Fucose-containing bacterial exopolysaccharides: Sources, biological activities, and food applications

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**ABSTRACT**

Bacterial exopolysaccharides are high molecular weight polysaccharides that are secreted by a wide range of bacteria, with diverse structures and easy preparation. Fucose, fucose-containing oligosaccharides (FCOs), and fucose-containing polysaccharides (FCPs) have important applications in the food and medicine fields, including applications in products for removing *Helicobacter pylori* and infant formula powder. Fucose-containing bacterial exopolysaccharide (FeEPS) is a prospective source of fucose, FCOs, and FCPs. This review systematically summarizes the common sources and applications of FCPs and FCOs and the bacterial strains capable of producing FeEPS reported in recent years. The repeated-unit structures, synthesis pathways, and factors affecting the production of FeEPS are reviewed, as well as the degradation methods of FeEPS for preparing FCOs. Finally, the bioactivities of FeEPS, including anti-oxidant, prebiotic, anti-cancer, anti-inflammatory, anti-viral, and anti-microbial activities, are discussed and may serve as a reference strategy for further applications of FeEPS in the functional food and medicine industries.

**Keywords:** Fucose, Bacterial exopolysaccharides, Structure, Bioactivity, Food application

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**Introduction**

**t**-fucose (6-deoxy-\(\alpha\)-galactose), a rare monosaccharide in nature, is distinct from other \(\alpha\)-monosaccharides owing to its unique structure, in which a hydroxyl group is lacking on carbon 6 (Becker & Lowe, 2003). Fucose has attracted increasing attention in the food, cosmetic, and pharmaceutical industries owing to its important physiological functions, including anti-cancer, anti-allergic, anti-coagulant, and anti-aging activities (Hong, Choi, Chang, & Mun, 2019). However, the complexity and high cost of fucose chemical synthesis make it unable to meet the demands of large-scale industrial production. Recent years, fucose-containing polysaccharides (FCPs) and fucose-containing oligosaccharides (FCOs) have attracted more and more attentions owing to their abundant sources (plants, sea animals, and microorganisms) and functional activities (Freitas, Alves, & Reis, 2011; Xiao et al., 2021).

Microbial exopolysaccharides (EPS) are promising sources of fucose, FCOs and FCPs. EPS are high molecular weight carbohydrate polymers produced by many microorganisms, including bacteria, fungi, and microalgae (Xiao et al., 2021). Bacterial EPS can be secreted extracellularly in two different states: capsular polysaccharides that are closely associated with the cell surface and form a capsule or as slime polysaccharides that are loosely attached or even totally secreted into the cell environment (Barcelos, Vespermann, Pelissari, & Molina, 2019). EPS could be further divided into homopolysaccharides and heteropolysaccharides based on the type of monosaccharides. Homopolysaccharides are usually made up of single monosaccharides, such as glucose and fructose (Oerlemans, Akkerman, Ferrari, Walvoort, & Vos, 2020). Heteropolysaccharides consist of not only glucose, fructose, and galactose, but also some rare monosaccharides, such as mannose, rhamnose, fucose, and occasionally N-acetylgalactosamine and uronic acids (Jiang & Yang, 2018; Oerlemans et al., 2020). Common heteropolysaccharides contain xanthan gum produced by *Xanthomonas* sp.,

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**Abbreviations:** FCPs, fucose-containing polysaccharides; FCOs, fucose-containing oligosaccharides; EPS, exopolysaccharides; FeEPS, fucose-containing EPS; \(2'\)-FL, \(2'\)-fucosyllactose; \(3'\)-FL, \(3'\)-fucosyllactose; HMOS, human milk oligosaccharides; ROS, reactive oxygen species; DPPH, 2,2-diphenyl-1-picrylhydrazyl; ABTS, 2,2′-azino-bis(3-ethylbenzothiazoline-6-sulphonate); SCPAs, short-chain fatty acids; PBMCs, peripheral blood mononuclear cells; MAPK, mitogen-activated protein kinase.

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gellan produced by *Sphingomonas paucimobilis*, alginites produced by *Azotobacter* sp. and *Pseudomonas* sp., fucogel produced by *Klebsiella pneumoniae*, clavan produced by *Clavibacter michiganensis*, fucoPol produced by *Enterobacter* sp. A47, or kefiran produced by *Lactobacillus kefiranofaciens* (Barcelos et al., 2019; Freitas et al., 2011). Accumulating research has shown that bacterial EPS have anti-cancer, anti-inflammatory, anti-diabetes, anti-viral, anti-oxidant, cholesterol-lowering, immune regulation, and probiotic activities (Freitas et al., 2011; Oerlemans et al., 2020). Marine microalgae, such as green algae, diatom and red algae, and fungi, such as *Auricularia auricula-judae* and *Ganoderma lucidium*, are also considered as abundant sources of EPS containing fucose. And microalgal and fungal EPS have promising applications in food, medicine and cosmetic industries, owing to their important physicochemical and biological properties (Osemwegie et al., 2020; Rui & Yi, 2016). The diversity of monosaccharide compositions, junction positions, branching patterns, and molecular weights resulted in different structures and activities of EPS. EPS have characteristic pseudoplastic rheological, emulsifying, and thickening properties, as well as water binding capacity, which make EPS to be applied as a thickener, emulsifier, and stabilizer to change the appearance, rheological properties, texture, and taste of food products (Li et al., 2017; Rani, Anandharaj, & Ravindran, 2018).

Although FCPs and FCOs are also found in plants, seaweeds, and marine invertebrates, bacterial production of such carbohydrates is demonstrably superior for several factors, namely easily controlled processing procedures and fast and reproducible production (Torres et al., 2012). Fucose-containing bacterial EPS (FcEPS) with high yield and diverse structures can be achieved by liquid fermentation of specific bacterial strains. In this sense, this review aims to summarize the specific FcEPSs, their structures, and 96 kinds of FcEPSs-producing bacteria. Various regulatory health properties of FcEPSs are discussed in depth, covering previous research on this subject. Finally, the applications of FcEPSs in different areas, especially in the food industry, are reviewed.

**Research progress on FCPs and FCOs**

FCPs and FCOs are considered attractive bioactive compounds owing to their abundant sources and diverse activities and have been applied in the food, medicine, and cosmetic industries. Here, we review the common sources, structural characteristics, activities, and applications of FCPs and FCOs, providing a reference for further efficient acquisition and application of FCPs and FCOs.

**Fig. 1.** Structures of fucose-containing polysaccharides and fucose-containing oligosaccharides (FCOs). (A) Two types of backbones in fucoidans extracted from brown seaweeds. (B) Structures of the main FCOs in human milk. 2′-FL: 2′-fucosyllactose; 3-FL: 3-fucosyllactose, DFL: difucosyllactose, LNFP: lacto-N-fucopentaose, LNDFH: lacto-N-difucohexaose; MFLNH: monofucosyllacto-N-hexaose.
Fucoidan is a type of FCP that is commonly found in the cell wall matrix of brown seaweeds (Fucus distichus, F. evanescens, F. serratus, F. vesiculosus, and Undaria pinnatifida) (Pradhan, Patra, Nayak, Behera, & Jena, 2020; Vo & Kim, 2013). Other FCPs, sulfated fucans, and fucosylated chondroitin sulfate are derived from marine invertebrates, including sea cucumbers (Apostichopus japonicus, Pearsornothuria graeffei, Stichopus tremulus, and Holothuria vagabunda) and sea urchins (Lytechinus variegatus, Ly. grisea, Arbacia lixula, Strongylocentrotus purpuratus, and S. franciscanus) (Shida, Mikami, Tamura, & Kitagawa, 2017). Fucoidan mostly consists of fucose and sulfate ester groups, with a small amount of other monosaccharides (glucose, galactose, mannose, rhamnose, and xylose) and uronic acids. The backbone of fucoids are known as two types: one consisting of repeating \((1 \rightarrow 3)\)-linked \(\alpha\)-fucosyl residues and another consisting of alternated \((1 \rightarrow 3)\)- and \((1 \rightarrow 4)\)-linked \(\alpha\)-fucosyl residues (Fig. 1A) (Vo & Kim, 2013). The fucoids extracted from sea cucumbers are composed of \((1 \rightarrow 3)\)-linked tetrafucose repeated units, each with one or two HSO\(_4\) substitutions (Chang, Hu, Long, Meclements, & Xue, 2016). The structure of fucan is characterized as \((1 \rightarrow 3)\)- and/or \((1 \rightarrow 2)\)-linked fucosyl residues and sulfated or non-sulfated fucose residues on the side chains, similar to fucosylated chondroitin sulfate (Cao, Surayot, & You, 2017).

Human milk is an important source of natural FCOs. Human milk oligosaccharides (HMOs) are the third most abundant solid component in human milk and have a significant influence on infant health (Bode, 2015; Bych et al., 2019). There are \(>\)200 kinds of oligosaccharides in HMOs, which are roughly divided into acidic sialylated HMOs and neutral HMOs. Most of the neutral HMOs are fucosylated HMOs, accounting for 60% of the total HMOs, including \(2\)-fucosyllactose (2\'-FL, 31%), 3-fucosyllactose (3-FL, 5%), difucosyllactose (4%), lacto-N-fucopentaose I/II/III (8/2/2%), lacto-N-fucopentaose V, lacto-N-difucohexaoise I (4%), and monofucosylacto-N-hexaose III (Bych et al., 2019; Pérez-Escalante et al., 2020). All nine FCOs are formed by the connection of three or four monosaccharides (glucose, galactose, fucose, and/or \(N\)-acetylgalcosamine), with fucose as the non-reducing end and lactose as the reducing end (Fig. 1B).

**Biological properties and applications of FCPs and FCOs**

During the last decades, many studies have demonstrated that fucoids extracted from brown seaweeds or marine invertebrates possess promising application prospect in marine functional foods owing to their various biological functions, including anti-oxidant, anti-inflammatory, anti-allergic, anti-tumor, anti-obesity, anti-coagulant, antiviral, anti-hepatopathy, anti-uropathy, and anti-renalpathy activities (Pradhan et al., 2020). In addition, fucoids are considered as superior dietary fiber, which may be attributed to their functions of promoting gastrointestinal peristalsis and increasing the abundance of beneficial bacteria in the intestine (Li, Xue, Zhang, & Wang, 2020). Fucoids also play a positive part in adsorbing toxic substances (especially toxic heavy metals) in intestine, thereby reducing the harm of toxic substances accumulation (Gao et al., 2020). Nowadays, fucoidan has been applied in the preparation of functional foods and beverages, including tablets, capsules, and granules, with the functions of enhancing immune, relieving constipation, reducing allergy, clearing Helicobacter pylori, etc. Although there are various extraction methods to prepare FCPs from brown algae and marine invertebrates, the exploration of optimal reaction conditions and new purification methods should be taken into consideration to simplify the extracted process and improve the yield of FCPs (Vo & Kim, 2013). In addition, FCPs extracted from different species, and even from the same species, have various structures that depend on the harvesting season and location. Special attention should be paid to the precise structural characterization of FCPs, and extensive in vivo studies is necessary to accurately assess their potential therapeutic applications.

Accumulating research has shown that fucosylated HMOs play a vital role in regulating intestinal health in early life by promoting the growth of dominant bacterial strains (bifidobacteria strains) in the gut (Pérez-Escalante et al., 2020). Fucosylated HMOs exert anti-microbial activity by modifying the host’s epithelial cell-surface glycome (Zhu et al., 2020). In addition, fucosylated HMOs are beneficial for promoting the maturation of the infant immune system and improving the cognitive ability of the baby brain, especially in the first months of life (Bode, 2015). 2\'-FL is the most abundant oligosaccharide in human milk, and it has unique biological effects. Many clinical studies have shown that milk powder supplemented with 2\'-FL is safe and well tolerated in infants, and the immune development of infants receiving 2\'-FL supplemented milk powder is similar to that of breastfed infants (Zhu et al., 2020). To date, 2\'-FL has attracted great attention in large-scale production and commercial applications, and infant formula supplemented with 2\'-FL is available in some countries. Moreover, 2\'-FL prepared by the fermentation of Escherichia coli BL21 (DE3) \#1540 has passed the safety certification of the European Food Safety Authority (EFSA) (EU, 2017/2470) and the American Food and Drug Administration (FDA, GRN 650). In addition, 3-FL is also one of the abundant HMOs in human milk, and the concentration of 3-FL will increase with the extension of lactation. At present, 3-FL is considered to reduce the risk of intestinal microbiota imbalance caused by harmful bacteria and selectively stimulate the growth of beneficial bifidobacteria (Bych et al., 2019). And 3\'-FL prepared by the fermentation of E. coli K12MG1655 has been authorized to apply in food field as a new resource food. However, the availability of 2\'-FL and 3\'-FL is limited by the high cost associated with its relatively complex synthesis process (Bych et al., 2019; Zhu et al., 2020). Therefore, new sources or preparation processes for FCPs and FCOs require further investigation.

**Physiochemical and structural features of FeEPSs**

FeEPSs produced by microorganisms have greater development potential for applications in the food, cosmetic, and medical industries than other natural materials. The preparation of fucose, FCOs, and FCPs via chemical synthesis or traditional extraction from natural sources (plants, algae, and animals) is not an easy task to meet the demands of large-scale industrial production. Production via microorganisms is a new strategy for the efficient preparation of fucose FCOs, and FCPs. Microorganisms capable of producing FeEPSs include a broad range of bacteria, as reviewed in Table 1, and the repeated-units structures of FeEPSs produced by several bacteria are displayed in Fig. 2.

**FeEPSs-producing bacteria**

Bacteria capable of producing FeEPSs mainly include Enterobacter sp., Clavibacter sp., and Klebsiella sp. Enterobacter sp., a gram-negative bacterium, is widely distributed in the natural environment and has a wide host range. Enterobacter sp. has shown a strong adaptability to both abrupt changes in the environment and bio-contamination, as well as good proliferation and differentiation capabilities. Several species within the genus Enterobacter have been reported to produce EPS containing fucose. The EPS secreted by Enterobacter sp. A47 (DSM 23193), named Fucopol, is a high molecular weight polymer composed of fucose, galactose, glucose, and glucuronic acid at a ratio of 4:2.5:3:1 (Freitas et al., 2011). The marine bacteria E. cloacae and E. amnigenus can produce heteropolymers containing glucose, galactose, fucose, mannose, glucuronic acid, and pyruvul (Gescutti et al., 2005; Iyer, Mody, & Jia, 2005). FeEPS is commonly obtained by liquid fermentation of E. sakazakii strains, including ATCC 53017, ATCC 29004, and ATCC 12868 (Vanhooren & Vandamme, 1999). In addition, a previous study showed that FeEPS extracted from E. sakazakii M1 was mainly composed of fucose, galactose, and glucose, in which the content of fucose reached 42.72 mol% (Xiao et al., 2021).

*C. michiganensis* subsp. is a plant pathogenic bacterium that spreads...
## Table 1

The culture conditions of fucose-containing exopolysaccharides (FcEPS) producing bacteria, and monosaccharide compositions and molecular weights of these FcEPSs.

| No. | Bacteria Source | Main carbon source | Temperature/time | Maximum yield | Monosaccharide composition | Molecular weight | References |
|-----|----------------|--------------------|------------------|---------------|---------------------------|------------------|------------|
| 1   | Acidianus sp. DSM 29099 | Yeast extract | 65 °C/7 d | – | Glucose/mannose/fucose | – | Zhang et al., 2019 |
| 2   | Acidithiobacillus ferrooxidans R1 | – | 28 °C | – | Rhamnose/fucose/xylene/ mannose/glucose/glucuronic acid = 10.8/17.1/0.8/0.7/15.2/3.9/0.6 (by molar ratio) | – | (Kinzler, Gehrke, Telegdi, & Sand, 2003) |
| 3   | Aerobacter aerogenes ATCC 12657 | – | 37 °C/16 h | – | 3-fucose/mannose | – | (Kornfeld, 1966) |
| 4   | Aerobacter cloaca | – | – | – | Galactose/fucose/xylene/ uronic acid | – | (Salton, 1960) |
| 5   | Aeromonas hydrophila | Yeast extract | 30 °C | – | Fucose/mannosyl/glucose/N- acetylgalactosamine | – | (Castro et al., 2014) |
| 6   | Alcaligenes faecalis NCTC 8764 | – | – | – | Glucose/arabinose/fucose/ rhamnose | – | (Salton, 1960) |
| 7   | Alcaligenes latus B-16 | – | – | – | 25 g/L Fucose/glucose/xylene/ glucuronic acid – 1/1.8/1.1/1 (by molar ratio) | – | (Nagayama, Karaisaki, Ueta, & Imai, 2002) |
| 8   | Alteromonas macieedi subsp. fiuusis HYD657 | Hydrothermal vent | Glucose | 28 °C/50 h | Galactose/glucose/rhamnose/ glucuronic acid/galacturonic acid/mannose/fucose – 5.9/2.6/2.5/2.0/1.4/1.0 (by molar ratio) | 1.1 × 10^6 Da | (Costanzo et al., 2012) |
| 9   | Azotobacter vinelandii MTCC 2460 | Sucrose | 30 °C/2 d | – | Glucose/galactose/fucose/ glucuronic acid – 2.2/2.7/5.6/1.6 (by molar ratio) | – | (Vermani, Kelkar, & Kamat, 1995) |
| 10  | Bacillus atrophaeus WYZ | Mangrove system | Peptone, yeast extract, glucose | 37 °C/40 h | 0.58 g/L | 3.19 × 10^3 Da | (Zhu et al., 2018) |
| 11  | Bacillus coagulans RK-02 | Soil sample | Yeast extract, glucose | 37 °C/36 h | 0.33 ± 0.005 g/L | – | (Kodoli et al., 2009) |
| 12  | Bacilluslicheniformis BioE-BL11 | Korean kimchi | Tryptone, sucrose | 37 °C/3 d | 9.18 g/L | 6.69 × 10^4 Da | (Kook et al., 2019) |
| 13  | Bacilluslicheniformis T8 | Chinese Academy of Sciences | Yeast extract and peptone | 37 °C/3 d | 3.07 g/mL | BL-P1: 3.96 × 10^6 Da; BL-P2: 1.23 × 10^5 Da | (Xu et al., 2019) |
| 14  | Bacilluslicheniformis T14 | Hydrothermal vent | Sucrose and yeast extract | 50 °C/2 d | 366 mg/L | 1 × 10^6 Da | (Gugliandolo et al., 2014; Spanò et al., 2015; Spanò et al., 2016) |
| 15  | Bacillus megaterium RB-05 | Glucose | 33 °C/90 h | 0.065 ± 0.013 g/L | N-acetyl glucosamine/glucose/galacturonic acid/glucuronic acid/mannose/fucose = 4/14.03/37.58/19.33/20.16/4.9 (by mass percentage) | 1.7 × 10^5 Da | (Chowdhury, Tank, Sen, & Adhikari, 2011) |
| 16  | Beijerinckia indica TX-1 | Soil | Glucose and peptone | 30 °C/4 d | – | Glucose/fucose/glucurono-manno-heptose/glucuronic acid = 5/1/2.0/0.9 (by molar ratio) | 6.5 × 10^5 Da | (Ohtani et al., 1995) |
| 17  | Bifidobacterium longum N73 | Human intestinal microbiota | MRSC broth | 37 °C/5 d | – | Rhamnose/galactose/glucose/fucose | 10^4–10^6 Da (70.7%), < 10^4 Da (29.3%) | (Salazar et al., 2019) |
| 18  | Bifidobacterium longum N63 | – | – | – | Rhamnose/galactose/glucose/ fucose | 10^5 – 10^6 Da (52.6%), | (Salazar et al., 2009) |

(continued on next page)
| No. | Bacteria | Source | Main carbon source | Temperature/ time | Maximum yield | Monosaccharide composition | Molecular weight | References |
|-----|----------|--------|--------------------|------------------|---------------|-----------------------------|-----------------|------------|
| 19  | Bifidobacterium pseudocatenulatum E34 | Human intestinal microbiota | – | – | Galactose/glucose/fucose/N-acetyl-glucosamine | < 10^4 Da (47.4%) | | |
| 20  | Burkholderia viemaniensis LMG 10929 | BCMMTM bacteria collection | Mannitol and yeast extract | 30 °C/4 d | 35 mg/Petri dish | Rhamnose/fucose/mannose/glucose = 0.31/0.23/0.08/1.1 (by molar ratio) | > 1 × 10^9 Da | (Cescutti, Cuzzi, Herasimenka, & Rizzo, 2013) |
| 21  | Chromobacterium violaceum | NCTC 7917 | CCY broth | 37 °C/22 h | – | Galactose/glucose/xylitol/arabinose/fucose/galacturonic acid | – | (Davies, 1955) |
| 22  | Clavibacter michiganensis subsp. michiganensis | NCPPB 382 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 43.5/25.9/36.6/1 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 23  | Clavibacter michiganensis subsp. michiganensis | CMM 100 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 48.8/24.7/47.1/1.8 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 24  | Clavibacter michiganensis subsp. michiganensis | NCPPB 1574 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 46.6/25.9/27.3/1 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 25  | Clavibacter michiganensis subsp. michiganensis | NCPPB 1496 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 44.5/33.2/22.3/1 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 26  | Clavibacter michiganensis subsp. michiganensis | NCPPB 515 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 9.6/31.2/6.4/52.8 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 27  | Clavibacter michiganensis subsp. michiganensis | NCPPB 254 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 11.1/27.9/24.4/36.6 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 28  | Clavibacter michiganensis subsp. michiganensis | NCPPB 399 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 26.4/20.6/32.2/20.8 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 29  | Clavibacter michiganensis subsp. michiganensis | NCPPB 1064 | Yeast extract and glucose | 25 °C/12 d | – | Glucose/galactose/fucose/pyruvate/succinate/acetate = 0.97/1.02/1.01/0.52/1.55 (by molar ratio) | > 1 × 10^9 Da | (Bulk et al., 1991) |
| 30  | Clavibacter michiganensis subsp. insidiosus | NCPPB 2581 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 22.85/23.7/41.7/6.1 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 31  | Clavibacter michiganensis subsp. neapolitana | NCPPB 1686 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 43.7/25.7/36.6/1 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 32  | Clavibacter michiganensis subsp. neathausi | NCPPB 2140 | Yeast extract and glucose | 25 °C/12 d | – | Fucose/galactose/glucose/mannose = 19.9/24.4/22.9/29.8 (by molar percentage) | > 1 × 10^9 Da | (Bermpohl et al., 1996) |
| 33  | Corynebacterium inosidans | – | – | – | – | Glucose/galactose/fucose/pyruvic acid = 1/1/2/1 (by molar ratio) | – | (Gorin, Spencer, Lindberg, & Lindh, 1980) |
| 34  | Enterobacter sp. A47 | DSM 23139 | Lactose | 30 ± 0.2 °C/4 d | 5.22 g/L | Fucose/galactose/glucose/glucuronic acid = 25/22/24/29 (by molar percentage) | 4.7 × 10^8 Da | (Antunes et al., 2015) |
| | | | Cheese whey | 30 ± 0.2 °C/4 d | 6.40 g/L | Fucose/galactose/glucose/glucuronic acid = 29/21/21/29 (by molar percentage) | 1.8 × 10^8 Da | (Antunes et al., 2015) |
| | | | Glycerol | 30 ± 0.1 °C/7 d | 13.28 ± 0.74 g/L | Fucose/galactose/glucose/galacturonic acid = 36/48/21/25/27/32 (by molar percentage) | 0.9 ± 1.3 × 10^7 Da | (Alves et al., 2010) |
| | | | Glycerol byproduct | 15.9 ± 4.1 °C/4 d | 7.79 g/L | Fucose/galactose/glucose/glucuronic acid/rhamnose/glucosamine = 0/26/2/42/27/61/6/12/0/29/0 (by molar percentage) | 0.26 ± 1.46 × 10^6 Da | (Torres et al., 2012) |
| | | | Glucose | 30 ± 0.1 °C/4 d | 13.4 g/L | Fucose/galactose/glucose/glucuronic acid = 29/29/26/16 (by molar percentage) | 4.2 × 10^6 Da | (Freitas et al., 2015) |
| | | | Xylose | 30 ± 0.1 °C/4 d | 5.39 g/L | Fucose/galactose/glucose/glucuronic acid = 36/18/27/17 (by molar percentage) | 1.7 × 10^5 Da | (continued on next page) |
Table 1 (continued)

| No. | Bacteria | Source | Main carbon source | Temperature/time | Maximum yield | Monosaccharide composition | Molecular weight | References |
|-----|----------|--------|-------------------|-----------------|--------------|-----------------------------|-----------------|------------|
| 35  | Enterobacter amnigenus BPT 165 | Helsinki University of Technology | Yeast extract, bacoptepo and sucrose | 32 °C/6 h | – | Fucose/mannose/galactose/glucose = 1.5/0.2/1.1/1 (by molar ratio) | – | (Cescutti et al., 2005) |
| 36  | Enterobacter cloacae | Marine sediment | Sucrose, peptone and yeast extract | 27 – 30 °C/76 h | – | Fucose/galactose/glucose/glucuronic acid = 2/1/1/1 (by molar ratio) | – | (Iyer et al., 2005) |
| 37  | Enterobacter cloacae Z0206 | Zhejiang University | Potato, bacto-peptone yeast extract and sucrose | 30 °C/2 d | – | Fucose/glucose/galactose/glucuronic acid/pyruvic acid = 2/1/3/1/1 (by molar ratio) | 1.1 × 10^6 Da | (Wang, Yang, & Wang, 2013) |
|     |          |        | Potato, bacto- peptone, yeast extract and sucrose | – | – | Se-ECZ-EPS-1: glucose/mannose = 91.75/0.66/7.59 (by molar percentage) | Se-ECZ-EPS-1: 2.93 × 10^6 Da | (Xu, Wang, Jin, & Yang, 2009) |
| 38  | Enterobacter ludwigii Ez-185-17 | Root nodules | Glutamke and mannitol | 30 °C/3 d | 0.7 g/L | Galactose/mannose/galacturonic acid = 2/1/2/1 (by molar ratio) | 2.9 × 10^5 Da | (Pau-Roblot et al., 2013) |
| 39  | Enterobacter sakazakii M1 | Ocean University of China | Glucose | 36 °C/2 d | 1.5 g/L | Fucose/glucose/galactose/galacturonic acid/gluconic acid/mannose = 2/1/2/1/1/1 (by molar percentage) | 2.5 × 10^5 Da | (Xiao et al., 2021) |
| 40  | Escherichia coli EC100. Loc1 | – | – | 37 °C/1 d | – | Fucose/arabinose/galactose (N-acetyl glucosamino) | – | (Li et al., 2019) |
| 41  | Flavobacterium aggregatum | Sea water | Glucose, polyephtone and yeast extract | 28 °C/2 – 3 d | – | Glucose/mannose/fucose = 7/2/1 (by molar ratio) | – | (Umezawa et al., 1983) |
| 42  | Geobacillus sp. 1A60 | Hydrothermal vents | Sucrose and yeast extract | 50 °C/3 d | 185 mg/L | Mannose/galactose/galactosamine/fucose/glucose = 0.06/0.65/0.59/0.35 (by molar ratio) | – | (Gugliandolo, Lentini, Spano, & Maugeri, 2012) |
| 43  | Geobacillus tepidimans V264 | Hot spring | Maltose and yeast extract | 60 °C | 114.1 mg/L | Glucose/galactose/fucose/fructose = 1/0.07/0.04/0.02 (by molar ratio) | > 1 × 10^6 Da | (Kambourova et al., 2009) |
| 44  | Gruclibacillus sp. SCU50 | Saline soil | Sucrose, tryptone and yeast extract | 30 °C/3 d | – | Mannose/galactose/galactose/fucose = 90.81/5.76/2.22/1.21 (by molar percentage) | 5.88 × 10^4 Da | (Gan et al., 2020) |
| 45  | Halomonas stenophila HK30 | Soil | Dextrose, peptone, yeast extract and malt extract | 32 °C/5 d | 3.89 ± 0.1 g/L | Glucose/galactose/mannose/fucose/rhamnose = 0.37/5.5/0.66/7.59 (by molar percentage) | 1.4 × 10^6 Da | (Amjgtes et al., 2015) |
| 46  | Halomonas stenophila B100 | Hypersaline soils | Dextrose, peptone, yeast extract and malt extract | 32 °C/5 d | – | Mannose/galactose/galactose = 4.4/15/46.5 (by molar percentage) | 3.75 × 10^5 Da | (Ruiz-Ruiz et al., 2011) |
| 47  | Halomonas stenophila N127 | Hypersaline soils | Dextrose, peptone, yeast extract and malt extract | 32 °C/5 d | – | Glucose/mannose/fucose = 48.82/25.47/25.69 (by molar percentage) | 2.5 × 10^5 Da | (Ruiz-Ruiz et al., 2011) |
| 48  | Klebsiella type 1 | – | – | – | – | Glucose/glucuronic acid/fucose/pyruvic acid = 1/1/1/1 (by molar ratio) | – | (Rieger-Hug & Stirm, 1981) |
| 49  | Klebsiella type 6 | – | – | – | – | Glucose/glucuronic acid/fucose/pyruvic acid = 1/1/1/1 (by molar ratio) | – | (Rieger-Hug & Stirm, 1981) |
| 50  | Klebsiella type 16 | – | – | – | – | Glucose/galactose/fucose | – | (Rieger-Hug & Stirm, 1981) |
| 51  | Klebsiella type 54 | – | – | – | – | Glucose/glucuronic acid/fucose = 2/1/1 (by molar ratio) | – | (Rieger-Hug & Stirm, 1981) |
| 52  | Klebsiella type 60 | – | – | – | – | Glucose/mannose/fucose | – | (Rieger-Hug & Stirm, 1981) |
| 53  | Klebsiella type 63 | – | – | 30 °C/4 d | – | Fucose/galactose/galacturonic acid = 1/1/1 (by molar ratio) | – | (Joseena & Marais, 1997) |
| 54  | Klebsiella oxytoca | Glucose, yeast extract and peptone | 30 °C/7 d | – | – | Rhamnose/fucose/arabinose/xylose/mannose/galactose/glucose = 3.29/6/4/1.085 | 116/018Da | (Feng, Li, Du, & Chen, 2009) |

(continued on next page)
| No. | Bacteria                     | Source                  | Main carbon source | Temperature/time | Maximum yield | Monosaccharide composition                                                                 | Molecular weight | References                          |
|-----|------------------------------|-------------------------|--------------------|------------------|---------------|--------------------------------------------------------------------------------------------|------------------|-------------------------------------|
| 55  | *Klebsiella pneumoniae*      | ATCC 31646              | –                  | 30 °C/4 d        | –             | Fucose/galactose/galacturonic acid = 1/1/1 (by molar ratio)                                  | –                | (Johansson, Jansson, & Widmalm, 1994) |
| 56  | *Klebsiella pneumoniae* subsp. pneumoniae BECT1000 CNCMI-1507 | Sludge                  | Sorbitol, peptone and yeast extract | 30 °C/2 – 4 d   | 12 g/L        | Fucose/galactose/galacturonic acid = 1/1/1 (by molar ratio)                                  | 1 × 10^9 Da      | (Paul, Perry, & Mons, 1999)         |
| 57  | *Kosakonia sp.*              | CCTCC M2018092          | Glucose and yeast extract | 30 °C/20 h      | –             | Fucose/glucose/galactose/galuronic acid/pyruvic acid = 2.03/1.00/1.18/0.64/0.67 (by molar ratio) | 3.65 × 10^3 Da   | (Li et al., 2020)                   |
| 58  | *Lactobacillus casei* SB27   | Yak milk                | Skim milk containing glycerol | 37 °C/36 h      | –             | LW1: rhamnose/fucose/arabinose/xyllose/mannose/galactose = 3.1/1.9/7.2/1.4/4.9/29.1/52.4/LW2: rhamnose/fucose/arabinose/xyllose/mannose/glucose/galactose = 2.0/2.6/5.6/1.6/8.5/22.5/57.4 (by molar percentage) | 3.65 × 10^3 Da   | (Di et al., 2017)                   |
| 59  | *Lactobacillus gasseri* FR4  | Gastrointestinal tract of free range chicken | Sucrose | – | 7.5 g/L | Glucose/mannose/galactose/rhamnose/fucose = 65.31/16.51/8.45/6.56/3.18 (by molar percentage) | 1.86 × 10^3 Da | (Rani et al., 2016)                |
| 60  | *Lactobacillus plantarum* JLAU103 | Hurood in Inner Mongolia of China | Bacto proteose peptone, bacto yeast extract and α-sorbitol | 37 °C/1 d     | 75 mg/L | Arabinose/rhamnose/fucose/xyllose/mannose/fructose/galactose/glucose = 4.05/6.04/6.29/5.22/1.47/5.21/2.24/1.83 (by molar ratio) | 1.24 × 10^4 Da | (Min et al., 2018; Wang et al., 2020) |
| 61  | *Lactobacillus plantarum* KX041 | Chinese Paocai          | Lactose, soy peptone, beef extracts and yeast extract | 35 °C/25 h    | 0.6 g/L | EPS-1: arabinose/mannose/glucose/galactose = 1.09/88.53/3.99/6.39 (by molar percentage) | 57201 Da         | (Xu et al., 2019)                   |
| 62  | *Leuconostoc mesenteroides* BioE-1MD18 | –                      | –                  | –                | 5.03 g/L | Mannose/arabinose/galactose/fucose = 8.71/0.07/1.22/79.8/10.21 (by molar percentage) | 1.24 × 10^3 Da | (Kook et al., 2019)                 |
| 63  | *Microbacterium auranticum* FSW-25 | Rashthakadu beach      | Glucose             | 28 °C/3 d       | 7.81 g/L | Glucuronic acid/glucose/mannose/fucose = 7.0/7.10/10.5/4.62/4.07/27.81/44.16/3.73 (by molar percentage) | 7.0 × 10^6 Da | (Sran et al., 2016)                |
| 64  | *Pantoeaecus edaphicus* NUST16 | Coastal soil            | Sucrose             | 30 °C/108 h     | 12.5 ± 0.5 g/L | Mannose/glucuronic acid/glucose/fucose = 3.11/8.53/0.9/1.89 (by molar ratio) | 1.2 × 10^7 Da   | (Li et al., 2017)                   |
| 65  | *Pediococcus pentosaceus* KFT18 | KCCM11309P              | Sucrose             | –/2 d           | 3.94 g/L | Glucose/mannose/galactose/2-methyl xyllose/fucose/arabinose/2-methyl fucose/xyllose/arabinose/acidic acid = 67.7/13.4/8.85/7.55/1.5/0.4/0.15/0.05/0.05/0.025 (by molar percentage) | ≥ 2.56 × 10^7 Da | (Shin et al., 2016)                |
| 66  | *Polaribacter riguellii* CAM006 | Sea ice and seawater   | Glucose             | 20 °C/7 d       | –             | Arabinose/fucose/mannose/galactose/glucose/glucuronic acid/N-acetylglactosamine/N-acetyl-glucosamine = 2/11/33/38/4/6/1.4 (by mass percentage) | 2.1 × 10^6 Da  | (Nichols et al., 2005)             |
| 67  | *Polaribacter sp.* SM1127    | Brown algae            | Glucose, peptone and yeast extract | 15 °C/5 d     | 2.11 g/L | Rhamnose/fucose/glucuronic acid/mannose/galactose/glucose/N-acetylglucosamine = 0.8/7.4/21.4/23.4/17.3/3.4 | 2.2 × 10^6 Da  | (Sun et al., 2015)                |

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| No. | Bacteria | Source | Main carbon source | Temperature/time | Maximum yield | Monosaccharide composition | Molecular weight | References |
|-----|----------|--------|-------------------|-----------------|---------------|---------------------------|-----------------|------------|
|     |          |        |                   |                 |               | Water-insoluble fraction: fucose/mannose/glucose/galactose = 7/22/40/31 (by mass percentage) | – | (Racine, Dumont, Champagne, & Morin, 1991) |
|     |          |        |                   |                 |               | Arabinose/rhamnose/fucose/mannose/glucose/glucuronic acid/N-acetyl galactosamine | 1.8 × 10^6 Da | (Nichols et al., 2005) |
|     |          |        |                   |                 |               | – | – |
| 68  | Propionibacterium acid-propionici VM-25 | ATCC 25562 | Partially deproteinated whey and lactose | 25 °C/3 d | 10 – 15 g/L | 1.6/28.0 (by molar percentage) | – | – |
| 69  | Pseudoalteromonas sp. CAM003 | – | – | – | – | – | – |
| 70  | Pseudoalteromonas sp. CAM025 | Sea ice Yeast extract and bacteriological peptone | –2 °C/14 d; 10 °C/14 d; 20 °C/7 d | 97.2 ± 9.3/99.9 ± 8/3.6 ± 0.2 mg/g (dry weight) | –2 °C: arabinose/rhamnose/fucose/galacturonic acid/mannose/galactose/glucose = 1.2 ± 0.9/4.8 ± 0.5/1.6 ± 0.4/15.8 ± 0.4/16.5 ± 0.7/5.7 ± 0.3/53.3 ± 1.8 (by mass percentage); 20 °C: arabinose/rhamnose/fucose/galacturonic acid/mannose/galactose/glucose = 3.1 ± 1.5/1.6 ± 0.2/18.8 ± 3.1/7.7 ± 0.4/8.1 ± 1.0/9.6 ± 1.5/19.7 ± 3.2/30.9 ± 5.4 (by mass percentage); 10 °C: arabinose/rhamnose/fucose/galacturonic acid/mannose/galactose/glucose = 3.1 ± 1.5/1.6 ± 0.2/18.8 ± 3.1/7.7 ± 0.4/8.1 ± 1.0/9.6 ± 1.5/19.7 ± 3.2/30.9 ± 5.4 (by mass percentage); 20 °C: arabinose/rhamnose/fucose/galacturonic acid/mannose/galactose/glucose = 11.3 ± 2.5/25.9 ± 5.8/6.9 ± 2.9 ± 0.2 ± 0.8/2.8 ± 0.8/23.6 ± 2.0/23.3 ± 9.2 (by mass percentage) | 5.7 × 10^6 Da | (Nichols et al., 2005) |
| 71  | Pseudomonas sp. | – | – | – | – | Glucose/fucose/rhamnose | – | (Salton, 1960) |
| 72  | Pseudomonas fluorescens Biovar II | ATCC 55421 Soy broth | 37 °C/12 h | – | – | Rhamnose/fucose/arábino/rhamnose/xylono/mannono/galactono/glucose | – | (Jhung et al., 2005) |
| 73  | Pseudomonas fluorescens H13 | Discolored lesions on mushroom caps ATCC 10844 | – | 20 – 28 °C/2 d; 3 d | 7 – 30 mg/5 culture dishes | Glucose/fucose/glucosano/rhamnose/fucose/arábino/rhamnose/xylono/mannono/galactono/glucose | – | (Fett, Wells, Cescutti, & Wijey, 1995) |
| 74  | Pseudomonas marginalis type C | An industrial effluent | – | 28 °C/1 d | – | Glucose/fucose/propionic acid = 2/1 (by molar ratio) | 1.49 × 10^6 Da | (Fishman et al., 1997) |
| 75  | Pseudomonas mendocina P2d | – | – | – | – | Glucose/fucose/propionic acid = 2/1 (by molar ratio) | – | (Yovan et al., 1999) |
| 76  | Pseudomonas elodeorum NRRL B-14682 | Glycerol byproduct | 30 ± 0.2 °C/5 d | 15 g/L | – | Galactono/mannono/glucose/fucose/arábino/rhamnose = 68/17/0.7 Da | 4.6 × 10^6 Da | (Alves et al., 2010) |
| 77  | Pseudomonas sp. ID1 | Marine sediment | 11 °C/5 d | – | – | Glucose/galactono/fucose = 17.04 ± 3.2/8.57% ± 1.15/8.21% ± 1.12 (by molar percentage) | > 2 × 10^5 Da | (Carrión, Delgado, & Mercade, 2015) |
| 78  | Pseudomonas syringae pv. phaseolicola Ex-4 | Institute collection no. 65S, IPO-38-2R7 | – | 25 °C/2 d | 761 mg/L | Rhamnose/fucose/glucose/amino sugars | – | (Gross & Rudolph, 1987) |
| 79  | Rhizobium sullae A6 | Mannitol and yeast extract | 28 °C/1 d | 7.5 ± 2.0 mg/g | – | Glucose/galactono/fucose/mannono/galactono/glucose/arábino/rhamnose = 42.7 ± 6.5/33.4 ± 1.0/19.9 ± 13.5 ± 1/10/0.1/2 (by molar percentage) | < 1.5 × 10^5 Da, 0.1 – 6 × 10^4 Da | (Ghazrourdi, Carpent, Couderc, Benguedouar, & Poinset, 2013) |
|     |          |         |                   |                 |               | Sucrose and yeast extract | 10.6 ± 0.6 mg/g | – |
|     |          |         |                   |                 |               | Glucose and yeast extract | 10.7 ± 1.1 mg/g | – |
|     |          |         |                   |                 |               | Sorbitol and yeast extract | 11.0 mg/g | – |

(continued on next page)
| No. | Bacteria                          | Source                      | Main carbon source                                  | Temperature/time | Maximum yield | Monosaccharide composition                                                                 | Molecular weight | References                                      |
|-----|---------------------------------|-----------------------------|----------------------------------------------------|------------------|---------------|-------------------------------------------------------------------------------------------|------------------|------------------------------------------------|
| 80  | *Rhizobium sullae* RHF           | –                           | Mannitol and yeast extract                         | 28°C/1 d         | 11.6 ± 1.3 mg/g | Glucose/galactose/fucose/mannose/galactonic acid – 34.1 ± 4.7/29.5 ± 2.0/23.6 ± 8.2/12.3 ± 12.3/±<1/1 (by molar percentage) | < 1.5 × 10⁵ Da, 0.1 – 6 × 10⁴ Da | (Gharzouli et al., 2013) |
|     |                                 |                             | Sucrose and yeast extract                          |                  |               | Glucose/galactose/fucose/mannose/galactonic acid – 39.5 ± 6.3/28.8 ± 0.3/25.5 ± 12.5/±<1/1/10/±<1 (by molar percentage) |                 |                                                |
|     |                                 |                             | Glucose and yeast extract                          |                  |               | Glucose/galactose/fucose/mannose/galactonic acid – 35.5 ± 2.0/33.6 ± 0.5/29.5 ± 2.7/±<1/1 (by molar percentage) |                 |                                                |
|     |                                 |                             | Sorbitol and yeast extract                         |                  |               | 3.4 ± 1.0 mg/g                                                                                 |                 |                                                |
| 81  | *Rhodospirillum rubrum*          | –                           | –                                                  |                  |               | Glucose/fucose/rhamnose                                                                     |                 | (Salton, 1960)                                  |
| 82  | *Rhodococcus erythropolis* HX-2 | Xingjiang oil field         | Yeast powder                                       | 25°C/3 d         | 8.957 g/L     | Glucose/galactose/fucose/mannose/galactonic acid – 27.29/24.83/4.79/26.66/15.84 (by molar percentage) | 1.04 × 10⁶ Da   | (Hu et al., 2019)                               |
| 83  | *Salmonella enteritidis*         | –                           | –                                                  |                  |               | 3Fucose/rhamnose                                                                              |                 |                                                |
| 84  | *Salmonella grumpeis*            | NCTC 6533                   | –                                                  | 37°C/22 h        | –             | Glucosamine/chondrosamine/galactose/glucose/fucose                                             |                 | (Davies, 1955)                                  |
| 85  | *Salmonella paraatyphi* B       | –                           | –                                                  |                  |               | 3Fucose                                                                                 |                 | (Grabrer et al., 1988)                        |
| 86  | *Salmonella poona*              | NCPPB 254                   | Yeast extract and glucose                          | 37°C/22 h        | –             | Glucosamine/chondrosamine/galactose/glucose/fucose                                             |                 | (Iernpol et al., 1996)                        |
| 87  | *Salmonella typhimurium*         | –                           | –                                                  |                  |               | 3Fucose                                                                                 |                 | (Grabrer et al., 1988)                        |
| 88  | *Salmonella wandsworth*          | –                           | –                                                  |                  |               | 3Fucose                                                                                 |                 | (Grabrer et al., 1988)                        |
| 89  | *Salipiger mucous* A3T           | Hypersaline soil (CECT 5855 T) | Dextrose, peptone, yeast extract and malt extract  | 32°C/5 d         | 1.35 g/L      | Glucose/mannose/galactose/fucose – 19.7/34/32.9/13.4 (by molar percentage)                   | 2.5 × 10⁴ Da    | (Llamas et al., 1988)                         |
| 90  | *Shigella dysenteriae*           | –                           | –                                                  |                  |               | 3Fucose/rhamnose                                                                              |                 | (Gehrke, Telegdi, Thiery, & Sand, 1998)        |
| 91  | *Streptococcus pneumoniae*       | –                           | –                                                  |                  |               | 3Fucose/rhamnose                                                                              |                 | (Grabrer et al., 1988)                        |
| 92  | *Streptococcus thermophilus* MR-1C | –                          | Skim milk powder supplemented with a mixture of amino acids | 40°C/1 d         | –             | Galactose/rhamnose/fucose – 5/2/1 (by molar ratio)                                           |                 | (Low et al., 1998)                            |
| 93  | *Streptomyces sp. A-1845*       | Soil sample                 | Glucose, corn starch, soybean meal and yeast extract | 25°C/5-6 d       | 0.785 g/L     | Mannose/galactose/xylose/glucosamine/rhamnose/glucose/fucose/ribose/galactosamine – 7.6/4.3/4.4/3.1/2.6/1.9/1.7/1.1/0.6 (by molar ratio) | 1.0 × 10⁶ Da    | (Iinoue, Murakawa, & Endo, 1992)               |
| 94  | *Thiobacillus ferrooxidans*      | –                           | –                                                  |                  |               | Rhamnose/fucose/xylose/mannose/galactose/glucuronic acid – 13.9/20.5/0.9/0.4 /1.1/4/4.4 (by molar ratio) |                 | (Grabrer et al., 1988)                        |
| 95  | *Vibrio sp. QY101*              | A decaying thallus of *Laminaria* | –                                                  | 25°C/4 d         | –             | Rhamnose/galactose/xylose/glucosamine/rhamnose/galactose/glucose/fucose/mannose – 23.90/23.05/21.47/12.15/6.89/6.57/3.61/2.36 (by molar percentage) | 5.46 × 10³ Da   | (Jiang et al., 2011)                          |
| 96  | *Yersinia pseudotuberculosis*    | –                           | –                                                  |                  |               | 3Fucose/rhamnose                                                                              |                 | (Grabrer et al., 1988)                        |

* limited information of monosaccharide compositions according to available references.
Fig. 2. The repeating units structure of bacterial fucose-containing exopolysaccharides (FcEPS) produced by some bacteria. *The No. refers the serial number of each reported FcEPS-producing strains in Table 1.
through the xylem, leading to bacterial wilt and canker in tomato and other plants (Gartemann et al., 2003). The EPS produced by C. michiganensis subsp. may protect bacteria by inhibiting the plant defense system and is conducive to the adhesion of bacteria on the plant surface, thus promoting the infection and colonization of host plants. The EPS, named Clavan, is a repeated-unit tetrasaccharide containing glucose, galactose, fucose, and pyruvate and is produced by C. michiganensis strains (Bulk, Zevenhuizen, Cordewener, & Dons, 1991).
For example, *C. m. subsp. michiganensis* NCPPB 1574, *C. m. subsp. nebraskensis* NCPPB 2581, *C. m. subsp. insidiosus* NCPPB 1686, and *C. m. subsp. sepedonicus* NCPPB 2140 are all capable of producing FeEPSs, with fucose content of 46.6, 28.5, 43.7, and 20.9 mol%, respectively (Bermphol, Dreier, Bahro, & Eichenlaub, 1996; Bulk et al., 1991).

Colanic acid is a type of FeEPS generally produced by members of Enterobacteriaceae, including *Escherichia* and *Klebsiella* spp. (Ratto et al., 2006). *Klebsiella* sp. is a special gram-negative bacterium. Its polysaccharide capsule surrounds the cell wall, leading to the formation of K-antigen. All K-antigens of *Klebsiella* strains have been divided into 82 different types, in which only six strains have been reported to contain fucose, namely, K1, K6, K16, K54, K60 and K63 (Rieger-Hug & Strim, 1981). The EPSs of several *K. pneumoniae* strains (ATCC 12657, 4208, 13886, 31646, and 31488) were reported to contain fucose (Vanhooren & Vandamme, 1999). Fucogel, an EPS prepared by fermentation of *K. pneumoniae* strain I-1507, is a high-viscosity polysaccharide developed by BioEurope and sold by Solabia. Fucogel has been used in the cosmetics industry because of its soft psychosensorial qualities, hydration, and emulsifying properties (Guetta, Mazeau, Auzely, Milas, & Rinaudo, 2005).

**Synthesis of FcEPS**

FcEPS is commonly composed of fucose, glucose, galactose, mannose, rhamnose, and uronic acid. FeEPSs can be synthesized by combining the intracellular and extracellular pathways, as shown in Fig. 3. In general, the biosynthesis of FeEPS occurs in four steps (Chaisuwon et al., 2020; Freitas et al., 2011). First, the nutrients in the extracellular environment enter the cells via active or passive transport and are transformed into different monosaccharides. When glucose is used as the carbon source, it is converted into glucose-6-phosphate under the action of glucokinase; three pathways are then used to synthesize the nucleotide sugar: (i) glucose-6-phosphate is converted into glucose-1-phosphate under the action of α-phosphoglucomutase, from which UDP-glucose, UDP-glucuronic acid, UDP-xylene, and UDP-galactose are synthesized; (ii) glucose-6-phosphate is converted to mannose-6-phosphate through phosphomannose mutase, followed by the production of GDP-mannose and GDP-fucose; and (iii) fructose-6-phosphate is produced from glucose-6-phosphate by phosphoglucomutase, and then glucosamine-6-phosphate, N-acetylglucosamine-6-phosphate, and UDP-N-acetylglactosamine are obtained step by step (Jiang & Yang, 2018). According to Fig. 3, GDP-fucose can be obtained through the conversion of a variety of monosaccharides. Second, monosaccharides are bound to a lipid carrier located in the cytoplasmic membrane. Thereafter, repeated units were formed by the linkage of different monosaccharides and extended into high molecular weight polysaccharides. Finally, these high molecular weight polysaccharides are secreted outside the cell to form FeEPS. In the last step, the polysaccharide must pass through the cell membrane without damaging its barrier characteristics. In the cell wall of gram-negative bacteria, FeEPS could be secreted out of the cells following the Wzx-Wzy-dependent pathway, in which the repeating units are assembled at the inner face of the cytoplasmic membrane and polymerized at the periplasm, or ABC transporter-dependent pathway, in which polymerization occurs at the cytoplasmic face of the inner membrane (Barcelos et al., 2019).

**Factors affecting FeEPS production**

The characteristics of FeEPS are mainly determined by the genetic factors of producing bacteria. The ability to produce different FeEPSs under the same culture conditions was exhibited within different strains of bacteria, although they belonged to the same species and genus, such as *Bacillus licheniformis* BioE-Bl11 and T8; *Bifidobacterium longum* H73 and H63; and *C. m. subsp. michiganensis* strains (Bermphol et al., 1996; Kook, Lee, Jeong, & Kim, 2019; Salazar et al., 2009). In addition, two or more kinds of FeEPSs may be synthesized by the same strain at the same time, although these FeEPSs exhibit different characteristic properties (molecular weight and monosaccharide composition) and activities; such FeEPSs can be produced by *Bacillus* sp. T14, *L. plantarum* KX041, *L. plantarum* JLAU103, and *L. gasser* FR4 (Spano et al., 2013; Gugliandolo et al., 2012; Min et al., 2018; Rani et al., 2018; Xu et al., 2019).

The production of FeEPS is highly influenced by the medium composition and culture conditions. The structure and yield of FeEPSs are commonly related to the type of carbon sources in the culture medium. Taking the FeEPS produced by *Enterobacter* sp. A47 as an example, the yield produced using glucose as the main carbon source was 2.48-fold higher than that using xylose, whereas the molar proportion of fucose in the FeEPS produced using glucose as the main carbon source was lower than that using xylose (Freitas et al., 2014). Sugars are frequently used as a carbon source during the fermentation of FeEPSs, and some cheaper substitutes have been shown as valuable for bacterial production of FeEPS. For example, the maximum FeEPS production of *Enterobacter* sp. A47 (13.3 g/L) was reached with glycerol used as the carbon source, whereas using out-of-specification tomato paste as the carbon source led to a maximum FeEPS production of 8.77 g/L (Antunes, Freitas, Sevrin, Grandfils, & Reis, 2017; Cruz, Freitas, Torres, Reis, & Alves, 2011). These low-cost materials are suitable carbon sources for the production of FeEPS to reduce the cost of industrial production. The existence of an excess carbon source is conducive to the synthesis of FeEPS, which is further limited by the nitrogen source and oxygen (Miuleto, Dolosic, Pozzi, Foresti, & Zaiat, 2010). And the production of FeEPS is commonly performed under aerobic conditions. FeEPSs can be synthesized throughout the logarithmic and stable phases of bacterial growth. However, the maximum yield of FeEPS generally occurs in the late logarithmic phase, rather than in the stable phase (Freitas et al., 2011).

**FeEPSs served as new sources of FCOs**

FeEPSs with high yield and diverse structures can be obtained by liquid fermentation of specific bacteria. FCOs are then prepared by depolymerizing FeEPSs using suitable degradation tools. Chemical degradation methods (acid hydrolysis and oxidative degradation) are commonly used for the preparation of oligosaccharides. Hydrochloric acid, sulfuric acid, and trifluoroacetic acid are widely used in acid hydrolysis degradation processes, while sodium periodate and hydrogen peroxide are common oxidants used to produce oligosaccharides (Cescutti et al., 2005; Wei et al., 2012). However, chemical degradation methods are usually performed at high concentrations and temperatures, leading to the production of more monosaccharides.

Enzymatic methods are more efficient and mild in comparison with chemical degradation methods. Enzymes capable of degrading EPS are usually produced in three ways. First, endogenous enzymes secreted by host EPS-producing bacterial strains (Lelchat, Cozien, Costauae, Brandilily, & Boisset, 2014). Second, exogenous enzymes produced by other bacterial strains (Li et al., 2019). Third, polysaccharides depolymerases from phage particles or phage-induced bacterial lysates. Glycanase produced during phage infection of host EPS-producing bacteria has lytic effects on the EPS secreted by that host bacteria, which is conducive to the adsorption and infection of the phage (Xiao et al., 2021). Bacteriophage-borne glycanase is a promising tool for the preparation of FCOs. Based on the effective degradation effect of bacteriophage-borne glycanase on EPS, the structures of some FeEPSs produced by *Klebsiella* sp. strains have been characterized (Rieger-Hug & Strim, 1981; Shang et al., 2014). Moreover, two FCOs with new structures were successfully obtained via degradation of the FeEPS produced by *E. sakazakii* M1 by bacteriophage-borne glycanase (Xiao et al., 2021).

**Activities and applications of FeEPSs**

Although FeEPSs have been applied in the cosmetic, food, medicine,
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and environmental remediation industries, applications related to health will become an important trend in the future of FcEPSs development. Accumulating evidence has shown that FcEPSs exert various biological activities, including anti-oxidant, prebiotic, anti-cancer, anti-inflammatory, anti-viral, and anti-microbial activities (Fig. 4).

**Anti-oxidant activity**

The overproduction of reactive oxygen species (ROS) may result in oxidative stress and free radical-induced oxidation, leading to a series of diseases, such as diabetes, inflammatory and neurological diseases (Rani et al., 2018). Natural materials could serve as a highly promising source of anti-oxidants, especially polysaccharides obtained from plants, animals, and microorganisms.

Many studies have demonstrated the anti-oxidant activity of FcEPSs in vitro. FcEPSs prepared from bacteria exhibited anti-oxidant activity mainly by scavenging free radicals, including 2,2-diphenyl-1-picrylhydrazyl (DPPH), hydroxyl, 2,2'-azinobis-3-ethylbenzothiazoline-6-sulphonic acid (ABTS), superoxide radicals, etc. Three Lactobacillus strains, *L. plantarum* KX041, *L. plantarum* JLAU103, and *L. gasseri* FR4, displayed strong anti-oxidant activities against DPPH, ABTS, superoxide, and hydroxyl radicals, thus demonstrating their potential to reduce oxidation (Min et al., 2018; Rani et al., 2018; Xu et al., 2019). The FcEPSs of *B. licheniformis* T8, *Polaribacter* sp. SM1127, *Microbacterium aurantiacum* FSW-25, and *Zunongwangia profunda* SM-A87 also exhibited similar anti-oxidant activity by scavenging free radicals (Sran, Bisht, Mayilraj, & Choudhury, 2019; Sun et al., 2015; Xu, Chen, Xue, Zhang, & Zheng, 2019). Among them, two FcEPSs of *B. licheniformis* T8, BL-P1 (3.96 × 10^6 Da) and BL-P2 (1.23 × 10^5 Da), showed strong scavenging ability to DPPH and hydroxyl radicals. The scavenging abilities of the two EPSs increased with increasing concentrations until the maximum scavenging rate reached 62.33% and 67.31% at 140 μg/mL, respectively, indicating that FcEPS with low molecular weights may demonstrate better anti-oxidant activity than high molecular weight FcEPS (Xu et al., 2019).

The anti-oxidant activities of FcEPSs are influenced by their fucose content. Two EPSs, high-fucose-content EPS (41.89%) and low-fucose-content EPS (4.9%), are biosynthesized by *B. megaterium* RB-05 under two different fermentation processes, and high-fucose-content EPS exhibited better free radical scavenging activities than low-fucose-content EPS. High-fucose-content EPS can directly eliminate intracellular ROS induced by hydrogen peroxide and reduce oxidative stress in WI38 cells by regulating the Nrf2/Keap1 signaling pathway and cytoprotective genes related to mitogen-activated protein kinase (MAPK) and mitochondrial-mediated pathways (Chowdhury et al., 2014). Anti-oxidant enzymes also play a vital role in preventing oxidative stress by catalyzing the stable formation of free radicals. Two fungal EPS (ALF1 and ALF2) were prepared from the fermentation liquid of *Flocularia lateovirens* but only ALF1 contained fucose. ALF1 exerts antioxidant activity by improving the activity of superoxide dismutase, glutathione peroxidase, and catalase (Liu, Jiao, Lu, Shu, & Chen, 2020). Anti-oxidation is one of the most valuable properties of FcEPS, resulting in its potential application prospects in the food, medicine, and cosmetic fields.

**Prebiotic activity**

Prebiotics are beneficial for improving the intestinal health of the host by selectively stimulating the growth or metabolism of one or more bacteria in the colon (Gibson, Probert, Loo, Rastall, & Roberfroid, 2004). A FcEPS was prepared from a gene-recombinant *E. coli* with overexpression of the gene cluster ycd-fabI-yciW-rnb, and the interaction of this FcEPS with gut microbiota was evaluated. The results showed that 96% of FcEPS could be degraded and utilized by the gut microbiota, with the enrichment of the genera *Collinsella*, *Butyricimonas*, and *Hafnia*. In addition, more short-chain fatty acids (SCFAs) can be produced by human fecal

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**Fig. 4.** The main functional activities of bacterial FcEPS, including anti-oxidant, prebiotic, anti-cancer, anti-inflammatory, anti-viral and anti-microbial activities.
microbiota using FcEPS as the carbon source than using starch as the carbon source (Li, Chen, Cao, Hu, & Yin, 2019). Other FCPs, for example, fucoidans, extracted from brown algae and sea cucumber also exhibited prebiotic activity. Fucoidans extracted from Laminaria spp. play a positive role in regulating intestinal microbiota by increasing the abundance of beneficial bacteria (especially Lactobacilli spp.) in the intestine and the concentration of SCFAs in the colon, which has been proved to alleviate dyslipidemia and obesity caused by high-fat diet. Similarly, fucoidans extracted from Acanthina molpadioides are also effective in repairing the intestinal mucosal barrier damage caused by cyclophosphamide treatment through improving the expression of tight junction protein, promoting the production of SCFAs (particularly propionate and butyrate), and increasing the abundance of SCFAP-producing bacteria, such as Coprococcus, Rikenella, and Butyricicoccus species (Li et al., 2020).

**Anti-cancer/anti-tumor activity**

Despite advanced technology and in-depth research, cancer is still the largest cause of death worldwide and is caused by the uncontrolled division of cells. FcEPS, as a natural material, serves not only as a functional food product but also as a source of anti-tumor drugs (Hu, Li, Qiao, Wang, & Huang, 2019).

Colon cancer, further affecting other organs and tissues, is the most common type of cancer. Two FcEPSs with different fucose contents and molecular weights have been prepared from L. casei SB27, a strain isolated from yak milk obtained from the Gansu Tibetan region of China. In vitro anti-tumor tests showed that both FcEPSs could significantly inhibit the proliferation of HT-29 colorectal cancer cells and upregulate the expression of Bad, Bax, Cas3, and Cas8 genes (Di et al., 2017).

Leukemia is a serious disease caused by malignant cloning of hematopoietic stem cells, also known as “blood cancer”. Ruiz-Ruiz et al. (2011) screened a new type of halophilic bacterium and studied the anti-tumor activity of its EPS. This EPS is a miscellaneous polysaccharide containing fucose, which has anti-tumor activity against T-cells in acute lymphoblastic leukemia. Only tumor cells were susceptible to apoptosis, whereas primary T-cells were resistant. The newly discovered EPS was the first bacterial EPS shown to have an effective and selective pro-apoptotic effect on leukemia T-cells. Umezawa et al. (1983) obtained a FcEPS from Flavobacterium uliginosum inhabiting the ocean and studied its anti-tumor activity against mouse sarcoma 180 solid tumors. Complete tumor regression was observed in some mice treated with FcEPS indicating it could prolong the survival of tumor mice. And some fungal FcEPSs also demonstrated anti-cancer activities. The anti-cancer effects of FcEPS extracted from Trichoderma pseudokoningii on human leukemia K562 cells were also studied. The findings showed that FcEPS could induce the apoptosis of K562 cells, mainly involving the mitochondrial pathway, suggesting that EPS may become a new potential adjuvant chemotherapeutic agent against human leukemia (Huang et al., 2012).

In addition, another study reported the anti-cancer activity of FcEPS prepared from T. pseudokoningii on human breast cancer MCF-7 cells. These findings suggested that FcEPS induced the apoptosis of MCF-7 cells through an intrinsic mitochondrial apoptotic pathway and that FcEPS may serve as an effective drug against human breast cancer (Wang, Liu, Liu, Bo, & Chen, 2016). Two EPSs, ALF1 with 13.86% fucose and ALF2 without fucose, were prepared from the fermentation liquid of Floccularia luteovirens, and the proliferation of tumor cells was inhibited by ALF1 without affecting the metabolic proliferation of normal cells (Liu et al., 2020).

**Anti-inflammatory activity**

Inflammation is a response of the host immune system to viral infection and tissue damage, and may cause leukocyte accumulation and plasma protein leakage through blood vessels. Long-term inflammatory reactions may lead to inflammatory diseases or cancer. Many studies have reported that EPS could serve as an immune regulator of the anti-inflammatory response of the immune system, in which the regulatory mechanism may be that some EPS with specific components and branches or high molecular weight may inhibit the immune response (Chaisuwan et al., 2020). However, further research is needed to understand the detailed mechanism.

Macrophages play an important role in the host immune defense system against various infections and cancers by secreting several mediators, such as nitric oxide, tumor necrosis factor α, interleukin (IL)-1β, and prostaglandin E2. RAW264.7 macrophages, which are commonly used in immune studies, can be activated by EPS, leading to the proliferation of macrophages, improvement of phagocytic phagocytosis, and secretion of cytokines (Min et al., 2018; Wang et al., 2020). Two FcEPSs with fucose contents of 37.1% and 10.21% were prepared from B. licheniformis BioE-BL11 and L. mesenteroides BioE-LMD18, respectively. Both FcEPSs inhibited the secretion of pro-inflammatory cytokine IL-6 in lipopolysaccharide-stimulated RAW264.7 mouse macrophage with the inhibition rate of 40.7% and 32.1%, respectively, and enhanced the secretion of anti-inflammatory cytokine IL-10 in a dose-dependent manner (Kook et al., 2019). L. plantarum, as a probiotic strain, is capable of producing FcEPS, which also has strong immunomodulatory activity. The release of IL-6, tumor necrosis factor α, and nitric oxide by RAW264.7 were enhanced by the FcEPS of L. plantarum JLAU103 through the NF-κB signaling pathway (Wang et al., 2020). Another study also showed that FcEPS purified from the fermentation broth of L. plantarum KX041 also has potential immunomodulatory activity (Xu et al., 2019).

According to previous studies, FcEPS of T. pseudokoningii demonstrated not only anti-tumor activity but also immunomodulatory activity, which was attributed to the activation of toll-like receptor-4 and dectin-1 specific antibodies by FcEPS through the NF-κB and MAPK signaling pathways, thereby inhibiting the secretion of cytokines (Wang et al., 2016). Moreover, FcEPS of T. pseudokoningii exhibited the ability to induce morphological changes in dendritic cells and enhance the expression of the dendritic cell surface characteristic molecules CD11c, CD86, CD80, and major histocompatibility complex II, which is also associated with NF-κB and MAPK signaling pathways (Xu et al., 2016). These characteristics indicate that FcEPS is a promising anti-inflammatory agent.

**Anti-viral and anti-microbial activity**

Viral diseases are commonly targeted by vaccination, chemoprevention, and chemotherapy. Bacterial EPS, as natural products, are potential anti-viral drugs. Arena et al. (2006) isolated a heat-resistant strain, B. licheniformis, from marine hot springs and evaluated the immunomodulatory effects of its FcEPS. The results showed that the replication of HSV-2 in human peripheral blood mononuclear cells (PBMCs) was blocked after treating with FcEPS. Moreover, both Th1 and Th2 cytokines were detected in the PBMCs supernatant, indicating that the anti-viral effect of FcEPS on PBMCs was related to the pattern of cytokines induced. In addition, another study reported the anti-viral and immunomodulatory effects of FcEPS obtained from B. licheniformis T14 on HSV-2; however, only Th1 cytokines were detected in the FcEPS-treated PBMCs supernatant (Gugliandolo, Spanò, Lentini, Arena, & Maugeri, 2014).

There are few studies on the anti-bacterial activity of FcEPSs. The FcEPS produced by L. gasseri FR4 exhibited anti-bacterial activity against E. coli MTCC 2622, Listeria monocytogenes MTCC 657, Staphylococcus aureus MTCC 3160, and Enterococcus faecalis MTCC 439, with the maximum inhibitory effect on Listeria monocytogenes MTCC 657 (Rani et al., 2018). The anti-bacterial effect of FcEPS produced by L. gasseri FR4 is related to the prevention of biofilm formation. An EPS containing fucose produced by B. licheniformis T14 also showed anti-bacterial and anti-biofilm properties against E. coli 463, K. pneumonia 2659, P. aeruginosa 445, and Staphylococcus aureus 210 (Spanò, Laganà, Visalli,
FcEPSs have important applications in various industries owing to their anti-oxidant, prebiotic, anti-cancer, anti-inflammatory, and anti-viral activities. In addition, the emulsification, pseudoplasticity, and stability of FcEPSs also provide the possibility for their applications in the food industry.

FcEPSs have potential applications in the food industry by stabilizing emulsions between water and hydrophobic materials (Freitas et al., 2011). Natural biological emulsifiers have the advantages of degradability, low toxicity, selectivity, and environmental compatibility compared to artificial emulsifiers (Mata et al., 2008). The activity of FcEPS extracted from *Pseudomonas* sp. ID1 against different food and cosmetic oils was much higher than commercial polysaccharides, such as xanthan gum and gum arabic. Emulsifying activity is a common property of the FcEPS produced by *Enterobacter* sp. A47, *Salipiger mucosus* A3, *B. coagulans* RK-02, *Graecilibacillus* sp. SCU50, *P. mendocina* P3y, and *P. oleovorans* NRRL B-14682 (Alves et al., 2010; Freitas et al., 2011; Gan, Li, Wang, Peng, & Tian, 2020; Kodali, Das, & Sen, 2009; Llamas et al., 2010; Royan, Parulekar, & Mavinckurve, 1999). However, emulsifiers may be exposed to high or low temperatures, high or low pH, and high salinity during food processing (Freitas et al., 2009). Research has shown that FcEPS produced by *Enterobacter* sp. A47 is stable within a wide range of pH and temperatures (Cruz et al., 2011). The degradation temperature of the FcEPS produced by *Rhodococcus erythropolis* HK-2 reached 255.4 °C (Hu et al., 2019). The FcEPS produced by low temperature-resistant strains, *Polaribacter igerensis* CAM006, *Pseudooalteromonas* sp. CAM003 and CAM025, could be served as cryoprotectants (Nichols, Bowman, & Guezenne, 2005). Another study suggested that the FcEPS of *B. licheniformis* T14 exhibited better thermal stability, which may be correlated with the presence of fucose (Caccamo et al., 2018).

Pseudoplastic rheological behavior is another common characteristic of FcEPS. Polysaccharides with better pseudoplasticity could be used in the preparation of different types of food, such as dairy products, cakes, syrups, and puddings. The pseudoplasticity of FcEPS is conducive to the perception of comfort when eating food (Antunes, Freitas, Alves, Grandfils, & Reis, 2015). Most FcEPSs have a high molecular weight (>100 kDa) and high viscosity and can serve as thickeners in the food industry. Several probiotics (*L. plantarum* H2, *L. rhamnosus* E41, and *L. rhamnosus* E43R) were isolated from human intestinal microbiota, and the FcEPSs of these strains could increase the viscosity of fermented milk, indicating their good viscosity-intensifying properties (Salazar et al., 2009).

Many studies have discussed potential biomedical and food applications from FcEPSs but only some outstanding results are reviewed here. However, whether these molecules can be marketed in food and pharmaceutical fields needs to be further evaluated. Unfortunately, few studies have determined the relationship between the structures and activities of FcEPSs, and the conclusions cannot be widely used. This paper systematically summarized the activities of FcEPSs to provide a research basis for the structure–activity relationship, which is also decisive for their potential application. In addition, the activity of natural products such as EPS needs to be simulated in animals before clinical development and application; however, so far, these aspects have been seldom studied.

**Conclusion and future perspectives**

Fucose and FCOs play a vital role in food industry application owing to their specific activities and physicochemical properties. However, the complexity and high cost of chemical synthesis of fucose or FCOs make them unable to meet the demands of large-scale industrial production. FcEPS could serve as a promising source of fucose and FCOs. To date, chemical degradation and enzymatic hydrolysis are effective means to degrade FcEPS for the preparation of FCOs, especially bacteriophage-borne glycans.

FcEPSs produced by microorganisms have great development potential with regard to food, cosmetics, and medical applications in comparison with other natural materials. In addition, FcEPSs have various important functions, including anti-oxidant, prebiotic, anti-tumor, anti-inflammatory, anti-viral, and anti-microbial activities. The preparation, structural analysis, and functions of FcEPSs have been extensively explored over the past several years. However, the relationships between the structural characteristics and bioactivities of FcEPSs are still not fully established owing to the structural diversity and complexity of FcEPS. Well-designed researches on the structure–activity relationship of FcEPSs are needed, which may serve as a reference strategy for the further applications of fucose-containing carbohydrates in the functional food and medicine industries.

**Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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