



Beneficial features of pediococcus: from starter cultures and inhibitory activities to probiotic benefits

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Abstract

Pediococci are lactic acid bacteria (LAB) which have been used for centuries in the production of traditional fermented foods. Their fermentative abilities were explored by the modern food processing industry in use of pediococci as starter cultures, enabling the production of fermented foods with distinct characteristics. Furthermore, some pediococci strains can produce bacteriocins and other antimicrobial metabolites (AMM), such as pediocins, which are increasingly being explored as bio-preservatives in various food matrices. Due to their versatility and inhibitory spectrum, pediococci bacteriocins and AMM are being extensively researched not only in the food industry, but also in veterinary and human medicine. Some of the pediococci were evaluated as potential probiotics with different beneficial areas of application associated with human and other animals' health. The main taxonomic characteristics of pediococci species are presented here, as well as their potential roles and applications as starter cultures, as bio-preservatives and as probiotic candidates.

Keywords *Pediococcus* · Starter · Bacteriocins · Probiotics · Food · Animal · Human · Health

Introduction

The role of lactic acid bacteria (LAB) as a starter, bio-preservative and adjunct cultures in the food industry has been investigated prior to the dawn of the modern microbiology,

and even before to our knowledge of the existence of microorganisms. The evolution of various subfields of microbiology over the past two centuries, as well as the contributions of pioneers in the basic and applied sciences, clearly demonstrated the importance of bacterial cultures for human health and nutrition. The scientific foundations of food microbiology, bio-preservation, probiotics, and other beneficial properties of microorganisms have been studied and arguments for their applications have been developed.

Pediococcus spp., a member of LAB, has been shown to be effective in the production of antimicrobial peptides (bacteriocins) with applications in the food and health industries. Numerous studies have been published on the production of bacteriocins, their use in biopreservation processes, and more recently, their use in human and veterinary medicine (Albano et al. 2007; Cavicchioli et al. 2018; Chikindas et al. 1993; Drider et al. 2006; Fugaban et al. 2021, 2022; Gutierrez-Cortes et al. 2018; Kuniyoshi et al. 2021; Martino et al. 2013; Queiroz et al. 2022; Niamah 2018; Osmanaoglu et al. 2010; Papagianni 2003; Porto et al. 2017; Ray 1992; Rodríguez et al. 2002; Todorov and Dicks 2005; Tomé et al. 2009). Moreover, the second most widely used bacteriocin in the scientific community is pediocin PA-I, which is produced by various *Pediococcus* strains (Garsa et

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al. 2014; Rodriguez et al. 2002; Simha et al. 2012) and used by the food industry as a bio-preservative, especially to prevent and control the contamination by Gram-positive pathogens, particularly *Listeria monocytogens* (Cabo et al. 2009; Garsa et al. 2014; Papagianni and Anastasiadou 2009; Ray and Hoover 1993; Rodrigue et al. 2002; Simha et al. 2012). Probiotic properties of pediococci have been successfully proposed for humans and other animals with the aim of immunomodulation, control of pathogens, improved recovery after COVID-19, antibiotic therapy and improved health status (Table 1). Deep analysis of the probiotic features of pediococci was subject to research projects, in which beneficial roles of strains belonging to the genus *Pediococcus* were investigated, including their role in immunomodulation (Kim et al. 2021; Shan et al. 2021; Shweta et al. 2021), growth improvement of farm animals (Castex et al. 2021; Liu et al. 2022; Wang et al. 2022; Wanna et al. 2021), reduction of the incidence of respiratory tract infections and the management of lactose intolerance (Chang et al. 2020; Otunba et al. 2021), resistance to infections (Li et al. 2021; Villagran-de la Mora et al. 2019; Yoon et al. 2021), infantile colic treatment (Chen et al. 2001), anti-obesity properties (Barathikannan et al. 2022), post COVID-19 recovery of the patience (Gutiérrez-Castrellón et al. 2022).

The taxonomy of *pediococcus*

Pediococci has a coccus morphology and forms specific tetrads, as a result of cells dividing along two planes of symmetry (typical feature for *Pediococcus* spp., *Aerococcus* spp., and *Tetragenococcus* spp.). Perhaps, pediococci are one of the most emblematic microorganisms due to their distinct morphology, being widely used as examples in microbiology teaching. Pediococci are Gram-positive, non-catalase producing, facultative anaerobic, homofermentative, non-motile and non-sporulating lactic acid bacteria (LAB) that belong to the family *Lactobacillaceae* in the order *Lactobacillales* (Schlegel 1993; Wieme et al. 2012; Holzapfel et al. 2015). Over the years, the classification of pediococci modified several times. Genus *Pediococcus* includes species such as *P. pentosaceus*, *P. acidilactici*, *P. stilesii*, *P. siamensis*, *P. cellicola*, *P. argentiniensis*, *P. parvulus*, *P. ethanolidurans*, *P. claussenii*, *P. inopinatus*, *P. perniciosus* and *P. damnosus* (Wieme et al. 2012), *P. halophilus*, *P. dextrinicus*, and *P. urinaequi* (Garvie 1986). In addition, strains previously classified as *P. cerevisiae* have been reclassified and distributed among *P. damnosus*, *P. acidilactici* and *P. pentosaceus* (Dallaglio et al. 1981; Garvie 1986). The taxonomic status of *P. halophilus* (known also as *Tetragenococcus halophila*) and *P. urinaequi* is uncertain (Collins et al. 1990; Dallaglio et al. 1981). It has been demonstrated that *P.*

lolii is a later subjective synonym of *P. acidilactici* (Wieme et al. 2012). Later, in 2015, only nine *Pediococcus* species (*P. acidilactici*, *P. claussenii*, *P. cellicola*, *P. damnosus*, *D. dextranicus*, *P. inopinatus*, *P. parvulus*, *P. pentosus* and *P. stilesii*) were included in the Bergey's Manual of Systematics of Archaea and Bacteria and considered as legitimate representatives of this genus (Holzapfel et al. 2015).

Pediococci are group of microorganisms, normally with exigence for cultivation in rich growth media, with their specific biochemical and physiological characteristics (Dallaglio et al. 1981; Garvie 1986; Holzapfel et al. 2015; Ray 1995). Most LAB, including different *Pediococcus* strains differ in their tolerance to oxygen, pH levels, temperature and NaCl (Dallaglio et al. 1981; Garvie 1986; Holzapfel et al. 2015). *Pediococcus* spp. can ferment carbohydrate based on species specific assimilation patterns. Even with development of biomolecular methods for taxonomical purposes of bacterial species, biochemical, physiological test and sugar fermentation profiles are still essential steps in the correct and descriptive classification of microorganisms. Glucose is always fermented via the homofermentative pathway and associated to the production of racemic DL-lactate via the Embden-Meyerhof-Parnas (EMP) pathway (Gasson and De Vos 1994). Bergey's Manual of Systematic of Archaea and Bacteria (Holzapfel et al. 2015) and Gasson and De Vos (1994) recommend taxonomy of pediococci based on physiological, biochemical, morphological, and biomolecular characteristics. However, different biomolecular and genetic tools were also used historically to assess the genomic diversity of *Pediococcus* spp. over the last few decades, such as specific DNA target probes (Mora et al. 1997, 1998, 2000), ribotyping (Barney et al. 2002; Jager and Harlander 1992; Satokari et al. 2000), DNA-DNA hybridization (Dallaglio et al. 1981), 16 S rRNA gene sequencing (Barney et al. 2002; Omar et al. 2000), repPCR, RAPD-PCR and PFGE (Albano et al. 2007; Cavicchioli et al. 2018; Gutierrez-Cortes et al. 2018; Simpson et al. 2002). In addition to classical DNA-DNA homology (Dallaglio et al. 1981), 16S rRNA immunoassays (Woo et al. 2009), frequently used to identify distinct pediococci, one other classical approach from the recent past was that proposed by Bhunia and Johnson (1992) - an ELISA test with a specific monoclonal antibody for the effective differentiation of closely related species, such as *P. pentosaceus* an *P. acidilactici*. However, nowadays DNA associated techniques were significantly improved and are considered as more rapid and more relevant approaches for identification and differentiation for pediococci.

In general, representatives of *Pediococcus* spp. can be described as chemoorganotrophs. Most pediococci require the presence in the growth media of amino acids and B vitamins for their growth, while *P. acidilactici* and *P. pentosaceus* are requiring folic acid and riboflavin, respectively

Table 1 Some examples of application of probiotic *Pediococcus* spp. as probiotics with focus on years 2020–2022

Species, strains	Application	Reference
<i>Pediococcus acidilactici</i> *, <i>Pediococcus pentosaceus</i> *	Improve growth performance on Holstein calves, 12 weeks of age	Wang et al. 2022
<i>Pediococcus pentosaceus</i> *	Improve growth performance of Holstein calves	Liu et al. 2022
<i>Pediococcus acidilactici</i> FS2	Reduction of blood cholesterol in mice model	Jang et al. 2021
<i>Pediococcus pentosaceus</i> PB2	Suggested to prevent some enteropathogen-induced gastrointestinal disorders; reduce the incidence of respiratory tract infections and for the management of lactose intolerance	Otunba et al. 2021
<i>Pediococcus pentosaceus</i> I44	Suggested potential probiotic properties	Vasudevan et al. 2021
<i>Pediococcus acidilactici</i> LA412	Suggested potential probiotic properties	Liu et al. 2021
<i>Pediococcus acidilactici</i> MA18/5 M	Improves on the growth, nutritional indices, and metabolic status of the adult western blue shrimp, <i>Litopenaeus stylirostris</i> .	Castex et al. 2021
<i>Pediococcus acidilactici</i> LS, part of the multistrain probiotic preparation (<i>L. acidophilus</i> LAP5, <i>L. fermentum</i> P2, and <i>L. casei</i> L21)	Modulate intestinal microbiota (increase <i>Lactobacillaceae</i> abundance and reduce <i>Enterobacteriales</i> abundance), increase the gene expression of tight junction proteins (ZO-1 and Mucin 2) and the immunomodulatory activity (downregulation of mRNA levels of interferon- [IFN-] and lipopolysaccharide-induced tumor necrosis factor- [TNF-], and upregulation of IL-10) in broiler chickens	Chang et al. 2020
<i>Pediococcus acidilactici</i> * (in combination with <i>L. rhamnosus</i> HN001 phytobiotics, <i>Agave tequilana fructans</i>)	Induced morphological modifications in the duodenal mucosa of broilers that, in turn, promoted resistance to infections caused by <i>S. typhimurium</i> and <i>C. perfringens</i>	Villagran-de la Mora et al. 2019
<i>Pediococcus pentosaceus</i> MBP003	Suggested potential probiotic properties	Adnan et al. 2021
<i>Pediococcus acidilactici</i> NMCC-11	Suggested potential probiotic properties	Kanwal et al. 2021
<i>Pediococcus acidilactici</i> NCDC 252	Stimulation of arginine aminopeptidase (EC 3.4.11.6) called aminopeptidase B production	Attri et al. 2021
<i>Pediococcus acidilactici</i> BNS5B	<i>Pseudomonas aeruginosa</i> PAO1 biofilm formation inhibition and control	Chandla et al. 2021
<i>Pediococcus acidilactici</i> CRL1888, CRL902, CRL904, CRL907, CRL913, CRL919, CRL911	Inhibit growth and surface colonization of Enterohemorrhagic <i>Escherichia coli</i> (EHEC) O157:H7 at 10 °C.	Cisneros et al. 2021
<i>Pediococcus pentosaceus</i> CRL791, CRL908, CRL909, CRL922, ATCC10791, CRL2145	Suggested potential probiotic properties	Kim et al. 2022
<i>Pediococcus acidilactici</i> MG5001, <i>Pediococcus pentosaceus</i> MG5078	Suggested potential probiotic properties	Kim et al. 2022
<i>Pediococcus pentosaceus</i> YC	Enhances host resistance against pathogen by increasing IL-1b production	Shan et al. 2021
<i>Pediococcus pentosaceus</i> KABP041	Potential to counteract functional gastrointestinal disorders in an observational pilot trial in infants	Asto et al. 2022
<i>Pediococcus pentosaceus</i> IM96	Protective effects against enterohemorrhagic <i>Escherichia coli</i> O157:H7 infection in vivo	Li et al. 2021
<i>Pediococcus pentosaceus</i> (29 strains) *	Suggested potential probiotic properties	Tsigkrimani et al. 2022
<i>Pediococcus pentosaceus</i> CECT8330	A randomized, double-blind, placebo-controlled trial for infantile colic treatment	Chen et al. 2001
<i>Pediococcus pentosaceus</i> strains (CICC 24,444, QK-1, MQ-1 and RQ-1)	Suggested potential probiotic properties	Hu et al. 2021
<i>Pediococcus acidilactici</i> (isolates M1, M3, 13, and 27)	Suggested potential probiotic properties and bacteriocin production	Desiderato et al. 2021
<i>Pediococcus acidilactici</i> MNL5	Anti-obesity efficacy of in <i>Canorhabditis elegans</i> gut model	Barathikannan et al. 2022
<i>Pediococcus acidilactici</i> CECT9879	Counteracts the effect of a high-glucose exposure in <i>C. elegans</i> by affecting the insulin signalling pathway (IIS)	Yavorov-Dayliev et al. 2022
<i>Pediococcus acidilactici</i> PMC202	Anti-tuberculosis activity against <i>Mycobacterium tuberculosis</i>	Yoon et al. 2021
<i>Pediococcus acidilactici</i> NCDC 252	<i>In vitro</i> studies on anti-inflammatory, antioxidant and antihyperglycemic activities	Shweta et al. 2021
<i>Pediococcus pentosaceus</i> OBK05	An <i>in vitro</i> study for cholesterol assimilation potential and antibiotic resistance status	Bhukya et al. 2021
<i>Pediococcus acidilactici</i> BK01	Suggested potential probiotic properties	Melia et al. 2021

Table 1 (continued)

Species, strains	Application	Reference
<i>Pediococcus pentosaceus</i> MG9015(YH9015))	Antioxidant and anti-inflammatory effect and probiotic properties	Kim et al. 2021
<i>Pediococcus acidilactici</i> JBCC105117	Probiotic properties of lactic acid bacteria with high conjugated linoleic acid converting activity	Song et al. 2021
<i>Pediococcus acidilactici</i> F21	Potential probiotic and postbiotic characteristics including immunomodulatory effects	Alameri et al. 2022
<i>Pediococcus pentosaceus</i> *	Potential probiotic properties and effect of simulated gastrointestinal digestion on its bioactivity	Mushtaq et al. 2021
<i>Pediococcus acidilactici</i> pA1c	Antidiabetic effects of probiotic on HFD-induced mice	Cabello-Olmo et al. 2022
<i>Pediococcus acidilactici</i> KABP021	Probiotic improves symptomatic and viral clearance in Covid19 outpatients	Gutiérrez-Castrellón et al. 2022
<i>Pediococcus pentosaceus</i> CECT 8330	Protects DSS-induced colitis and regulates the intestinal microbiota and immune responses in mice	Dong et al., 2022
<i>Pediococcus pentosaceus</i> SL4	A synthetic probiotic engineered for colorectal cancer therapy modulates gut microbiota	Chung et al. 2021
<i>Pediococcus acidilactici</i> 72 N (in combination with <i>Lactobacillus plantarum</i> 22 and 25 F)	Use of <i>Lactobacillus plantarum</i> (strains 22 and 25 F) and <i>Pediococcus acidilactici</i> (strain 72 N) as replacements for antibiotic-growth promotants in pigs	Pupa et al. 2021
<i>Pediococcus pentosaceus</i> MR001	Potential probiotic for application in shrimp's aquaculture	Wanna et al. 2021
<i>Pediococcus pentosaceus</i> MF000967	Encapsulated within sodium alginate, camel casein (CC), camel skin gelatin (CSG) and CC: CSG (1:1 wt/wt) wall materials to improve viability	Devarajan et al. 2022
<i>Pediococcus acidilactici</i> CCFM28 and CCFM18	<i>Pediococcus acidilactici</i> bac negative NT17-3 control was applied; Firmicutes were decreased, Proteobacteria were increased; Downregulation of <i>Blautia</i> , upregulation of <i>Ruminococcus</i> and <i>Lactobacillus</i> .	Qiao et al. 2021

*Strain identity not specified in the study

(Atlas 2004). Manganese, a microelement, is required in trace amounts for the growth of most of pediococci, including *P. acidilactici* and *P. pentosaceus* (Biswas et al. 1991; Holzapfel et al. 2015). Moreover, *P. acidilactici* and *P. pentosaceus* do not have a specific NaCl growth requirement and can tolerate of up to 4% NaCl (Ray 1995; Holzapfel et al. 2015). *P. halophilus*, on the other hand, as implied by its name, requires more than 5% NaCl to grow (Ray 1995). However, later *P. halophilus* was reclassified as *T. halophilus* (Raccach 2014). Although most pediococci are described as facultative anaerobes or microaerophilic bacteria, they can grow rapidly aerobically. However, some representatives, such as *P. halophilus*, can grow better in aerobic conditions (Ray 1995; Racchach 2014). Taking in consideration specific behaviour of *P. halophilus* was some of the arguments for the reclassification to *T. halophilus*, in addition to other properties and DNA specificity (Raccach 2014). Although oxygen can may not be limiting factor for pediococci growth, a comparison of aerobic, semi-aerobic culture conditions (dissolved oxygen tension levels (DOT) of 60%) or anaerobic culture conditions for bacteriocinogenic *P. acidilactici* NRRL B 5627, showed that aerobic conditions resulted in significantly higher biomass formation and lactate production levels, but lower pediocin

levels (Anastasiadou et al. 2008a, b) found similar results for biomass, acidification and pediocin production by *P. pentosaceus*.

Sugar fermentation profiles of LAB, including for pediococci are fundamental for biochemical taxonomy. Taxonomy classification of the microorganisms is a complex approach, combining evidences from biomolecular, biochemical and physiological test. According to Holzapfel et al. (2015), most of *Pediococcus* spp. can ferment glucose, fructose, galactose, mannose, cellobiose, arabinose, ribose, salicin, amygdalin, esculin, but not sorbose, melibiose, inulin, starch, dextrin, and sugar alcohols. Other carbohydrates associated with *Pediococcus* biochemical taxonomy can be described as strain dependent. It is worth noting that the presence of glucose has been reported to be an inhibitory factor for the growth of *P. acidilactici* strains (Vazquez et al. 2003), which is most likely due to species/strain specificity in enzymes responsible for EMP pathway.

Furthermore, the ability of pediococci to ferment carbohydrates such as lactose, sucrose, trehalose, rhamnose and others varies greatly between strains were initially specified by Mundt et al. (1996) and later amended by Holzapfel et al. (2015). Cavicchioli et al. (2018) described *P. pentosaceus* strain with limited lactose metabolism. In addition, this strain was isolated from artisanal cheese and characterized

as potential bacteriocins producers. Since this strain was unable of metabolizing lactose, the primary carbohydrate in dairy products, the question is whether they play a fermentation role in the ripening of the cheese from which they were isolated or should they be considered as contaminants? This is a question that requires further investigation and clarification.

Some *P. pentosaceus* strains can possess a pseudo-catalase system, which is associated with conversion of glucose to pyruvate under aerobic conditions (Pay 1995). Moreover, the glycerol inducible oxidizing system is involved in bacterial aerobic glycerol metabolism, and evaluation of the end products revealed that glycerol was oxidized to the pyruvate level, producing lactate, acetate, acetoin and CO₂ in a molar ratio of approximately 1:1:1:3 (Dobrogosz and Stone 1962). In the subsequent stage, acetoin can be converted to diacetyl. Diacetyl is considered as beneficial metabolite specially used by the dairy industry, since it is associated as dairy aromatic compound and previously described as antimicrobial agent (Jay 1982). Application of diacetyl as antimicrobial compound was suggested even before his role in dairy industry was explored. Classical example can be suggested by Myrvi and Volk (1954) proposed application of diacetyl as the antibacterial compound for inhibition of *Mycobacterium tuberculosis*, where 3 µg/ml was reported as the lowest inhibitory concentration; however, for the inhibitory activity of diacetyl against *Escherichia coli*, 10 times higher concentration needed to be applied as effective inhibitory doses; or example from last decade, where Langa et al. (2014) suggested that effect of the diacetyl as inhibitory compound to *E. coli* and *L. monocytogenes* can be enforced by synergetic effect with reuterin.

The majority of pediococci utilizes the lactate oxidation system, which has been extensively studied in *P. pentosaceus*. The lactate oxidation system is inducible, and cells can diverge energy from the oxidation of lactate to acetate (Ray 1995). Under aerobic conditions, L-(+)-lactate is oxidized to acetate and CO₂ in equimolar amounts. Production of acetate and CO₂ can play a role in the development of distinctive flavour and it is considered as essential step in the ripening of cheddar cheese (Eugster et al. 2019; Ray 1995). However, under anaerobic conditions, no production of acetate is realised, but conversion of L-(+)-lactate to D-(-)-lactate was conducted. Negative consequences of increased levels of D-(-)-lactate were pointed by Kowlgi and Chhabra (2015), evaluated links between D-lactic acidosis and complications of short bowel syndrome. Moreover, increased levels of D-(-)-lactate can be associated with some other negative consequences for the consumers and some of them were reviewed by Pohanka (2020).

The dairy industry values the formation of diacetyl, a metabolite with distinct sensorial properties as primary

benefits from citrate metabolisms. As secondary effect, antimicrobial properties of diacetyl were additionally contributed to the safety of the different fermented food products (Jay 1982; Langa et al. 2014). Citrate metabolism was investigated in several LAB, including pediococci strains isolated from soy products and cheeses (Kanbe and Uchida 1987; McSweeney et al. 2017; Quintans et al. 2008). It was observed that citrate-negative strains lack a particular enzyme, inducible citrate lyase [citrate (pro-3 S)-lyase; EC 4.1.3.6]. Moreover, it has been demonstrated that the citrate degradation pathway in *P. halophilus* is distinct from that of other LAB, and that the main products of citrate degradation are acetate and formate, whereas *P. halophilus* is incapable of producing acetoin or diacetyl. In addition, the transformation of citrate to formate was drastically reduced when glucose was present in the substrate (Papagianni and Anastasiadou 2009). Some specificity on the metabolism of *P. pentosaceus* includes an inducible enzymatic system for the metabolism of phenolic acids, which may be useful for bio-decontamination of industrial wastes. *P. pentosaceus* exhibited a substrate-inducible phenolic acid decarboxylase (PAD) enzymatic activity on *p*-coumaric acid (Barthelmebs et al. 2000).

Most of the pediococci are incapable of producing extracellular proteases. However, like the majority of LAB, pediococci express different intracellular proteases, dipeptidases and amino peptidases associated with protein metabolism (Bhowmik and Marth 1990; Bhowmik et al. 1990), with different strain-dependent levels of activity (Ray 1995). Additionally, it is likely that pediococci probably do not produce extracellular lipases; however, they can contain intracellularly lipases, which have been extensively studied in some strains of *P. pentosaceus* (Bhowmik and Marth 1990). It was proposed that certain intracellular enzymes of pediococci play a significant role in cheese ripening. Mora et al. (2003) examined the involvement of various enzymes from *P. acidilactici* and *P. pentosaceus*, such as N-acetyl-muramidases, N-acetyl-glucosaminidases, l-alanine amidase and endopeptidases (peptidoglycan hydrolases) in the autolysis processes of cheese ripening. Mora et al. (2003) examined the enzymatic profiles of different strains of *P. acidilactici* and *P. pentosaceus* isolated from plant, animal and dairy sources. Specific peptidoglycan hydrolases associated with *Pediococcus* spp. were active at high salt concentrations and different pHs, implying a potential role in the fermentation of different salted meat, fermented vegetable products and cheese ripening when the pH decreases due to the growth of different LAB starter cultures in increased salt concentration and decreased water activity.

Beneficial features of *Pediococcus* spp

The role of pediococci in food and health cannot be clearly defined as beneficial or detrimental (spoilage). Be good or bad, it is a clearly strain specific characteristic associated with genetic heritage of each *Pediococcus* spp. representative. Several reports provided information on various pediococci isolated from food and beverage products, describing them as starters, probiotics or spoilage agents (Bhowmik et al. 1990; Leroy et al. 2006). Analysis of strain behaviour reveals that specific strains of *Pediococcus* spp. are well-adapted to different food systems, as well as the gastrointestinal tract (GIT) of humans and other animals (Lv et al. 2014; Varsha et al. 2014).

Analysis of the whole genome sequences (WGS) of pediococci strains revealed complex information about the beneficial properties and potential hazards related to mapping of the specific genes of these specific strains and added essential information to the scientific knowledge of pediococci. Lv et al. (2014), for example, examined the WGS of *P. pentosaceus* LI05 (CGMCC 7049), a strain isolated from faecal samples of healthy volunteers and proposed its use as a potential probiotic (Lv et al. 2014; Oliveira et al. 2022) sequenced the entire genome of *P. pentosaceus* ST65ACC, a strain isolated from artisanal cheese that has been described as a bacteriocin producer (Cavicchioli et al. 2018; Todorov et al. 2019) and an effective strain for bio-control of *Listeria monocytogenes* (Cavicchioli et al. 2018) and mapped essential genes associated with production of antimicrobials. In addition to previously reported microbiological tests pertaining to the application of *P. pentosaceus* ST65ACC (Cavicchioli et al. 2018; Todorov et al. 2019), WGS revealed explanations of previously observed features (bacteriocin production) and provided arguments for additional applications of the studied strain based on recorded genes, as safe beneficial strain with potential applications as adjunct culture in dairy industry (Oliveira et al. 2022). Moreover, Kuniyoshi et al. (2021) reported on *P. pentosaceus* ET34, originally isolated from smoked salmon, described as bacteriocin producer and shown to be effective in control of *L. monocytogenes* in salmon production (Tomé et al. 2009). This strain was also characterized as a potentially probiotic candidate, as well as an effective producer of pediocin using a sugarcane bagasse as substrate (Todorov et al. 2011; Kuniyoshi et al. 2021) also reported the WGS of *P. pentosaceus* ET34, demonstrating additional beneficial features that can be explored in further studies.

Queiroz et al. (2022), performed the WGS on three different *Pediococcus* spp. isolated from boza: two different strains of *P. pentosaceus*: ST75BZ and ST87BZ, and one representee of *P. acidilactici*: ST31BZ. In addition to biomolecular analysis of WGS and comparisons with other

pediococci, microbiological approaches were used to characterize the strains in terms of their bacteriocinogenic properties, safety and additional beneficial properties (Queiroz et al. 2022). Combining biomolecular approaches, such as the analysis of WGS, and conventional microbiological assays results, results in the better understanding of potential positive/negative effects of the application of bacterial cultures as result of collection of information from the improved analytical methods. This complete approach for strains analysis is valuable, once predictions on their safety can be done based on the presence of virulence and pathogenic markers, as well as antibiotic resistance related genes.

Diverse beneficial properties, including probiotic potential, were described for numerous pediococci: *P. pentosaceus* OZF (Osmanagaoglu et al. 2010) isolated from breast milk was suggested as putative probiotic; strain of *P. pentosaceus* LP28 isolated from plant material was evaluated regarding his effect on reduction of obesity and fatty liver (Zhao et al. 2012); beneficial role of *P. pentosaceus* on antioxidant activity and fatty acid profile of fermented milk was reported (Balakrishnan and Agrawal 2014). Moreover, bacteriocin production and application in bio-preservation of different *Pediococcus* spp. have been reported by Albano et al. (2007), Bhunia et al. (1988), Cavicchioli et al. (2018), Cintas et al. (1995), Fugaban et al. (2021, 2022), Gutierrez-Cortes et al. (2018), Martino et al. (2013), Nieto Lozano et al. (1992), Todorov et al. (2019), Todorov and Dicks (2005), Tomé et al. (2009). Some of them will be discussed in depth later on this review.

Starter cultures and fermentation

Numerous studies have evaluated different strains of pediococci for their potential safe application, and other, pointing on their virulence properties. Moreover, the Bulletin of the International Dairy Federation (Bourdichon et al. 2018) describes the application of *Pediococcus* spp. as starter cultures in fermented food products as follows: *P. acidilactici* in dairy and meat, *P. pentosaceus* in meat, fish, dairy, beer, wine, fruit, vegetable, and beverages, *P. parvulus*, *P. cerevisiae*, and *P. inopinatus* in wine, and *P. damnosus* in beer and wine (Arevalo-Villena et al. 2010; Leroy et al. 2006; Snauwaert et al. 2015).

P. acidilactici, *P. pentosaceus*, and *P. halophilus* are the most frequently isolated and characterized food fermentation-associated pediococci according to most pediococci-related literature sources. *P. acidilactici* and *P. pentosaceus*, as both autochthonous microbiota and selected starters, can play an essential role in the fermentation processes of fermented vegetables and meat produced in a natural and controlled manner (Knorr 1998; Papagianni and Anastasiadou

Table 2 Some examples of application of probiotic *Pediococcus* spp. in farm animals and aquaculture

Species, strains	Application	Reference
<i>Pediococcus pentosaceus</i>	Review on application of <i>P. pentosaceus</i> as probiotics	Jiang et al. 2021
<i>Pediococcus</i> spp.	Role of pediococci in animal feed	Renata et al. 2003
<i>Pediococcus pentosaceus</i> NB-17	Application of <i>P. pentosaceus</i> NB-17 in farm animal feed	Jon-ganurakkun et al. 2018, 2008
<i>Pediococcus acidilactici</i>	<i>P. acidilactici</i> as feed additive for fish	EFSA Panel on Additives and Products or Substances used in Animal Feed (FEEDAP), 2012 and (FEEDAP) 2018
<i>Pediococcus</i> spp.	Effect on promoting broiler performance and modulating cecal microflora composition and metabolic activities	Mountzouris et al. 2007
<i>Pediococcus acidilactici</i>	Improve antioxidant defenses and oxidative stress status of shrimp	Castex et al. 2009
<i>Pediococcus acidilactici</i>	Effects of <i>P. acidilactici</i> on performance, nutrient digestibility, egg traits, egg yolk cholesterol, and fatty acid profile in laying hens	Mikulski et al. 2012
<i>Pediococcus acidilactici</i>	Effect on productive performance and cecal microbial counts of floor housed laying hens	Pineda-Quiroga et al. 2017
<i>Pediococcus acidilactici</i> , <i>Pediococcus pentosaceus</i>	Improve growth performance on Holstein calves, 12 weeks of age	Wang et al. 2022
<i>Pediococcus pentosaceus</i>	Improve growth performance of Holstein calves	Liu et al. 2022
<i>Pediococcus acidilactici</i> MA18/5 M	Improves on the growth, nutritional indices, and metabolic status of the adult western blue shrimp, <i>Litopenaeus stylirostris</i>	Castex et al. 2021
<i>Pediococcus acidilactici</i>	induced morphological modifications in the duodenal mucosa of broilers that, in turn, promoted resistance to infections caused by <i>S. typhimurium</i> and <i>C. perfringens</i>	Villagrande la Mora et al. 2019
<i>Pediococcus acidilactici</i> 72 N	Use of <i>Lactobacillus plantarum</i> (strains 22 and 25 F) and <i>Pediococcus acidilactici</i> (strain 72 N) as replacements for antibiotic-growth promotions in pigs	Pupa et al. 2021
<i>Pediococcus pentosaceus</i> MR001	Potential probiotic for application in shrimp's aquaculture	Wanna et al. 2021

2009; Wood 1997). Due to the fact that pediococci are typically incapable of fermenting lactose (Garvie 1986), the

use *Pediococcus* spp. as starter culture in dairy products is limited. Some reports (Bhowmik and Marth 1990; Bhowmik et al. 1990; Reinbold and Reddy 1978) suggest that non-starter and adjunct *Pediococcus* spp. may play a role in dairy fermentation and impart desirable characteristics to cheese, suggesting that they may be good dairy starters if they have the ability to use lactose (Caldwell et al. 1996). The ability of most *Pediococcus* spp. to produce antimicrobial peptides, such as bacteriocins, has attracted the scientific interest in using of such strains as protective cultures or biopreservatives, not only in dairy products, but also in other fermented food products (Albano et al. 2007; Cavicchioli et al. 2018; Chikindas et al. 1993; Drider et al. 2006; Fugaban et al. 2021, 2022; Gutierrez-Cortes et al. 2018; Kuniyoshi et al. 2021; Martino et al. 2013; Queiroz et al. 2022; Niamah 2018; Osmanagaoglu et al. 2010; Papagianni 2003; Porto et al. 2017; Rodríguez et al. 2002; Todorov and Dicks 2005; Tomé et al. 2009). Different pediococci, such as *P. acidilactici* and *P. pentosaceus*, were used in fermentation of silage, dairy products, meat commodities, dough and fruit juices (Fugaban et al. 2022; Papagianni and Anastasiadou 2009). Several commercial probiotic feeds currently available on the market are also enriched with different pediococci (Table 2).

Strains of *P. acidilactici* have been reported in association with fermented food products of plants and animal origin (Abbasiliasi et al. 2017; Bhagat et al. 2020; Fugaban et al. 2022; Surachat et al. 2021). These strains were characterized as moderate thermophiles with an optimum growth temperature at 40 °C, with some of them exhibiting the ability to grow even at 50 °C (Papagianni and Anastasiadou 2009). Their sugars fermentation ability was directly associated with specific substrates metabolization and potential applications in different areas of food industry. Strains of *P. acidilactici* are able to metabolize a variety of carbohydrates, including glucose, ribose, xylose, fructose and galactose to DL-lactate, accompanied by pH reduction as low as 3.6 (Anastasiadou et al. 2008). Some strains of *P. acidilactici* can ferment lactose, sucrose and maltose (Ray 1995; Holzapfel et al. 2015). Application of different strains of *P. acidilactici* is connected with the fermentations of vegetables (sauerkraut, Papagianni and Anastasiadou 2009), cheese (Bhagat et al. 2020), grains (Abbasiliasi et al. 2017) and various meat-based products (dry sausages, Albano et al. 2007; Surachat et al. 2021; smoked salmon, Tomé et al. 2009). However, while not a common feature, some vancomycin-resistant *P. acidilactici* strains have been linked to cases of septicemia (Sire et al. 1992).

Even though very similar in specificity to *P. acidilactici*, *P. pentosaceus* is a mesophile organism with optimal growth at 28-35°C and cannot grow at 50 °C; yet, it can tolerate salt concentrations of up to 10%, an point important

for the application of pediococci in preparation of pickled fermented food products. Most of the *P. pentosaceus* strains can ferment glucose, ribose, galactose, arabinose, and fructose to DL-lactate (Garvie 1986). Only a few *P. pentosaceus* strains can ferment lactose and xylose (Ray 1995). *P. pentosaceus* is widely used in different fermentation processes, including the brewing industry (Skytta et al. 1993; Vizoso Pinto et al. 2004), the production of fermented meat products (Raccach 1984), as well as silage fermentations (Fugaban et al. 2021, 2022). *P. pentosaceus* strains were isolated from several fermented dairy products (Cavicchioli et al. 2018; Gutierrez-Cortes et al. 2018), but their significance as starter or adjunct cultures is still a matter of scientific debate due to the lactose-fermenting specialization of pediococci. Diverse *P. pentosaceus* strains are associated with fermentation of vegetables, cereals and other plant-based products (Queiroz et al. 2022; Kimura et al. 1997; Kuniyoshi et al. 2021; Raccach 1984; Ray 1995; Todorov and Dicks 2005, 2009). Some strains of *P. pentosaceus* have been characterized as opportunistic pathogens (Barton et al. 2001; Corcoran et al. 1991), whereas other strains are considered as probiotics (Qi et al. 2021).

The taxonomical identification of *P. halophilus* is still question of discussions. According to recent description of genus *Pediococcus*, *P. halophilus* was reclassified as *Tetragenococcus halophilus* (Raccach 2014) and does not belong to the group of pediococci (Holzapfel et al. 2015). Associated with previous taxonomical position of *T. halophilus* as *P. halophilus* will be relevant to be providing some of the characteristics for that species and related probiotic properties. Several specific beneficial properties of *T. halophilus* were reported, including that this species plays an important role in the fermentation of miso and soy sauce (Nakagawa and Kitahara 1959; Papagianni and Anastasiadou 2009; Sakaguchi 1958; Wood 1997). *P. halophilus* (reclassified as *T. halophilus*) is described as salt-tolerant and homofermentative lactic acid bacteria that is capable to metabolize citrate and malate as part of the lactic acid fermentation in the soy sauce brewing process. As the end metabolites of carbohydrate fermentation, citrate and malate are the predominant acids found in their food environments and can play a role in the production of fermented products. Furthermore, they can metabolize citrate and malate into acetoin and diacetyl, both responsible to enrich the flavour of cheese, butter and other fermented dairy products. Moreover, acetoin and diacetyl can have antimicrobial properties and can contribute to the safety of the final products (Jay 1982). Nevertheless, citrate biotransformation is a strain specific trait, and several *T. halophilus* strains have been described as non-citrate-metabolizing ones (Kanbe and Uchida 1987).

The species *P. damnosus* is phylogenetically distant from *P. acidilactici* and *P. pentosaceus* (Collins et al. 1991;

Garvie 1986). The optimum growth temperature of *P. damnosus* is 22 °C, and it does not growth at 35 °C, in a clear contrast with mesophilic *P. acidilactici* and *P. pentosaceus*. In addition, *P. damnosus* cannot grow at 4% NaCl and is not able to metabolize arginine, arabinose, xylose and lactose. Most of *P. damnosus* strains can ferment glucose, sucrose and galactose via the homofermentative pathway, and only some strains can metabolize maltose and sucrose (Collins et al. 1991; Garvie 1986). *P. damnosus* is a beer and wine spoilage bacterium that has been subjected to extensive biomolecular studies (Calmin et al. 2008; Suzuki et al. 2004, 2006). However, several *P. damnosus* strains were described as exopolysaccharide (Dimopoulou and Dols-Lafargue 2021; Dueñas-Chasco et al. 1997; Li and Kong 2004; Snuwaert et al. 2015) and bacteriocin producers (Bauer et al. 2005; Nel et al. 2001; Skytta et al. 1993).

Bacteriocins produced by *Pediococcus* spp.

Bacteriocins are antimicrobial peptides that are produced by ribosomal machinery of several microorganisms, including Gram-positive, Gram-negative bacteria and Archaea representatives (Chikindas et al. 2018; Meade et al. 2020; Todorov et al. 2019). Unlike antibiotics with peptide structure, bacteriocins are not post-translationally modified in the microbial cytoplasm, and their production is related with suitable genes clustered in representative operons (Daw and Falkner 1996). Bacteriocin operon includes genes encoding for the production of antimicrobial peptides, often including leader peptide that will be separated from the mature peptide during the transportation of the bacteriocin via dedicated ABC-transporter, immunity protein, responsible for the self-protection of the bacteriocin producers from their own bacteriocins, proteins associated with ABC-transporters and other assessor proteins (Duhan et al. 2013). Bacteriocins are generally active against microbial species closely related to the producer species (Todorov et al. 2019). However, in last few decades, there have been reports of bacteriocins with a broader spectrum of activity of bacteriocin produced by LAB, including activity even against some Gram-negative, molds, *Mycobacterium* spp. and viruses (Todorov et al. 2019; Chikindas et al. 2018) reported that bacteriocins must be considered not only as killing metabolites, but also for their role in the bacterial communication. Some studies highlight the potential application of bacteriocins as selective inhibitors/killers of the cancer cells and associated with these applications in cancer treatments (Kaur and Kaur 2015).

Pediocin PA-1, produced by several *Pediococcus* spp. strains, was the first thoroughly characterized class IIa bacteriocin (Chikindas et al. 1993; Rodríguez et al. 2002).

Moreover, its anti-*Listeria* activity and the presence of constitutive amino acid motif became a landmark in the classification and study of bacteriocins. The class IIa bacteriocins, often designated as pediocin-like bacteriocins, constitute the most prevalent group of antimicrobial peptides produced by LAB. Class IIa have a highly conserved hydrophilic and positively charged N-terminal region containing the consensus sequence YGNGV(X)C(X)₄C(X)V(X)₄A, where X denotes any amino acid (Drider et al. 2006).

The majority of pediocins produced by different strains of *Pediococcus* spp., such as *P. acidilactici*, *P. claussenii*, *P. cellicola*, *P. damnosus*, *P. ethanolidurans*, *P. inopinatus*, *P. parvulus*, *P. pentosaceus* and *P. stilesii*, belong to subclass IIa (Haakensen et al. 2009; Porto et al. 2017). Pediocin N5p, on the other hand, was characterized as Class IV (Heng and Tagg 2006). Pediocins codes have been added to distinguish different isomers or variants of pediocins, being associated with the specificity of producing strains or specific bacteriocin modifications, such as pediocin AcH, pediocin SJ, pediocin JD, and pediocin PA-1, pediocin ST18, and so on (Bhunia et al. 1991; Christensen and Hutkins 1992; Niamah 2018; Rodríguez et al. 2002; Todorov and Dicks 2005).

It has been shown that strains of *P. parvulus* isolated from vegetables, as well as *Lactobacillus plantarum* isolated from cheese (Ennahar et al. 1996), can produce pediocin PA-1 (Bennik et al. 1997). The production of pediocin PA-1 by diverse of pediococci strains, and even lactobacilli, can be used to argue that this antimicrobial has more than just killing characteristics and may be involved in *quorum sensing* intracellular communications (Chikindas et al. 2018). Bacteriocin production by various strains of *Pediococcus* spp., particularly *P. pentosaceus*, *P. acidilactici* and *P. damnosus*, are well documented and the majority of the strains are associated with the ability to produce pediocin PA-1 (Albano et al. 2007; Bauer et al. 2005; Bhunia et al. 1988; Cintas et al. 1995; Nel et al. 2001; Kaur et al. 2004; Nieto Lozano et al. 1992; Osmanagaoglu et al. 2011; Skytta et al. 1993; Todorov and Dicks 2005).

Some strains of *P. damnosus* isolated from wine, cider and brewery environments associated with spoilage were shown to be pediocin producers. It is important to point out that *P. damnosus* bacteriocin producers are sensitive to bacteriocins like nisin produced by *Lactococcus lactis* (Delves-Broughton 1990) and pediocin PA-1/AcH by *P. acidilactici* H (Ray 1995), implying that expressed pediocin is a different bacteriocin (Green et al. 1997).

Bacteriocin production by different strains of *Pediococcus* spp. is often reported. However, the number of studies describing the amino acid structure of expressed bacteriocins by different pediococci is still very limited. Moreover, evidences for their amino acid structures obtained by protein sequencing or relevant biomolecular approaches validating

expression of the targeted genes are required in order to claim creating a novel bacteriocin (Todorov et al. 2012).

Several studies have revealed that particular strains of *Pediococcus* can harbour genes related with the production of pediocin-PA1 and penocin based on WGS and metagenomic analysis (Oliveira et al. 2022; Queiroz et al. 2022; Kuniyoshi et al. 2021). However, the presence of these genetic markers confers only that these strains have the ability to produce the above mentioned bacteriocins. The capability of specific strain/s to express *de facto* specific bacteriocin can be only assessed through functional techniques, based on phenotypical and/or molecular assays. However, pediococci strains obtained from different niches are capable of producing a same bacteriocin, like pediocin PA-1, is clear evidence that such substances play an important role in the life cycle of this genus, besides than just killing target bacteria. The multipart role of the bacteriocins in the life cycle of the bacterial producer strains were already pointed by Chikindas et al. (2018), showing that bacteriocins needs to be considered not only as killing molecules, but as metabolites with signalling functions. This is/are function/s, that deserve a deep investigation, including for behaviour of pediocin PA-1 and other bacteriocins produced by pediococci.

Pediocins are usually described as small unmodified peptides, with a molecular weight (MW) of less than 5 kDa, composed of 40–44 amino acids containing aliphatic and aromatic amino acids, but without posttranslational polypeptide modification (Papagianni and Anastasiadou 2009; Todorov et al. 2019). As most of pediocins belongs to class IIa, their amino acid sequences share a specific similarity: a conserved N-terminal hydrophobic region in the YGNGV motif and a highly variable C-terminal hydrophobic or amphiphilic region (Niamah 2018; Kaur et al. 2014; Papagianni 2003; Porto et al. 2017; Todorov et al. 2019).

Most of the known pediocins are heat-resistant, small-structured, hydrophobic peptides which retain their activity even after sterilization temperatures and low temperatures even at -80°C (Anastasiadou et al. 2008b; Ghosh et al. 2019; Niamah 2018; Papagianni and Anastasiadou 2009; Porto et al. 2017; Todorov and Dicks 2005). As polypeptides, pediocins are sensitive to most protease enzymes such as papain, pepsin and trypsin (Anastasiadou et al. 2008 a, b; Espitia et al. 2016; Niamah 2018; Papagianni and Anastasiadou 2009; Todorov and Dick, 2005; Wu et al. 2004). Moreover, the majority of pediocins has an isoelectric point between 8.6 and 10, and a positive charge between (+3) and (+7) estimated at pH 6 (Niamah 2018; Porto et al. 2017; Venema et al. 1997).

Khorshidian et al. (2021) summarized research on pediocin and pediocin-like bacteriocins with prospective use for the control of *L. monocytogenes* in various food products

(Bari et al. 2005; Loessner et al. 2003). Different pediocin PA-1 producers were described in the literature (Albano et al. 2007; Chikindas et al. 1993; Gutierrez-Cortes et al. 2018; Queiroz et al. 2022; Kuniyoshi et al. 2021; Piva and Headon 1994) described pediocin A with an approximate MW of 80 kDa produced by *P. pentosaceus* FBB61 and provided detailed characterization of the expressed bacteriocin. Pediocin 34, produced by *P. pentosaceus* 34 and described by Kaur et al. (2013) was proposed as an effective agent for *L. monocytogenes* control. Pediocins with MW of 5.0 kDa produced by *P. acidilactici* NCIM 2292 was characterized and shown to be active against *L. monocytogenes* and *Staphylococcus aureus* (Mandal et al. 2014), with a spectrum of activity comparable to pediocin PA-1 (Simha et al. 2012). Other pediocins were denominated as Pediocin 05–10 (Hu et al. 2009), Pediocin LB-B1 (Xie et al. 2011) and Pediocin 18 (Todorov and Dicks 2005). However, since all authors have not provided information on the amino acid sequence of the expressed bacteriocins, definitive conclusions regarding the novelty and differences of the reported bacteriocins must be further investigated (An et al. 2011; Hu et al. 2009; Mandal et al. 2014; Simha et al. 2012; Todorov and Dicks 2005).

Pediocin F is produced by a *P. acidilactici* isolated from a fermented sausage (Osmanagaoglu et al. 1998). This pediocin has been demonstrated to be effective against a variety of food spoilage bacteria, including *E. coli*, *S. aureus*, *B. cereus* and *L. monocytogenes* (Osmanagaoglu et al. 1998) some of which pose significant health risks. Based on the sodium dodecyl sulphate- polyacrylamide gel electrophoresis (SDS-PAGE), Pediocin F was determined to have a MW of approximately 4.46 kDa (Osmanagaoglu et al. 1998; Todorov et al. 2019) reported that *P. pentosaceus* ST65ACC, a bacteriocin with strong anti-listerial activity, isolated from artisanal cheese, and a producer of coagulin A, has a high amino acid similarity to pediocin PA-1. However, the WGS of *P. pentosaceus* ST65ACC revealed that this strain carries an operon for the production of Pediocin PA-1 (Oliveira et al. 2022). Differences in case of the *P. pentosaceus* ST65ACC observed between the predicted bacteriocin based on WGS (Oliveira et al. 2022) and the results obtained from partial purification of the expressed bacteriocin (Todorov et al. 2019) may be due to some post-translational modification or oxidation of the produced antimicrobial peptide.

Probiotic potential

Antineoplastic activity of pediocin and some other bacteriocins

Cancer and cancer-related treatments are often challenges for the health care system. Different types of cancer are successfully treated with a variety of conventional chemotherapeutic drugs, but the side effects are severe. Cancer therapy is a complex process, involving not only direct targets of the cancer cells, but also resistance to some of the chemotherapy drugs associated with numerous factors related to increased expression of drug transporters and other drug detoxifying enzymes (Raguz and Yague 2008). In addition, chemotherapy often has a deleterious effect on the GIT microbiota and probiotics might be prescribed as an option to mitigate these side effects (de Moreno de Leblanc and Perdigon 2010; del Carmen et al. 2017). Some studies have proposed that certain bacteriocins might antineoplastic properties, making them a viable co-therapy for the treatment of cancer. Bacteriocins such as pediocin (Beaulieu 2004), colicins, microcin and pyocin (Abdi-Ali et al. 2004; Chumchalova and Smarda 2003; Hetz et al. 2002) have demonstrated promising results for the treatment of certain types of breast carcinoma, breast adenocarcinoma, osteosarcoma, leiomyosarcoma, fibrosarcoma, T cell lymphoma, cervix carcinoma, Burkitt lymphoma, pulmonary carcinoma, colon adenocarcinoma, lymphoblastic leukemia and hepatocarcinoma (reviewed by Kumar et al. 2012). Potential application of bacteriocins in with cytotoxic effect against cancer cells (Farkas-Himsley and Cheung 1976) was related to the highly specific recognition and interaction with the cell surface of the target cells without penetrating it and affecting their cell division and DNA synthesis (Jayawardene and Farkas-Himsley 1969; Todorov et al. 2019).

In addition to naturally produced pediocin (Beaulieu 2004), experiments with recombinant Rec-Pediocin CP2 were shown *in vitro* that specific cytotoxic effect against cancer cell lines can be a promising treatment and induction of programmed cell death or apoptosis (Kumar et al. 2012). Furthermore, experiments with naturally expressed pediocin CP2 produced by *P. acidilactici* MTCC 5101, and its recombinant analogue expressed as a synthetic fusion protein in recombinant *E. coli* BL21(DE3)-*pedA*, were tested for cytotoxicity against HepG2 (hepatocarcinoma), HeLa (cervical adenocarcinoma), MCF7 (mammary gland adenocarcinoma) and Sp2/0-Ag14 (spleen lymphoblast) cell lines (Kumar et al. 2012). Moreover, studies showed that recombinant pediocin had a strong cytotoxic impact and chromosomal DNA damage in bacteriocin-tested cell lines (Kumar et al. 2012).

In addition to the applications of different bacteriocins produced by pediococci, it is interesting to mention that microcin B17 was discovered to have a structural homology with bleomycin, a peptide used as a drug for the treatment of cancers, particularly Hodgkin disease and germinal cancers (Heddle et al. 2001). Pyocin has been shown to have antineoplastic effects in some cases of hepatocarcinoma and lymphoblastic leukaemia (Kumar et al. 2012). Additional evaluations for anticancer properties for some pediococci bacteriocins maybe will be interesting future scientific projects and potential medical application area. However, the majority of the reports are based on cell line investigations, and appropriate in vivo experiments on the potential use of pediocins as therapeutic or prophylactic compounds are necessary.

Probiotics are live microorganisms, which when consumed in adequate amounts can provide health benefits to the host (Hill et al. 2014). Bacteriocin production is not required, but it is a highly valued feature in the selection of novel probiotic strains since it can improve the ability of a strain to compete with other organisms in the GIT (including pathogens) and can positively influence the health of the host (Corr et al. 2007). It was suggested that pediocin-producing strain of *P. acidilactici* used as probiotics will be able to survive and express the bacteriocin/s in the host GIT, effectively inhibiting some bacterial pathogens or interfering with gastric adhesion of opportunistic pathogens such *Klebsiella*, *Pseudomonas* or *Shigella* (Speelmans et al. 2006; Piva et al. 2006). Moreover, in vitro studies showed the potential inhibitory activity of probiotic *P. acidilactici* BA28 (pediocin producer) against *Helicobacter pylori*. Treatment with pediocin BA28 was suggested as an option for *H. pylori* infection eradication (Kaur et al. 2014). In the case of *P. pentosaceus* OZF, immunomodulatory effects were assessed in vivo, implying its role as a probiotic (Osmanagaoglu et al. 2012).

Role of *P. acidilactici* in the modulation of immune response via interferences with gut microbiota in red tilapia was evaluated by Ferguson et al. (2010), and elevations of blood leucocyte levels and serum lysozyme activity were reported. Hao et al. (2021) reported on effect of *P. pentosaceus* ZJUAF-4 on relieves of oxidative stress and role in the restauration of the gut microbiota after intestinal injuries. *P. pentosaceus* ZJUAF-4 was influenced recovery of liver injury, monitored by alanine transaminase (ALT) and aspartate aminotransferase (AST) enzymatic markers; jejunum reactive oxygen species (ROS) parameters and expression of nuclear factors (Nrf2) were marker monitored associated to functionality of jejunum. Authors suggested that *P. pentosaceus* ZJUAF-4 protect the intestinal barrier functions and is involved in the balancing intestinal redox homeostasis, playing essential role in the prevention and treatment of

oxidative stress-related intestinal diseases (Hao et al. 2021; Xue et al. 2021) suggested application of *P. pentosaceus* as probiotic for the modulation of intestinal microbiota, increasing resistance to *Aeromonas hydrophila* in freshwater prawns. Role of *P. acidilactici* FZU106 in the modulation of intestinal microbiota in model animals and effect on lipid metabolism disorders were evaluated by Zhang et al. (2022). Recovery of the liver as consequence of the alcohol injury and modulations of the gut microbiota and short-chain fatty acids metabolism by *P. pentosaceus* was evaluated by Jiang et al. (2020). Authors pointed on lower levels of alanine aminotransferase, AST and triglyceride levels, as well on decreased neutrophil infiltrations. Application of studied strain of *P. pentosaceus* as well reduced levels of endotoxins and inflammatory cytokines, tumor necrosis factor- α , macrophage inflammatory protein-1 α , as well monocyte chemoattractant protein-1. Moreover, *P. pentosaceus* was able to restore microbial gut balance after negative effect of ethanol. Authors as well pointed on increasing the levels of some specific proteins, including tight junction protein ZO-1, mucin proteins (mucin [MUC]-1, MUC-2 and MUC-4) and the antimicrobial peptide Reg3 β (Jiang et al. 2020). Moreover, Bian et al. (2020) provided interesting results on role of *P. pentosaceus* LI05 in immune-modulation properties in recovery from DSS-induced colitis in mouse model, including role of the applied probiotic in regulation of gut microbiota and production of short-chain fatty acids.

Pediocins as spermicidal and vaginal health promoters

Despite the usual association of bacteriocins and their activity against close related bacteria to the producer species, the inhibitory activity of these substances can also affect other microorganisms, eukaryotic cells and even spermatozooids (Chikindas et al. 2018). Most of the conventional chemical contraceptive spermicides have been linked to vaginal microbiota disruption, and in some cases, the promotion of urinary tract infections (Balzaretto et al. 2015). Some bacteriocins, particularly Pediocin CP2 (native and recombinant analogue), have been shown to alter sperm motility and so interfere with their biological roles (Kumar et al. 2012).

Moreover, Borges et al. (2013) showed that pediocin produced by *P. pentosaceus* SB83 can have an effective activity against *Gardnerella vaginalis* and *Prevotella bivia*, *Bacteroides*, *Peptostreptococcus* and *Mobiluncus* spp. and can contribute to the development of a healthy balance in the vaginal microbiota.

Pediocin against bovine mastitis

The role of bacteriocins as an alternative treatment for bovine mastitis was proposed by Pieterse and Todorov (2010). By definition, bovine mastitis is an inflammatory disease of the mammary gland caused by the growth of different microorganisms (Turovskiy et al. 2009). It was proposed that pediocin produced by *P. pentocaceus* SA131 (isolated from jeotgal) can be used as an agent for the treatment of bovine mastitis pathogens with effective inhibition of related pathogens, including *Streptococcus uberis* E290, *Enterococcus gallinarum* E362, and *Staphylococcus epidermis* ATCC 12228 (Park et al. 2017).

Use of pediocin in animal feedstuff

According to U.S. Patent no. 0176910A1, pediocin can be associated to other feed additives to improve the hygiene and productivity in agricultural livestock (Razek 2002). Bacteriocins, bacteriocin producing organisms, and probiotics are some of the proposed alternatives to antibiotics in the animal feed industry, where the search for alternatives is expanding.

Different areas of applications of *Pediococcus* spp. were proposed, including improvement of human and other animals' health, lowering of blood cholesterol levels, control of inflammatory bowel disease (IBD), diabetes, obesity, prevention of some enteropathogen-induced gastrointestinal disorders, inhibition of growth and surface colonization of Enterohemorrhagic *E. coli* (EHEC) O157:H7, anti-tuberculosis activity against *Mycobacterium tuberculosis*, *M. bovis*, improvement of symptomatic and viral clearance in COVID-19 outpatients, colorectal cancer therapy, infantile colic treatment, modulation of the GIT microbiota, reduction of the incidence of respiratory tract infections and for the management of lactose intolerance, anti-inflammatory, antioxidant and antihyperglycemic activities, immunomodulatory effects, applications in aqua cultures, broilers farming, control of biofilm formations by different pathogenic species etc. Table 1 provides a summary of these applications. In addition, it is significant to note that the assessed strains were isolated from diverse ecological niches, demonstrating the well-adapted nature of pediococci.

Trends and perspectives

Pediococci have a relevant role as a member of LAB, and their diverse beneficial features demonstrate how this group can be explored as starter cultures, bio-preservatives and even probiotics candidates. The current use of Pediocin PA-1 in the food industry highlights the bio-preservative

potential of pediococci, leading further studies to characterize novel strains and pediocin variants, with clear application in food systems to assure safety and quality. In addition, such pediocins must also be assessed for their potential application in human and animal health, as alternative for conventional antibiotics treatments, and even to treat and control non-infectious diseases, such as cancers.

As the molecular tools are becoming usual and accessible to the scientific community, known pediococci strains, previously isolated and characterized based on their technological features, can be deeply investigated regarding their additional beneficial features. In this sense, *Pediococcus* spp. strains that are currently used by the food industry with technological purposes can be further explored, in order to select potential probiotic candidates to be used in medical and veterinary treatments. In addition, *in silico* analysis of bacteriocins and their potential target interactions can be currently assessed, allowing relevant predictions to identify potential candidates to control pathogenic agents, supporting the control of worldwide distributed diseases, such as COVID-19 (Erol et al. 2021). The same approach can be adopted to predict potential interactions with specific targets, enhancing the potential application of pediocins in different areas.

Independently of the vast beneficial potential and applications of pediococci and their bacteriocins, the safety of the beneficial strains must be assessed (EFSA Panel on Additives and Products or Substances used in Animal Feed (FEEDAP) et al. 2018; Fugaban et al. 2021; Todorov et al. 2021). Molecular tools, as WGS, are allies in this task, allowing quite complete characterizations of the virulence factors presented in pediococci strains genome, as well as antimicrobial resistance (AMR) related genes. Conventional microbiology, or even molecular assays, that allow the identification of the expression of such virulence and AMR related genes must be considered to assess the safety of potential candidates to be applied directly in food and/or as therapeutics.

The beneficial features presented by *Pediococcus* spp. were widely presented and discussed in this review, demonstrating how this genus can contribute with the pharmaceutical and food industries. These beneficial aspects of *Pediococcus* spp. are determinant to improve human and animal health, once different strains of this genus can be used as probiotics, starters cultures and biopreservatives. *Pediococcus* strains that present such beneficial features must be subjected to deep analysis based on molecular and phenotypical approaches for proper characterization of their applications, as well as their safety status. Such approaches must also be adopted to characterize *Pediococcus* strains already described as beneficial, supporting their use with different purposes.

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