

Microbiological characteristics of cheeses aged in animal skins and natural caves

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Azzouz Safae, Ahadaf Soumaya, Haouali Wessal, El Galiou Ouïam, Hassani Zerrouk Mounir, Laglaoui Amin*

Abdelmalek Essaâdi University, Faculty of Science and Technology, 416, Tetouan, Morocco

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*Corresponding author: bdd.azzsafae@gmail.com

Abstract

This review investigates the microbial communities present in cheeses aged in animal skin sacks and natural caves. These traditional aging techniques preserve cultural practices and contribute to the unique flavours and textures of cheese. Analysis revealed that cheeses aged in animal skins exhibit a higher number of shared species and a more complex bacterial composition than those aged in caves. The dominant species identified in skin-aged cheeses have shown to be *Lactococcus lactis*, *Lactiplantibacillus plantarum*, *Enterococcus faecalis*, and *Lactobacillus delbrueckii*, while cave-aged cheeses predominantly contain *Brevibacterium* species, *Lactococcus lactis*, and *Debaryomyces hansenii*, with *Kluyveromyces lactis* dominating the core microbiota. Additionally, cheeses aged in skin sacks exhibited a notable presence of anaerobic flora due to the enclosed environment, whereas the surface of cave-aged cheeses harboured more halophilic microorganisms due to salt treatments.

Keywords: natural caves; traditional aging; microbial communities; skin-aged cheeses; cave-aged cheeses

Introduction

The practice of aging cheeses in animal skin sacks is deeply rooted in history and is believed to have originated with the accidental discovery of cheese when milk was stored in a sheep's stomach, according to Shafiei Babil Oliaei (2017). Over time, this method evolved into the production of various cheeses, many of which are named after the specific skin sacks used for their maturation. For example, the Greek cheese Touloumotyri is named after the "touloumia" skin sack in which it matures (Pappa and Kondyli, 2023). Similarly, Turkish Tulum cheese takes its name from the word "tulum", which means animal skin sack, while the Greek Tomas cheese derives its name from the Greek word for "skin" or "leather" (Hayaloglu et al., 2007). In Lebanon, Darfiyeh cheese is named after "*Dariff*", the term for the goatskin sack used during its aging process (Serhan, 2008). "Mišina" is the Croatian word for animal skin sack, after which the Croatian sir iz mišine is named (Kalit et al., 2024). Other examples of cheeses traditionally aged in animal skin sacks include Bouhezza from Algeria, which is ripened in goatskin sacks called "*chekoua*" (Aissaoui Zitoun, 2014); Mehovo Sirene from Bulgaria, ripened in ewe skin sacks (Dimov et al., 2023); and Kurdish cheese, which is traditionally aged in goatskin sacks (Milani et al., 2014).

The cultural significance of these cheeses is profound, as they are often linked to specific regions and traditional practices, reflecting the local terroir and the rich cultural heritage that shapes these unique products (Tudor Kalit et al., 2020). Their distinctive characteristic lies in their ability to enclose the cheese in a humid environment with restricted gas exchange (Montel et al., 2005), fostering the development of intense flavours primarily driven by anaerobic lipolytic reactions (Kalit, 2017).

In the same context, natural caves have also been used in traditional cheese aging for centuries. Unlike modern industrial facilities, which rely on advanced systems to control temperature and humidity, caves offer a naturally stable microclimate (Farnham and Druart, 2011). Temperatures in caves typically range from 6 °C to 10 °C, with high humidity levels between 95 % and 98 %. These conditions are maintained through natural ventilation systems, often facilitated by vertical cracks, known as *fleurines* that allow a constant exchange of air (Kindstedt, 2012). While industrial cheese production has largely shifted towards controlled environments, several traditional cheeses such as Pecorino di Filiano, Cabrales, Roquefort, Taleggio, Gorgonzola, and Stilton varieties continue to be aged in natural caves, which remain crucial to their production process (Donnelly, 2017).

The slightly warmer temperature of caves, when compared to modern refrigeration, promotes the growth of a variety of microorganisms essential for cheese maturation. Bacteria, moulds, and yeasts thrive in these environments, contributing to the breakdown of proteins and fats, which enhances flavour development (Sennett, 2017). Cheeses aged in natural caves often host a diverse range of fungal species. Commonly found genera include *Alternaria*, *Chrysosporium*, *Geotrichum*, *Mucor*, and *Penicillium* (Marcellino and Benson, 2014).

Cheeses aged in animal skins or natural caves are exposed to complex microbial ecosystems, which play a crucial role in the fermentation, ripening, and overall quality of the final product. This review aims to identify the dominant, shared, and variable microbial species found in cheeses aged in animal skins and natural caves. By examining various case studies, the aim is to gain insights into the key microbiota that influence both the fermentation and ripening processes within these traditional aging environments.

Cheeses aged in animal skins

Animal skin sacks

Animal skins, particularly from sheep and goats, have historically played a key role in the traditional aging of a variety of cheeses (Shafiei Babil Oliaei, 2017). These skins serve as natural containers, providing unique conditions that influence the ripening process and the final characteristics of the cheese.

The use of either the inner or outer side of skin bags varies according to the type of cheese. For instance, Tulum cheese in Turkey is aged using the inner side of the skin bag (Tekin and Guler, 2019). In contrast, Greek Touloumotyri and Algerian Bouhezza cheeses are ripened using the outer side (Senoussi et al., 2022; Pappa and Kondyli, 2023).

The raw goat skin comprises four main layers: the outer epidermis, the dermal surface containing hair follicles (where hair originates), the dermal-epidermal junction, and the endoderm, which forms the primary part of the dermis used in leather production. The endoderm consists of fiber bundles whose density and interweaving determine the texture and strength of the leather. Leathers that are resilient and elastic have a well-interlaced structure with dense fibers and are less penetrated by hair follicles. Indeed, goatskins are preferred because they are stronger and less penetrated by twisted hair follicles compared to sheepskins, resulting in firmer leathers suitable for a variety of uses (Serhan, 2008).

In terms of chemical composition, raw goatskins contain 60-70 % water, 25-32 % protein, 2.2-3.2 % fiber protein, and 7-7.3 % crude fat. The high protein content, particularly collagen, which forms strong protein-binding bonds in a triple helix structure, contributes to their strength and durability (Hakim et al., 2021).

The microscopic analysis of *chekoua*, a type of goatskin sack used in Bouhezza cheese production, reveals a distinctive surface characterized by wrinkled folds and thick, well-defined fibers. These skins exhibit pores of varying diameters, ranging from less than 50 µm to over 100 µm, enhancing their ability to interact with the environment. Microscopic observations further revealed the microbial enrichment of *chekoua*'s biofilm after contact with Lben, a traditional beverage obtained by partial skimming of spontaneously fermented milk (Aissaoui Zitoun et al., 2011). The use of Lben in *chekoua*'s preparation serves both to neutralize odours (Medjouj et al., 2017) and to enrich the microbial communities within the skin sacks (Aissaoui Zitoun, 2014). The microorganisms identified in *chekoua* after contact with Lben included diplococci, bacilli, and yeasts (Aissaoui Zitoun, 2014). Thus, it can be concluded

that the contact between Lben and *chekoua* promotes the transfer of microbial communities, which in turn play a crucial role in the development of the distinct microbiological characteristics of traditionally aged cheeses (Senoussi et al., 2024).

As previously discussed, goatskins are of exceptional quality and ideal for fabricating ripening containers. However, producing these containers requires meticulous techniques to avoid damaging the skin and to maintain the anaerobic conditions essential for the cheese ripening process (Tudor Kalit et al., 2010). The production methods for Tulum, Bouhezza, and Darfiyeh goatskin sacks illustrate both shared practices and distinct approaches tailored to regional cheese-making traditions. Tulum skins, as outlined by Hayaloglu et al. (2007), involve scraping off meat and fat residues, sprinkling with salt, and drying in shaded, low-moisture areas. On the other hand, Darfiyeh skins, described by Serhan et al. (2010), emphasize internal salting that lasts for 10 days, with subsequent removal of excess salt using a knife. Similarly, Bouhezza skins, detailed by Senoussi et al. (2022), undergo a process that includes, besides salting, depilation of the skin through putrefaction, treatment with juniper, and overnight filling with Lben. Salt is crucial across all methods for skin preservation and microbial control while juniper serves as both a deodorant and an antibacterial agent (Aouadi et al., 2021). These diverse preparation techniques underscore regional adaptations aimed at maintaining the structural integrity and microbial balance crucial for effective cheese ripening.

Throughout the ripening process, regular cleaning and occasional soaking of Bouhezza skins (Aissaoui Zitoun, 2014), along with periodic salting of Darfiyeh goatskins (Serhan et al., 2008), contribute to sustaining their effectiveness and cleanliness (Aissaoui Zitoun, 2014; Serhan et al., 2008).

Animal skins and modern ripening containers

Historically, the use of animal skins for milk storage emerged from the practical need to transport milk. Animal stomachs were naturally suited for this purpose as they were readily available and could be easily sealed. The enzymes present in the stomachs facilitated the curdling of milk, which increased its shelf life by turning it into curds through acidification (Fox et al., 2016). This method of storage was a practical solution that early civilizations employed to extend the usability of milk, leveraging the natural properties of these organic containers.

Expanding on this traditional practice, goat skins have long been integral to cheese-making, yet their acquisition has become increasingly challenging (Erginkaya et al., 2020), primarily due to the laborious and time-intensive preparation process (Pappa and Kondyli, 2023). This difficulty has been compounded by factors such as declining animal populations, economic constraints, and logistical hurdles (Tekin and Guler, 2021). Consequently, alternative materials such as wood, plastic, and earthenware have gained popularity. Among these options, plastic containers have emerged as a preferred choice due to their widespread availability and affordability (Cakmakci et al., 2007). However, despite their prevalent use, goatskin bags offer distinct advantages

that justify their continued use, particularly in artisanal and specialty cheese production: Hygienic advantages. Goatskin bags exhibit superior hygienic qualities compared to plastic containers (Shafiei Babil Oliaei, 2017). Research by Cakmakci (2007) demonstrated higher levels of *Enterococcus faecalis* isolates in cheeses aged in plastic containers than in those aged in goatskin bags. Similarly, Hayaloglu et al. (2007) found higher microbial counts in cheeses aged in plastic barrels compared to those in goatskin bags.

Physicochemical properties. According to Shafiei Babil Oliaei (2017), goatskin sacks have superior porosity compared to plastic barrels, enabling cheeses to rapidly lose moisture and achieve the desired textural characteristics. Indeed, Hayaloglu et al. (2007) reported that cheeses ripened in goatskin sacks exhibit lower moisture content and higher levels of protein, fat, and salt-in-moisture than those matured in plastic containers. Quantitative differences in some volatile and aroma compounds were also observed, underscoring the influence of the ripening environment on flavour development. Moreover, Cakmakci et al. (2011) demonstrated that proteolysis is more extensive in cheeses aged in goatskin sacks, as evidenced by elevated levels of TCA-soluble and phosphotungstic acid-soluble nitrogen fractions.

Sensorial preferences. Attempts to use plastic barrels for aging certain cheeses, such as Tulum, have often resulted in lower acceptability among panellists (Tekin and Guler, 2021). Panel preference studies consistently show a stronger preference for cheeses aged in goatskin bags, highlighting their superior sensory attributes. The natural materials of goatskin contribute to the unique aroma and flavour profiles desired by discerning consumers and cheese enthusiasts.

Case studies of skin bag cheeses: Microbiological aspects

Cheeses aged in animal skins are a rare tradition, particularly those that are acid-coagulated (Kamber et al., 2007). One such example is Bouhezza cheese, which relies on spontaneous fermentation and coagulation. This cheese is primarily crafted by gradually adding salted Lben throughout the aging process, with raw milk introduced in the final weeks of maturation (Aissaoui Zitoun, 2014). Tulum cheese, on the other hand, undergoes coagulation, draining, and salting before being placed into its skin bag (Demirci et al., 2021). Similarly, Darfiyeh cheese is coagulated and drained before being introduced into the skin bag along with whey cheese prepared from raw goat milk added to scalded whey (Serhan et al., 2009) (see Table 1).

In this review, we compared the bacterial communities reported in previous studies of four cheeses aged in animal skins: Bouhezza, Tulum, Darfiyeh, and Mehovo Sirene, alongside *chekoua*, the goatskin used for aging Bouhezza cheese. Table 2 compiles bacteria found commonly across at least two ecosystems. Table 3 details bacteria exclusively found in either one ecosystem.

Shared microbiota between skin bag cheeses. Two species frequently employed in cheese-making technology, *Lactococcus lactis* and *Lactiplantibacillus plantarum*, were detected in all analyzed cheeses. These species belong to the

Table 1. Characteristics of selected cheeses ripened in animal skin sacks

Properties	Tulum	Darfiyeh	Bouhezza	Mehovo sirene
Milk type	Raw goat, ewe and cow milk	Raw goat milk	Cow milk	Raw ewe milk
Starter addition	No	No	No	No
Bag type	Goat skin	Goat skin	Goat skin	Ewe skin
Steps prior to aging in skin bags	Tulum's Curd preparation: - Coagulation - Curd's heat treatment (45-55 °C) - Drainage - Salting	Darfiyeh's curd preparation: - Coagulation - Drainage Whey cheese preparation: - Whey boiling - Raw goat milk	Lben preparation and salting	ND
Ripening T°	10 °C for one week 4 °C for 6 months	10-12 °C	26.8 °C	In cellars at ambient temperature
Sampling interval during ripening	7 days - 6 months	20 days - 2 months	45 days - 4 months	5 months
Coagulation method	Renneting	Renneting	Spontaneous fermentation	Spontaneous fermentation
Country of origin	Turkey	Lebanon	Algeria	Bulgaria
Cheese type	Semi-hard	Semi-hard	Soft	Semi-hard
References	Demirci et al. (2021)	Serhan et al. (2009)	Aissaoui Zitoun (2014)	Dimov et al. (2023)

^aNot determined

genera most commonly isolated from artisanal cheeses made with raw milk (Azzouz et al., 2024a). *Lactococcus lactis* is renowned for its acidifying and aromatic properties and is extensively used as a starter culture in the cheese industry. On the other hand, *L. plantarum* is recognized for its enzymatic activities that primarily contribute during the ripening process (Corsetti and Valmorri, 2011; Bintsis and Athanasoulas, 2014). Notably, *L. plantarum* was also detected in *chekoua* used for aging Bouhezza cheese (Senoussi et al., 2024), suggesting a potential transfer from *chekoua* to Bouhezza cheese.

Enterococcus faecalis was also found in all four cheeses. This species is ubiquitous (Giraffa, 2003) and was found to be dominant in diverse raw milk cheeses such as Iranian Koozeh and Lighvan cheeses, as well as the artisanal PDO Ossau-Iraty cheese (Edalatian et al., 2011a; Edalatian et al., 2011b; Feutry et al., 2012). Although enterococcal species are commonly used as indicators of faecal contamination in water (Tamai and Suzuki, 2023), studies have demonstrated that their presence in food products does not necessarily indicate poor hygienic practices (Biorollo et al., 2001).

The cheeses investigated in this study also revealed the presence of thermophilic bacteria, such as *Lactobacillus delbrueckii*, *Lactobacillus helveticus*, and *Streptococcus thermophilus*. These species are commonly used as starter cultures in the production of various dairy products (Cogan, 2014a). *Lactobacillus delbrueckii* was detected in all cheeses except Darfiyeh. Its presence in Bouhezza cheese could be attributed to the goatskin used for aging, as this species was also found in *chekoua*. Alternatively, it may originate from the Lben used in Bouhezza production, as *L. delbrueckii* is known to be present in naturally fermented milk. This species, characterized by its proteolytic, aromatic, and preservative properties, is globally used in the production of fermented milk products (Teixeira, 2014). *Streptococcus thermophilus* was found in both Darfiyeh and Mehovo sirene cheeses. This

species is a versatile starter used in producing various dairy products, including yogurt, fermented milks, and cheeses (Gobbetti and Calasso, 2014). In Darfiyeh cheese, its presence is likely due to the boiled whey used during the cheese-making process (Serhan et al., 2009).

Lactobacillus paracasei has been identified in Tulum and Bouhezza cheeses as well as in *chekoua*. Importantly, research by Serhan et al. (2009) demonstrated that *Lb. paracasei* was not present in Lben prior to its contact with *chekoua*. This species was originally found in *chekoua* and subsequently appeared in Lben after their interaction, indicating a transfer of this bacterium. *Lactobacillus paracasei* is a key component of various fermented milks (Litopoulou-Tzanetaki and Tzanetakis, 2014) and is commonly found in semi-hard and hard cheeses (Ozer, 2014). This species may occur as a contaminant in milk or cheese-making equipment (Gobbetti and Minervini, 2014). However, when intentionally introduced as a secondary culture in fermented milk, *Lb. paracasei* is valued more for its health-promoting benefits than for its acidification capabilities (Gobbetti and Minervini, 2014).

Lactococcus cremoris has been identified in Darfiyeh and Bouhezza cheeses, as well as in *chekoua*. Its presence in Bouhezza cheese can thus be explained by its occurrence in *chekoua*, as well as by its presence in Lben, which is used in the production of Bouhezza cheese (Senoussi et al., 2024). *Lactococcus cremoris* primarily originates from contamination during milking (Demarigny, 2014). However, it is also often intentionally used as a mesophilic starter culture due to its acidifying and aromatic properties (Chandan, 2014). Some strains of *L. cremoris* are noted for their high salt tolerance and are used in the production of white-brined cheeses (Ozer, 2014). This tolerance may account for its presence in *chekoua*, which is prepared with salt, and in Darfiyeh and Bouhezza cheeses, which are produced using

significant amounts of salt (Serhan et al., 2009; Aissaoui Zitoune, 2014).

Staphylococcus equorum was detected in Mehovo Sirene and Bouhezza cheeses, as well as in *chekoua*. This species is coagulase-negative (Irlinger et al., 2012) and has never been associated with diseases (Cogan, 2014b). *Staphylococcus equorum* is predominant in the microbiota of various fermented food products, such as Galician chorizo (Fonseca et al., 2013), Sardinian fermented sausages (Mangia et al., 2024), llama sausage (Rebecchi et al., 2020), Vorarlberger Bergkäse cheese (Schornsteiner et al., 2014), French cheeses (Coton et al., 2010), and Mehovo Sirene cheese, where it constitutes over 50 % of the total bacterial population (Dimov et al., 2023). The presence of *S. equorum* in Bouhezza cheese and its goatskin sack can be explained by its halophilic nature. This species thrives in salty environments and has been isolated from cheese brines used in Danbo cheese production (Haastrup et al., 2018) and from the surfaces of various French cheeses using salt-based media (Kothe, 2021).

Two species from the genus *Eubacterium*, *Eubacterium rangiferina* and *Eubacterium tenue*, were identified in Tulum and Darfiyeh cheeses, respectively. Being a significant component of the adult intestinal microbiota (Taban et al., 2014), dairy wastewaters (McGarvey et al., 2004), and the faecal microbiome of beef cattle (Corrêa et al., 2021), *Eubacterium* species are likely present in these cheeses due to faecal contamination. Furthermore, their persistence during the ripening process is likely supported by the

anaerobic conditions within the aging bags.

Lactobacillus brevis was identified in both Tulum and Bouhezza cheeses, likely due to its microaerophilic nature (Teixeira, 2014). This species is a key member of the non-starter lactic acid bacteria (NSLAB) group, commonly found in various cheeses, such as Pecorino Abruzzese (Centi et al., 2017), Motal (Azizi et al., 2017), and Nicastrese (Pino et al., 2018). This species is known for its high proteolytic activity (Zaaraoui et al., 2021), antibacterial activity (Dehghani Champiri et al., 2022; Abarquero et al., 2023) and its ability to produce volatile compounds (Pino et al., 2018).

Lactococcus garvieae was identified in Tulum and Mehovo Sirene cheeses. This species is more commonly associated with infections in fish, ruminants, and humans (Gibello et al., 2016). However, it has been previously detected in certain cheeses such as Moroccan *Jben*, Italian goat cheese (Colombo et al., 2010; Azzouz et al., 2024b), and notably, as a dominant species in Mozzarella cheese (Morea et al., 1999; De Angelis et al., 2006).

Streptococcus gallolyticus, found in Tulum and Bouhezza cheeses, belongs to the *S. bovis* group, which is associated with animal and human diseases (Sanhoun et al., 2020). However, *S. gallolyticus* subsp. *macedonicus* found in Bouhezza cheese is considered non-pathogenic (Gobbetti and Calasso, 2014). This facultative anaerobic species (Andyanti et al., 2019) is promising as NSLAB and has been found in several cheeses, including Vastedda della Valle del Belice (Gaglio et al., 2013) and Sprezza delle Giudicarie (Andrighetto

Table 2. Commonly found bacteria across skin bag cheeses and *chekoua* skin bag

Species	Tulum	Darfiyeh	Bouhezza	Mehovo sirene	Bouhezza goat skin ^a
<i>Lactococcus lactis</i>	X	X	X	X	
<i>Lactiplantibacillus plantarum</i>	X	X	X	X	X
<i>Enterococcus faecalis</i>	X	X	X	X	
<i>Lactobacillus delbrueckii</i> subsp. (<i>lactis/bulgaricus</i>)	X		X	X	X
<i>Lactobacillus helveticus</i>	X		X		
<i>Lactobacillus paracasei</i>	X		X		X
<i>Lactococcus cremoris</i>		X	X		X
<i>Streptococcus thermophilus</i>		X		X	X
<i>Staphylococcus equorum</i>			X	X	X
<i>Enterococcus durans</i>	X	X			
<i>Enterococcus faecium</i>	X	X			
<i>Eubacterium</i> spp. (<i>rangiferina/tenue</i>)	X	X			
<i>Lactobacillus Brevis</i>	X		X		
<i>Lactococcus garvieae</i>	X			X	
<i>Streptococcus gallolyticus</i>	X		X		
<i>Clostridium</i> spp.	X	X			
<i>Weissella paramesenteroides</i>	X			X	
<i>Escherichia coli</i>		X		X	
<i>Limosilactobacillus fermentum</i>				X	X
<i>Leuconostoc mesenteroides</i>			X		X
References	Demirci et al. (2021)	Serhan et al. (2009)	Aissaoui Zitoun (2014)	Dimov et al. (2023)	Senoussi et al. (2024)

^aThe biodiversity results for both *chekoua* and Bouhezza cheese are derived from different production methods and studies.

et al., 2004), as well as other dairy products like Koumiss (Zhou et al., 2020).

The presence of the *Clostridium* genus in both Tulum and Darfiyeh cheeses is primarily attributed to the anaerobic conditions that prevail in the aging bags. Species belonging to this genus are involved in the industry and in disease-related cases. They are phylogenetically very heterogeneous, with the most feared being *C. botulinum* and *C. perfringens* due to their foodborne origin and pathogenic traits (Blaschek, 2014). Other species are associated with the blowing defect in cheeses such as Grana Padano. For instance, *C. tyrobutyricum* and *C. butyricum* were found to be among the most prevalent *Clostridium* species in 83 analysed Grana Padano spoiled samples (Bassi et al., 2015).

Tulum and Mehovo Sirene cheeses also shared the species *Weissella paramesenteroides*. The genus *Weissella* belongs to the family *Leuconostocaceae*, which can thrive under anaerobic conditions, explaining its occurrence in cheeses ripen in animal skin sacks. *Weissella paramesenteroides*, in particular, is commonly found in artisanal cheeses that rely on environmental flora for ripening and/or are made from raw milk (Dimov, 2023). For example, Raclette cheese made with raw milk has been characterized by the dominance of *W. paramesenteroides* (Egger et al., 2021). This species has also been found in other traditional cheeses such as Kırklareli white brined cheese (Çetin et al., 2024) and artisanal milk cheese from China (Shi et al., 2018).

Escherichia coli was detected in both Mehovo Sirene and Darfiyeh cheeses, confirming its common occurrence in raw milk cheeses (Azzouz et al., 2024a). *Escherichia coli* is a common inhabitant of the intestines of both humans and animals, encompassing non-pathogenic and pathogenic strains. Therefore, its presence in food does not directly imply a health risk (Batt, 2014). Nevertheless, it is important to note that *E. coli* is classified as part of the coliform group, which is widely recognized as a key indicator of hygiene in food products (Sandle, 2014).

The species *Limosilactobacillus plantarum* was notably found in Mehovo Sirene cheese and in *chekoua* used for Bouhezza ripening. This species is capable of growing under both aerobic and anaerobic conditions and is widespread. It is commonly found in the guts of humans and animals, in fecal samples (Ksiezarek et al., 2022), and in fermented vegetables (Tigrero-Vaca et al., 2022). Recognized as generally safe (Zhao et al., 2022), *L. plantarum* is valued for its probiotic (Murtaza et al., 2024) and antibacterial properties (Sornsene et al., 2024). Additionally, it has been identified in various dairy products such as Bulgarian yogurt (Ivanov et al., 2021), Brazilian Buffalo Mozzarella (Silva et al., 2021), and artisanal Feta-type Kefalonian cheese (Lappa et al., 2024).

The species *Leuconostoc mesenteroides* was identified in both Bouhezza cheese and *chekoua*. Interestingly, in the investigations by Senoussi et al. (2024), this species was absent in the Lben used to prepare *chekoua* but was found in both the fresh and dried *chekoua* used for Bouhezza aging. According to the same research, contact of Lben with *chekoua* for 30 minutes, 60 minutes, and overnight did not result in the transfer of *Ln. mesenteroides* from *chekoua* to Lben. This might be due to the species being present in insufficient levels (possibly because of the lack of favorable conditions) and therefore not appearing in the DGGE profiles, where it could have been masked by the amplification of more abundant species. It appears that this species becomes active during the later stages of aging. In fact, the study by Aissaoui Zitoun (2014) on Bouhezza cheese detected *Ln. mesenteroides* between the 7th and 21st days of ripening.

Comparing the biodiversity of *chekoua* with that of Bouhezza cheese reveals that all species found in *chekoua* were also present in Bouhezza cheese, except for *S. thermophilus*, *L. fermentum*, and *Brevibacterium casei* (Figure 1). It is important to note that the biodiversity results for both *chekoua* and Bouhezza cheese are derived from different productions and studies. This consistency suggests that the two studies may have been conducted

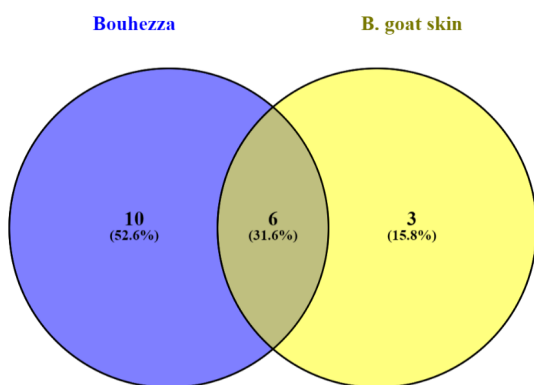
Table 3. Variable microbiota found in skin bag cheeses

Cheeses	Tulum (Mut region)	Darfiyeh	Bouhezza	Mehovo sirene
Detection method	DGGE ^a	TTGE ^b	TTGE	NGS ^c
Identified species	<i>E. hirae</i> <i>S. lutetiensis</i> , <i>S. alactolyticus</i> <i>S. suis</i>	<i>E. malodoratus</i> , <i>Lb. curvatus</i> , <i>S. haemolyticus</i> ,	<i>B. cereus</i> <i>C. variabil</i> <i>C. flavescent</i> <i>Lb. buchneri</i> <i>S. xylosus</i>	<i>Lb. kefirano</i> faciens, <i>L. raffinolactis</i> , <i>L. coryniformis</i> . <i>S. parauberis</i> <i>E. italicus</i> <i>T. halophilus</i> <i>T. muriaticus</i> <i>Schmidhempelia</i> subsp. <i>S. alvi</i> <i>G. apicola</i> , <i>B. apis</i> <i>F. perrara</i> <i>L. apis</i> <i>B. asteroides</i> <i>B. pseudolongum</i>
References	Demirci et al. (2021)	Serhan et al. (2009)	Aissaoui Zitoun (2014)	Dimov et al. (2023)

^aDGGE = Denaturing Gradient Gel Electrophoresis

^bTTGE = Temporal Temperature Gel Electrophoresis

^cNGS = Next Generation Sequencing



B. goat skin = Bouhezza goat skin (chekoua)

Figure 1. Venn diagram of similar and different microbial communities (the number and percentage) between Bouhezza goat skin and Bouhezza cheese

in the same geographical area, highlighting the resilience of the microbiota. However, the observed variability may be attributed to prevailing environmental conditions and differences in sampling and analysis techniques used in each study. Additionally, it is possible that these bacteria were initially present in *chekoua* but did not persist or develop in the final cheese due to competition with other microbes or changes in environmental conditions. Another observation is that *E. faecalis*, *Lb. helveticus*, and *S. gallolyticus* subsp. *macedonicus* appeared as dominant species in *chekoua* used for Bouhezza production after contact with the Lben during *chekoua*'s preparation. This suggests that these species in Bouhezza cheese are likely introduced by the Lben used in its production rather than through direct transfer from *chekoua* to Lben during Bouhezza cheese making.

The second Venn diagram (Figure 2) illustrates the percentages of similarity and dissimilarity among the four cheeses. It shows that the cheeses with the highest number of shared species are Bouhezza and Tulum, with eight common species; whereas the cheeses with the fewest shared species are Darfiyeh and Bouhezza, with only four species in common. This variation could be attributed to factors such as geographical and climatic conditions, manufacturing practices, and interactions between microorganisms.

Based on a study documenting microorganisms frequently detected in various types of raw milk cheeses (Azzouz et al., 2024a), species such as *L. fermentum*, *S. gallolyticus*, and *S. equorum* are rarely encountered, appearing in only one or two cheeses. The presence of the first two species may be due to their ability to thrive in anaerobic environments, while the third species is noted for its halophilic nature. Additionally, species such as *E. rangiferina* and *E. tenue* were not found in any of the cheeses included in the study (Azzouz et al., 2024a). This may be due to their strictly anaerobic nature, which allows them to flourish in confined environments like skin bags.

Variable microbiota of skin bag cheeses. In addition to the shared microbial communities previously discussed, each

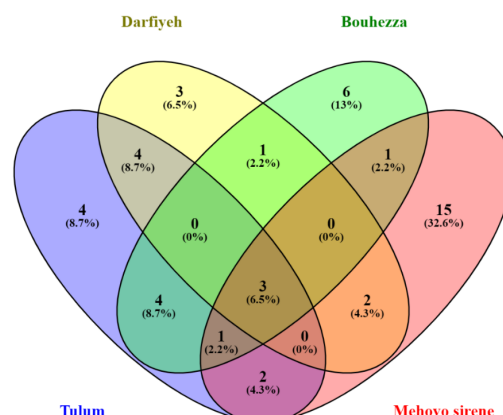


Figure 2. Venn diagram of similar and different microbial communities (the number and percentage) between four skin sacks aged cheeses: Mehovo Sirene, Bouhezza, Tulum and Darfiyeh

of the four skin sack cheeses studied contains a unique microbiota (Table 3), whose members contribute to the cheese's distinct characteristics. These include:

- Probiotic activities: *Lactobacillus coryniformis* and *Bifidobacterium pseudolongum* (Yu et al., 2022; Zhang et al., 2023).
- Bacteriocin production: *Enterococcus hirae* and *Enterococcus italicus* (El-Ghaish et al., 2015; Merlich et al., 2019).
- Potential GABA production: *Enterococcus malodoratus* (Cunha et al., 2022).
- Halotolerant bacteria: *Corynebacterium* and *Tetragonococcus* (Cogan, 2014b; Mullan, 2014; Innocente et al., 2023).
- Fermented milk-related species: *Lactobacillus kefirifaciens* (kefir) and *Lactobacillus buchneri* (koumiss) (Ozer and Kirmaci, 2014).
- Disease-related species in humans or animals: All *Streptococcus* species, *Bacillus cereus*, and *Staphylococcus haemolyticus* (Beattie and Williams, 2014; Gobetti and Calasso, 2014; Nunez, 2014; Crippa et al., 2024; Chakrabarty et al., 2024).
- Promising Starter Species: *Lactococcus raffinolactis* (Kimoto-Nira et al., 2012).
- Flavour-Developing NSLAB: *Lactobacillus curvatus* (Cogan, 2014a).

Safety aspects of cheeses aged in skin bags

Cheeses aged in skin bags, while contributing unique flavours and characteristics, also present certain safety concerns. The microbiological safety of these cheeses can vary significantly, with some reported instances highlighting potential risks. For instance, Croatian cheese matured in lamb skin sacks was found to have higher counts of staphylococci and enterobacteria than those permitted by food safety regulations. This included a high incidence of *Staphylococcus aureus* and the detection of staphylococcal enterotoxins, which are linked to foodborne illnesses (Frece et al., 2016). Furthermore, Kurdish cheese

made from thermised ovine milk and ripened in goatskins exhibited contamination with coliforms, *E. coli*, *Salmonella*, and staphylococci before reaching 60 days of ripening (Milani et al., 2014). Similarly, 13 % of animal skin sack cheeses from Herzegovina failed to meet microbiological quality standards due to elevated levels of β -glucuronidase-positive *Escherichia coli* (Sesar et al., 2022). Another concern involves fungal contamination. For example, *Penicillium roqueforti*, the dominant fungal species in Moldy Civil cheese, has been found to produce mycotoxins. As a result, this cheese, made using natural flora, can pose health risks. In addition to fungal risks, the presence of antibiotic-resistant bacteria has also been documented. A study on artisanal Tulum cheese from the Taurus Mountains revealed that it harbors *E. faecium* strains resistant to several antibiotics, including gentamicin, kanamycin, streptomycin, and erythromycin (Özkan et al., 2021).

Cheeses aged in natural caves

The origins of cheeses matured in natural caves are often associated with the discovery of Roquefort cheese. According to legend, Roquefort was first created when a herder abandoned his meal of fresh cheese and bread in a cave. Upon returning weeks later, he found the cheese transformed, veined with blue mould, revealing the unique effects of cave environments on cheese maturation (Betancourt, 2013).

Roquefort is one of the earliest cheeses to be officially recognized for its aging in natural caves. In 1411, King Charles VI of France granted the people of Roquefort exclusive rights to mature their cheese in the caves of Combalou, securing the traditional method of production and boosting the cheese's

renown. This royal decree not only protected the unique cave-aging process but also contributed to Roquefort's enduring reputation as a prestigious blue cheese (Verdellet, 2017).

Since that time, natural caves have continued to play a vital role in the production of numerous well-known cheeses, such as Cabrales, where similar environmental conditions help foster the development of blue moulds that define their distinct flavours and textures (Harbutt, 2017).

Cabrales is primarily made from cow's milk, with seasonal additions of goat and sheep's milk. The curd, which is intensely acidic and left unpressed, allows the natural blue mould to penetrate easily. Cabrales cheeses are coated with coarse salt before they are transported to natural caves for an extended maturation period. Within these caves, the stable humidity and cool temperatures foster the growth of *Penicillium roqueforti*, which infuses the cheese with its signature pungent and spicy flavour. Traditionally wrapped in sycamore leaves, Cabrales is now typically packaged in green foil to comply with modern health regulations (Harbutt, 2017).

In addition to Cabrales, this section will also explore other case studies such as Fontina PDO and Pecorino di Filiano PDO, which are similarly matured in natural caves (see Table 4 for more details).

Surface microbiota

This section describes the bacterial and fungal populations found on the surface of Fontina, Pecorino, and Cabrales cheeses.

Based on the data from Table 5, particularly regarding the bacterial populations, species from the *Brevibacterium* genus were detected on the surface of both Fontina and Pecorino cheeses. This genus is part of the coryneform

Table 4. Characteristics of selected cheeses aged in natural caves

Cheeses properties	Fontina PDO cheese	Pecorino di Filiano PDO	Cabrales
Country of origin	Italy	Italy	Spain
Cheese type	Surface-ripened	Surface-ripened	Blue-veined
Milk used	Raw cow's milk	Heated ewe's milk (68 °C - 20s)	Raw cow's milk (seasonal additions of raw goats' and sheep's milk)
Starters	<i>S. thermophilus</i> and/or <i>L. lactis</i>	Not added	Not added
Method of salting	Dry salted and brine washed (1 st month)	Salt can be added as a dry rub or brine before ripening	Covered in coarse salt before ripening
Curd processing	Heated (46-48 °C) Pressed	Heated (60-65 °C) Manually pressed	Not heated Not pressed
Ripening time	3 months (5-12 °C)	4 months (12-14 °C)	2 months (9-12 °C)
Used techniques for microbial identification	Plating/PCR-DGGE	RAPD, 16S-23S rDNA ISR, ARDRA, Species-specific PCR (Bacterial populations) Restriction analysis of 18S and ITS regions (Fungal populations)	PCR-DGGE
Sampling interval during ripening	1-84 days	0-120 days	Day 60
Targeted microbial populations	Fungal/bacterial populations	Bacterial populations (study 1) Yeasts populations (study 2)	Bacterial and fungal populations
Targeted part of the cheese	Surface	Surface and core	Surface and core
References	Dolci et al. (2009)	Bonomo and Salzano (2012) Capece et al. (2009)	Flórez and Mayo (2006)

group, which is frequently linked to smear-ripened cheeses (Cogan, 2011a), especially in the later phases of maturation (Gobbetti and Rizzello, 2014). Their ability to thrive in these environments is largely due to their salt tolerance, with some strains capable of withstanding salt concentrations as high as 20 % (Forquin and Weimer, 2014). These bacteria are typically introduced through the brine used for salting, but can also be transferred via aging shelves and manual handling during the cheese-making process (Cogan, 2011a). Within the *Brevibacterium* genus, *Brevibacterium linens* stands out as the most relevant species in the food industry (Mullan, 2014). It is renowned for producing proteolytic and lipolytic enzymes (Cogan, 2011b), as well as volatile and antimicrobial compounds, including bacteriocins (Ratray and Eppert, 2011). Additionally, *Brevibacterium* plays a key role in the distinctive orange pigmentation that develops on the cheese surface during ripening (Cogan, 2011b). An interesting aspect of these bacteria is their dependence on yeasts and moulds, such as *Debaryomyces hansenii*, which was also detected on the surface of both Fontina and Pecorino cheeses. These yeasts metabolize lactate and raise the pH, creating favorable conditions for the growth

of *Brevibacterium* and other coryneform bacteria, such as *Corynebacterium* and *Arthrobacter*, as these bacteria cannot proliferate in environments with a pH lower than 6 (Mullan, 2014).

Fontina cheese also showed the presence of other genera from the coryneform group, such as *Corynebacterium* and *Arthrobacter*. This may be due to the prolonged salting process it undergoes, unlike Pecorino and Cabrales cheeses, which are salted only once before ripening (Table 5). The genera *Corynebacterium* and *Arthrobacter* are also among the main coryneform bacteria found on the surface of smear-ripened cheeses, alongside *Brevibacterium* (Cogan, 2011a). The *Corynebacterium* species identified in Fontina cheese is *Corynebacterium glutamicum*. This bacterium is widely known in the pharmaceutical industry for its role in the fermentation of amino acids, especially glutamic acid, from which it derives its name. However, it also plays a role in cheese production (Gopinath and Nampoothiri, 2014).

The genus *Arthrobacter* was represented in Fontina cheese by the species *Arthrobacter nicotianae*, a strictly aerobic bacterium (Gobbetti and Rizzello, 2014). It is recognized for its role in producing aromatic compounds and contributing to

Table 5. Microbiology of cheeses matured in natural caves

Microbiota	Fontina PDO cheese	Pecorino di filiano PDO ^a	Cabrales
SURFACE			
Bacterial populations	<i>L. lactis</i> <i>Brevibacterium</i> sp. <i>B. casei</i> <i>S. thermophilus</i> <i>M. mesophilicum</i> <i>A. nicotianae</i> <i>C. glutamicum</i>	<i>Brevibacterium linens</i> <i>Lb. paracasei</i> <i>Lb. delbrueckii</i> <i>Ln. mesenteroides</i> <i>Ln. lactis</i> <i>P. acidilactici</i>	<i>L. lactis</i> <i>Lc. garvieae</i> <i>Lc. raffinolactis</i> <i>S. equorum</i> <i>Lb. farciminis</i> <i>Lb. casei</i> <i>L. plantarum</i>
References	Dolci et al. (2009)	Bonomo and Salzano (2012)	Flórez and Mayo (2006)
Fungal populations	<i>D. hansenii</i> <i>Candida. sake</i> <i>Goetrichum silvicola</i> <i>Torulaspora delbrueckii</i> <i>Trichotecium domesticum</i> <i>Fusarium solani</i>	<i>D. hansenii</i> <i>K. lactis</i>	ND ^b
References	Dolci et al. (2009)	Capece et al. (2009)	-
CORE			
Bacterial populations	ND	<i>Lb. paracasei</i> <i>Ln. mesenteroides</i> <i>Ln. lactis</i> <i>Ln. citreum</i> <i>P. acidilactici</i>	<i>L. lactis</i> <i>Lb. casei</i> <i>Lb. garvieae</i> <i>L. plantarum</i> <i>Lb. raffinolactis</i>
References	-	Bonomo and Salzano (2012)	Flórez and Mayo (2006)
Fungal populations	ND	<i>K. lactis</i> <i>D. hansenii</i> <i>D. anomala</i>	<i>K. lactis</i> <i>P. roqueforti</i> <i>P. chrysogenum</i> <i>G. candidum</i>
References	-	Capece et al. (2009)	Flórez and Mayo (2006)

^aThe information on fungal and bacterial populations in Pecorino di Filiano cheese is derived from two distinct studies

^bNot Determined

pigmentation in red smear cheeses (Comi and Cantoni, 2011). Furthermore, it has been noted for its inhibitory effect against *Listeria monocytogenes* (Gobbetti and Rizzello, 2014).

Interestingly, Fontina cheese also harboured less typical genera, such as *Methylobacterium*. This genus is found in various environmental contexts and has been associated with clinical cases. The presence of *Methylobacterium mesophilicum* in Fontina is likely the result of its halotolerant nature (Egamberdieva et al. 2015).

A particular NSLAB species, *Pediococcus acidilactici*, was detected in Pecorino cheese. This species is one of the most frequently isolated from white-brined cheeses (Ozer, 2014). Its presence in Pecorino may be attributed to the thermal treatments applied to the curd and milk during production, as it thrives at an optimal temperature of 40 °C. Additionally, its occurrence in both the surface and core of the cheese can be explained by its ability to grow in both aerobic and microaerophilic environments (Raccach, 2014).

Cabrales cheese contained two specific bacteria: *S. equorum*, already described in section 1.3.1, whose occurrence can be attributed to its halophilic nature, and *Lactobacillus farciminis*, which may be present due to environmental contamination, given its use as a feed additive for animals (Bampidis et al., 2020). Its presence has also been detected in Doble Crema cheese, where it acts as a halotolerant bacterium (Morales et al., 2011).

When examining the fungal populations of Fontina and Pecorino cheeses, it was found that Fontina harboured a more complex fungal ecosystem compared to Pecorino. The only shared species between the two is *Debaryomyces hansenii*, a yeast commonly found on the surfaces of mould-ripened (Hocking, 2014) and smear-ripened cheeses (Cogan, 2014b). Known for its halotolerance (Wrent et al. 2014), *D. hansenii* is often introduced via brines, which serve as a primary source. In some cases, it is even intentionally added through commercial starter cultures containing other important microorganisms like *B. linens* and *Geotrichum candidum*, due to its technological importance (Cogan, 2014b). *Debaryomyces hansenii* plays a crucial role in metabolizing lactic acid, which raises the pH, thereby facilitating the growth of proteolytic bacteria during ripening. Additionally, it contributes to the aromatic and sensory qualities of the cheese. This yeast also produces various enzymes of industrial relevance and is a valuable biocontrol agent against pathogenic species such as *Clostridium* (Wrent et al., 2014).

The genus *Candida* was also detected on the surface of Fontina cheese. *Candida* species are known for their ability to tolerate high salt concentrations and typically do not grow under anaerobic conditions (Hommel, 2014). This may explain their occurrence specifically on the cheese's surface. Species such as *Candida versatilis* (Sheehan, 2011), *Candida zeylanoides*, and *Candida lipolytica* (Desmaures, 2014) are frequently found in cheeses. However, in this case, a less common species, *Candida sake*, was identified. This marine yeast (Warwas et al., 2023), often isolated from oysters (Hommel, 2014), was likely introduced through environmental contamination. However, *C. sake* has also been previously found in Queijo da Beira Baixa PDO cheese (Cardinali et al., 2022).

The species *Geotrichum silvicola* has also been detected on the surface of Fontina cheese. However, to our knowledge, this species has not been found on other cheeses aged in similar conditions. Instead, it has been identified in a few cheeses, including Queijo de Azeitão PDO, Turkish Mihalic, and Italian Caciofore (Karasu-Yalcin et al. 2019; Cardinali et al. 2021; Rampanti et al., 2023). Its presence in Fontina cheese may stem from a contamination of the milk used in its production, as demonstrated in the case of Caciofore, where significant amounts of this microorganism were found both in the milk and the resulting cheese. Additionally, the identification of *G. silvicola* in Fontina could be due to its close genetic relationship with *Geotrichum candidum*, a species widely associated with surface-ripened cheeses (Hocking, 2014). In fact, the strong similarity between their sequences has already been demonstrated, showing 99.9 % for 18S, 100 % for ITS, and 99.6 % for 28S regions (Abed et al., 2023).

A well-researched yeast species, *Torulaspora delbrueckii*, has also been detected on the surface of Fontina cheese. This species is known for its ability to tolerate high salt concentrations (up to 14 %) (Buchl and Seiler, 2011) and its strong resistance to cleaning agents (Sheehan, 2011). *Torulaspora delbrueckii* is one of the predominant species in brines and possesses several important technological properties (Innocente et al., 2023). It has also been identified as a dominant species in several cheeses, such as Canastra, Cerrado, and Serro-type cheeses (Câmara et al., 2024).

Two species from the *Fusarium* genus have been identified in Fontina cheese. The first, *Fusarium domesticum* (formerly *Trichotecium domesticum*), is a species unique to cheese. It typically coexists on the cheese surface in symbiosis with other microorganisms and is known for reducing stickiness in cheese. This species is commonly used to inoculate cheeses like Saint-Nectaire and Reblochon (Ropars et al., 2012). The second species, *Fusarium solani*, is primarily a soilborne plant pathogen (Thrane, 2014). However, it has also been detected in cheeses like Canastra (Martin et al., 2023). The probable source of this species in cheese is the aging environment, as demonstrated by De Souza (2021).

In addition to *Debaryomyces hansenii*, the yeast *Kluyveromyces lactis* was also found on the surface of Pecorino cheese. *Kluyveromyces lactis* is commonly isolated from white-mould and blue cheeses (Desmaures, 2014), and is frequently detected in dairy-related environments such as raw milk, cheese brines, and dairy equipment. This yeast plays a crucial role in cheese ripening due to its ability to break down lactose, proteins, and fats, which are essential for the development of both texture and flavour. Although *K. lactis* initially colonizes the surface of cheeses like Pecorino, as the cheese matures, it migrates inward and proliferates, driven by its ability to ferment lactose (Belloch et al. 2011).

Core microbiota

The bacterial and fungal populations in Cabrales and Pecorino cheeses remained relatively stable, even though the surface and core of Pecorino cheese were not studied in the same research. The only bacterial species that appeared in the core but not on the surface was *Leuconostoc citreum*,

a species well-known as a dominant microorganism in white-brined cheeses (Özer, 2014).

As for fungal species, the yeast *Dekkera anomala* was detected exclusively in the core of Pecorino cheese. This yeast has previously been found in certain dairy products, but its role remains unclear (Ciani and Comitini, 2014). It is likely of environmental origin, as another study investigating yeast diversity in blue-veined cheeses found this species on equipment, floors, and walls (Viljoen, 2003).

Three fungal species were found to be unique to Cabrales cheese: two moulds, *P. roqueforti* and *Penicillium chrysogenum*, and one yeast, *G. candidum*. *Penicillium chrysogenum* is one of the most commonly isolated *Penicillium* species from food products (Pitt, 2014). Although it is intentionally used in the fermentation of certain meats (Temperini et al., 2021; Li et al., 2024), it is not deliberately added to cheeses (Frisvad, 2014). Instead, it typically predominates as a contaminant in certain cheeses, such as Turkish Divle Cave, Spanish semi-hard ripened cheeses, and some Alpine varieties (Ozturkoglu Budak, 2016; Ramos-Pereira, 2019; De Respinis, 2023). *Penicillium roqueforti* is the mould responsible for the characteristic blue veins in many cheeses, such as Cabrales (Chandan, 2014). Unlike other *Penicillium* species, it cannot tolerate high salt concentrations (Frisvad, 2014) but thrives in low-oxygen environments (around 5 %), which explains its prevalence inside cheeses (Uraz and Ozer, 2014). It produces ketones that give blue cheeses their strong, pungent aroma (Cogan, 2014a; Maslov Bandić, 2023). While *P. roqueforti* is often intentionally introduced during cheese production, it can also occur naturally in cheeses aged in caves, as is the case with Cabrales (Chandan, 2014). *Geotrichum candidum* is a yeast-like fungus commonly found in surface-ripened cheeses (Hocking, 2014). However, its growth is sensitive to salt, with its development being restricted when the salt

concentration exceeds 1-2 % (Desmaures, 2014), which could explain its absence on the surface of Cabrales cheese. *Geotrichum candidum* is also used in synergy with species from the genus *Penicillium* (inoculated into the curd) for the production of certain cheeses, such as Brie and Camembert (Botha and Botes, 2014). Typically, it grows alongside *D. hansenii* and *K. lactis* during the first week of ripening, contributing to the complex microbiota that shapes the final cheese (Eliskases-Lechner et al., 2011).

Conclusion

This review aimed to reveal and analyse the shared and unique microbial communities in cheeses aged under specific conditions: animal skin sacks and natural caves. The analysis showed that cheeses aged in animal skin sacks have a significantly higher number of shared species compared to those aged in caves, with a more complex bacterial composition. The dominant species in skin-aged cheeses included *L. lactis*, *L. plantarum*, *E. faecalis*, and *L. delbrueckii*. In contrast, cave-aged cheeses were primarily characterized by species from the genus *Brevibacterium*, with *L. lactis* and *D. hansenii* found on the surface, while *K. lactis* dominated the core microbiota. Additionally, cheeses aged in skin bags exhibited a notable presence of anaerobic flora, which can be attributed to the enclosed environment, while cave-aged cheeses harboured more halophilic microorganisms on their surfaces due to the salt treatment. Overall, this review emphasizes the significant impact of aging conditions on the microbial communities in cheese, highlighting the complexity and diversity that define these traditional methods.

Mikrobiološka svojstva sireva dozrijevanih u životinjskim kožama i prirodnim špiljama

Sažetak

Ovaj pregledni rad istražuje mikrobne zajednice prisutne u sirevima koji dozrijevaju u mišinama od životinjske kože i prirodnim špiljama. Ove tradicionalne metode dozrijevanja ne samo da čuvaju kulturnu baštinu, već i pridonose jedinstvenim okusima i teksturama sira. Analiza je pokazala da sirevi dozrijevani u životinjskim kožama sadrže veći broj zajedničkih vrsta i složeniji sastav bakterija u usporedbi sa sirevima dozrijevanim u špiljama. U sirevima dozrijevanim u kožama prevladavaju vrste *Lactococcus lactis*, *Lactiplantibacillus plantarum*, *Enterococcus faecalis* i *Lactobacillus delbrueckii*, dok u sirevima iz špilja dominiraju vrste roda *Brevibacterium*, *Lactococcus lactis* i *Debaryomyces hansenii*, pri čemu jezgrenom mikrobiotu najčešće čini *Kluyveromyces lactis*. Također, u sirevima koji dozrijevaju u mišinama zabilježena je značajna prisutnost anaerobne flore zbog zatvorenog okruženja, dok je površina sireva iz špilja bila bogatija halofilnim mikroorganizmima, što se povezuje s tretmanima solju.

Ključne riječi: prirodne špilje; tradicionalno dozrijevanje; mikrobne zajednice; sirevi iz mišine; sirevi iz špilja

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