**Pediococcus pentosaceus**, a future additive or probiotic candidate

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**Abstract**

**Background:** *Pediococcus pentosaceus*, a promising strain of lactic acid bacteria (LAB), is gradually attracting attention, leading to a rapid increase in experimental research. Due to increased demand for practical applications of microbes, the functional and harmless *P. pentosaceus* might be a worthwhile LAB strain for both the food industry and biological applications.

**Results:** As an additive, *P. pentosaceus* improves the taste and nutrition of food, as well as the storage of animal products. Moreover, the antimicrobial abilities of *Pediococcus* strains are being highlighted. Evidence suggests that bacteriocins or bacteriocin-like substances (BLISs) produced by *P. pentosaceus* play effective antibacterial roles in the microbial ecosystem. In addition, various strains of *P. pentosaceus* have been highlighted for probiotic use due to their anti-inflammation, anticancer, antioxidant, detoxification, and lipid-lowering abilities.

**Conclusions:** Therefore, it is necessary to continue studying *P. pentosaceus* for further use. Thorough study of several *P. pentosaceus* strains should clarify the benefits and drawbacks in the future.

**Keywords:** *Pediococcus pentosaceus*, Bacteriocin, Probiotics, Food additives, Biopreservative

**Background**

Screening useful bacteria from complex microbial communities is becoming increasingly commonplace. There are billions of microorganisms in the world, but few of them have been tested to determine their features and applications. Among them, the microorganisms called probiotics have already received much publicity for their beneficial effects on humans, animals, plants and foods. In fact, there are not enough probiotics on the market or in clinical practice, which has prompted us to seek insights into other novel bacteria that are both functional and harmless. Currently, only a limited number of probiotics are used for daily maintenance of the intestinal microecological balance and in clinical treatment. Among them, lactic acid bacteria (LAB) have proven worthy of exploration. LAB play important roles in food manufacturing and storage as well as human health promotion [1]. LAB were first recorded in 1907 and used as starter cultures, and they have long been applied as food additives and health promoters [2]. It has already been shown that certain kinds of probiotics can boost disease treatment and improve homeostasis. Both the gut and nonintestinal organs are modulated by probiotics [3]. In addition to *Lactobacillus* and *Bifidobacterium* species, which are the most widely used, *Clostridium* species have recently been proven to possess potent probiotic characteristics [4]. However, these strains are not sufficient for the various demands of humans and industry [5]. Therefore, additional types of bacteria need to be discovered to enrich the application spectrum of probiotics and their applications in food and agriculture.

*Pediococcus pentosaceus*, one type of LAB, has played an increasingly pivotal role in LAB applications in recent
years. Isolated from fermented food, aquatic products, raw animal, plant products and faeces, many strains of *P. pentosaceus* were finally proven to have links of the human gastrointestinal tract (GIT) [6]. To date, there is increasing experimental evidence indicating that *P. pentosaceus* may be usable as a biopreservative for foods, plants or animals or as an emerging possible probiotic candidate, as shown in Table 1. *P. pentosaceus* is a coccio-shaped, gram-positive, nonmotile and homofermentative LAB with facultative anaerobic and carbohydrate degradation features [7]. It was already known in the 1990s that some *P. pentosaceus* strains can be applied in fermentation, as an animal growth biopromoter and as a probiotic [8]. However, most of the properties of *P. pentosaceus* were not well studied at that time. Furthermore, after more than two decades of investigation of *P. pentosaceus*, many other previously undiscovered features have been studied. To date, the problems associated with the practical use of *P. pentosaceus* as a probiotic remain unsolved, for example, there is a lack of knowledge regarding mechanisms, side effects, usage and dosage. There is growing evidence that *P. pentosaceus* and its bacteriocins perform well in both the food industry and intestinal health. Some strains of *P. pentosaceus* produce several functional compounds for different uses, as illustrated in the Fig. 1. Moreover, genomic sequencing verified the ability of both food-derived and animal-derived bacteria to metabolize carbohydrates and horizontally transfer prophage DNA and bacteriocins, etc. [9].

In this review, we have summarized a majority of the studies on *P. pentosaceus* and explored the possibility of its further development as biopreservatives or probiotics. We assume that *P. pentosaceus* has a great impact on the health of animals and especially humans.

**Evidence of *P. pentosaceus* use in food engineering, agriculture and animal husbandry**

Different strains of *P. pentosaceus* were detected in foods, plants and animals, acting as flavour enhancers, storage agents or growth stimulators. Some species of bacteria have been gradually shown to provide an array of flavouring agents and food additives in recent years [60]. As food supplements defined by European Food Safety Authority (EFSA), these bacteria play important roles in nutrition supply and physiological functions maintain. Furthermore, members of the *Pediococcus* genus were shown to lack known antibiotic resistance genes [61]. Both traditional and industrial foods are supplemented with particular bacteria to improve taste, nutrition and food safety. Fermentation is an important process to transform bioengineered food to safe, healthy, and green products. In the process of fermentation, *P. pentosaceus* greatly increased the concentration of nitriles and alcohols in Suancai, a Chinese pickled vegetable [62]. Isolated from fermented seeds of *Chrysophyllum albidum* Linn (African star apple), *P. pentosaceus* (ProbtA2b), as a beneficial LAB, changed the physicochemical properties of the fermented food [63].

Notably, *P. pentosaceus* acts as a food additive, providing improved flavour by elevating the concentration of short-chain fatty acids (SCFAs) [10], the protein hydrolysis of meat [11]. Jang et al. [12] found that *P. pentosaceus* T1 improved texture, sourness and other organoleptic senses and thus could be a starter for original kimchi. Through suppressing LAB, *P. pentosaceus* T1 delayed the maturation of kimchi to improve its utility. *P. pentosaceus* CRAG3 (GenBank accession number JX679020) was first shown to have glucansucrase-producing and prebiotic-utilizing abilities. Then, its high glucansucrase output was certified for contributing to the flavour of dairy products [13,14]. *P. pentosaceus* OA1 and S3N3 stand out among 41 candidate strains for their superior acidification abilities and proteolytic roles in whole wheat dough fermentation [15]. Gong et al. [64] showed that *P. pentosaceus* could ferment a large number of meats and vegetables, especially Chinese Lamian, and recently, kefir grain-derived *P. pentosaceus* SP2 was proven to be a new candidate for bread fermentation due to its acidity and resistance to mold and rope spoilage [65]. Isolated from traditional sour meat, *P. pentosaceus* SWU73571 and *Lactobacillus curvatus* LAB26, when combined as double-starter culture, improved the flavour, quality and safety of the sour meat [66].

Moreover, in the fields of agriculture and animal husbandry, some studies found that *P. pentosaceus* improved the characteristics and growth abilities of animals and plants. As a major advance in the application of animal husbandry, *P. pentosaceus* DSM 16,244 was certified as safe additive for all animal species by the Panel on Additives and Products or Substances used in Animal Feed (FEEDAP) [67]. With regard to crops, *Elymus nutans*-derived *P. pentosaceus* Q6 was beneficial for the storage quality of *Elymus nutans* silages at low temperature [16]. Thus, *P. pentosaceus* Q6 might be a cold-resistant candidate for high-quality silage storage. With regard to animals, cobia intestine-derived *P. pentosaceus* 4012 was found to act against *Photobacterium damselae* subsp. *Piscicida* (*Pdp*) and hasten cobia growth. In a subsequent experiment, the immune-enhancer *P. pentosaceus* 4012 eliminated vibriosis; this strain was isolated from cobia intestine, making it a promising and profitable strain for use in orange-spotted grouper [17, 18]. *P. pentosaceus* SL001, isolated from many soil samples, not only greatly increased the expression of complement 3 and immunoglobulin M but also ameliorated damage to the intestinal villi and goblet cells, indicating promotion of the immune
Table 1 Summary of studies on Pediococcus pentosaceus

| The purpose                                           | The strain used                                                                 | The main findings                                                                 | References                      |
|-------------------------------------------------------|---------------------------------------------------------------------------------|----------------------------------------------------------------------------------|---------------------------------|
| Improve the taste of food                             | P. pentosaceus T1, P. pentosaceus CRAG3, P. pentosaceus QA1 and S3N3            | Improving texture, sourness and other organoleptic properties                     | [10–15]                        |
| Improve the growth abilities of plants and animals    | P. pentosaceus Q6, P. pentosaceus 4012, P. pentosaceus SL001, P. pentosaceus PP8 | Promoting biological growth and storage                                           | [16–20]                        |
| Inhibit bacteria and fungi without bacteriocins or BLISs | P. pentosaceus T1, P. pentosaceus Z13P, P. pentosaceus BahBio02, P. pentosaceus SK25, P. pentosaceus –DPS, P. pentosaceus L1, P. pentosaceus 411, P. pentosaceus MP12, P. pentosaceus TG2, P. pentosaceus No. 183, P. pentosaceus KCC-23, P. pentosaceus PPCS, P. pentosaceus HM, P. pentosaceus L006 | Fighting against bacteria or fungus directly or with EPS, especially L. monocytogenes | [12, 21–27]                    |
| Inhibition of inflammation                            | P. pentosaceus AK-23, P. pentosaceus ONB9A, P. pentosaceus KFT18, P. pentosaceus NB-17, P. pentosaceus Sn26 | Exerting anti-inflammatory effects by regulating cytokines and boosting immunity | [28–34]                        |
| Antagonism of cancer                                  | P. pentosaceus M41, P. pentosaceus SL4(PP), P. pentosaceus CRAG3, P. pentosaceus PP3 | Inhibiting the proliferation of cancer, especially CRC                           | [22, 35–37]                    |
| Antioxidant                                           | P. pentosaceus Be1, P. pentosaceus S-SU6, P. pentosaceus MYU759, P. pentosaceus AR243, P. pentosaceus KCC-23, P. pentosaceus AOA2017, P. pentosaceus DK1 | Exerting antioxidant effects by scavenging DPPH free radical, O2-, and so on     | [38–43]                        |
| Reduction of lipids                                   | P. pentosaceus LAB6, P. pentosaceus LP28, P. pentosaceus KID7                   | Affecting cholesterol metabolism and ameliorating some related diseases           | [44–48]                        |
| Antidotal action                                      | P. pentosaceus FB145 and FB181, P. pentosaceus xy46                           | Degrading or antagonizing toxic substances, such as Cd, ZEA, etc                  | [49–51]                        |
| Utilization of minerals and nutrients                 | P. pentosaceus B3, B11, P. pentosaceus CFR R38, R35, P. pentosaceus GF23, P. pentosaceus UP-2, P. pentosaceus TL-3, P. pentosaceus HN8 | Promoting the biotransformation and utilization of nutrients and minerals, especially phytate | [44, 52–58]                    |
| Vaginal protection                                   | P. pentosaceus SB83                                                          | Surviving manmade vaginal gel and producing antibacterial bacteriocin             | [58, 59]                       |
system of grass carp. Its broad-spectrum antibacterial properties also provided an opportunity for probiotic use in freshwater fish [19]. *P. pentosaceus* was found to be beneficial to mud crabs because of its bacteriostatic, immune-enhancing and growth-promoting virtues [68]. Moreover, the application of *P. pentosaceus* PP8 in whiteleg shrimp had the same outcomes [20]. Treatment with *P. pentosaceus* PP8 derived from the gut of juvenile whiteleg shrimp promoted many functions in whiteleg shrimp, such as digestive enzyme activity, disease resistance, growth and immunity. Isolated from human colostrum, *P. pentosaceus* B49 relieved constipation not only by improving gastrointestinal motility and water and electrolyte absorption but also by promoting neurotransmitter transmission and the growth of beneficial short-chain fatty acid-producing bacteria [69]. Isolated from rumen fluid, *P. pentosaceus* S22, with low carbohydrate tolerance, exhibited good adaptability to the gastric juice environment. Research showed that *P. pentosaceus* S22 greatly improved the quality of fermentation of legume silage in vitro [70]. Eveno et al. [71] proposed that *P. pentosaceus* ICVB491 produced bacteriocins and biofilms with low pathogenic risks and high compatibility. Combined with three other LAB, *P. pentosaceus* LUHS183 is involved in the acidification process of feed, leading to great improvement of the hematology indexes, intestinal microorganism distribution and growth of piglets. All four LAB were obtained from the Lithuanian University of Health Sciences collection (Kaunas, Lithuania) [72].

As confirmed by various experiments, many *P. pentosaceus* strains not only could be applied as biopreservatives for foods, crops and livestock but also could be used to accelerate beneficial physical activities. Adding freshness and flavour to food, *P. pentosaceus* is used in the field of food research to promote the development of food engineering from chemical treatment to biological treatment. The usage of *P. pentosaceus* in agriculture is relatively rare, and this species is used mainly in the storage of crops. These strains increase the storage time for plants. But in animal husbandry, related characteristics of *P. pentosaceus* have been explored much more extensively. Through the action of *P. pentosaceus* on animals themselves, improvement of the growth and pathological state of animals can be achieved, so in a sense, *P. pentosaceus* can be called an animal probiotic. *P. pentosaceus* exhibits several beneficial properties, making it a competitive candidate strain for animal feed additives.

**Antimicrobial properties**

**Bacteriostatic capacity**

*P. pentosaceus* is a strain of LAB that not only enhances the flavour and preservation of food agents but also

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**Fig. 1** Some *Pediococcus pentosaceus* pathways involved in functional compound production
inhibits colonization by pathogenic bacteria. Many foodborne pathogens colonize food and multiply to cause food decay and poisoning, such as Salmonella [73], Escherichia coli [74] and Listeria [75]. P. pentosaceus behaves as a good antipathogen agent when faced with such harmful bacteria. Several experiments were conducted as described below to show that P. pentosaceus exhibits good performance against L. monocytogenes. L. monocytogenes is one of the most common human pathogens, causing meningitis, septicemia, and abortion [76].

Ubiquitous L. monocytogenes contaminates and reproduces in food, eventually resulting in listeriosis [77]. Several strains of P. pentosaceus have been shown to restrict the growth of Listeria spp., such as P. pentosaceus LJR1 [78] and P. pentosaceus ATCC 43,200 [79]. For instance, P. pentosaceus T1 showed better antilisterial ability in fish products than a disinfectant and nisin, which are famous for their antibacterial abilities [12]. Yukselkg and Aslim [21] found that five strains of Pediococcus spp. isolated from Turkish sausage suppress L. monocytogenes by secreting hydrogen peroxide, especially P. pentosaceus Z13P. In addition to its high anti-Listeria activity, P. pentosaceus was found to be effective against other special pathogens, such as Salmonella Typhimurium [80] and Streptococcus salivarius [81]. Beyond its role in promoting milk yield, P. pentosaceus BaltBio02 showed promising antimicrobial activity against Staphylococcus aureus and Pseudomonas aeruginosa [22]. The traditional Chinese pickle-derived P. pentosaceus SK25 produces a large amount of 3-phenyllactic acid, which results in broad-spectrum antibacterial properties, including against a variety of food-spoiling bacteria and fungi [23]. In fact, several strains of P. pentosaceus have been shown to have antimicrobial activities for further application [82, 83]. Faba bean contains 8 strains of P. pentosaceus that effectively fight against L. monocytogenes and E. coli [84].

In addition to bacteriocins and bacteriocin-like inhibitory substances (BLISs), exopolysaccharides (EPSs) were confirmed as important metabolites with special functions secreted by P. pentosaceus. The EPSs of P. pentosaceus-DPS are thermostable and destroy harmful biofilms. P. pentosaceus-DPS survived in the human GIT, fighting against L. monocytogenes and E. coli, and its thermostolerant EPSs destroyed harmful pathogenic bacteria-derived biofilms by inhibiting adhesion [24]. The supernatant of P. pentosaceus 411, derived from freshwater fish, was effective against foodborne pathogens, such as E. coli O157:H7 and Staphylococcus aureus KCTC-1621 [26]. P. pentosaceus MP12 was obtained from pickled vegetables for inhibiting Salmonella invasion to extend the shelf life of pickles [27]. In addition to adhering to the intestinal epithelium, other factors contribute to preventing Salmonella invasion.

**Antifungal ability**

P. pentosaceus, one of the major fungus-inhibiting LAB, behaved well in research [85]. Fungi and their mycotoxins are hazards to the health of their parasitifers and food security. In addition to activity against pernicious bacteria, some P. pentosaceus even have antifungal abilities, including P. pentosaceus TG2 (collected from Silent Valley National Park) [86], P. pentosaceus No. 183 (collected from a spontaneous rye sourdough) [87], and P. pentosaceus KCC-23 (collected from Italian ryegrass) [42]. P. pentosaceus was found to fight against several common fungi, especially Aspergillus, Penicillium, Fusarium and Candida albicans. For instance, P. pentosaceus PPCS originated from an Indian traditional fermented dairy product, and the cell-free supernatant (CFS) of P. pentosaceus PPCS has the ability to suppress zearalenone (ZEA) activity and inhibit Fusarium graminearum [88]. The CFS of P. pentosaceus HM (collected from Al-Maray honey) shows fungicidal activity against Candida species [89]. The secreted factors of maize leaf-derived P. pentosaceus L006 have an impact on fumonisin-producing fungi [90].

**Bacteriocins or BLISs**

To date, only one bacteriocin has been applied in food biopreservative use and approved for clinical use by the Food and Drug Administration (FDA): nisin, which is produced by Lactococcus [91]. However, more bacteriocins should be identified for use in food supplements and clinical applications. Recently, an increasing number of studies have shown that P. pentosaceus antagonizes pathogens through secreting bacteriocins or BLISs [92]. In 2017, Porto et al. [93] provided a detailed overview of the cultivation and mechanisms of Pediococcus spp. and their pediocins [93]. Bacteriocins, polypeptides synthesized by ribosomes, have antibacterial properties, especially against foodborne pathogens. The bacteriocins of class II-a consist of pediocin-like single peptides. Bacteriocins from Pediococcus spp. are small and heat-stable peptides known as pediocins and have hydrophobic and cationic properties [92, 94]. The pediocins known so far are listed in Table 2. The bacteriocin of P. pentosaceus exhibits bactericidal ability against pathogens, such as L. monocytogenes and Clostridium perfringens [95]. By screening thousands of bacteria from kimchi, P. pentosaceus K 23–2 and its pediocin K 23–2 were found to inhibit various gram-positive pathogens [96]. P. pentosaceus LMQS 331.3, isolated from traditionally fermented German sausages, produces a bacteriocin with good stability and effective suppression of Listeria spp. [97]. In addition to antagonistic activity against pathogens, P. pentosaceus CFF4, as an isolate from different food matrices, was found

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to adhere to Caco-2 cells [98]. Fermented triticale silage-derived *P. pentosaceus* (TC48) not only produced better-quality silage but also inhibited *Pseudomonas aeruginosa, Enterococcus faecalis, S. aureus* and *E. coli* [99]. *P. pentosaceus* ST65ACC, a poorly cytotoxic coagulin A producer from raw milk cheese, survived in the GIT and coaggregated with *L. monocytogenes* of pathogens, especially *Clostridium sporogenes* ATCC 11,259 [109]. *P. pentosaceus* DT016 weakened the proliferation of *L. monocytogenes* by pediocin DT016 in vegetable storages. In short, bacteriocins produced by *P. pentosaceus* showed good antibacterial performance, but their food safety needs to be evaluated for further clinical and food application.

Similar to bacteriocins, BLISs, a previously unidentified category of molecules, lead to bacteria death through depolarized membrane and cytoplasmic content release. *P. pentosaceus* ATCC 43,200, also known as *P. pentosaceus* FBB61, was first isolated from fermented cucumbers in 1953 [116], and further studies were carried out. The BLIS pediocin A is most active at pH 5.0 with no additional sugar supplements in the medium [114, 117]. Then, it was determined that inulin and sucrose accelerate the production of pediocin A [92]. However, it was proven that a *P. pentosaceus* BLIS produced by *P. pentosaceus* ATCC 43,200 not only inhibits the growth of *Listeria seeligeri* but also improves the appearance of pork ham. Moreover, the BLIS may have better antibacterial effects than Nisaplin [79, 118]. Furthermore, the secretion of BLISs by *P. pentosaceus* is influenced by many factors, such as pH and temperature. Gutierrez-Cortes et al. [119] designed an experiment to elucidate pediocin upregulation during coculture with *Lactobacillus*. In summary, both bacteriocin and BLIS produced by *P. pentosaceus* were competent substitutes for antimicrobial agents. As a strain of bacteriocinogenic LAB, *P. pentosaceus* has the ability to inhibit a wide variety of pathogens.

### Table 2 Bacteriocins produced by *Pediococcus pentosaceus*

| Bacteriocin | Producing organism | Source | Classification | Reference |
|------------|--------------------|--------|----------------|-----------|
| LJR1       | *P. pentosaceus* LJR1 | Goat rumen liquor | 4.6 kDa | [78] |
| GS4        | *P. pentosaceus* GS4 | Indian fermented food (Khadi) | Class II-a | [94] |
| MZF16      | *P. pentosaceus* MZF16 | Artisinal Tunisian meat, dried Ossban | Class II-a | [110] |
| LB44       | *P. pentosaceus* LB44 | Dary soil | ~6 kDa | [111] |
| Coagulin A | *P. pentosaceus* ST65ACC | Raw milk cheese | Class II-a | [102] |
| VJ13B      | *P. pentosaceus* VJ13B | Idly batter | Class II-a | [103] |
| OZF        | *P. pentosaceus* OZF | Human breast milk | - | [104] |
| ST44AM     | *P. pentosaceus* ST44AM | Marula | Class II-a | [105] |
| K23-2      | *P. pentosaceus* K23-2 | Kimchi | ~5 kDa | [96] |
| A          | *P. pentosaceus* ATCC 25745 | Plant | 4684.6 Da | [108] |
| PA-1 (AcH) | Multiple LAB (pS34 from *P. pentosaceus* S34) | Food products | Class II-a | [112] |
| ACCEL      | *P. pentosaceus* ACCEL | Vacuum-packaged meat | Class II-a | [113] |
| L          | *P. pentosaceus* L | Refrigerated pork | 27 kDa | [109] |
| S          | *P. pentosaceus* S | Refrigerated pork | 25 kDa | [109] |
| A          | *P. pentosaceus* FBB61 (ATCC 43200) | Fermented cucumbers | 80 kDa | [114] |
| N5p        | *P. pentosaceus* N5p | Wine | - | [115] |
Probiotic applications

Until now, basic and clinical research on probiotics has progressed rapidly, but probiotics still have not been applied as drugs worldwide [120]. In the United States, probiotics have been recommended by clinical doctors as evidence-based conventional or medical foods and dietary supplements under the guidance of the US Food and Drug Administration (FDA). Many probiotic strains are considered Generally Recognized as Safe (GRAS) to use in foods (https://www.fda.gov/animal-veterinary/animal-food-feeds/generally-recognized-safe-gras-notification-program). In addition, the European Food Safety Authority (EFSA) evaluated a number of traditional species of probiotics as safe for application in food by the Qualified Presumption of Safety (QPS) [121]. From October 2019 to March 2020, EFSA found that only 6 microorganisms met the standard from 39 notifications [122].

The interactions between *P. pentosaceus* and the gut microbiota alone have been widely analysed, but not many studies have evaluated them by -omics approaches, such as transcriptomic, proteomics, metagenomics, and 16S rDNA/rRNA gene sequencing. For example, gastrointestinal peristalsis was partially improved by treatment with *P. pentosaceus* B49, as determined by analysing the transcriptomic outcome in the colon [69]. The cell adherence function of *P. pentosaceus* GS4 was proved to produce a 98 kDa surface layer protein, as determined by proteomic technology such as SDS-PAGE and size exclusion chromatography [123]. Through metagenomic sequencing, *P. pentosaceus* strains were selected from hundreds of LAB for their beneficial characteristics. For instance, *P. pentosaceus* strains were found in a dominant position in wheat fermentation, in addition to *Lactobacillus plantarum* and *Lactobacillus fermentum* [124]. The most widely used method is 16S rDNA/rRNA gene sequence analysis, which identified *P. pentosaceus* among a variety of bacteria. Hundreds of *P. pentosaceus* strains were selected by screening various samples and further identified based on the results of 16S rRNA gene sequencing [125]. Through -omics approaches, additional features and functions of *P. pentosaceus* were determined for further probiotic application.

Anti-inflammatory ability

*P. pentosaceus* was verified to sustain internal environmental homeostasis, for example, by enforcing systemic immunity and enhancing anti-inflammatory ability. *P. pentosaceus* showed its anti-inflammatory abilities in the host through upregulating or downregulating lipopolysaccharides (LPS) or cytokines. Many studies were conducted to examine the relationship between inflammatory response and *P. pentosaceus*, as described below. High burdens of gram-negative pathogens give rise to intestinal health disorders because of their LPS. The heat shock protein (HSP) of pickled-derived *P. pentosaceus* AK-23 is useful for neutralizing LPS, which is finally degraded to polysaccharides and fatty acids [28]. Onion-derived *P. pentosaceus* ON89A improves the anti-inflammatory effect of the Chinese herb Cordyceps militaris (*C. militaris*) via the GRC-ON89A hexane fraction (GRC-ON89A-Hex). LPS-stimulated RAW 264.7 macrophages were affected by GRC-ON89A-Hex, resulting in decreases in TNF-α, cyclooxygenase 2 (COX2) and inducible NO synthase (iNOS). Enterotoxigenic *E. coli* F4+ antagonism by *P. pentosaceus* L1 showed anti-inflammatory effects by downregulating the levels of interleukin (IL)-6, tumour necrosis factor (TNF)-α and IL-8 [25]. Furthermore, oral administration of fermented *C. militaris* with *P. pentosaceus* ON89A in cyclophosphamide (CY)-induced mice improved its immunostimulatory abilities and obtain more nutrition acquisition [29, 30]. Moreover, the PE-EPS of [31] kimchi-derived *P. pentosaceus* KFT18 was administered to CY-mediated immunosuppressed mice, which mediated spleen and thymus development and lymphocyte and cytokine production. *P. pentosaceus* KFT18, which could even act as an immunomodulator, stimulated a protective immune response [32]. In vitro, pickled vegetable-isolated *P. pentosaceus* NB-17 was applied to ovalbumin (OVA)-sensitized mouse spleen cells. The improvement in IL-12 and interferon (IFN)-γ levels showed a possibility for improved immunity [33]. In the model of OVA-treated diarrheic mice, *P. pentosaceus* Sn26 also downregulated OVA-specific IgE levels in serum and upregulated IL-12 and IFN-γ levels. Maintaining the Th1/Th2 balance, the Japanese Sunki pickle-derived *P. pentosaceus* Sn26 is good for modulating type 1 allergic reactions [34].

Anticarcinogenic properties

Several cancers, especially colorectal cancer (CRC), were found to be ameliorated by certain kinds of probiotics. Also, some experiments were conducted to determine the anticancer functions of *P. pentosaceus*. As a new probiotic candidate, *P. pentosaceus* might stand out from a range of already known probiotics. *P. pentosaceus* M41, derived from a marine source, excreted EPS-M41 with antitumor and antioxidant activities, including high anti-Caco-2 and anti-MCF-7 efficacy [35]. Protein p8 is a therapeutic substance that is certified to decrease the mass of CRC and enhance antiproliferative activity. Lele et al. [22] invented p8-secreting induction kit targets based on *P. pentosaceus* SL4 (PP). Recombinant *P. pentosaceus* SL4 offers an alternative means of delivering p8 for oncotherapy. Dextran, a product of *P. pentosaceus* CRAG3, inhibited colon cancer (HT29) and cervical cancer.
(HeLa) cell lines. Extracted from fermented cucumber, P. pentosaceus CRAG3 is a novel probiotic candidate with anticancer functions [36]. Among 81 isolates from infant faeces, P. pentosaceus FP3 inhibited the proliferation of colon cancer and induced the production of SCFAs [37]. This study proved that P. pentosaceus FP3 might serve as a prophylactic or therapeutic approach for colon cancer. As mentioned above, some strains of P. pentosaceus may have a brighter future.

Antioxidant applications
The antioxidant capacity of LAB includes the scavenging capacities of α,α-diphenyl-β-picrylhydrazyl (DPPH) free radical, O₂⁻, and so on. Through these abilities, some related diseases, such as neurodegenerative disease, cardiovascular disease and, more importantly, senility, benefit greatly. Some strains of P. pentosaceus are adept at scavenging hydrogen peroxide, such as P. pentosaceus Be1 (collected from fermented food) [38] and P. pentosaceus S-SU6 (collected from the gut of blue mackerel) [39]. P. pentosaceus MYU 759 was found to have hydroxyl radical antioxidant capacity (HORAC) due to the secretion of acidic EPS, which is highly beneficial in its isolation from soymilk yogurt as an antioxidant product [40]. Additionally, P. pentosaceus AR243, an isolated LAB from Chinese fermented foods, had significant scavenging abilities for hydroxyl radicals and DPPH free radicals, resulting in further inhibition of lipid peroxidation [41]. P. pentosaceus KCC-23 survived in the low-pH environment of gastric juice and not only inhibited fungus and bacteria effectively but also exhibited its own biological potential. Italian ryegrass-derived P. pentosaceus KCC-23 was determined to have a strong free radical-scavenging effect and cholesterol-lowering ability [42]. Eleusine coracana-derived P. pentosaceus AOA2017 amplified the antioxidant ability of Korean Yak-Kong, thereby possibly resulting in atherosclerosis prevention [43]. P. pentosaceus DK1 was applied to Lavandula angustifolia extract for its antiaging effect. In addition, it turned out that Diospyros kaki fruit-derived P. pentosaceus DK1 effectively downregulated UVB-mediated MMP-1 expression and collagen [126]. Additionally, a strain of P. pentosaceus in Harbin dry sausage possessed the ability to scavenge radicals. It might also be an antioxidant of meat [127].

Lipid-lowering effects
Recently, probiotic supplementation was shown to decrease cholesterol levels in humans via several mechanisms [47]. P. pentosaceus strains were also shown to affect cholesterol metabolism. For instance, Malaysian P. pentosaceus LAB6 decreased cholesterol without bile salts by 54% and cholesterol with bile salts by 58% compared to other LAB [44]. Applied to obese mice with high-fat diets, P. pentosaceus LP28 resulted in weight reduction and decreased the concentrations of cholesterol and triglycerides. These plant-derived LAB were confirmed as promising antiobesity bacteria for preventing metabolic syndrome [45, 46]. Both in vitro and in vivo experiments were carried out, and P. pentosaceus KID7 survived in the gastrointestinal environment and lowered cholesterol levels. Oral administration of KID7 in atherogenic diet-induced mice greatly ameliorated elevated cholesterol levels [47]. Through modulating the gut microbiota, finger millet gruel-derived P. pentosaceus KID7 ameliorates the nonalcoholic fatty liver disease (NAFLD) state [48]. As an isolate from Northeast pickled cabbage, P. pentococcus PP04 ameliorated blood lipids and markers of liver injury and inflammation in hyperlipidemia model C57BL/6 N mice through the AMPK signaling pathway [128].

Detoxification
P. pentosaceus strains might act as novel potent biological antidotes for reducing or preventing the presence of toxic substances in human bodies. Through physical methods, detoxification abilities have been reported for several strains of P. pentosaceus. P. pentosaceus not only affected the substance absorption and excretion of the intestine but also upregulated toxic substance decomposition by the detoxification ability of the liver, such as reducing blood ammonia, heavy metal ion, and endotoxin levels [49]. Le and Yang [50] carried out experiments to show that P. pentosaceus FB145 and FB181, derived from fermented seafood, were capable of reducing the toxicity of cadmium (Cd). They found that Cd combined with bacterial cells by specific several functional groups and thus decreased Cd bioaccessibility in vitro to 44.7–46.8%. Administration of P. pentosaceus xy46 (CCTCC number: M2018352) protected the male reproductive system of mice from the poisonous effects of ZEA at a relatively low dose [51]. The ability to detoxify heavy metal ions and other toxic metabolites gives P. pentosaceus a bright future.

Promotion of mineral and nutrient utilization
P. pentosaceus converts food into nutrients and promote mineral utilization. To the best of our knowledge, phytic acid is harmful to mineral bioavailability. Moreover, sour-dough-derived P. pentosaceus B3 and B11 and chicken intestine-derived P. pentosaceus CFR R38 and R35 were able to degrade phytate and promote mineral bioavailability [52, 53]. Similarly, from among 60 strains of LAB from cereal- and pulse-based fermented mixtures, P. pentosaceus CFR R123 not only significantly improved the availability of calcium but also reduced cholesterol and β-galactosidase levels. P. pentosaceus CFR R123
degraded 43% of phytate in one hour in an experiment designed by Raghavendra et al. [54, 55]. These phytate-degrading *P. pentosaceus* have potential as nutritive food additives [54, 55]. In the model of grass carp sausages, *P. pentosaceus* GY23 showed a proteolytic profile that was different from that of other LAB [56]. With high proteolysis ability, Malaysian food-derived *P. pentosaceus* UP-2 could produce 15 extracellular amino acids (AAs) for body nutrition or biological functions [57]. Isolated from tempah-fermented soybean cake, *P. pentosaceus* TL-3 was confirmed to have the highest threonine and methionine production among LAB [44]. γ-Aminobutyric acid (GABA) is an amino acid that has been reported to ameliorate diabetes, hypertension, and even cancer development. There are several kinds of LAB that produce GABA, and *P. pentosaceus* HN8, which was collected from Thai fermented pork sausage, is one such LAB [58]. Moreover, one strain of *P. pentosaceus* in Assam produced dextran, which is nonpoisonous and bioactive. It might be a future delivery system material for drugs or bioengineered tissue [129].

**Vaginal delivery connection**

Some probiotics are versatile and can be used in the protection of the vagina, especially when giving birth, including *P. pentosaceus*. From a total 35 strains of bacteriocinogenic *P. pentosaceus*, *P. pentosaceus* SB83 was selected for vaginal protection. *P. pentosaceus* SB83 is sensitive to a wide spectrum of antibiotics [58]. Apart from bacteriocin production, *P. pentosaceus* SB83 was tested for survival in glycerol and in manmade vaginal gel [59].

**Dilemma**

When applied to the human body, *P. pentosaceus* is definitely also harmful to health if it is not in the correct location. Duchaine et al. [130] found that *P. pentosaceus* produced abrupt inflammation in clinical use, resembling *Saccharopolyspora rectivirgula*. Additionally, the contradiction between the research and development of probiotics and practical use is currently a conundrum. As Suez et al. [131] mentioned, the supervision of the safety, efficacy and cost effectiveness of probiotics is essential to optimize the whole industry. Moreover, the evaluation of all aspects of probiotics has not been fully studied. The risk of probiotics for the human body, in particular, has not been sufficiently evaluated in either scientific research or clinical practice [132].

Overall, even though it is increasingly clear that additional safety assessment is needed for screening and selection of probiotics, *P. pentosaceus* is a preferable choice for probiotics.

**Potential special ability of *P. pentosaceus***

Several strains of *P. pentosaceus* have been studied more deeply than others and achieved special stats as candidate probiotics, such as *P. pentosaceus* ATCC 43,200 and *P. pentosaceus* KID7. For instance, *P. pentosaceus* GS4, a likely future probiotic, had been tested for its basic characteristics, biological processes and effects on the body. Sukumar and Ghosh [133] found that Indian fermented food-derived *P. pentosaceus* GS4 has antibacterial ability, in addition to being equipped with basic antioxidative properties, cholesterol absorption ability, and acid and bile salt tolerance. Furthermore, Dubey et al. [134–136] carried out experiments to determine that *P. pentosaceus* GS4 can become biohydrogenated, that it produces conjugated linolenic acid, that it has reduced toxicity, and that it inhibits mouse colon carcinogenesis. *P. pentosaceus* GS4 also survived under sustained gastric acid irritation and during cold storage. Recently, pediocin GS4 was purified and certified for hard denaturation [94, 137]. Similarly, *P. pentosaceus* MZF16 colonized and improved the intestinal tract without any cytotoxicity, secreting a BLIS named pediocin MZF16 with anti-*Listeria* ability [110]; this strain was collected from artisanal Tunisian meat. Adhering to the surface of the GIT, human breast milk-derived *P. pentosaceus* OZF might be a probiotic because of its antipathogen bacteriocin [104]. Even ginseng root-extracted *P. pentosaceus* HLJG0702 was found to be able to produce HLJG0701. HLJG0701 also significantly improved the concentration of the ginsenosides Rg5/Rk1 to inhibit acetylcholinesterase in scopalamine-induced memory dysfunction mice, which manifested as an improvement in brain function [138].

Moreover, *P. pentosaceus* LI05, identified by screening the faeces of healthy volunteers, has achieved substantial success in recent years. In a D-galactosamine-treated rat model, *P. pentosaceus* LI05 obviously ameliorated liver enzyme levels and the morphology of the terminal ileum and liver. The microflora distribution was altered, and bacterial translocation was reduced upon oral administration of *P. pentosaceus* LI05 [139]. Shi et al. [140] found that *P. pentosaceus* LI05 corrected hepatic fibrosis by ameliorating inflammatory cytokine levels and the intestinal bacterial flora distribution in a CCl₄-damaged liver cirrhosis model. Furthermore, *P. pentosaceus* LI05 was certified to inhibit *Clostridium difficile* infection (CDI) in mice. By reducing inflammation and upregulating tight junction proteins, *P. pentosaceus* LI05 prevented pathogen colonization of the intestine [141]. In a DSS-induced colitis model, *P. pentosaceus* LI05 improved the status of colitis and remarkably augmented the diversity of the microbiota and the level of SCFAs [142]. These *Pediococcus* spp. showed infinite potential for the maintenance of body health status. Despite counteracting diseases and
maintaining health, no side effects of these *Pediococcus* spp. have been discovered yet.

**Technological potential**
With regard to converting *P. pentosaceus* to a commercial product, several properties are desired. For instance, the property most worth discussing is the resistance of *P. pentosaceus* to different procedures, such as lyophilization, atomization, salinization, etc. An oro-gastrointestinal transit (OGT) tolerance assay [143] and a Caco-2 cell culture and adhesion assay [144] were performed and showed that *P. pentosaceus* is resistant to gastric acid and can adhere to the intestines. Given its tolerance to the freeze-drying and storage conditions, *P. pentosaceus* KID7 was approved for storage by lyophilization [47]. *P. pentosaceus* CRAG3 has tolerance for bile salts and even the ability to degrade bile salts [13]. Additional features are needed, for example, adhesion ability and bacteriocin-producing ability. The biofilm formation ability of *P. pentosaceus* has potential industrial applications, such as in drug research and development, as only in biofilm cells of *P. pentosaceus* can proteins related to probiotic properties be expressed and enriched [145]. Much more research is needed to test the possibility of commercial use of *P. pentosaceus*.

**Future direction**
Identifying the potential uses and commercial properties of *P. pentosaceus* is the most important next step. As a promising candidate in the world of probiotics and beneficial bacteria, selecting the most promising strain of *P. pentosaceus* is the next most important task, not to mention the preparation of complete bacterial formulations and systematic and complete evaluation of the characteristics and disadvantages of *P. pentosaceus*, which are also necessary. Then, the bacteria can be prepared for direct application in agriculture, animal husbandry, the food industry or clinical settings in the near future.

**Conclusions**
*P. pentosaceus*, a potentially predominant probiotic strain in the future, has been studied by many researchers since it was first described in the 1960s. In playing an all-important role in the food industry and animal husbandry, *Pediococcus* spp. acts on the intestines and improves overall body condition. *P. pentosaceus* has high potential to achieve probiotic status.

**Abbreviations**
LAB: Lactic acid bacteria; BLISs: Bacteriocin-like substances; GIT: Human gastrointestinal tract; EFSA: European Food Safety Authority; FEEDAP: Panel on Additives and Products or Substances used in Animal Feed; SCFAs: Short-chain fatty acids; EPSs: Exopolysaccharides; IL: Interleukin; TNF: Tumor necrosis factor; IFN: Interferon; CFS: Cell-free supernatant; ZEA: Zearalenone; FDA: Food and Drug Administration; LPS: Lipopolysaccharide; HSP: Heat shock protein; COX2: Cyclooxygenase 2; iNOS: Inducible NO synthase; CY: Cyclophosphamide; OVA: Ovalbumin; IFN: Interferon; CRC: Colorectal cancer; DPPH: o-Diphenyl-

β-picrylhydrazyl; HORAC: Hydroxyl radical antioxidant capacity; NAFLD: Nonalcoholic fatty liver disease; Cd: Cadmium; AAs: Amino acids; GABA: γ-Aminobutyric acid; CDI: Clostridium difficile.

**Acknowledgements**
Not applicable.

**Authors' Contributions**
SJ and LC contributed equally to writing the manuscript. LLv helped modify this paper. LL provided funding and projects. All authors read and approved the final manuscript.

**Funding**
This work was supported by the National Key Research and Development Program of China (2018YFC2000500) and the Natural Science Foundation of Zhejiang Province, China (LQ19H1030007).

**Availability of Data and Materials**
Not applicable.

**Ethics Approval and Consent to Participate**
Not applicable.

**Consent for Publication**
Not applicable.

**Competing Interests**
The authors declare that they have no competing interests.

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