipolytica</i> , <i>Zygosaccharomyces</i> spp.	API 50 CHL, API Rapid ID32C	(Witthuhn et al., 2004)
Kule naoto	Kenya	Spontaneously fermented cow milk, at least 5 days	4.4	M17 7.9 MRS 8.0 PDA 5.9	<b>Predominant:</b> <i>E. faecium</i> , <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>Lc. lactis</i> <b>Others:</b> <i>Lb. acidophilus</i> , <i>Lb. casei</i> , <i>Lb. paracasei</i> , <i>Lb. rhamnosus</i> , <i>Leuc. mesenteroides</i> , yeasts not identified to genus or species	basic phenotypic characterization and API 50 CHL	(Mathara et al., 2004)
Leben	Algeria	Fermented cow, ewe, goat, camel milk	n/a	M17, no CFU data	<i>E. faecalis</i> , <i>E. faecium</i> , <i>Lc. lactis</i> , <i>S. thermophilus</i> . No predominance data reported.	Basic phenotypic characterization, 16S rRNA gene, <i>pepN</i> and <i>pepO</i> sequencing	(Bensalah et al., 2009)
Lben	Morocco	Fermented cow or goat milk	4.6	M17 9.6 MRS 2.3 GYEP (yeast) 5.7	<b>Predominant:</b> <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>Lc. lactis</i> subsp. <i>lactis</i> biovar <i>diacetyllactis</i> ; <i>Kluyveromyces lactis</i> , <i>Saccharomyces cerevisiae</i> <b>Others:</b> <i>E. faecalis</i> , <i>Lb. brevis</i> , <i>Lc. lactis</i> subsp. <i>cremoris</i> , <i>Leuc. lactis</i> , <i>Leuc. mesenteroides</i> subsp. <i>dextranicum</i>	API 50 CHL, API 20 STREP, API 20C AUX	(Mangia et al., 2014)
Lben and raw milk	Morocco	Fermented cow milk	4.2–4.6	MRS 10–11	<b>Predominant:</b> <i>Lb. plantarum</i> , <i>Lc. lactis</i> , <i>Leuc. mesenteroides</i> , <i>Leuc. pseudomesenteroides</i> , <i>E. faecium</i> <b>Others:</b> <i>Lb. brevis</i> , <i>Lb. paracasei</i> , <i>Lb. rhamnosus</i> , <i>Lc. garvieae</i> , <i>Leuc. citreum</i> , <i>Leuc. pseudomesenteroides</i> , <i>E. faecium</i> , <i>E. hirae</i> , <i>P. pentosaceus</i> , <i>W. cibaria</i> , <i>W. confusa</i> , <i>W. paramesenteroides</i> , <i>W. viridescens</i>	GTG-5 fingerprinting, <i>pheS</i> sequencing, SDS PAGE whole-cell protein analysis; methodology of representative isolation not described	(Quadhiri et al., 2009)
Mabisi	Zambia	Fermented milk	4.0–4.5	M17 8 MRS 8	<b>Predominant:</b> <i>Acinetobacter ursingii</i> , <i>Citrobacter freundii</i> , <i>Lc. lactis</i> , <i>S. equinus</i> <sup>f</sup> , <i>S. thermophilus</i> <b>Others:</b> <i>E. durans</i> , <i>Lb. brevis</i> , <i>Lb. kefiranoferiensis</i> , <i>Lb. plantarum</i> , <i>Leuc. garlicum</i> , <i>Leuc. pseudomesenteroides</i>	V1–V4 region analysis of 16S rRNA gene	(Schoustra et al., 2013)
Mafi/amasi	South Africa/Namibia	Fermented milk (likely cow)	4.0–5.4	M17 6.1–9.3 MRS 5.7–9.1	<b>Predominant:</b> <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>Lb. delbrueckii</i> subsp. <i>lactis</i> , <i>Lb. plantarum</i> , <i>Leuc. mesenteroides</i> subsp. <i>dextranicum</i>	Basic phenotypic characterization, API 50 CH	(Beukes et al., 2001)
Masai fermented milk	Tanzania	Fermented cow milk	n/a	BCP, GAM, MRS, SMA, TSA: LAB 8–10; PDA n.d.	<b>Predominant:</b> <i>Lb. confusus</i> ( <i>W. confusa</i> ), <i>Lc. lactis</i> subsp. <i>lactis</i> <b>Others:</b> <i>E. faecium</i> , <i>Lb. brevis</i> , <i>Lc. garvieae</i> ,	API 20 STREP and API 50 CH for LAB, API 20C AUX for yeast; methodology of representative	(Isono et al., 1994)

(continued on next page)

Table 1 (continued)

Name	Country	Description	pH (range)	Agar media <sup>a</sup> and log <sub>10</sub> CFU/mL	LAB and yeast species <sup>b</sup>	Methodology of identification	Reference
				to 9	<i>S. bovis</i> (possibly <i>S. infantarius</i> group by esculin test), <i>Streptococcus</i> spp.; <i>Candida</i> spp., <i>Saccharomyces</i> spp.	isolation not described	
Milk curds	Chad	Fermented milk <sup>d</sup>		M17 9.9–10.7 MRS 9.9–10.2	<b>Predominant:</b> <i>Lb. delbrueckii</i> subsp. <i>bulgaricus</i> , <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>Lc. lactis</i> subsp. <i>cremoris</i> , <i>Lc. lactis</i> subsp. <i>diacetylactis</i> , <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>S. thermophilus</i> <sup>e</sup> <b>Others:</b> <i>Leuconostoc</i> spp., <i>Lb. acidophilus</i> , <i>Lb. brevis</i> , <i>Lb. lactis</i> , <i>Lb. casei</i> , <i>Lb. helveticus</i>	API 50 CH for MRS isolates; methodology of representative isolation not described	(Doutoum et al., 2013)
Mursik	Kenya	Fermented milk	3.5	FAA 10.4 BA n.d. SP n.d.	<b>Predominant:</b> <i>Lb. kefirii</i> , <i>Lb. casei</i> , <i>Lb. paracasei</i> , <i>Lb. rhamnosus</i> , <i>Candida krusei</i> <b>Others:</b> <i>Bacillus pumilus</i> , <i>Bacillus cereus</i> , <i>Lb. brevis</i> , <i>Lb. helveticus</i> , <i>Lb. pontis</i> , <i>Candida sphaerica</i> , <i>Candida kefir</i> , <i>Saccharomyces fermentati</i>	16S and 18S rRNA gene sequencing, API 32C AUX; methodology of representative isolation not described	(Nieminen et al., 2013)
Mutandabota	Zimbabwe	Mixed cow/goat milk with dry baobab fruit pulp (acidic)	3.5	MRS 5.3 OGYEA (yeast) 5.0	Not identified. No predominance data reported.	n/a	(Mpfu et al., 2014)
Nunu	Ghana	Fermented cow milk	3.0–3.1	MRS 8.4–8.7 MEA (yeast) 5.0–5.8	<b>Predominant:</b> <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>Leuc. mesenteroides</i> ; <i>Pichia kudriavzevii</i> , <i>Saccharomyces cerevisiae</i> <b>Others:</b> <i>E. italicus</i> , <i>Lactococcus</i> spp., <i>Lb. helveticus</i> , <i>E. faecium</i> , <i>W. confusa</i> ; <i>Candida parapsilosis</i> , <i>Candida rugosa</i> , <i>Candida tropicalis</i> , <i>Galactomyces geotrichum</i>	Basic phenotypic characterization followed by GTG-5 fingerprinting and 16S rRNA gene/26S rRNA gene sequencing	(Akabanda et al., 2013)
Omashikwa	Namibia	Fermented buttermilk with Omunkunzi tree roots ( <i>Boscia albitrunca</i> )	3.25	MRS 8.0 RBCA (yeast) 1.7	Not identified. No predominance data reported.	n/a	(Bille et al., 2007)
Pendidam	Cameroon	Fermented cow milk	4.0–4.5 3.6–4.0	MRS, no quantification MRS 7–9 Elliker 7–9	Presumptive <i>Lb.</i> spp. and <i>Streptococcus/Enterococcus</i> spp. (Mbawala et al., 2013); <b>Predominant:</b> <i>Lb. delbrueckii</i> , <i>Lb. helveticus</i> , <i>Lb. fermentum</i> , <i>Lb. plantarum</i> , <i>E. faecalis</i> , <i>E. faecium</i> , <i>S. thermophilus</i> <sup>c</sup> <b>Others:</b> <i>Lb. casei</i> , <i>Leuc. mesenteroides</i> , <i>Leuc. paramesenteroides</i> (Jiwoua and Milliere, 1990)	Basic phenotypic characterization (Mbawala et al., 2013); Extended phenotypic characterization (Jiwoua and Milliere, 1990)	(Mbawala et al., 2013) (Jiwoua and Milliere, 1990)
Nyarmie	Ghana	Fermented cow milk	3.5–4.3	PCA 6.9–8.2 M17 7.4–9.0 MRS 7.1–9.0 MYPGA 7.0–7.5	<b>Predominant:</b> <i>Leuc. mesenteroides</i> subsp. <i>mesenteroides</i> , <i>S. thermophilus</i> , <i>Lb. delbrueckii</i> subsp. <i>bulgaricus</i> , <i>Lb. helveticus</i> , <i>Lb. delbrueckii</i> subsp. <i>lactis</i> and <i>Lc. lactis</i> ; <i>Saccharomyces cerevisiae</i>	16S and 18S rRNA gene DGGE, API 50 CHL, API 20 STREP, API 20C AUX	(Obodai and Dodd, 2006)
Raw dromedary milk	Algeria	Unfermented	n/a	MRS M17 no CFU values stated	<i>E. durans</i> , <i>E. faecalis</i> , <i>E. faecium</i> , <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>Lb. paracasei</i> subsp. <i>paracasei</i> , <i>Lb. plantarum</i> , <i>Lb. rhamnosus</i> . No predominance recorded.	Phenotypic. Methodology of representative isolation not described	(Hassaine et al., 2007)
Raw dromedary milk	Morocco	Raw camel milk	n/a	MRS 2.4–7.8 Elliker 2.7–7.8 MSE 2.7–7.7 M17 2.6–7.9	<b>Predominant:</b> <i>E. casseliflavus</i> , <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>Lb. delbrueckii</i> , <i>Lb. casei</i> subsp. <i>casei</i> , <i>Lb. helveticus</i> , <i>Lb. plantarum</i> , <i>S. thermophilus</i> <sup>c</sup> <b>Others:</b> <i>E. faecalis</i> , <i>Lb. amylophilus</i> , <i>Lb. brevis</i> , <i>Lb. rhamnosus</i> , <i>Lc. lactis</i> subsp. <i>cremoris</i> , <i>Lc. lactis</i> biovar <i>diacetylactis</i> , <i>Lc. garvieae</i> , <i>Lc. raffinolactis</i> , <i>Leuc. mesenteroides</i> subsp. <i>mesenteroides</i> , <i>Leuc. mesenteroides</i> subsp. <i>cremoris</i> , <i>Leuc. lactis</i> , <i>P. acidilactici</i> , <i>P. damnosus</i> , <i>P. pentosaceus</i>	Phenotypic only	(Khedid et al., 2009)
Raw dromedary milk	Morocco	Raw camel milk	n/a	M17, no CFU values	<i>S. cameli</i> , <i>S. tangierensis</i> . No predominance reported.	16S rRNA gene sequencing and MALDI-TOF, API 50 CHL, API 20 STREP	(Kadri et al., 2015)
Sethemi	South Africa	Fermented cow milk	4.1–4.3	M17 9–9.8 MRS 9–9.8 RBCA 6.2	<b>Predominant:</b> <i>Lactobacillus</i> spp., <i>Lactococcus</i> spp., <i>Leuconostoc</i> spp., (LAB not further identified) <i>Cryptococcus curvatus</i> , <i>Debaryomyces hansenii</i> , <i>Saccharomyces cerevisiae</i> <b>Others:</b> <i>Candida albicans</i> , <i>Candida parapsilosis</i> , <i>Clavispora lusitanae</i> , <i>Kluyveromyces marxianus</i> , <i>Yarrowia</i>	LAB: identified based on isolation agar medium (MRS: <i>Lactobacillus</i> spp. and <i>Leuconostoc</i> spp.; M17: <i>Lactococcus</i> spp.) Yeast: phenotypic and DNA-based	(Kebede et al., 2007)



Table 1 (continued)

Name	Country	Description	pH (range)	Agar media <sup>a</sup> and log <sub>10</sub> CFU/mL	LAB and yeast species <sup>b</sup>	Methodology of identification	Reference
Suusac	Kenya/Somalia	Fermented camel milk	4.9	M17 8 MRS 8 KFS 7 YM 2.0–5.4	<i>lipolytica</i> <b>Predominant:</b> <i>E. faecium</i> , <i>Lb. helveticus</i> , <i>Sii</i> , <i>S. salivarius/thermophilus</i> , <i>W. confusa</i> ; <i>Candida famata</i> , <i>Candida inconspicua</i> <b>Others:</b> <i>E. faecalis</i> , <i>Lb. fermentum</i> , <i>Lc. lactis</i> subsp. <i>lactis</i> , <i>Leuc. lactis</i> , <i>Leuc. mesenteroides</i> , <i>Sgm</i> ; <i>Candida lusitanae</i> , <i>Cryptococcus laurentii</i> , <i>Rhodotorula mucilaginosa</i> , <i>Saccharomyces cerevisiae</i> , <i>Trichosporon mucoides</i> , <i>Trichosporon cutaneum</i>	Rep-PCR for clustering, species-specific PCR assay, 16S rRNA gene sequencing Yeasts: API 20C AUX and DNA-based	(Jans et al., 2012a; Njage et al., 2011)
Raw milk	Kenya	Raw camel milk	6.2–6.5	M17 2.6–6.7 MRS 1.7–6.6 KFS 7 0.7–3.7 YM 4.4–5.0	<b>Predominant:</b> <i>E. faecalis</i> , <i>S. agalactiae</i> , <i>W. confusa</i> ; <i>Rhodotorula mucilaginosa</i> , <i>Cryptococcus albidus</i> , <i>Candida lusitanae</i> <b>Others:</b> <i>E. faecium</i> , <i>Lc. lactis</i> , <i>S. salivarius/thermophilus</i> , <i>Vagococcus</i> spp.; <i>Candida famata</i> , <i>Candida inconspicua</i> , <i>Candida krusei</i> , <i>Cryptococcus laurentii</i> , <i>Trichosporon mucoides</i>		
Zabady	Egypt	Fermented buffalo milk, possible also with cow milk	n/a	n/a, culture independent only	<b>Predominant:</b> <i>S. thermophilus</i> , <i>Lc. garvieae</i> , <i>Lc. raffinolactis</i> , <i>Lc. lactis</i> , <i>Leuc. citreum</i> , <i>Lb. delbrueckii</i> subsp. <i>bulgaricus</i> , <i>Lb. johnsonii</i>	Total DNA extraction, TTGE, DGGE of V3 region of 16S rRNA gene	(El-Baradei et al., 2008)

<sup>a</sup> On agar media: azide blood agar + Slanetz/Berteley agar: streptococci; BA: lysed trypticase soy blood agar with horse blood, total aerob bacteria; BCP: plate count agar with bromocresol purple for LAB; Elliker: lactococci; FAA: fastidious anaerobe agar with horse blood for total viable bacteria; GAM: gentamicin agar for strict anaerobes; GYEP: glucose yeast extract peptone agar with chloramphenicol for yeast; KCA: potassium carboxymethyl cellulose agar with triphenyl tetrazolium chloride for lactococci; KCA-V: KCA with vancomycin for leuconostoc; KFS: selective for streptococci, enterococci; M17: selective for streptococci, enterococci, lactococci; MEA: Malt extract agar with chloramphenicol and chlortetracycline for yeast; MRS: Man-Rogosa-Sharp for lactobacilli; MSE: selective for *Leuconostoc*; MYPGA: Malt yeast peptone glucose agar for yeast; OGYEA: oxytetracycline glucose yeast extract agar for yeast; PCA: Plate Count Agar; PDA: Potato Dextrose Agar for yeast; RBCA: Rose Bengal Chloramphenicol Agar for yeast; Rogosa Agar: selective for lactobacilli which served as a basis for the development of MRS; SMA: Standard Method Agar for total viable cell count; SP: Sabouraud dextrose agar with penicillin and streptomycin for yeast; TSA: blood agar for streptococci; YEC: yeast extract chloramphenicol agar for yeast; YM: Yeast mold agar, selective for yeast.

<sup>b</sup> Genus abbreviations: *Lb.* = *Lactobacillus*, *Lc.* = *Lactococcus*, *Leuc.* = *Leuconostoc*, *E.* = *Enterococcus*, *S.* = *Streptococcus*, *W.* = *Weissella*.

<sup>c</sup> Phenotypic re-evaluation of identification as *S. thermophilus* vs. *Sii* (African variant) critical based on data provided and current knowledge available.

<sup>d</sup> Likely cow milk.

<sup>e</sup> *S. thermophilus* identified using API 50 CH strips is not distinguishable from dairy adapted *Sii*.

<sup>f</sup> 16S rRNA gene sequence differentiation power critical between *Sii* and *S. equinus* using the chosen sequence as reference.

<sup>g</sup> *Lb. mesenteroides* is not an official species designation according to DSMZ standing nomenclature, likely *Leuc. mesenteroides*.

risks not commonly found in other geographical areas (Table 1) (Jans et al., 2012a; Manning et al., 2010; Zadoks et al., 2011). For further in-depth insights into the general microbiology of milk and the burden of foodborne diseases, the authors would like to refer to the excellent reviews by Quigley et al. (2013b), Kirk et al. (2015) and Havelaar et al. (2015). In Africa and particularly sub-Saharan Africa, milk products provide key nutrients and income, but they also contribute to human zoonotic and foodborne pathogen infections. Thus, methods of enhancing quality and safety of existing milk products are required.

### 3. Basic characterization of African dairy products

In Africa, milk products, particularly from pastoral regions, are usually consumed and traded either as raw milk or traditional FDP. Africa features a unique richness of cereal- and milk-based fermented products (Franz et al., 2014). Fermentation extends the shelf life of food products and is particularly important in the absence of other conservation options such as pasteurization and cooling. For this narrative review, we specifically collected scientific publications that reported the fermentative microbiota of raw milk and FDP in Africa. For this, we searched for peer-reviewed journal articles on pubmed, sciencedirect and webofscience using Boolean search terms for fermented dairy/milk products, dairy/milk fermentation, Africa, sub-Saharan Africa and individual African country names in the time frame of 1990–2015. Products were considered as either basic raw or milk types analyzed for microbiota content or specific types of food carrying a product name. Studies were included if microbial data such as microbial enumeration or identification of microorganisms were reported. Studies without sufficient methodology description on predominance determination

were marked as such and included in order to still obtain valuable information on microbiota observations. Studies solely focusing on human or animal pathogens in milk as well as review articles and books lacking methodological descriptions were excluded at this stage. We identified 29 publications covering 25 products from 17 African countries fitting these criteria of which four however did not allow to deduct any information on microorganism predominance (Table 1). Data obtained referred to end point microbiota content as determined by the respective studies from direct product analysis.

Among these 25 products analyzed for this review, cow, buffalo, camel, goat or ewe milk were used as a basis for FDP such as fènè (cow; Mali), mabisi (cow; Zimbabwe), nunu (cow; Ghana) or suusac (camel; Kenya and Somalia) and gariss (camel; Sudan) in sub-Saharan Africa, as well as zabady (buffalo; Egypt) and lben/leben (cow, ewe, goat or camel; Algier, Morocco) in North Africa (Table 1). In other countries of sub-Saharan Africa, milk was also mixed with cereals or other plant materials before fermentation to yield products such as omashikwa in Namibia (Bille et al., 2007). Milk preservation did not always rely on direct action by a fermentative microbiota, but was also achieved through the addition of acidic material such as baobab fruit pulp in mutandabota from Zimbabwe (Mpofu et al., 2014). Similar to the acidifying effect of the fermentation process, the acidic material reduces the pH of the product to inhibit spoilage organisms and modify the predominating microbiota.

Given the high diversity of African FDP and the multitude of involved dairy animals, the available data on milk and FDP was not further stratified by animal species. Unfortunately, current microbiota data on African milk and FDP is still limited and requires further studies before relevant conclusions can be drawn with respect to dairy animals as

well as physico-chemical characteristics of the products with the exception of pH. Therefore, this review focuses on the microbiota of African dairy products.

#### 4. The fermentative and technologically important microbiota of African dairy products

##### 4.1. Predominant lactic acid bacteria and yeast in raw and fermented dairy products

The fermentative microbiota of African milk products surveyed for this review was predominated by lactic acid bacteria (LAB). LAB were most abundant and accompanied by yeasts in selected products (Table 1). Of the LAB, *Lactococcus lactis* and its subspecies *lactis* and subspecies *cremoris* were the most widely detected species, as they were described in 20 products, followed by *Lactobacillus* spp., *Streptococcus bovis*/*Streptococcus equinus* complex (SBSEC) members and *Streptococcus infantarius* subsp. *infantarius* (*Sii*), *Enterococcus* spp. and yeasts (Table 1).

*Lc. lactis* represents a typical technologically important LAB in dairy products (Teuber, 2009). *Lc. lactis* was isolated from FDP in Algeria, Chad, Egypt, Ethiopia, Mali, Morocco, Kenya, South Africa, Tanzania and Zambia, as well as raw milk in Algeria, Kenya and Morocco. *Lc. lactis* was detected at  $10^6$  to  $10^{10}$  CFU/mL in the final products, indicating its wide adaptability and contribution to fermentation processes (Table 1). *Lc. lactis* is a mesophilic bacterium with highly adapted lactose metabolism, formation of diacetyl and limited proteolysis for optimal food preservation and flavor development, which has led to widespread application in industrial dairy fermentations (Teuber, 2009). These characteristics also render *Lc. lactis* optimally adapted to the prevailing fermentation conditions at ambient temperatures in Africa.

In contrast to *Lc. lactis*, *Streptococcus infantarius* subsp. *infantarius* (*Sii*) was less known for its role in dairy fermentation until *Sii* was first identified as the predominant species from traditional fermented camel milk gariss in Sudan in 2008 (Abdelgadir et al., 2008). Subsequently, *Sii* was also identified as a predominant LAB species in fermented camel and cow milk products in Côte d'Ivoire, Kenya, Mali and Somalia (Jans et al., 2012a; Jans et al., 2013b; Wullschlegel et al., 2013). In all products, *Sii* was present at over  $10^8$  live cells per mL of product (Table 1). *Sii* were isolated from African FDP under conditions selective for mesophilic aerobic cocci, anaerobic lactobacilli and thermophilic enterococci (Abdelgadir et al., 2008; Jans et al., 2012a; Jans et al., 2013b), indicating their wide range of growth abilities and competitiveness during fermentation processes. Furthermore, *Sii* strains involved in African dairy fermentations have adapted to the milk environment, which has yielded unique variants of *Sii* dairy lineages (Jans et al., 2016a). These dairy-adapted African *Sii* variants harbor a *lacS/lacZ* directed lactose metabolism while the otherwise commonly utilized lactose phosphotransferase pathway is inactivated in these variants. *lacS* and *lacZ* were likely obtained from *S. thermophilus* via horizontal gene transfer (Jans et al., 2013a; Jans et al., 2012b). *Sii*, particularly the African variant *Sii*, represent a previously undescribed and possibly overlooked component of the dairy fermentation microbiota. However, *Sii* of the ancestral lineages are human and animal commensal inhabitants of the gastrointestinal tract and possibly opportunistic pathogens (Jans et al., 2015). *Sii* are not classified by the qualified presumption of safety (QPS) of the European Food Safety Authority (EFSA) nor have the status of Generally Recognized as Safe (GRAS) (EFSA Panel on Biological Hazards, 2016; U.S. Food and Drug Administration FDA, 2017). Given the distribution and predominance, as well as their adaptation to dairy that parallels that of *S. thermophilus*, their role in dairy fermentations requires in depth investigations accompanied by a thorough safety assessment (see Section 4.3 for further elaboration).

Besides the predominant organisms *Lc. lactis* and *Sii*, *Lb. delbrueckii*, *Lb. plantarum* and *Lb. fermentum* were regularly identified. These organisms were detected at titers ranging from  $10^2$  to  $10^8$  CFU/mL in raw milk

and  $10^8$  to  $10^{10}$  CFU/mL in FDP (Table 1). While *Lb. delbrueckii* and *Lb. fermentum* represent typical dairy organisms, *Lb. plantarum* is more commonly associated with plants, plant fermentations and, to some extent, meat and fish products (Hammes and Hertel, 2009). This suggests that *Lb. plantarum* from plant or animal sources likely contaminates milk during production. In general, the role of lactobacilli in FDP of certain regions, particularly West Africa, might be underestimated. Not all studies enabled a comprehensive overview of the involved LAB, particularly through restricted use of approaches to isolate and identify lactic cocci (mainly *Lactococcus*, *Enterococcus* and *Streptococcus*) in combination with *Lactobacillus* and related genera.

*Enterococcus* spp. are further representatives of milk contaminants that played a predominant role in 13 of the various milk products analyzed (Table 1). Most enterococci are part of the intestinal microbiota of mammals and birds, and they are also associated with plants or water (Ludwig et al., 2009). Their presence, particularly in water, is regarded as an indicator of fecal contamination from animal and human sources (Franz et al., 1999; Godfree et al., 1997). In dairy products, the species *E. faecalis* and *E. faecium* are among the often detected enterococci (Quigley et al., 2013a). However, *Enterococcus* is a controversial genus in terms of food safety and human infections. Similar to *Sii*, they are not included in the current QPS scheme EFSA for general application in food (EFSA Panel on Biological Hazards, 2016). Enterococci have also been described as emerging pathogens in nosocomial infections, and they are implicated in the spread of antibiotic resistance, particularly in the case of vancomycin. This renders them potentially less suitable for safe product development (Byers et al., 2001; Fisher and Phillips, 2009; Ogier and Serror, 2008) despite the approval on a strain by strain basis of some enterococci strains for application in starter cultures in cheese production where they contribute to flavor and aroma development (Ogier and Serror, 2008).

While enterococci play a controversial but detectable role in FDP, yeasts are often underestimated in raw milk (Quigley et al., 2013b). They contribute significantly to product development during many fermentation processes through lactose and galactose metabolism, proteolysis, lipolysis and enzymatic degradation, which contributes to flavor development (Quigley et al., 2013b). Yeasts such as *Candida* spp., *Cryptococcus* spp., *Debaryomyces* spp., *Geotrichum* spp., *Issatchenkia* spp., *Kluyveromyces* spp. and *Saccharomyces cerevisiae* are typical representatives of the raw milk microbiota (Quigley et al., 2013b), and were detected at  $10^3$  to  $10^8$  CFU/mL in FDP in Africa (Table 1). Their presence in raw milk suggests that they likely contribute to product development (Table 1). *Candida* spp. represented the largest genus group with eight different species detected in nine different products (Table 1). However, most yeast species were attributed only to a single product, with the exception of *Saccharomyces cerevisiae* attributed as the predominant yeast species in five products (Table 1). In contrast to LAB, the predominant yeast species in the dairy products analyzed varied between products, suggesting a much more product-specific yeast microbiota.

##### 4.2. Streptococci in food fermentation: an example for the discrimination power required to identify unexpected species variants in the case of *Streptococcus infantarius* subsp. *infantarius*

Members of the genus *Streptococcus* were regularly detected in dairy products worldwide. In Africa, this included *Sii*, *Streptococcus gallolyticus* subsp. *macedonicus* (*Sgm*), *S. thermophilus*, *Streptococcus salivarius* and *Streptococcus agalactiae* (Table 1). *S. agalactiae* is a pathogen of public health relevance in Africa for neonatal sepsis and meningitis in humans and mastitis in animals (Fischer et al., 2013; Le Doare and Heath, 2013). *S. salivarius* is a human commensal and opportunistic pathogen closely related to *S. thermophilus* (Delorme et al., 2015). Of the genus *Streptococcus*, only the species *S. thermophilus* is currently approved for use in dairy fermentations by EFSA (EFSA Panel on Biological Hazards, 2016). However, in Africa, many traditional dairy fermentations are predominated by novel variants of *Sii* instead of *S.*

*thermophilus*. Thus, further investigation is required into the phylogenetic and taxonomic background of *Sii*, and its role in fermentation processes as well as implications for public health.

The presence and predominance of *Sii* in African FDP was a novel discovery in 2008 first reported for the Sudanese FDP gariss (Abdelgadir et al., 2008). Since then, knowledge into its potential role in fermentation has grown and revealed interesting insights into its evolution into several lineages and adaptation of specific lineages to the dairy environment (Jans et al., 2016a; Jans et al., 2013a; Jans et al., 2012b).

*Sii* is a member of the *Streptococcus bovis*/*Streptococcus equinus* complex (SBSEC). The SBSEC is a group of commensal inhabitants of the gastrointestinal tract of animals and humans. However, they are also opportunistic pathogens of humans and animals that have been associated with bacteremia, bloat, meningitis, infective endocarditis and colorectal cancer, which potentially qualifies them as pathobionts (Chow et al., 2011; Jans et al., 2015; Schlegel et al., 2003). The pathogenic potential of *Sii* and several other novel SBSEC species remains unclear, as most epidemiological data was obtained using the less discriminative biotype classifications that was state of the art prior to taxonomic rearrangements and current DNA-based classifications (Jans et al., 2015; Schlegel et al., 2003). The refined taxonomy is needed to draw more coherent conclusions on specific SBSEC species.

The SBSEC currently comprises seven (sub)species grouped into four branches based on sequence identities: the *Streptococcus gallolyticus* branch, the *Streptococcus equinus* branch, the *Streptococcus infantarius* branch and the *Streptococcus alactolyticus* branch (Jans et al., 2015). This advanced taxonomy allows for a more detailed differentiation than previous biotype classifications of *S. bovis* biotype I (*S. gallolyticus* subsp. *gallolyticus*, Sgg), *S. bovis* biotypes II.1 (*Sii* and *S. lutetiensis*) and II.2 (*S. gallolyticus* subsp. *pasteurianus*, Sgp), as well as the more recently-established species *S. gallolyticus* subsp. *macedonicus* (Sgm) and *S. alactolyticus* that were not properly classified by biotypes (Jans et al., 2015; Whiley and Hardie, 2009). Even by DNA-based identification, *Sii* and *S. lutetiensis* (formerly *S. infantarius* subsp. *coli*), including strains identified as *S. bovis* or *S. equinus*, were not always given reliable species assignments. Differentiation by 16S rRNA gene sequencing within the SBSEC is limited to the *S. gallolyticus* vs. the *S. infantarius*/*S. equinus* type strains and the *S. alactolyticus* branches. Within each branch, the identity of the 16S rRNA gene between species and subspecies exceeds 99.7% sequence identity over 1400 bp, making separation less reliable (Jans et al., 2015). Furthermore, the report of horizontal gene transfer reduced the reliability of single gene assays (Jans et al., 2016a; Jans et al., 2013a; Jans et al., 2012b). This indicates the clear need for more advanced identification tools, especially when investigating microorganisms in new ecosystems and the association of the pathogenic potential of a species and should also be considered when analyzing traditional GRAS or QPS-approved LAB and yeast species from novel microbiota.

Recently developed multi locus sequence typing (MLST) schemes for Sgg (Dumke et al., 2014; Shibata et al., 2014) and an overarching SBSEC assay (Jans et al., 2016a) finally allowed elucidation of the phylogeny of SBSEC members in sufficient detail across ecological niches. The MLST analysis of SBSEC and *Sii* yields a main branch of *Sii*, with *S. lutetiensis* and *S. equinus* confirming single gene phylogenetic trees. Within the *Sii* branch, *Sii* delineates, besides few minor branches, into a West and an East African dairy lineage as well as a third lineage that shares an association with bacteremia (Jans et al., 2016a). Potential human commensal isolates of mainly of European and Asian origin are distributed among sub branches of these main clades. Unfortunately, little background knowledge on host health status is available to draw relevant conclusions for some of the older *Sii* strains, including several strains identified as *S. bovis* or *S. equinus* under former taxonomy. In addition, the currently small strain pool of presumptive commensal *Sii* from humans does not yet allow for in-depth analyses of virulence traits in food, commensal and potentially pathogenic lineages. Thus, elucidation

of *Sii* prevalence, history, evolution and epidemiology requires the analysis of African human isolates to provide vital missing information.

#### 4.3. Literature re-evaluation of microbiota in raw and fermented milk focusing on dairy streptococci and *Sii* under consideration of the current state of knowledge

The new *Sii* variant and its novel pheno- and genotypic characteristics stimulated re-evaluation of previous studies on African dairy products reporting *S. thermophilus*, *S. salivarius* and *S. equinus* species (Table 1). Studies that identified *S. thermophilus* or *S. salivarius* were selected and subsequently assessed for the identification methods used. Past studies often had to rely on phenotypic assays, growth under different salt or temperature conditions, and API 50 CHL strips or *lacZ* functionality, which could not provide the resolution necessary to discriminate *Sii* and particularly the dairy-adapted African *Sii* variant from *S. thermophilus* or *S. salivarius* (Facklam, 2002; Jans et al., 2012b; Whiley and Hardie, 2009). These classifications were therefore considered uncertain, and the organisms were classified as potential novel *Sii* candidates requiring further confirmation.

DNA-based identification approaches were re-evaluated using current SBSEC taxonomy, sequence length and sequence identity (Jans et al., 2015; Schlegel et al., 2003). Generally, the differentiation between *Sii* and the *S. thermophilus*/*S. salivarius* group is supported by 96.0% sequence identity over 1544 bp between the two. Therefore, 16S rRNA sequence data identified as *S. thermophilus*/*S. salivarius* was considered reliable. Short sequence data for general SBSEC members in mabisi of Zambia (Schoustra et al., 2013) was re-evaluated and found to fit the *S. infantarius* branch of current SBSEC taxonomy. However, the short reads available of only 16S rRNA genes did not allow proper assignment of a species or subspecies. Therefore, these isolates were also considered as potential novel *Sii* candidates.

While *Sii* was not detected in FDP of North Africa, this *in-silico* pheno- and genotypic re-evaluation of published data (Table 1), as explained in the previous paragraphs, suggests a possibly wider distribution of SBSEC and *Sii* in sub-Saharan African dairy products from Cameroon, Chad, Ethiopia, Kenya, Tanzania and Zambia (Doutoum et al., 2013; Gonfa et al., 1999; Isono et al., 1994; Jiwoua and Milliere, 1990; Nyambane et al., 2014; Schoustra et al., 2013) and potentially also in raw camel milk from Morocco (Khedid et al., 2009). Certainly, this *in-silico* re-evaluation requires further confirmation that potential “*Sii* candidates” were disguised as *S. thermophilus*, but it is a key step in unravelling the role of *Sii* in African dairy fermentations. Furthermore, the seemingly wider distribution of *Sii* in sub-Saharan Africa and its detection in fermented food in Bangladesh (Jans et al., 2016a; Rashid et al., 2007) and Mexico (Díaz-Ruiz et al., 2003) (unpublished *Sii* MLST data, Kaindi et al. in preparation) supports the theory that it has a longer history of use in fermentation, which is one of the key pillars of establishing food fermentation bacteria for starter culture applications according to QPS (EFSA Panel on Biological Hazards, 2016).

*Sii* is not the only SBSEC member with a potential role in food fermentation. *Sgm* was a predominant microorganism in fermented dairy and plant foods of Bangladesh, Mexico, southern Europe and Nigeria (Jans et al., 2015; Oguntoyinbo et al., 2011). This suggests the involvement of *Sii* and other SBSEC in different ecological niches in food processing worldwide, with a potential hotspot in sub-Saharan Africa. In addition, the commensal occurrence of SBSEC and *Sii* in the gastrointestinal tracts of animals and humans, along with its presence in fermented food products, requires epidemiological research to clarify their phylogeny, host associations and ability to jump between ecological niches and hosts (Jans et al., 2015; Schlegel et al., 2003).

In Africa, where livestock, humans and food are closely interrelated within communities, there is an optimal setting to study these aspects of niche adaptation. The specific dairy adaptations only present in African *Sii*, and the strong link of these adaptations only to specific MLST branches, suggest that at least some *Sii* lineages could be food bacteria originating



from traditional FDP. Further thorough evaluation of potential virulence factors through comparative genomics and functional analysis of SBSEC is required to ensure that interventions and innovations (Jans et al., 2016b) such as designing novel starter cultures with optimized manufacturing processes can be implemented based on science.

## 5. Embedding interventions in the socioeconomic context

For more sustainable implementation, interventions must be developed around the pillars of food safety, food security, technology, community preferences and socioeconomics, with involvement of stakeholders from academia, governmental and regulatory authorities, producers and consumers (Swiss Commission for Research Partnerships with Developing Countries (KFPE), 2014). Food safety, security and technology are tightly connected to raw material quality, presence of zoonotic agents, spoilage and good manufacturing practices. Basic good manufacturing practices (GMPs) enhance food safety and quality by avoiding initial contamination, reducing pathogenic microorganisms (processing and heat treatment), avoiding recontamination (processing and storage) and preventing growth of microorganisms (transportation and storage). To be effective, such GMPs need to be tailored to the setting of rural Africa. Several aspects have to be considered, including the milk production systems of pastoralists, collection systems of milk cooperatives, varying technology standards, economics, cultural products and manufacturing preferences. Building on existing traditional preservation processes including FDP is likely a key element for acceptance and sustainability. Predominant local fermentative microorganisms represent a key component that gives FDPs their typical flavor. Such microorganisms must be considered when trying to enhance FDPs while retaining product characteristics and manufacturing processes. This in turn requires careful studies on handling, production, transportation and consumption patterns in the different communities to design incentives to use safer starter cultures.

## 6. Conclusion

African raw and FDP are predominated by many LAB and yeasts. Predominance of specific yeast species seems to be largely product specific. For LAB, *Lc. lactis*, *Sii* and several *Lactobacillus* spp. predominate in the products analyzed although their exact roles, prevalence and predominance might also be product-specific. Furthermore, the detection of associations between microorganisms, dairy animals and physicochemical properties is unfortunately still limited by the relatively small number of studies given the large diversity of raw and FDP in Africa, which highlights the need for more comprehensive studies on the technological microbiota of these products. The technologically important microorganisms are pivotal to building locally adapted starter cultures that could be used to enhance product quality and safety as well as improved food security. While several predominant species such as *Lc. lactis* or *Lb. fermentum* are typical for dairy products, African *Sii* variants represent a unique example of novel and well-adapted species variants in new ecosystems. *Sii* also exemplifies the recommendation formulated in this review to apply recent identification methods and taxonomy to detect and classify microorganisms to achieve innovations in uncharacterized ecosystems. As described for the African *Sii* variants, the safety of any novel food species or variant must be thoroughly evaluated. Standard safety evaluation procedures established by food safety agencies such as EFSA should serve as a foundation for such evaluations. Besides the absence of virulence factors, the history of safe use represents one of the main pillars of establishing food-grade microorganisms. Unfortunately, there is no written history of safe use of *Sii* in Africa. However, the data on dairy adaptation of African variants, separation of phylogenetic lineages and the re-evaluation of other studies suggest a widespread prevalence, predominance and contribution of *Sii* in milk fermentations across sub-Saharan Africa. These together indicate a potentially safe history of use of *Sii* variants in milk fermentation.

Nevertheless, further research is urgently needed to validate and assess *Sii* predominance beyond those confirmed for Kenya, Somalia, Sudan, Mali and Côte d'Ivoire, to evaluate potential virulence factors, evolution and epidemiology of *Sii* and to assess its individual lineages, given the millions of daily consumers across Africa. This research will contribute to the identification of variants, lineages or strains of *Sii* that might be considered as safe or unsafe for the food production process. Thereby, novel interdisciplinary research initiatives will have a strong impact in elucidating whether African *Sii* lineages could become a novel local food-grade *Streptococcus* lineage. The results of these initiatives will help develop local, sustainable and technologically feasible interventions and starter culture formulation to enhance food safety and security of locally-produced milk products in Africa.

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