Microbial exopolysaccharides (EPS) are high molecular hydrocarbonic exogenous products of microbial metabolism [1–3]. They are widely used in industry (food production, chemistry, oil production, etc.) due to their ability to gel, emulsify, flocculate, form suspensions and to change rheological parameters of aqueous systems [3–5].

Most of currently known microbial EPS have similar functional properties that determine their practical significance [2, 4]. Thus, it is not surprising that only a few of many isolated, described and studied polysaccharides of microbial origin (xanthan, gellan, alginate, dextran) are produced industrially [1, 4].

A polysaccharide must now have unique properties to enter the free niches of rapidly developing fields like medicine, pharmacy, cosmetics, and nature conservation.

Since late XX century, scientists actively study microorganisms living in habitats previously overlooked in the search for bioactive compounds-producing microorganisms (permafrost, hot springs, oceanic depths, salt marshes, etc.). Quite possibly, they survive in such places due to specific adaptive mechanisms and synthesis of protective compounds [5], including EPS with new properties.

Such organisms are known as extremophiles, or microorganisms isolated from extreme habitats [6, 7]. We argue that the terms “extremophile” and “extreme” are not quite applicable, since microbiology considers “extreme” conditions in which only specialized microorganisms survive and many other taxa perish. Therefore this review refers to them simply as “nontraditional”.

To date, a number of reviews have been published about synthesis of EPS by nontraditional producers [6–17]. However, the reviewers mostly paid attention to habitat description, physico-chemical properties and environmental significance of the synthesized polysaccharides and almost ignored the possibility of practical applications [13]. In addition, the reviews were devoted to a specific group of microorganisms (thermophilic [15], halophilic bacteriae [14, 16] and archaea [18], cryophilic yeast [19], sea microbes [9, 10, 17], and microorganisms isolated from hydrothermal vents [8]). Only a few papers reviewed several unusual producers at once [6, 7, 12]. The listed studies were published in 2010–2012 and include mostly summaries of specifics of EPS biosynthesis and their physico-chemical properties. A recent paper [11] discusses practical applications of several polysaccharides, synthesized by bacteriae isolated from hydrothermal sources.
This review aimed to summarize the available information on EPS synthesis by non-traditional producers (thermo-, cryo-, halophilic microorganisms and bacteriae isolated from deep-sea hydrothermal vents), and properties of polysaccharides that support their potential practical application in medicine, pharmaceutical, food industries and nature conservation.

**Thermophiles**

The studies of thermophilic microorganisms started approximately in 1967 [20]. The paper briefly summarized the available knowledge about the microorganisms. In those days, attention was mostly paid to their environmental niche and the mechanisms enabling their survival at high temperatures.

One of those adaptive mechanisms is synthesis of microbial EPS. It should be noted that, unlike industrial mesophilic producers, using thermophils for the preparation of polysaccharides has a number of technological advantages, in particular, at elevated temperatures, the viscosity of the culture fluid and the possibility of the process infection are reduced, as well as mass exchange processes increase, etc. [21–25].

**Archaea.** The first reports of EPS synthesis by thermophilic archaea began to appear at the end of XX century [26–29]. In 1993, Nicolaus et al. [26] found out that the thermoacidophilic archaea Sulfolobus solfataricus MT4 and MT3, isolated from a hot acidic spring (Agnano volcanic crater, Italy) produced EPS at 75–88°C.

The main disadvantage of those archaea as well as almost all other thermophilic producers of EPS is the low concentration of the target product (Table 1). This can be caused by low concentrations of the carbon and energy source (2–9 g/l) in the cultivation medium. Special attention was paid to the polysaccharide effect on physiology. Thus, several papers [27, 28, 30] presented data on synthesis of EPS by archaea linked to biofilm formation. Rinker et al. [27, 28] studied the growth of hyperthermophilic anaerobic organism Thermococcus litoralis DSM 5473. They established that biofilms formed on hydrophilic surfaces (polycarbonate filters) followed by accumulation of sulfated mannan (over 0.3 g/l EPS). Other researchers [30] studied the biofilm structure in thermocaidophilic archaea of the genus Sulfolobus.

Polysaccharides can perform other vital functions other than the formation of biofilms which protect the microorganisms from unfavorable factors and toxins. Thus, a hypothesis was formulated [29] that EPS of thermophilic methanogenic archaea Methanosarcina thermophila TM-1 can be an osmoprotectant.

Notably, researchers [26–30] did not try to intensify EPS synthesis by thermophilic archaea. Due to the low concentration of the target product, this microorganisms are hardly going to be industrially important in the near future. Another complication is the difficulty of culturing most thermophilic archaea that require complex media with a lot of vitamins, amino acids, etc. [27, 28].

**Bacteriae.** Simultaneously with studying EPS-synthesizing archaea, researchers turned to thermophilic bacteriae. Almost all of them belong to the family Bacillaceae (the genera Bacillus [31–33], Geobacillus [22, 34–36], Anoxybacillus [37], Aeribacillus [24]) and Paenibacillaceae (the genus Brevibacillus [23, 25]) with optimal growth temperature of 45–65°C (Table 1). Notably, the first reports of EPS synthesis by thermophilic bacteriae also included representatives of these families. Thus, Manca et al. [35] in 1996 reported isolation of extremely thermophilic bacteriae Geobacillus thermoantarcticus, which at 65°C synthesized up to 400 mg/l sulfated EPS from soil near the crater of Melbourne volcano (Antarctica).

Besides representatives of Bacillaceae and Paenibacillaceae, synthesis of polysaccharides is known for hyperthermophilic bacteriae of the genus Thermotoga (optimal temperatures 80–85°C) [27] and thermophiles of the genus Thermus (optimal temperature 60°C) [38].

All thermophilic bacteriae in the literature produce less than 1 g/l EPS [22–25, 32, 33, 35, 36, 38]. Recently, bacteriae Anoxybacillus sp. R4-33, able to produce 1.1 g/l polysaccharide and tolerant of high temperature and radiation were isolated from geothermal radon springs (China) [37].

Thermophilic obligate methanotroph Methylcoccus thermophilus 111n synthesizes up to 5 g/l EPS [2] and thus is a much better choice. Those amounts were achieved after a complex investigation of pH, temperature, diluted oxygen concentration, gaseous methane to oxygen ratio conditions, and the pre-treatment of the inoculum. The exogenous addition of 0.5 g/l aspartic acid (obtained by transferring amino group to oxaloacetic acid) to the culture medium of strain 111n was followed by an almost two-fold increase in the polysaccharide biosynthesis rate [2].

The EPS of several thermophilic and thermotolerant bacteriae were observed to
have antiviral [31, 34, 39] and immunomodulating [38] activities and to inhibit biofilm formation [40].

Treatment of mononuclear cells of human peripheral blood with polysaccharide solutions (300 μg/ml) of strains Geobacillus thermodenitrificans B3-72, Bacillus licheniformis B3-15 and T14 stimulated the production of IFN-γ, IFN-α, TNF-α, IL-12 and IL-18 and inhibited the replication of herpes simplex virus type 2 [31, 34, 39]. In the presence of EPS of strains B3-72, T14 and B3-15 the virus was inhibited by 67, 77 and 85%, respectively [39]. Notably, antiviral activity is usually seen in sulfated polysaccharides [41], and the compounds described in [31, 34, 39] did not contain sulfate groups.

Lin et al. [38] isolated from the biofilm of Thermus aquaticus YT-1 a polysaccharide that heightened immune response. That EPS was observed to act as an agonist of TLR2 receptor and helped induce synthesis of cytokines IL-6, TNF-α, and nitrogen monoxide (NO) by murine macrophages and human monocytes. That immunoregulatory activity supposedly was caused by galactofuranose in its structure [38].

Several thermophilic representatives of the genus Bacillus were also observed to synthesize polysaccharides with anticytostatic activity [22, 33]. Fraction 1 EPS B. licheniformis T14, consisting of fructose, fucose and glucose (1:0.75:0.28), at 500 ppm raised LD50 of avarol (a cytostatic agent) from 0.18 to 0.99 mg/ml [33], and EPS of Geobacillus tepidamans V264 raised it to 2.24 mg/ml [22].

Recently Španò et al. [40] found that EPS of B. licheniformis T14 at 400 μg/ml inhibited biofilm formation by multiresistant strains Escherichia coli 463, Klebsiella pneumoniae 2659, Pseudomonas aeruginosa 445 and Staphylococcus aureus 210 by 74, 56, 54 and 60%, respectively. The researchers suggested that due to the emulsifying properties of the polysaccharide it is able to impact the hydrophobicity of bacterial cells and so prevent their primary adhesion to surfaces [40].

A summary of EPS biosynthesis by thermophilic and thermotolerant microbes is given in Table 1. Currently, the microbes are not considered promising due to low EPS synthesis ability. Meanwhile such polysaccharides have properties important for medicine and pharmacy (antiviral, immunomodulating, anticytostatic, etc.), which can stimulate work on intensifying their synthesis.

**EPS-producing microbes from deep-sea hydrothermal vents.** Deep-sea hydrothermal vents, characterized by high concentrations of toxic compounds (sulfides and heavy metals), sharp changes in temperature and pressure, are habitats of thermophilic bacteriae with various properties [8, 21, 42–44].

Since the first such vent was discovered in 1977 near the Galapagos, a great many other hydrothermal vents with various unique microorganisms were found [43, 44]. Thus, from the East-Pacific Rise (2600 m deep), EPS-synthesizing strains of bacteriae from the genera Alteromonas [45–48] and Vibrio [49] were isolated; at Mid-Atlantic Ridge (3500 m deep), bacteriae Alteromonas macleodii subsp. fijensis var. medioatlantica were found [50]; at Guaymas Basin and North Fiji Basin (2000 m deep), strains A. macleodii [43] and Alteromonas infernus [44] were isolated, respectively.

Despite the fact that these EPS-producing bacteriae were isolated from extreme habitats, most of them turned out to be mesophilic neutrophils with optimal growth temperature 25–35 °C and pH 6–8 [43–45, 46–50], and only a few of them were thermophiles (40–45 °C) [49].

The EPS-producing bacteriae isolated from deep-sea hydrothermal vents became a subject of active research in 1990s [42–44, 47–49]. In 1994, Guezenec et al. [42] published results of screening EPS-producing bacteriae isolated from hydrothermal vents. Almost all polysaccharides except for neutral monosaccharides contained sulfate moieties (to 21.5%) and glucuronic acids (to 7.9%), several had amino sugars (to 2.5%).

Interestingly, EPS-producing bacteriae are isolated not only from soil or water near hydrothermal vents [42], but from the surfaces of various organisms living there (shrimps, worms, etc. [45, 46, 48–50]). The strain Alteromonas macleodii subsp. fijensis var. medioatlantica MS907, producing 9 g/l EPS after 72 hours of culturing was found on carapax of the shrimp Rimicaris exoculata [50].

The outer shell of a sea polychaete Alvinella pompejana (at the depth of 2600 m) yielded EPS-synthesizing bacteriae Alteromonas sp. HYD1545 and A. macleodii subsp. fijensis biovar deepsane HYD657 [45, 48]. The strain HYD1545 after 120 hours of culturing produced 11 g/l of polysaccharide [48], and strain HYD657 produced 7 g/l EPS after
**Table 1. Synthesis of exopolysaccharides by thermophilic and thermotolerant microorganisms**

| Microorganism                      | Culture temperature | Carbon source, g/l | EPS concentration, g/l | Physico-chemical properties of EPS | Molecular mass, kDa | Physiological role, functional properties and prospects of EPS application | References |
|------------------------------------|---------------------|--------------------|-------------------------|-----------------------------------|--------------------|--------------------------------------------------------------------------|------------|
| **EPS of thermophilic archaea**    |                     |                    |                         |                                   |                    |                                                                          |            |
| *Methanosarcina thermophila* TM-1  | 45–55 °C            | Trimethylamine, 4.8 | –                      | Glucuronic acid (over 40%)        | –                  | Osmo-protectant                                                           | [29]       |
| *Sulfolobus acidocaldarius*        | 76 °C               | –                  | –                      | Glucose, galactose, mannose, N-acetylg glucosamine | –                  | Biofilm formation                                                         | [30]       |
| *Sulfolobus solfataricus* MT3      | 75 °C               | Glucose, 3         | 7.0 mg/l               | Glucose, mannose, glucosamine, galactose (1:2:1:0:6:0:7:0:73). Sulfates 5–12% | –                  | –                                                                        | [26]       |
| *Sulfolobus solfataricus* MT4      | 88 °C               | Glucose, 3         | 8.4 mg/l               | Glucose, mannose, glucosamine, galactose (1:2:1:0:6:0:13). Sulfates 5–12% | –                  | –                                                                        | [26]       |
| *Sulfolobus tokodaii*              | 76 °C               | –                  | –                      | Glucose, galactose, mannose, N-acetylg glucosamine | –                  | Biofilm formation                                                         | [30]       |
| *Thermococcus litoralis* DSM 5473  | 88 °C               | Maltose, 2         | 0.18–0.32              | Mannan, sulfates 1–2%             | 41                 | Biofilm formation                                                         | [27, 28]  |
| **EPS of thermophilic and thermotolerant bacteriae** | |                    |                         |                                   |                    |                                                                          |            |
| *Aeribacillus pallidus* 418        | 55 °C               | Maltose, 9         | 0.17                   | Fraction 1: mannose, glucose, galactosamine, glucosamine, ribose (1:0.16:0.1:0.09:0.07:0.06:0.04) Fraction 2: mannose, galactose, glucose, galactosamine, glucosamine, ribose, arabinose (1:0.5:0.46:0.35:0.24:0.16:0.14) | Fraction 1: 700; Fraction 2: 1000 | Emulgent                                 | [24]       |
| *Anoxybacillus* sp. R4-33          | 55 °C               | Glucose, 10        | 1.1                    | Fraction 2: mannose, glucose (1:0.45) | 1000               | Adsorbs heavy metals                                                   | [37]       |
| *Bacillus licheniformis* B3-15     | 45 °C               | Glucose, 6         | 0.165                  | Fraction 1: mannose, glucose (1:0:3); Fraction 2: mannose; Fraction 3: glucose | 600                | Antiviral and immunomodulatory                                            | [31, 32]  |
| Microorganism                          | Culture temperature | Carbon source, g/l | EPS concentration, g/l | Physico-chemical properties of EPS                                                                 | Physiological role, functional properties and prospects of EPS application | References |
|---------------------------------------|---------------------|-------------------|------------------------|----------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------|-------------|
| *Bacillus licheniformis* T14          | 50 °C               | Sucrose, 50       | 0.366                  | Fraction 1: fructose, fucose, glucose and traces of galactosamine, mannose (1:0.75:0.28:traces:traces) | 1000 Antiviral, immunomodulatory and anticytotoxic. Inhibits biofilm formation | [33, 39, 40]|
| *Brevibacillus thermoruber* 423       | 55 °C               | Maltose, 18       | 0.897                  | Glucose, galactose, galactosamine, mannose, mannosamine (1:3:0.25:0.16:0.04)                        | –                                                                        | [25]        |
| *Brevibacillus thermoruber* 438       | 55 °C               | Maltose, 18       | 78.1 mg/l              | –                                                                                                  | –                                                                        | [23]        |
| *Geobacillus tepidamans* V264         | 60 °C               | Maltose, 30       | 111.4 mg/l             | Glucose, galactose, fucose, fructose (1:0.07:0.04:0.02)                                            | >1000 Anticytotoxic                                                    | [22]        |
| *Geobacillus thermoantarcticus*       | 65 °C               | Mannose, 6        | 0.4                    | Fraction 1: mannose, glucose (1:0.7); Fraction 2: mannose and traces of glucose                    | Fraction 1: 300; Fraction 2: 300                                        | [35]        |
| *Geobacillus thermodenitrificans* B3-72 | 65 °C              | Sucrose, 6        | 70 mg/l                | Fraction 1: glucose, mannose, mannose (1:0.3); Fraction 2: mannose, glucose (1:0.2)              | Fraction 2: 400                                                        | [34, 36]    |
| *Methylococcus thermophilus* 111n     | 40 °C               | Methan             | 5                      | Fraction 1: mannose, galactose, glucose, fucose, xylose, rhamnose, glucuronic acid. Fraction 2: mannose, glucose, xylose, rhamnose | –                                                                       | [2]         |
| *Thermotoga maritima* DSM 3109        | 88 °C               | Maltose, 2        | 0.120                  | Glucose, ribose, mannose (1:0.06:0.03)                                                            | –                                                                        | [27]        |
| *Thermus aquaticus* YT-1              | 60 °C               | –                  | –                      | Galactofuranose, galactopyranose, N-acetylglucosamine (1:1:2)                                    | 500 Immunomodulatory activity; adjuvant to vaccines                       | [38]        |

*Note:* «—» — no data available.
HYD657 has an unusual component, a residue against irritation of sensitive skin [52]. Recommended for soothing and protection on the polysaccharide (deepsane). It is preparation Abyssine® was developed based on skin immune protection. Nowadays, cosmetic industry plays an important role in the system of human skin immune protection. The protective effect of EPS of strain HYD657 established that they efficiently protect keratinocytes from inflammation agents. The protective effect was also found towards Langerhans cells, which are sensitive to the ultraviolet and play an important role in the system of human skin immune protection. Nowadays, cosmetic preparation Abyssine® was developed based on the polysaccharide (deepsane). It is recommended for soothing and protection against irritation of sensitive skin [52].

Notably, the polysaccharide of strain HYD657 has an unusual component, a residue against irritation of sensitive skin [52]. Further research [51] of EPS of strain HYD657 established that they efficiently protect keratinocytes from inflammation agents. The protective effect was also found towards Langerhans cells, which are sensitive to the ultraviolet and play an important role in the system of human skin immune protection. Nowadays, cosmetic preparation Abyssine® was developed based on the polysaccharide (deepsane). It is recommended for soothing and protection against irritation of sensitive skin [52].

The strain Vibrio diabolicus HE800T was isolated from polychaete Alvinella pompejana. The strain produces a polysaccharide similar to hyaluronic acid [49]. The EPS is made up equally from glucuronic acid and hexosamines (N-acetylgalactosamine and N-acetylgalactosamine) [54]. The polysaccharide of strain HYD657 was found in EPS of the strain Alteromonas sp. HYD1644, isolated from the epidermis of the polychaete Alvinella caudata [46], and in drought-resistant cyanobacteria Nostoc commune DRH-1 [53]. Helm et al. [53] suggested that this and other uronic acids with carboxyethyl moieties play a key part in providing survival in unfavorable conditions. For example, such functional groups can help EPS attach to adjacent chains of the polymer, organic (biofilms) or inorganic surfaces, etc. The strain Vibrio diabolicus HE800T was isolated from polychaete Alvinella pompejana. The strain produces a polysaccharide similar to hyaluronic acid [49]. The EPS is made up equally from glucuronic acid and hexosamines (N-acetylgalactosamine and N-acetylgalactosamine) [54]. Treating damaged skullcap skin of Wistar rats with the EPS made the wound close sooner, while the trabecular and cortical anatomic structure of the defect fully recovered [55]. Zanchetta et al. [55, 56] suppose that the effect is caused by the ability of EPS to form extracellular matrix that helps direct adhesion of osteoblasts and pericytes, generally protect the damaged site while it heals, and to bind calcium.

Senni et al. [57] suggested that glycosaminoglycan polysaccharide of strain HE800T is a promising agent for various derivatives (heparan sulfate, chondroitin sulfate, etc.). Such depolymerization of native polysaccharide to molecular mass of 22 kDa with further deacetylation and sulfation (sulfate content 34%) resulted in a polymer similar to heparan sulfate. Those derivatives were observed to stimulate proliferation of dermal and gingival fibroblasts and inhibit secretion of matrix metalloproteinases [57]. The EPS of Alteromonas infernus GY785 after sulfation (sulfate content 40%) and controlled depolymerization by free radicals to molecular mass of 2 kDa substantially raised APTT (activated partial thromboplastin time) [58, 59]. The anticoagulant activity of the polysaccharide was on the level of calcium pentosan polysulfate though 2.3–6.5 times lower compared to heparin [58]. Notably, due to the low sulfate content in the native polysaccharide (5.5–10%) it did not have anticoagulant activity [58].

Recently the effect of depolymerized EPS of strains V. diabolicus HE800T and A. infernus GY785 on the complement system was studies [60]. The low molecular (2.9 kDa) derivative of the polysaccharide of strain HE800T to a large extent activated the system (60% activation at 50 μg EPS), while the depolymerized (molecular mass 23 kDa) and sulfated (sulfate content 37–42%) EPS of strain GY785, conversely, caused its significant inhibition (78% inhibition at 10 μg EPS). Due to those properties, the polysaccharides are promising for treating diseases caused by deregulation of immune system and over activation of the complement system.

Therefore, EPS of bacteria isolated from hydrothermal vents can become widely accepted into medical, pharmaceutical and cosmetic industries due to anticoagulant, protectant, immunomodulatory and regenerative activities. Notably, such microorganisms can synthesize up to 11 g/l of the product, and some polysaccharides from hydrothermal-dwelling bacteriae are already mass-produced. For example, EPS of A. macleodii subsp. fijiensis biovar deepsane HYD657 is used for cosmetics (Abyssine®).

Data on EPS of bacteria isolated from hydroterms are summarized in Table 2.

**Psychrophiles**

Cold environments are found from deep seas to snow-laden mountaintops, from Arctic to Antarctica. Temperature of almost 75–80% of the Earth surface is below 5 °C [60–62]. Cold habitats are characterized by frequent sharp changes in temperature (cycles of freezing and thawing, etc.), UV-radiation, nutrient concentration [63, 64]. Oceanic and sea waters also have pressure and salinity oscillations [21]. Evidently, microorganisms would not survive in such conditions without relevant adaptive mechanisms [62, 65, 66].

EPS play a large role in it. Exopolymers, including polysaccharides, take part in
Table 2. Exopolysaccharide synthesis by bacteria isolated from deep-sea hydrothermal vents

| Microbial source* | Carbon source, g/l | EPS content, g/l | Physico-chemical properties of EPS | Physiological effect, functional properties and possible implementations of the EPS | References |
|-------------------|--------------------|------------------|-----------------------------------|---------------------------------------------------------------------------------|------------|
| *Alteromonas infernus* GY785 | Glucose, 30 | Fraction 1: 5.5 Fraction 2: 4.3 | Fraction 1 (water-soluble): glucose, galactose, glucuronic and galacturonic acid (1.0:0.9:0.7:0.4). Sulfates 5.5–11% | Fraction 1: 1000 Anticoagulant, adsorbent | [44, 58, 59] |
| *Alteromonas macleodii* subsp. *fijiensis* ST716 | Glucose, 30 | 6 | Galactose, glucose, mannose, glucuronic and galacturonic acid (1.0:0.95:0.4:1.1:0.57). Sulfates 5% | 330 Thickener | [43] |
| *Alteromonas macleodii* subsp. *fijiensis* biovar deepsane HYD657 | Glucose, 30 | 7 | Galactose, glucose, rhamnose, fucose, mannose, glucuronic, galacturonic and 3-O-(1-carboxyethyl)-D-glucuronic acids (1.0:0.43:0.8 6:0.5:0.43:0.5:0.5:0.5). Sulfates 7.5% | 1100–1600 Protects keratinocytes and Langerhans cells from inflammation agents | [45, 51] |
| *Alteromonas macleodii* subsp. *fijiensis* var. medioatlantica MS907 | Glucose, 30 | 9 | Galactose, glucose, glucuronic and galacturonic acids (1.0:0.5:0.7:0.26) | 1500 Thickener | [50] |
| *Alteromonas sp.* HYD1545 | Glucose, 30 | 11 | Glucose, galactose, mannose, glucuronic and galacturonic acids (1.0:0.55:0.04:0.24:0.14) | 1800 – | [48] |
| *Alteromonas sp.* HYD1644 | Fructose, 40 | Fraction 1: 7.5 Fraction 2: 5.0 | Fraction 1 (water-soluble): galactose, glucose, rhamnose, mannose, glucuronic, galacturonic and 3-O-(1-carboxyethyl)-D-glucuronic acids (1.0:0.74:0.7:0.13:0.4:0.19:0.23) | Fraction 1: 5000 Thickener | [46, 47] |
| *Vibrio diabolicus* HE800† | Glucose, 40 | 2.5 | Glucuronic acid, N-acetylglucosamine, N-acetylgalactosamine (1:0.5:0.5) | 800–850 Raw material to obtain glycosaminoglycan derivatives. Fastens bone fusion | [49, 54–57] |
aggregation, adhesion to surfaces and other microorganisms, biofilm formation, nutrient storage, etc. in marine bacterial communities [66–68]. Often aggregates of salty drops remain unfrozen after the seawater freezes, and the microbes are trapped in salt canals [63, 66]. Then, EPS are cryoprotectants and protectants from high salinity [62, 65, 66].

The majority of microorganisms, able to survive at low temperature, are yeasts and bacteriae [8]. Notably, phylogenetic research also registers a lot of representatives of Archaea [61], although they have not been cultured.

**Fungi.** EPS synthesis by fungi at relatively low temperatures is a novel approach. The first report of polysaccharide production by cryotolerant mycelial fungi appeared only at the beginning of XXI century. In 2002, Selbmann et al. [69] established the ability of Phoma herbarum CCFEE 5080 cultured on medium containing sorbitol (60 g/l) to produce 13.4 g/l 17412 kDa glucan. Due to cryoprotectant properties of the polysaccharide, strain CCFEE 5080 is able to grow at 0–5 °C (optimal temperature 28°C) [70].

Another glucan-producing fungus is strain *Thelebolus* sp. IITKGP-BT12 [68]. Unlike the strain CCFEE 5080, at 18 °C it synthesizes only 1.94 g/l EPS. Experiments have shown that the glucan has significant antiproliferative effect on cells of skin cancer in B16-F0 mice. IC50 (the concentration at which maximal inhibition occurred) of the EPS was 275.4 μg/ml. The polysaccharide had almost no effect on normal fibroblasts of the L929 line (at the concentration of 187.5–1500 μg/ml cytotoxicity was almost absent) [67].

Recently, isolation of EPS-synthesizing cryotolerant yeasts of the genera *Sporobolomyces* [71] and *Cryptococcus* [72–74] was reported from Livingstone Island. Cultivation in medium with sucrose (40–50 g/l) and ammonium sulfate (0.25%) at 22–24 °C resulted in 4.6–6.4 g/l of polysaccharides (Table 3).

Research of economically valuable properties of EPS of yeasts from the Livingstone Island confirmed their possible use in cosmetics, food industry [73, 75, 76] and medicine [78]. EPS of strain *Cryptococcus laurentii* AL100 exhibited high emulgent activity, significantly enhanced by other polysaccharides (xanthan, guar gum, cellulose, etc.) [73].

Other researchers showed that cosmetic emulsions with 2% EPS *Sporobolomyces salmonicolor* AL1 remained stable for a month at –10 °C and for 3 months at 22 and 45 °C [75, 76]. To achieve similar results, concentration of synthetic emulgent Arlacel 165 or Rofetan N/NS was 5% [75]. Besides that, EPS of *S. salmonicolor* AL1 has anticytostatic activity. At 5 ppm it changed LD50 of (cytostatic) avarol from 0.18 to 0.10 ppm [77].

EPS of cryotolerant fungi can be used as emulgents and thickeners in food and cosmetic practices at low temperatures. They are promising for medicine and pharmacy due to antitumor and anticytostatic activities.

**Bacteria.** Reports of EPS synthesis by cryophilic and cryotolerant bacteriae started shortly after the first study about polysaccharides of cryotolerant fungi [69].

Polysaccharides of cryotolerant bacteriae isolated from free ice and marine aggregates in the Antarctic ocean, with *in situ* temperature of 4 °C were described in 2005 [78]. Six of the studied isolates belonged to the genus *Pseudoalteromonas*, three to the genera *Shewanella*, Polaribacter, and Flavobacterium. A strain CAM0301 represented the family *Flavobacteriaceae*, later it became a new taxon *Olleya marilimosa* [79]. Most cryophilic bacterial producers isolated after 2005 belong to the genera *Pseudoalteromonas*, Polaribacter and Flavobacterium (Table 3).

By their monosaccharide content, the polysaccharides of cryophilic bacteriae are similar to EPS of marine bacteriae (Table 2).

Lowering the growth temperature from 20 to 10, or to –2 °C caused an almost 30-fold rise in EPS-producing ability of strain *Pseudoalteromonas* sp. CAM025 (up to 99.9 and 97.2 mg EPS/g biomass, respectively), and a changed monosaccharide ratio [80].

Cryoprotectant properties of EPS of *Pseudoalteromonas* sp. SM20310 were studied in [63]. At 30 mg/ml EPS the number of living cells of strain SM20310 and *E. coli* DH5α was 7 to 18 times as high as in the control group (without EPS) after three cycles of freezing-thawing. Other researchers [68] report that adding the polysaccharide of cryotolerant bacteriae *Flavobacterium* sp. ASB 3–3 at 50 mg/ml led to a four times increase in the number of living cells of strains ASB 3–3 and *E. coli* DH5α after two cycles of freezing-thawing compared to the cultures without EPS.

Cryotolerant bacteriae *Pseudoalteromonas elyakovii* ArcPo 15 isolated from Chukchi Sea were observed to synthesize 1.7 MDa EPS with high cryoprotectant activity [81]. Adding the
EPS (0.5%) to a suspension of *E. coli* DH5α resulted in 94.2% survival of the cells after five cycles of freezing-thawing. Adding 20% glycerin resulted in 54.1% survival of the cells.

Due to the cryoprotectant ability of bacterial EPS we suggest using them as alternative cryoprotectant agents for long-term storage of suspended cultures [82, 83].

According to Carrión et al. at 10% EPS of *Pseudomonas* sp. ID1, survival of *E. coli* ATCC 10536 after freezing and storing for seven days at −20 and −80 °C was 36 and 64%, respectively [82]. Cell survival decreased at lower EPS concentrations. After similar freezing of EPS-synthesizing strain ID1, the cell survival rates were 75 and 94%, respectively. Another study [84] showed that EPS of cryophilic *Colwellia psychrerythraea* 34H are a better cryoprotectant agent for freezing cells at –80 °C than 10% glycerin solution.

Notably, cryoprotectant properties of polysaccharides are not limited to merely the protection of microbial cells. Sun et al. [84] reported that, survival rate of human dermal fibroblasts after 20 hours at 4 °C reached 76.1% with 500 μg/mg EPS of *Polaribacter* sp. SM1127, while without the polysaccharide it was only 44.2%.

In the native environment, other physico-chemical factors besides temperature can induce EPS synthesis, such as pressure and salinity [63, 83]. For example, culturing *C. psychrerythraea* 34H at high hydrostatic pressure (up to 400 atm) resulted in EPS content increasing 4.5–7.5 times.

Polysaccharides of cryophilic and cryotolerant bacteria can also hold moisture [84, 85], emulsify [82, 68, 86], flocculate [68, 86] and adsorb metal [86, 87].

Research of EPS of bacterial strains *Polaribacter* sp. SM1127 and *Zunongwangia profunda* SM-A87 [84, 85] showed that after 72 hours of incubation with silica gel (relative humidity 43%) the polysaccharide of strain SM1127 retained 76% moisture, which is higher than for hyaluronic acid, glycerin, sodium alginate. This is possibly due to not only a lot of glucuronic acid and N-acetylglucosamine (components of hyaluronic acid), but also fucose, which has moisturizing properties, in EPS [84]. The polysaccharides also have antioxidant activity [84, 85]. Thus, the level of neutralization of 2,2-diphenyl-1-picrylhydrazyl radical radical (DPPH·), hydroxyl radical (−OH) and superoxide anion (O₂·) at 10 mg/ml of EPS of SM1127 and SM-A87 10, was 27.2–55.4%. Further research [87] established the ability of EPS of strain SM-A87 to adsorb Cu²⁺ and Cd²⁺ (48 and 39.75 mg/g EPS, respectively).

After optimization of the culture medium [88] in the fed-batch culture [85], the concentration of EPS of strain *Z. profunda* SM-A87 increased to 17 g/l, which is 1.93 times higher compared to the initial.

Recently Sathiyanarayanan et al. [68, 86] isolated cryotolerant *Flavobacterium* sp. ASB 3–3 and *Pseudomonas* sp. PAMC 28620 (AS-06/29) from the soil of Svalbard Arctic glacier fore-field. The optimal carbon and energy source for those bacteriae, unlike other microbial sources of EPS (Table 3) is glycerin. At the medium with 30 g/l of this substrate, the bacteriae produced 7.25 g/l EPS with flocculant and emulgent properties.

In kaolinite suspension (0.5%), flocculant activity of 40 mg/l EPS for strains PAMC 28620 and ASB 3-3 70 was 71.2 and 91.3%, respectively [68, 86]. The polysaccharide of strain ASB 3-3 emulsified n-hexane (emulsification index 66.3%) and n-hexadecane (64.3%) just as efficiently as sodium dodecyl sulfate [68]. EPS of strain PAMC 28620 efficiently emulsified toluene (67.2%) and methyl octanoate (66.7%) [86]. Besides that, polysaccharide of strain PAMC 28620 expediently adsorbed Cu²⁺ and Cd²⁺ (48 and 39.75 mg/g EPS, respectively).

Unlike thermophilic and thermotolerant sources (Table 1 and Table 2), cryophilic and cryotolerant microorganisms synthesize more EPS (up to 17 g/l; Table 3), and their polysaccharides have cryoprotectant, emulsifying properties, retain moisture and adsorb heavy metals. That, consequently, makes the polysaccharides potentially attractive for various fields from food industry (foodstuffs storage) and cosmetics (production of protective cosmetics) to environment-friendly technology (purification of waste waters).

**Halophiles**

Halophiles are organisms able to survive in briny habitats, whose development requires salt. The salt in question is generally NaCl, while many researchers in their experiments on halophilic cultures use sea salt which contains not only NaCl but also comparatively small amounts of other salts of two- and monovalent metals [89].
Table 3. EPS synthesis by cryophilic and cryotolerant microorganisms

| Microbial source                  | Incubation temperature | Carbon source, g/l | EPS concentration, g/l | Physico-chemical properties of EPS | Physiological effect, functional properties and possible avenues of implementation of EPS | References |
|-----------------------------------|------------------------|--------------------|------------------------|-----------------------------------|-----------------------------------------------------------------------------------|------------|
| **EPS of cryotolerant fungi**     |                        |                    |                        |                                   |                                                                                   |            |
| Cryptococcus flavus AL51          | 24°C                   | Sucrose, 50        | 5.75                   | Mannose, glucose, xylose, galactose (1:0.47:0.17:0.03:0.08) | 1010                                                                               | [72]       |
| Cryptococcus laurentii AL62       | 22°C                   | Sucrose, 40/50     | 4.73/4.6               | Xylose, mannose, glucose (1:0.74:0.41) | 8                                                                                 | [74]       |
| Cryptococcus laurentii AL100      | 22°C                   | Sucrose, 40        | 6.4                    | Arabinose, mannose, glucose, galactose, rhamnose (1:0.25:0.2:0.1:0.05) | 4.2                                                               | Emulgent   | [73]       |
| Phoma herbarum CCFEE 5080         | 28°C                   | Sorbitol, 60       | 13.4                   | Glucan (glucose 100%)             | 7412                                                                            | Cryoprotectant | [69]       |
| Sporobolomyces salmonicolor AL1   | 22°C                   | Sucrose, 50        | 5.2–5.6                | Mannose, glucose, galactose       | >1000                                                                           | Thickener, emulgent | [71, 75–77] |
| Thelebolus sp. IITKGP-BT12        | 18°C                   | Glucose, 50        | 1.94                   | Glucan (glucose 100%)             | 500                                                                             | Antiproliferative activity | [67]       |
| **EPS of cryophilic and cryotolerant bacteria** |                        |                    |                        |                                   |                                                                                   |            |
| Flavobacterium sp. ASB 3-3        | 25°C                   | Glycerin, 30       | 7.25                   | Glucose, galactose (1:0.43). Sulfates were found | –                                                                              | Emulgent, flocculant, cryoprotectant | [68]       |
| Polaribacter sp. SM1127           | 15°C                   | Glucose, 30        | 2.11                   | N-acetylglucosamine, mannose, glucuronic acid, galactose, fucose, glucose, rhamnose (1:0.84:0.76:0.62:0.26:0.06:0.03) | 220 | Cryoprotectant, moisture-retention agent, antioxidant | [84]       |
| Pseudoalteromonas elyakovii ArcPo 15 | 15°C              | Glucose, 20        | 1.64                   | Mannose, galacturonic acid (3.3:1.0) | 17000                                                                 | Cryoprotectant | [81]       |
| Pseudoalteromonas sp. CAM025      | 10°C                   | Glucose, 30        | 99.9 mg/g biomass      | Glucose, galactose, rhamnose, mannose, fucose, arabinose, ribose, glucuronic acid (1:0.64:0.61:0.31:0.25:0.12:0.05:0.26). Sulfates 5% | 5700 | Cryoprotectant | [80]       |
As to salinity, halophiles can be halotolerant (upper salinity limit 15%), weak (NaCl content of 2–5%), moderate (5–5%) and extreme halophiles (20–30%) [16]. Usually, they can be found in various saline habitats such as salt lakes, salt evaporation ponds, saline soils, mines, food products, saline mud, etc. [21, 90]. Traditional halophilic sources are salterns, which usually have high salt content and intensive sunlight [90–95].

Archaea. Main papers on polysaccharide synthesis by halophilic archaea include research on isolation of new producers [94, 96], EPS structure [97–99], and the possibilities of their practical application [96].

In 1988, Antóñ et al. [96] established that extremely halophilic archaea Haloferax mediterranei ATCC 33500 cultured on a medium with 1% glucose and 25% sea salt produced 3 g/l of sulfated high molecular polysaccharide. Viscosity of EPS solutions was stable in wide ranges of pH, temperature and salinity. Hence EPS of strain ATCC 33500 can be utilized in increasing oil production from wells with high salt content. Later, researchers established the structure of repeating sequences of EPS strain ATCC 33500 [98] and other EPS-synthesizing archaea, in particular Haloferax gibbonsii ATCC 33959 [97] and Haloferax denitrificans ATCC 35960 [99].

At the end of the twentieth century, for new producers of polyhydroxyalkanoates and EPS, Nicolaus et al. [94] isolated three obligate halophilic strains Т5, Т6 and Т7, which synthesized 35–370 mg/l EPS, from the salt works of Tunisia. The isolates belonged to the genus Haloarcula. Among halophilic EPS-synthesizing archaea, in particular Haloferax mediterranei ATCC 33500 [97] and other EPS-synthesizing archaea, in particular Haloarcula mediterranei ATCC 33560 [99], research on polysaccharide synthesis by halophilic archaea after that, until a recent publication [90], is limited. Despite the fact that halophilic archaea are able to produce polysaccharides at salinities up to 20–30% (NaCl), the concentration of EPS in these organisms is usually below 1% of cell dry weight. Hence, research on isolation of new producers of EPS, especially those that can produce polysaccharides at moderate salinities (15–20%), is important. EPS structure [97–99], physiological effect of EPS on microbial growth, and the possibilities of their practical implementation [96] are among the main topics of recent research on this subject. The isolation of new EPS-producing halophilic archaea and bacteria is an urgent task for the development of new technologies for producing polysaccharides from renewable resources.
was not toxic for Huh7 human hepatocytes.

The polysaccharide of NaCl to 2.5% was followed by increased EPS production to 7.87 g/l [90]. The polysaccharide of strain S-30 to 3.8 g/l [103]. Further optimization of cultivation medium (reducing sea salt concentration, instead adding 2.5% NaCl and 0.05% MgCl₂·6H₂O) increased EPS production to 7.87 g/l [90]. The polysaccharide of strain S-30 resulted in 100% inhibition of leukemia line Jurkat (500 μg/ml sEPS of strain S-30) and 99% inhibition of T-cells of acute lymphoblast leukemia line Jurkat (500 μg/ml sEPS of strain S-30) [110]. Further studies aimed to lower the production cost of the target product by using various molasses instead of sucrose in the EPS biosynthesis medium [105]. EPS concentration reached 7.56 g/l (12.4 g/l after 210 hours of cultivation) in culture medium with beet pre-treated with calcium phosphate, sulfate acid and activated carbon. In culture medium with likewise pre-treated starch molasses (a side product of manufacturing dextrose from starchy materials) it was 4.38 g/l. Using starch molasses as a substrate resulted in levan with high emulgent activity [111]. Levan of strain AAD⁶T was shown to be useful in targeted delivery of drugs, in particular, of antibiotic vancomycin [118]. It also increased LD₅₀ of avarol from 0.18 ppm to 10 ppm [95]. Anticoagulant activity of artificially sulfated derivatives of that EPS was studied in [119].

Ruiz-Ruiz et al. [110] studied antitumor properties of polysaccharides of halophilic bacteria Halomonas stenophila B100 and N12³T. Artificially sulfated EPS (sEPS) of strains B100 and N12³T (sulfate content 23 and 17%, respectively) efficiently decreased proliferation of T-cells of acute lymphoblast leukemia line Jurkat (500 μg/ml sEPS of strain B100 resulted in 100% inhibition of cell proliferation). Only sEPS of strain B100 induced apoptosis of tumour cells (lines CEM, MOLT-4, HPB-ALL, etc.), while healthy T-cells resisted the apoptosis induction [111]. Authors considered that antitumor effect to directly depend on the concentration of sulfates. It was suggested that sulfates change the charge of polymer molecule to negative and affect its structure, increasing the interaction between EPS and the target cell surface [110].

Bacteriae of the genus Halomonas are not only moderately halophilic producers of polysaccharides. A strain isolated from the hypersaline soil of solar saltern (Spain), Salipiger mucosus A3³ (sEST 5855³) cultured in early 1990s, reports were published on the synthesis of sulfated polysaccharide (2.8 g/l) by moderately halophilic bacteriae Volcaniella eurihalina F2-7 [104, 109] (now Halomonas eurihalina [114]).

Soon, wide-scale screening of possibly halophilic producers isolated from solar salterns in Morocco was published [92]. Thirty two isolates of the genus Halomonas were selected for a more detailed analysis out of more than 500 isolates. Only four of them accumulated over 2 g/l polysaccharide, and the highest amount (2.8 g/l) was produced by strain S-30. According to phylogenetic analysis, the strain and isolates S-7, S-3¹ and S-36 were combined into a new species Halomonas maura [115]. Further optimization of the cultivation medium (reducing sea salt concentration, instead adding 2.5% NaCl and 0.05% MgCl₂·6H₂O) increased EPS production of strain S-30 to 3.8 g/l [103].

Strain Halomonas xianhensis SUR308, isolated from soil of a solar saltern (India) [90, 91], on a medium with glucose (1%) and NaCl (10%) produced 2.56 g/l EPS [91]. Further increase of glucose content to 3% and decrease of NaCl to 2.5% was followed by increased EPS production to 7.87 g/l [90]. The polysaccharide was not toxic for Huh7 human hepatocytes.
for 72 hours in a medium with 1% glucose and 7.5% sea salt produced 1.35 g/l EPS [93]. Approximately the same amount of EPS (1–1.5 g/l) was obtained from strains Idiomarina fontislapidosi F23^T, Idiomarina ramblicola R22^T and Alteromonas hispanica F32^T isolated similarly from hypersaline habitats [111]. Unlike these bacteriae, strain Halobacillus trueperi AJSK produced almost 13 g/l EPS on an optimized medium [112].

Many polysaccharides of moderate halophilic organisms can adsorb cations of various metals [93, 103, 106, 111, 117] (Table 4), emulsify carbohydrates, vegetable and mineral oils [91, 93, 102, 103, 106, 111, 117] (Table 5). Besides that, EPS of Halomonas

### Table 4. Adsorption of metal cations by polysaccharides of halophilic bacteriae

| EPS-producing microbe | Adsorption rate, mg/g EPS | References |
|-----------------------|---------------------------|------------|
|                       | Cu^{2+} | Pb^{2+} | Co^{2+} |          |
| Alteromonas hispanica F32^T | 6.95 | 30 | 4 | [111] |
| Halomonas almeriensis M8^T | 19.2 | 24.5 | 10 | [106] |
| Halomonas anticariensis FP35^T | 26.6 | 26.3 | 10.5 | [117] |
| Halomonas anticariensis FP36 | 28.1 | 25.15 | 10.5 | [117] |
| Halomonas maura S-30 | 4.24 | 46.4 | 0.72 | [103] |
| Halomonas ventosae A112^T | 12 | 24.8 | 2.5 | [117] |
| Halomonas ventosae A116 | 27.6 | 25.7 | 10 | [117] |
| Idiomarina fontislapidosi F23^T | 16.3 | 40 | 8 | [111] |
| Idiomarina ramblicola R22^T | 26.25 | 44.65 | 10 | [111] |
| Salipiger mucosus A3^T | 15.7 | 43.5 | 8.7 | [93] |

### Table 5. Emulsifying properties of polysaccharides of halophilic bacteriae

| EPS-producing microbe | Emulsifying index,% | References |
|-----------------------|---------------------|------------|
|                       | Oil: sunflower, olive, mineral | Tetra-decane, Octane, Kerosene |          |
| Alteromonas hispanica F32^T | 55, 40, 50 | 50, 55, 67.5 | [111] |
| Halomonas almeriensis M8^T | 65, 67.5, 67.5 | 62.5, 65 | 65 | [106] |
| Halomonas anticariensis FP35^T | 47.5, 40, 47.5 | 45, 45 | – | [117] |
| Halomonas anticariensis FP36 | 37.5, 42.5, 50 | 55, 42.5 | – | [117] |
| Halomonas stenophila HK30 | 70, 85, 55.8 | 41, 56.7, 80 | [102] |
| Halomonas ventosae A112^T | 51, 42.8, 35.5 | 57.5, 57.5 | – | [117] |
| Halomonas ventosae A116 | 60, 55, 62.5 | 60, 60 | – | [117] |
| Halomonas xianhensis SUR308 | –, 71.3, – | 80.3, 76.3 | – | [91] |
| Idiomarina fontislapidosi F23^T | 65, 60, 62.5 | 45, 60 | 55 | [111] |
| Idiomarina ramblicola R22^T | 60, 65, 62.5 | 55, 60 | 62.5 | [111] |
| Salipiger mucosus A3^T | 70, 60.3, 71 | 75, 70 | 70 | [93] |
| Control | 62.5–67.5, 60–62.5, 60–67.5, 62.5–65, 60–62.5, 60–62.2 | | [91, 93, 102, 106, 111, 117] |
| Triton X-100 | 62.5–67.5, 60–62.5, 60–67.5, 62.5–65, 60–62.5, 60–62.2 | | [91, 93, 102, 106, 111, 117] |
| Tween 80 | 62, 61.5–62.5, 60–70, 60–62.5, 60, 60 | | [91, 93, 102, 106, 111, 117] |
| Microbial source | Salt content | Carbon source, g/l | EPS content, g/l | Physico-chemical properties of EPS | Physiological effect, functional properties, possible avenues of implementation of EPS | References |
|------------------|--------------|--------------------|------------------|-----------------------------------|--------------------------------------------------------------------------------------------|------------|
| **EPS of halophilic archaea** | | | | | | |
| *Haloarcula sp. T6* | NaCl, 200 g/l | Glucose, 6 | 0.045 | Mannose, galactose and glucose (1:0.2:0.2) | – | [94] |
| *Haloarcula sp. T7* | NaCl, 200 g/l | Glucose, 6 | 0.035 | Mannose, galactose and glucose (1:0.2:0.2) | – | [94] |
| *Haloarcula japonica* | NaCl, 200 g/l | Glucose, 6 | 0.37 | Glucuronic acid, mannose and galactose (3:2:1) | – | [94] |
| *Halobacterium volcanii* | NaCl, 156 g/l | Galactose, 10 | 0.3 | Mannose, Hexuronic acids present. Sulfates 0.6% | – | [100] |
| *Halofex mediterranei* | Sea salt, 25% | Glucose, 10 | 3 | Mannose, glucose, galactose. Sulfates 6% | >100 | Thicker, intensification of oil production | [96] |
| *Haloterrigena turkmenica* | NaCl, 200 g/l | Glucose, 10 | 0.207 | Glucose, glucosamine, glucuronic acid, galactose, galactosamine (1:0.65:0.24:0.22:0.02). Sulfates 2.8% | Fractions 1-3: 801.7; 206; 37.6 | Emulgent, antioxidant, moisture retention agent | [101] |
| **EPS of moderately halophilic bacteriae** | | | | | | |
| *Alteromonas hispanica* | Sea salt (7.5%) | Galactose, 10 | 1.25 | Mannose, glucose, xylose (1:0.29:0.11). Sulfates 0.25% | 19000 | Biofilm formation. Emulgent, adsorbent | [111] |
| *Halobacillus trueperi* | NaCl (61.56 g/l) | Glucose, 22,2 | 12.93 | – | – | – | [112] |
| *Halomonas alkaliantarctica* CRSS | NaCl (100 g/l) | Sodium citrate, 3 | 2.9 g EPS/g biomass | Mannose, xylose, glucose, galactosamine, fructose, rhamnose, not indentified component (1:0.7:0.3:0.2:traces:traces:0.3) | – | Thickener | [64, 108] |
| *Halomonas almeriensis* M8* | Sea salt (7.5%) | Glucose, 10 | 1.7 | Fraction 1: mannose, glucose, rhamnose (1:0.38:0.01); Fraction 2: mannose, glucose (1:0.97). Sulfates 1.4% | Fraction 1: 6500; Fraction 2: 15 | Emulgent, adsorbent | [106] |
| *Halomonas anticariensis* PP35* | Sea salt (7.5%) | Glucose, 10 | 345.5 mg/l | Mannose, galacturonic acid, glucose (1:0.82:0.38). Sulfates 0.73% | 20 | Biofilm formation. Emulgent, adsorbent | [117] |
| *Halomonas anticariensis* FP36 | Sea salt (7.5%) | Glucose, 10 | 0.386 | Mannose, galacturonic acid, glucose (1:0.87:0.4). Sulfates 1.16% | 46 | Biofilm formation. Emulgent, adsorbent | [117] |
| *Halomonas eurhithina* F2-7 | Sea salt (7.5%) | Glucose, 10 | 2.8 | Glucose, mannose, rhamnose (molar ratio 2.9:1.5:1). Sulfates 2.7% | – | Thicker, emulgent, intensification of oil production | [104, 109] |
| Microbial source | Salt content | Carbon source, g/l | EPS content, g/l | Physio-chemical properties of EPS | Molecular mass, kDa | Physiological effect, functional properties, possible avenues of implementation of EPS | References |
|-----------------|--------------|-------------------|-----------------|----------------------------------|-------------------|---------------------------------------------------------------------------------|------------|
| *Halomonas maura* S-30 | Sea salt / NaCl (2.5%) | Glucose, 10 | 3.8 | Mannose, galactose, glucose, glucuronic acid (1:0.4:0.84:0.63). Sulfates 6.5% | 4700 | Emulgent, thickener; adsorbent | [92, 103] |
| *Halomonas smyrnensis* AAD6<sup>T</sup> | NaCl (137.2 g/l) | Sucrose, 50 | 1.84–8.84 | Fructose (levan) | >1000 | Flocculant [118]; targeted drug delivery [119], anticoagulant [120]; anticytotoxic activity | [95, 116] |
| *Halomonas stenophila* B100 | Sea salt (7.5%) | – | – | Glucose, galactose, mannose (1:0.91:0.34). Sulfates 7.9% | 375 | Antitumor activity | [110] |
| *Halomonas stenophila* HK30 | Sea salt (5%) | Glucose, 10 | 3.89 | Glucose, glucuronic acid, mannose, fucose, galactose, rhamnose (1:0.3:5.5:0.23:0.19:0.02) | Fraction 1: 1400; Fraction 2: 82 | Biofilm formation. Thickener, emulgent; flocculant | [102] |
| *Halomonas stenophila* N12<sup>T</sup> | Sea salt (7.5%) | – | – | Glucose, mannose, fucose (1:0.52:0.53). Sulfates 2.45% | 250 | Antitumor activity | [110] |
| *Halomonas ventosae* A112<sup>T</sup> | Sea salt (7.5%) | Glucose, 10 | 283.5 mg/l | Mannose, glucose, galactose (1:0.43:0.25). Sulfates 1.09% | 53 | Biofilm formation. Emulgent, adsorbent | [117] |
| *Halomonas ventosae* A116 | Sea salt (7.5%) | Glucose, 10 | 289.5 mg/l | Mannose, glucose, galactose (1:0.42:0.22). Sulfates 0.71% | 52 | Biofilm formation. Emulgent, adsorbent | [117] |
| *Halomonas xianhensis* SUR308 | NaCl (10% / 2.5%) | Glucose, 10 / 30 | 2.56 / 7.87 | Glucose, galactose, mannose, xylose, ribose (1:0.74:0.39:0.04:0.02) | – | Thickener, emulgent, antioxidant | [90, 91] |
| *Idiomarina fontispaladisi* F23<sup>T</sup> | Sea salt (7.5%) | Glucose, 10 | 1.45 | Fraction 1: mannose, glucose, galactose, xylose (1:0.61:0.32) | Fraction 1: 1500; Fraction 2: 15 | Biofilm formation, emulgent, adsorbent | [111] |
| *Idiomarina ramblicola* R22<sup>T</sup> | Sea salt (7.5%) | Glucose, 10 | 1.5 | Fraction 1: mannose, glucose, rhamnose (1:0.37:0.1); Fraction 2: mannose, glucose, galacturonic acid, rhamnose, xylose (1:0.35:0.47: traces). Sulfates 0.5% | Fraction 1: 550; Fraction 2: 20 | Biofilm formation. Emulgent, adsorbent | [111] |
| *Salipiger mucosus* A3<sup>T</sup> | Sea salt (2.5–7.5%) | Glucose, 10 | 1.35 | Mannose, galactose, glucose, fucose (1:0.97:0.58:0.39). Sulfates 0.9% | 250 | Emulgent, adsorbent | [93] |
polysaccharides is limited by the low efficiency of production. Non-traditional sources produce EPS in much lower concentrations than the traditional ones. In our opinion, solving this problem is only a question of time, because various approaches to metabolic and gene engineering for microbial synthesis intensification are already developed [88, 112, 120–122].

EPS biosynthesis by non-traditional sources currently requires expensive carbohydrate materials (glucose, fructose, sucrose, and maltose) (Tables 1–3, 6). At the same time, many new studies aim to substitute carbohydrate substrates with cheap industrial wastes (whey, crude glycerin, oil-containing wastes, and agricultural wastes) in culturing traditional producers of polysaccharides. Those approaches to microbial polysaccharide production are reviewed in [123]. We demonstrated that it is possible to obtain microbial EPS ethapolan using fried vegetable oil [124] and its mixture with molasses [125].

REFERENCES

1. Donot F., Fontana A., Baccou J. C., Schorr-Galindo S. Microbial exopolysaccharides: main examples of synthesis, excretion, genetics and extraction. Carbohydr. Polym. 2012, 87 (2), 951–962. https://doi.org/10.1016/j.carbpol.2011.08.083.

2. Grinberg T. A., Pirog T. P., Malashenko Yu. R., Pinchuk G. Microbial synthesis of exopolysaccharides on C1–C2–compounds. Kyiv: Naukova dumka. 1992, 212 p. (In Russian).

3. Pidgorsky V. S., Litinska G. O., Pirog T. P. Intensification of microbial synthesis technologies. Kyiv: Naukova dumka. 2010, 327 p. (In Ukrainian).

4. Freitas F., Alves V. D., Reis M. A. Advances in bacterial exopolysaccharides: from production to biotechnological applications. Trends Biotechnol. 2011, 29 (8), 388–398. https://doi.org/10.1016/j.tibtech.2011.03.008

5. Nwodo U. U., Green E., Okoh A. I. Bacterial exopolysaccharides: functionality and prospects. Int. J. Mol. Sci. 2012, 13 (11), 14002–14015. https://doi.org/10.3390/ijms131114002

6. Nicolaus B., Kambourova M., Oner E. T. Extrremophiles as sources of exopolysaccharides. Environ. Technol. 2010, 31 (10), 1145–1158. https://doi.org/10.1080/09593330903552094

7. Nicolaus B., Kambourova M., Oner E. T. Exopolysaccharides from extremophiles: from fundamentals to biotechnology. Environ. Technol. 2010, 31 (10), 1145–1158. https://doi.org/10.1080/09593330903552094

8. Nichols C. A., Guezenec J., Bowman J. P. Bacterial exopolysaccharides from extreme marine environments with special consideration of the southern ocean, sea ice, and deep-sea hydrothermal vents: a review. Mar. Biotechnol. (NY). 2005, 7 (4), 253–271. https://doi.org/10.1007/s10126-004-5118-2

9. Chi Z., Fang Y. Exopolysaccharides from marine bacteria. J. Ocean Univ. China. 2005, 4 (1), 67–74. https://doi.org/10.1007/s11802-005-0026-2

10. Poli A., Anzelmo G., Nicolaus B. Bacterial exopolysaccharides from extreme marine habitats: production, characterization and biological activities. Mar. Drugs. 2010, 8 (6), 1779–1802. https://doi.org/10.3390/md8061779

11. Guezenec J. Bacterial exopolysaccharides from unusual environments and their applications. The perfect slime: microbial extracellular polymeric substances (EPS). Fleming H. C., Neu T. R., Wingender J. (Ed.). IWA publishing. 2016, 155–152.

12. Barbara N., Gianluca A., Annarita P. Bacterial polymers produced by extremophiles: biosynthesis, characterization, and applications of exopolysaccharides. Extremophiles: sustainable resources and biotechnological implications. Singh O. V. (Ed.). John Wiley & Sons, Inc. 2012, 335–356. https://doi.org/10.1002/9781118394144.ch13

13. Molina I. J., Ruiz-Ruiz C., Quesada E., Bejar V. Biomedical applications of exopolysaccha-
ridges produced by microorganisms isolated from extreme environments. *Extremophiles: sustainable resources and biotechnological implications.* Singh O. V. (Ed.). John Wiley & Sons, Inc. 2012, 357–366. https://doi.org/10.1007/9781118394144.ch14

14. Quesada E., Béjar V., Ferrer M. R., Calvo C., Llamas I., Martínez-Checa F., Arias S., Ruiz-Garcia C., Pérez R., Martínez-Cánovas M. J., Moral A. Moderately halophilic, exopoly saccharide-producing bacteria. *Halophilic microorganisms.* Ventosa A. (Ed.). Springer, Berlin. 2004, 297–314. https://doi.org/10.1007/978-3-662-07656-9_22

15. Kambourova M., Radchenkova N., Tomova I., Bojadjieva I. Thermophiles as a promising source of exopolysaccharides with interesting properties. *Biotechnology of extremophiles. Grand challenges in biology and biotechnology, vol 1.* Rampelotto P. (Ed.). Springer, Cham. 2016, 117–139. https://doi.org/10.1007/978-3-319-13521-2_4

16. Kanekar P. P., Deshmukh S. V., Kanekar S. P., Dhakephalkar P. K., Ranjekar P. K. Exopolysaccharides of halophilic microorganisms: an overview. *Industrial biotechnology: sustainable production and bioresource utilization.* Thangadurai D., Sangeetha J. (Ed.). Apple Academic Press, 2016, 1–27.

17. Poli A., Finore I., Romano I., Gioiello A., Lama L., Nicolaus B. Microbial diversity in extreme marine habitats and their biomolecules. *Microorganisms.* 2017, 5 (2). https://doi.org/10.3390/microorganisms5020025

18. Poli A., Di Donato P., Abbamondi G. R., Nicolaus B. Synthesis, production, and biotechnological applications of exopolysaccharides and polyhydroxalkanoates by archaea. *Archaea.* 2011. https://doi.org/10.1155/2011/692535

19. Gientka I., Blażejak S., Stasiak-Różańska L., Chlebowska-Smigiels A. Exopolysaccharides from yeast: insight into optimal conditions for biosynthesis, chemical composition and functional properties — review. *Acta Sci. Pol. Technol. Aliment.* 2015, 14 (4), 283–292. https://doi.org/10.17306/J.AFS.2015.4.29

20. Brock T. D. Life at high temperatures. Evolutionary, ecological, and biochemical significance of organisms living in hot springs is discussed. *Science.* 1967, 158 (3804), 1012–1019.

21. Charlesworth J., Burns B. P. Extremophilic adaptations and biotechnological applications in diverse environments. *AIMS Microbiol.* 2016, 2 (9), 251–261. https://doi.org/10.3934/microbiol.2016.3.251

22. Kambourova M., Mandeva R., Dimova D., Poli A., Nicolaus B., Tomonaro G. Production and characterization of a microbial glucan, synthesized by *Geobacillus tepidamans* V264 isolated from Bulgarian hot spring. *Carbohydr. Polym.* 2009, 77 (2), 338–343. https://doi.org/10.1016/j.carbpol.2009.01.004

23. Radchenkova N., Tomova A., Kambourova M. Biosynthesis of an exopolysaccharide produced by *Brevibacillus thermoruber* 438. *J. Biotechnol.* 2011, 25 (4), 77–79. https://doi.org/10.5504/BBEQ.2011.0115

24. Radchenkova N., Vassileev S., Panchev I., Anzelmo G., Tomova I., Nicolaus B., Kuncheva M., Petrov K., Kambourova M. Production and properties of two novel exopolysaccharides synthesized by a thermophilic bacterium *Aeribacillus pallidus* 418. *Appl. Biochem. Biotechnol.* 2013, 171 (1), 31–41. https://doi.org/10.1007/s12010-013-0348-2

25. Yasar Yildiz S., Anzelmo G., Ozer T., Radchenkova N., Genc S., Di Donato P., Nicolaus B., Toksoy Onur E., Kambourova M. *Brevibacillus thermoruber*: a promising microbial cell factory for exopolysaccharide production. *J. Appl. Microbiol.* 2014, 116 (2), 314–324. https://doi.org/10.1111/jam.12362

26. Nicolaus B., Manca M. C., Romano I., Lama L. Production of an exopolysaccharide from two thermophilic archaea belonging to the genus *Sulfolobus*. *FEMS Microbiol. Lett.* 1993, 109 (2–3), 203–206. https://doi.org/10.1111/j.1574-6968.1993.tb06168.x

27. Rinker K. D., Kelly R. M. Effect of carbon and nitrogen sources on growth dynamics and exopolysaccharide production for the hyperthermophilic archaeon *Thermococcus litoralis* and bacterium *Thermotoga maritima*. *Biotechnol. Bioeng.* 2000, 69 (5), 537–547. https://doi.org/10.1002/1097-0290(20000905)69:5<537::AID-BIT8>3.0.CO;2-7

28. Rinker K. D., Kelly R. M. Growth physiology of the hyperthermophilic archaeon *Thermococcus litoralis*: development of a sulfur-free defined medium, characterization of an exopolysaccharide, and evidence of biofilm formation. *Appl. Environ. Microbiol.* 1996, 62 (12), 4478–4485.

29. Sowers K. R., Gunsalus R. P. Adaptation for growth at various saline concentrations by the archaeabacterium *Methanoscina thermophila*. *J. Bacteriol.* 1988, 170 (2), 998–1002. https://doi.org/10.1128/jb.170.2.998-1002.1988

30. Koordeit A., Gödeke J., Berger J., Thormann K. M., Albers S. V. Crenarchaeal biofilm formation under extreme conditions. *PLoS One.* 2010, 5 (11). https://doi.org/10.1371/journal.pone.0014104

31. Arena A., Maugeri T. L., Pavone B., Iannello D., Gugliandolo C., Bisignano G. Antiviral and immunoregulatory effect of a novel exopolysaccharide from a marine thermotolerant *Bacillus licheniformis*. *Int. Immunopharmacol.* 2006, 6 (1), 8–13. https://doi.org/10.1016/j.intimp.2005.07.004
32. Mauger T. L., Gugliandolo C., Caccamo D., Panico A., Lama L., Gambacorta A., Nicolaus B. A halophilic thermotolerant Bacillus isolated from a marine hot spring able to produce a new exopolysaccharide. Biotechnol. Lett. 2002, 24 (7), 515–519. https://doi.org/10.1023/A:1014891431233

33. Spanò A., Gugliandolo C., Lentini V., Mauger T. L., Anzelmo G., Poli A., Nicolaus B. A novel EPS-producing strain of Bacillus licheniformis isolated from a shallow vent off Panarea Island (Italy). Curr. Microbiol. 2013, 67 (1), 21–29. https://doi.org/10.1007/s00284-013-0327-4

34. Arena A., Gugliandolo C., Stassi G., Pavone B., Iannello D., Bisignano G., Mauger T. L. An exopolysaccharide produced by Geobacillus thermodenitrificans strain B3-72: antiviral activity on immunocompetent cells. ImmunoLett. 2009, 123 (2), 132–137. https://doi.org/10.1016/j.imlet.2009.03.001

35. Manca M. C., Lama L., Improta R., Esposito E., Gambacorta A., Nicolaus B. Chemical composition of two exopolysaccharides from Bacillus thermoantarcticus. Appl. Environ. Microbiol. 1996, 62 (9), 3265–3269.

36. Nicolaus B., Panico A., Manca M. C., Lama L., Gambacorta A., Mauger T. G., Gugliandolo C., Caccamo D. A thermophilic Bacillus isolated from an Eolian shallow hydrothermal vent, able to produce exopolysaccharides. Syst. Appl. Microbiol. 2000, 23 (3), 426–432. https://doi.org/10.1016/S0723-2020(00)80074-0

37. Zhao S., Cao F., Zhang H., Zhang L., Zhang F., Liang X. Structural characterization and biosorption of exopolysaccharides from Anoxybacillus sp. R4-33 isolated from radioactive radon hot spring. Appl. Biochem. Biotechnol. 2014, 172 (5), 2731–2746. https://doi.org/10.1007/s12010-013-0680-6

38. Lin M. H., Yang Y. L., Chen Y. P., Hua K. F., Lu C. P., Sheu F., Lin G. H., Tsay S. S., Liang S. M., Wu S. H. A novel exopolysaccharide from the biofilm of Thermus aquaticus YT-1 induces the immune response through Toll-like receptor 2. J. Biol. Chem. 2011, 286 (20), 17736–17745. https://doi.org/10.1074/jbc.M110.201113

39. Gugliandolo C., Spanò A., Lentini V., Arena A., Mauger T. L. Antiviral and immunomodulatory effects of a novel bacterial exopolysaccharide of shallow marine vent origin. J. Appl. Microbiol. 2014, 116 (4), 1028–1034. https://doi.org/10.1111/jam.12422

40. Spanò A., Lagano P., Visalli G., Mauger T. L., Gugliandolo C. In vitro antibiotic film activity of an exopolysaccharide from the marine thermophilic Bacillus licheniformis T14. Curr. Microbiol. 2016, 72 (5), 518–528. https://doi.org/10.1007/s00284-015-0981-9

41. Wang W., Wang S.-X., Guan H.-S. The antiviral activities and mechanisms of marine polysaccharides: an overview. Mar. Drugs. 2012, 10 (12), 2795–2816. https://doi.org/10.3390/md10122795

42. GuezenneC J. G., Pignet P., Raguenes G. Preliminary chemical characterization of unusual eubacterial exopolysaccharides of deep-sea origin. Carbohydr. Polym. 1994, 24 (4), 287–294. https://doi.org/10.1016/0144-8617(94)90073-6

43. Raguenes G., Pignet P., Gauthier G., Peres A., Christen R., Rougeaux H., Barbier G., GuezenneC J. G. Description of a new polymer-secreting bacterium from a deep-sea hydrothermal vent, Alteromonas macleodii subsp. fijensis, and preliminary characterization of the polymer. Appl. Environ. Microbiol. 1996, 62 (1), 67–73.

44. Raguenes G. H., Peres A., Ruimy R., Pignet P., Christen R., Loae C., Rougeaux H., Barbier G., GuezenneC J. G. Alteromonas infernus sp. nov., a new polysaccharide-producing bacterium isolated from a deep-sea hydrothermal vent. J. Appl. Microbiol. 1997, 82 (4), 422–430. https://doi.org/10.1046/j.1365-2672.1997.00125.x

45. Cembor Bonavita M. A., Raguenes G., Jean J., Vincent P., GuezenneC J. A novel polymer produced by a bacterium isolated from a deep-sea hydrothermal vent polychaete annelid. J. Appl. Microbiol. 2002, 93 (2), 310–315. https://doi.org/10.1046/j.1365-2672.2002.01689.x

46. Dubreucq G., Domon B., Fournet B. Structure determination of a novel uronic acid residue isolated from the exopolysaccharide produced by a bacterium originating from deep sea hydrothermal vents. Carbohydr. Res. 1996, 290 (2), 175–181. https://doi.org/10.1016/0008-6215(96)00155-3

47. Samain E., Milas M., Bozzi L., Dubreucq G., Rinaudo M. Simultaneous production of two different gel-forming exopolysaccharides by an Alteromonas strain originating from deep sea hydrothermal vents. Carbohydr. Polym. 1997, 34 (4), 235–241. https://doi.org/10.1016/S0144-8617(97)00129-X

48. Vincent P., Pignet P., Talmont F., Bozzi L., Fournet B., GuezenneC J., Jeantson C., Prieur D. Production and characterization of an exopolysaccharide excreted by a deep-sea hydrothermal vent bacterium isolated from the polychaete annelid Alvinella pompejana. Appl. Environ. Microbiol. 1994, 60 (11), 4134–4141.

49. Raguenes G., Christen R., GuezenneC J., Pignet P., Barbier G. Vibrio diabolicus sp. nov., a new polysaccharide-secreting organism isolated from a deep-sea hydrothermal vent polychaeta annelid, Alvinella pompejana. Int. J. Syst. Bacteriol. 1997, 47 (4), 989–995.
Guezennec J., Colliec-Jouault S., Sinquin C., Ratiskol J., Lutomski D., Godeau G., Senni K., Gueniche F., Changotad e S., Septier D., 2014. Exopolysaccharides isolated from hydrothermal vent bacteria can modulate the complement system. *PLoS One*. 2014, 9 (4). https://doi.org/10.3389/ijm.0094965

Cavicchioli R. Cold-adapted archaea. *Nat. Rev. Microbiol.* 2006, 4 (5), 331–343. https://doi.org/10.1038/nrmicro1390

De Maayer P., Anderson D., Cary C., Cowan D. A. Some like it cold: understanding the survival strategies of psychrophiles. *EMBO Rep.* 2014, 15 (5), 508–517. https://doi.org/10.1002/embr.201383170

Martins A., Vieira H., Gaspar H., Santos S. Structured and fibroblast activities in engineered connective tissues. *Acta. Biomater.* 2006, 3 (4), 595–609. https://doi.org/10.1016/j.actbio.2006.05.003

Raguéne G., Cambon-Bonavita M. A., Lo- hier J. F., Boisset C., Guezennec J. A novel, highly viscous polysaccharide excreted by an *Alteromonas* isolated from a deep-sea hydrothermal vent shrimp. *Curr. Microbiol.* 2003, 46 (6), 448–452. https://doi.org/10.1007/s00284-002-3922-3

Thibodeau A., Takeoka A. The applications and functions of new exopolysaccharide “Deepsane” from the deepest oceans. *Fragr. J.* 2006, 34 (3), 61–68.

Martins A., Vieira H., Gaspar H., Santos S. Marketed marine natural products in the pharmaceutical and cosmecutical industries: tips for success. *Mar. Drugs* 2014, 12 (2), 1066–1101. https://doi.org/10.3390/md12021066

Helm R. F., Huang Z., Edwards D., Leeson H., Peery W., Potts M. Structural characterization of the released polysaccharide of desic- cation-tolerant *Nostoc commune* DRH-1. *J. Bacteriol.* 2000, 182 (4), 974–982.

Rougeaux H., Kervarec N., Pichon R., Guezennec J. Structure of the exopolysaccharide of *Vibrio diabolicus* isolated from a deep-sea hydrothermal vent. *Carbohydr. Res.* 1999, 322 (1–2), 40–45. https://doi.org/10.1016/S0008-6215(99)00214-1

Zanchetta P., Lagarde N., Guezen nec J. A novel, biocompatible acid-like bacterial exopolysaccharide. *Calcif. Tissue Int.* 2003, 72 (1), 74–79. https://doi.org/10.1007/s00223-001-2091-x

Zanchetta P., Lagarde N., Guezennec J. Systemic effects on bone healing of a new hyaluronic acid-like bacterial exopolysaccharide. *Calcif. Tissue Int.* 2003, 73 (3), 232–236. https://doi.org/10.1007/s00223-002-2081-7

Senni K., Gueniche F., Changotade S., Septier D., Sinquin C., Ratischol J., Lutomski D., Godeau G., Guezennec J., Colliec-Jouault S. Unusual glycosaminoglycans from a deep-sea hydrothermal bacterium improve fibrillar collagen structuring and fibroblast activities in engineered connective tissues. *Mar. Drugs* 2013, 11 (4), 1351–1369. https://doi.org/10.3390/md11041351

Colliec Jouault S., Chevolot L., Helley D., Ratischol J., Bros A., Sinquin C., Roger O., Fischer A. M. Characterization, chemical modifications and in vitro anticoagulant properties of an exopolysaccharide produced by *Alteromonas infernus*. *Biochim. Biophys. Acta.* 2001, 1528 (2–3), 141–151. https://doi.org/10.1016/S0005-2760(01)00185-4

Guezennec J., Pignata P., Licourb Y., Gentrich E., Ratischol J., Colliec-Jouault S. Sul- fation and depolymerization of a bacterial exopolysaccharide of hydrothermal origin. *Carbohydr. Polym.* 1998, 37 (1), 19–24.
69. Selbmann L., Onofri S., Fenice M., Federici F., Petruccioli M. Production and structural characterization of the exopolysaccharide of the Antarctic fungus Phoma herbarum CCFEE 5080. *Res. Microbiol.* 2002, 153 (9), 585–592. https://doi.org/10.1016/S0923-2508(02)01372-4

70. Zuccconi L., Pagano S., Fenice M., Selbmann L., Tosi S., Onofri S. Growth temperature preferences of fungal strains from Victoria Land, Antarctica. *Polar Biol.* 1996, 16 (1), 53–61. https://doi.org/10.1007/BF01876829

71. Pavlova K., Koleva L., Krachanova M., Panchev I. Production and characterization of an exopolysaccharide by yeast. *World J. Microbiol. Biotechnol.* 2004, 20 (4), 435–439. https://doi.org/10.1023/B:WIBI.0000033068.45655.2a

72. Pavlova K., Panchev I., Krachanova M., Gocheva M. Production of an exopolysaccharide by yeast. *Folia Microbiol.* (Praha). 2009, 54 (4), 343–348. https://doi.org/10.1007/s12223-009-0049-y

73. Pavlova K., Rusinova-Videva S., Kuncheva M., Krachanova M., Gocheva M., Dimitrova S. Synthesis and characterization of an exopolysaccharide by Antarctic yeast strain Cryptococcus laurentii AL 150. *Appl. Biochem. Biotechnol.* 2011, 163 (8), 1038–1052. https://doi.org/10.1007/s12010-010-9107-9

74. Rusinova-Videva S., Pavlova K., Georgieva K. Effect of different carbon sources on biosynthesis of exopolysaccharide from Antarctic strain Cryptococcus laurentii AL 150. *Biotechnol. Biotec. Eq.* 2011, 25 (4), 80–84. https://doi.org/10.5504/BBEQ.2011.0121

75. Kuncheva M., Pavlova K., Panchev I., Dobrevska S. Emulsifying power of mannan and glucomannan produced by yeasts. *Int. J. Cosmet Sci.* 2007, 29 (5), 377–384. https://doi.org/10.1111/j.1468-2494.2007.00393.x

76. Vlaev S., Rusinova-Videva S., Pavlova K., Kuncheva M., Panchev I., Dobrevska S. Submerged culture process for biomass and exopolysaccharide production by Antarctic yeast: some engineering considerations. *Appl. Microbiol. Biotechnol.* 2013, 97 (12), 5303–5313. https://doi.org/10.1007/s00253-013-4864-3

77. Poli A., Anzelmo G., Tommonaro G., Pavlova K., Casaburi A., Nicolau B. Production and chemical characterization of an exopolysaccharide synthesized by psychrophilic yeast strain *Sporobolomyces salmonicolor* AL1, isolated from Livingston Island, Antarctica. *Folia Microbiol.* (Praha). 2010, 55 (6), 576–581. https://doi.org/10.1007/s12223-010-0092-8

78. Nichols C. M., Lardièvre S. G., Bowman J. P., Nichols P. D., A. E. Gibson J., Guézenne J. Chemical characterization of exopolysaccharides from Antarctic marine bacteria. *Microb. Ecol.* 2005, 49 (4), 578–589. https://doi.org/10.1007/s00248-004-0093-8

79. Nichols C. M., Bowman J. P., Guézenne J. Olleya marilimosa gen. nov., sp. nov., an exopolysaccharide-producing marine bacterium from the family *Flavobacteriaceae*, isolated from the Southern Ocean. *Int. J. Syst. Evol. Microbiol.* 2005, 55 (Pt4), 1557–1561. https://doi.org/10.1099/ijs.0.63642-0

80. Nichols C. M., Bowman J. P., Guézenne J. Effects of incubation temperature on growth and production of exopolysaccharides by an Antarctic sea ice bacterium grown in batch culture. *Appl. Environ. Microbiol.* 2005, 71 (7), 3519–3523. https://doi.org/10.1128/AEM.71.7.3519-3523.2005

81. Kim S. J., Kim B. G., Park H. J., Yim J. H. Cryoprotective properties and preliminary characterization of exopolysaccharide (P-Arcpo 15) produced by the Arctic bacterium *Pseudoalteromonas elyakovii* Arco 15. *Prep. Biochem. Biotechnol.* 2016, 46 (3), 261–266. https://doi.org/10.1080/10826068.2015.1015568

82. Carrion O., Delgado L., Mercade E. New emulsifying and cryoprotective exopolysaccharide from Antarctic *Pseudomonas* sp. ID1. *Carbohydr. Polym.* 2015, 117, 1028–1034. https://doi.org/10.1016/j.carbpol.2014.08.060

83. Marx J. G., Carpenter S. D., Deming J. W. Production of cryoprotectant extracellular polysaccharide substances (EPS) by the marine psychrophilic bacterium *Colwellia psychrerythraea* strain 34H under extreme conditions. *Can. J. Microbiol.* 2009, 55 (1), 63–72. https://doi.org/10.1139/W08-130

84. Sun M. L., Zhao F., Shi M., Zhang X. Y., Zhou B. C., Zhang Y. Z., Chen X. L. Characterization and biotechnological potential analysis of a new exopolysaccharide from the Arctic marine bacterium *Polaribacter* sp. SM1127. *Sci. Rep.* 2015, 5. https://doi.org/10.1038/srep18435

85. Sun M. L., Liu S. B., Qiao L. P., Chen X. L., Pang X., Shi M., Zhang X. Y., Qin Q. L., Zhou B. C., Zhang Y. Z., Xie B. B. A novel exopolysaccharide from deep-sea bacterium *Zunongwangia profunda* SM-A87: low-cost fermentation, moisture retention, and antioxidant activities. *Appl. Microbiol. Biotechnol.* 2014, 98 (17), 7437–7445. https://doi.org/10.1007/s00253-014-5839-8

86. Sathiyarayanan G., Bhatia S. K., Kim J.-H., Jeon J.-M., Kim Y. G., Park S. H., Lee S. H., Lee Y. K., Yang Y.-H. Metal removal and reduction potential of an exopolysaccharide produced by Arctic psychrotrophic bacterium *Pseudomonas* sp. PAMC 28620. *RSC Adv.* 2015, 5 (103), 84492–84502. https://doi.org/10.1039/C5RA14978A
the rheological properties and chemical composition of Volcaniella eurihalina exopolysaccharide. Appl. Biochem. Biotechnol. 1996, 59 (1), 77–86. https://doi.org/10.1007/BF02787859

105. Küçükbaşık F., Kazak H., Güney D., Finore I., Poli A., Yenigün O., Nicolaus B., Oner E. T. Molasses as fermentation substrate for levans production by Halomonas sp. Appl. Microbiol. Biotechnol. 2011, 89 (6), 1729–1740. https://doi.org/10.1007/s00253-010-3055-8

106. Llamas I., Amjres H., Mata J. A., Quesada E., Béjar V. The potential biotechnological applications of the exopolysaccharide produced by the halophilic bacterium Volcaniella almeriensis. Molecules. 2012, 17 (6), 7103–7120. https://doi.org/10.3390/molecules17067103

107. Mata J. A., Béjar V., Llamas I., Arias S., Bressollier P., Tallon R., Urdači M. C., Quesada E. Exopolysaccharides produced by the recently described halophilic bacteria Halomonas ventosae and Halomonas antarctica. Res. Microbiol. 2006, 157 (9), 827–835. https://doi.org/10.1016/j.resmic.2006.06.004

108. Poli A., Schiano Moriello V., Esposito E., Lama L., Gambacorta A., Nicolaus B. Exopolysaccharide production by a new Halomonas strain CRSS isolated from saline lake Cape Russell in Antarctica growing on complex and defined media. Biotechnol. Lett. 2004, 26 (21), 1635–1638. https://doi.org/10.1007/s10529-004-3187-y

109. Quesada E., Béjar V., Calvo C. Exopolysaccharide production by Volcaniella eurihalina. Experientia. 1993, 49 (12), 1037–1041. https://doi.org/10.1007/BF01929910

110. Ruiz-Ruiz C., Srivastava G. K., Carranza D., Mata J. A., Llamas I., Santamaría M., Quesada E., Molina I. J. An exopolysaccharide produced by the novel halophilic bacterium Halomonas stenophila strain B100 selectively induces apoptosis in human T leukaemia cells. Appl. Microbiol. Biotechnol. 2011, 89 (2), 345–355. https://doi.org/10.1007/s00253-010-2886-7

111. Mata J. A., Béjar V., Bressollier P., Tallon R., Urdači M. C., Quesada E., Llamas I. Characterization of exopolysaccharides produced by three moderately halophilic bacteria belonging to the family Alteromonadaeae. J. Appl. Microbiol. 2008, 105 (2), 521–528. https://doi.org/10.1111/j.1365-2672.2008.03879.x

112. Arun J., Satkishkumar R., Muneeswaran T. Optimization of extracellular polysaccharide production in Halobacillus trueperi AJSK using response surface methodology. Afr. J. Biotechnol. 2014, 13 (48), 4449–4457. https://doi.org/10.5897/AJB2014.14109

113. Poli A., Nicolaus B., Denizci A. A., Yavuzturk B., Kazan D. Halomonas smyrnensis sp. nov., a moderately halophilic, exopolysaccharide-producing bacterium. Int. J. Syst. Evol. Microbiol. 2013, 63 (Pt 1), 10–18. https://doi.org/10.1099/ijs.0.037036-0

114. Mellado E., Moore E. R. B., Nieto J. J., Ventosa A. Phylogenetic interferences and taxonomic consequences of 16S ribosomal DNA sequence comparison of Chromohalobacter marismortui, Volcaniella eurihalina and Delaya halophila and recification of V. eurihalina as Halomonas eurihalina comb. nov. Int. J. Syst. Bacteriol. 1995, 45 (4), 712–716. https://doi.org/10.1099/00207713-45-4-712

115. Bouchotroch S., Quesada E., del Moral A., Llamas I., Béjar V. Halomonas mauro sp. nov., a novel moderately halophilic, exopolysaccharide-producing bacterium. Int. J. Syst. Evol. Microbiol. 2001, 51 (Pt 5), 1625–1632. https://doi.org/10.1099/s00253-51-5-1625

116. Sarılımiser H. K., Ates O., Özdemir G., Arga K. Y., Oner E. T. Effective stimulating factors for microbial levans production by Halomonas smyrnensis AAD65. J. Biocell. Biotech. 2015, 119 (4), 455–463. https://doi.org/10.1016/j.jbiotec.2014.09.019

117. Sam S., Kucukbasik F., Yenigun O., Nicolaus B., Oner E. T., Yuksel M. A. Flocculating performances of exopolysaccharides produced by a halophilic bacterial strain cultivated on agro-industrial waste. Bioresour. Technol. 2011, 102 (2), 1788–1794. https://doi.org/10.1016/j.biortech.2010.09.020

118. Sezer A. D., Kazak Sarlımışer H., Rayaman E., Çevikbaş A., Toksoy Öner E., Akboga J. Development and characterization of vancomycin-loaded levans based-microparticulate system for drug delivery. Pharm. Dev. Technol. 2017, 22 (5), 627–634. https://doi.org/10.3109/10837450.2015.1116564.

119. Erginer M., Akcaay A., Coskunkan B., Morova T., Rende D., Bucka S., Baysal N., Ozisik R., Ergulu M. S., Agirbasli M., Toksoy Öner E. Sulfated levans from Halomonas smyrnensis as a bioactive, heparin-mimetic glycan for cardiac tissue engineering applications. Carbohydr. Polym. 2016, 149, 289–296. https://doi.org/10.1016/j.carbpol.2016.04.092

120. Ates O. Systems biology of microbial exopolysaccharides production. Front. Bioeng. Biotechnol. 2015, 3. https://doi.org/10.3389/fbioe.2015.00200

121. Schmid J., Sieber V., Rehm B. Bacterial exopolysaccharides: biosynthesis pathways and engineering strategies. Front. Micro-
122. Ruffing A., Chen R. R. Metabolic engineering of microbes for oligosaccharide and polysaccharide synthesis. Microb. Cell Fact. 2006, 5. https://doi.org/10.1186/1475-2859-5-25

123. Pirog T. P., Ivakhniuk M. O., Voronenko A. A. Exopolysaccharides synthesis on industrial waste. Biotechnol. acta. 2016, 9 (2), 7–18. https://doi.org/10.15407/biotech9.02.007

124. Pirog T. P., Ivakhniuk N. A., Voronenko A. A. Microbial synthesis of exopolysaccharide ethapolan on various types of waste vegetable oils. Vestsi Natsyunal’nai akademii nauk Belarusi. Seryya biyalagichnych nauk [Proceedings of the National Academy of Sciences of Belarus, biological series], 2017, 2, 87–93. (In Russian).

125. Pirog T. P., Voronenko A. A., Ivakhniuk M. O. Intensification of microbial exopolysaccharide ethapolan biosynthesis on mixture of molasses and sunflower oil. Biotechnol. acta. 2017, 10 (4), 25–33. https://doi.org/10.15407/biotech10.04.025

НЕТРАДИЦІЙНІ ПРОДУЦЕНТИ
МІКРОБНИХ ЕКЗОПОЛІСАХАРИДІВ
Т. П. Пирог
А. А. Вороненко
М. О. Івахнюк
Національний університет
харчових технологій, Київ, Україна
E-mail: tapirog@nuft.edu.ua

Наведено дані літератури щодо синтезу екзополісахаридів психрофільними грибами, гало- і термофільними археями та бактеріями, зокрема й віділенними з глибоко
водних гідротермальних вентів — джерел. Проаналізовано фізіологічну роль, фізико-
хімічні властивості та можливі галузі практичного використання екзополісаха
ридів, синтезованих нетрадиційними продуцентами. Відсоток з них притаманна імуномодулювальна, противірусна, антикоагулянтна, антиоксидантна активність, що робить їх перспективними для застосування у медицині та фармаце
вічні.

Бодночас аналіз літератури засвідчив необхідність розроблення ефективних техноло
гій одержання таких полісахаридів, оскіль
ки показники їх синтезу нетрадиційними продуцентами є значно нижчим порівняно з традиційними.

Ключові слова: екзополісахариди, термофіли, психрофіли, галофіли, гідротермальні венти.

НЕТРАДИЦИОННЫЕ ПРОДУЦЕНТЫ
МИКРОБНЫХ ЭКЗОПОЛИСАХАРИДОВ
Т. П. Пирог
А. А. Вороненко
Н. А. Ивахнюк
Национальный университет
пищевых технологий, Киев, Украина
E-mail: tapirog@nuft.edu.ua

Представлены данные литературы о синтезе экзополисахаридов психрофильными грибами, гало- и термофильными археями и бактериями, в частности выделенными с глубоковод
ных гидротермальных вентов — источников. Проанализированы физиологическая роль, физико-химические свойства и возможные отрасли практического использования экзо
полисахаридов, синтезированных нетрадиционными продуцентами. Большинство из них обладает иммуностимулирующей, противови
русной, антикоагулянтной, противопуховелой, антиоксидантной активностью, что делает их перспективными для применения в медицине и фармацевтике.

В то же время анализ литературы показал необходимость разработки эффективных техноло
гий получения таких полисахаридов, поскольку показатели их синтеза нетрадиционными продуцентами значительно ниже по сравнению с традиционными.

Ключевые слова: экзополисахариды, термофильы, психрофильы, галофильы, гидротермальные венты.