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EXPERIMENTAL ARTICLES

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## Cell Wall Galactofuranan of the *Paenarthrobacter* Actinobacteria

N. V. Potekhina<sup>a,\*</sup>, A. S. Shashkov<sup>b</sup>, E. M. Tul'skaya<sup>a</sup>, E. V. Ariskina<sup>c</sup>,  
L. V. Dorofeeva<sup>c</sup>, and L. I. Evtushenko<sup>c</sup>

<sup>a</sup>Biological Faculty, Moscow State University, Moscow, 119192 Russia

<sup>b</sup>Zelinsky Institute of Organic Chemistry, Russian Academy of Sciences, Moscow, 119991 Russia

<sup>c</sup>All-Russian Collection of Microorganisms (VKM), Skryabin Institute of Biochemistry and Physiology of Microorganisms,  
Russian Academy of Sciences, Pushchino, 142290 Russia

\*e-mail: potekhina56@mail.ru

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**Abstract**—The composition and structure of the cell wall glycopolymers of *Paenarthrobacter* species (*P. aurescens* VKM Ac-1105<sup>T</sup>, *P. histidinovorans* VKM Ac-1978<sup>T</sup>, and *P. nicotinovorans* VKM Ac-1988<sup>T</sup>, previously assigned to the genus *Arthrobacter*) were studied. All strains under study were found to contain a neutral polysaccharide, (1 → 6)-linked β-D-galactofuranan with the 2,3-diacetamido-2,3-dideoxy-α-glucopyranose (α-Glc<sub>p</sub>NAc<sub>3</sub>NAc) residues that glycosylate most of the hydroxyl groups at C-2 of galactofuranose. Acid hydrolysates of the cell walls contained galactose, glucose, arabinose, glucosamine, and galactosamine. The polysaccharide structure was established by chemical and NMR spectroscopic methods. The galactofuranan structure has not been previously described for representatives of other *Actinobacteria* genera. The data obtained expand our understanding of the chemical structure of microbial cell walls and may be used in taxonomy of actinobacteria, especially to differentiate at the phenotype level and to justify the description of new genera in the family *Micrococcaceae*.

**Keywords:** *Paenarthrobacter*, galactofuranan, polysaccharide, cell wall, chemotaxonomy

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The study of glycopolymers of microbial cell walls is of interest for a number of fields of basic and applied science, including microbial taxonomy. Though the classification system for prokaryotes is increasingly based on the data of genomics, the information about phenotypic traits, in particular, chemotaxonomic characteristics reflecting the chemical composition of cells and cell walls, is still relevant (Chun et al., 2018; Nouioui et al., 2018). A peptidoglycan characterized by the high level of structural diversity is known to be the major cell wall glycopolymer of gram-positive bacteria (Schleifer and Kandler, 1972; Schumann, 2011). The types (variations) of the structures of this polymer are the most important chemotaxonomic features of the taxa of actinobacteria of different ranks (Schumann et al., 2009; Schumann, 2011; Busse, 2016).

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**Abbreviations:** HSQC, proton-detected heteronuclear single quantum correlation; *J* (SSIC), spin-spin interaction constant; ROESY, rotating-frame nuclear Overhauser effect correlation spectroscopy; COSY, correlation spectroscopy; TOCSY, total correlation spectroscopy; HMBC, heteronuclear multiple bond correlation; TSP, 3-(trimethylsilyl)-2,2,3,3-tetraduteropropionic acid sodium salt; δ<sub>C</sub>, δ<sub>H</sub>, chemical shifts of the <sup>13</sup>C and <sup>1</sup>H atoms, respectively.

Apart from peptidoglycan, the cell wall of gram-positive bacteria usually contains glycopolymers of other types, which are covalently bound to peptidoglycan and are often referred to as secondary cell wall glycopolymers (Kohler et al., 2009; Schade and Weidenmaier, 2016). The latter are represented by phosphate-containing glycopolymers (teichoic acids and poly(glycosyl 1-phosphates) and phosphate-free glycopolymers: teichuronic and teichulosonic acids or polysaccharides of other types (Kohler et al., 2009; Potekhina et al., 2011; Tulskaia et al., 2011; Schade and Weidenmaier, 2016; Shashkov et al., 2020a). It has been shown that the set and structures of secondary glycopolymers are specific for some of the studied actinobacterial species, genera, and higher-level taxa (Takeuchi et al., 1990; Potekhina et al., 2011; Busse, 2012; Evtushenko and Ariskina, 2015; Magee and Ward, 2015; Goodfellow, 2015; Goodfellow and Jones, 2015; Nouioui et al., 2018; Shashkov et al., 2020a).

The genus *Paenarthrobacter* (the family *Micrococcaceae*) includes six species previously assigned to the genus *Arthrobacter* (group “*Arthrobacter nicotinovorans*”) (Busse, 2016). The genus was proposed on the basis of phylogenetic detachment (16S rRNA) of the species comprising this genus and of their phenotypi-

cal differences from *Arthrobacter sensu stricto* and other related genera, mainly chemotaxonomic (the structure of peptidoglycan, the composition of isoprenoid quinones and polar lipids) (Busse, 2016). Representatives of the genus *Paenarthrobacter* have an A3 $\alpha$  type peptidoglycan, var. A11.17 (L-lysine in the tetrapeptide chain, L-Ala–L-Thr–L-Ala interpeptide bridge) (Schumann et al., 2011; Busse, 2016). The data on the secondary glycopolymers of this genus are fragmentary. The absence of teichoic acids and the presence of neutral polysaccharides of unknown structure have been shown for the strains of two species (*P. aurescens* and *P. ureafaciens*) (Takeuchi and Yokota, 1989).

The goal of the present work was to study the structures of secondary cell wall glycopolymers of the type strains of three *Paenarthrobacter* species: *P. aurescens* (the type species of the genus), *P. histidinovorans*, and *P. nicotinovorans*.

## MATERIALS AND METHODS

The strains studied (*P. aurescens* VKM Ac-1105<sup>T</sup>, *P. histidinovorans* VKM Ac-1978<sup>T</sup>, *P. nicotinovorans* VKM Ac-1988<sup>T</sup>, and *Paenarthrobacter* sp. VKM Ac-2576) were provided by the All-Russian Collection of Microorganisms (VKM) (www.vkm.ru).

The cultures were grown aerobically at 28°C to the mid-exponential growth phase on a peptone yeast medium containing the following (g/L): peptone, 5; yeast extract, 3; K<sub>2</sub>HPO<sub>4</sub>, 0.2; glucose, 5; pH 7. Cell walls were obtained by differential centrifugation from the cells disintegrated with an UP100H sonicator (Hielscher, Germany) at 30 kHz, 3–5 × 10 min in ice water; glycopolymers were extracted from the cell walls with 10% TCA at 4°C (Potekhina et al., 2011).

The products of acid hydrolysis (2 M HCl, 3 h, 100°C) of the cell wall preparations and glycopolymers were identified by paper chromatography and electrophoresis using different solvent systems and specific reagents (Isherwood reagent, ninhydrin, AgNO<sub>3</sub>, aniline phthalate) (Potekhina et al., 2011).

The absolute configuration of galactose was determined by the modified method of GLC of acetylated glycosides with (*S*)-octane-2-ol as described (Potekhina et al., 2011).

The NMR spectra were recorded with an Avance 600 spectrometer (Bruker, Germany) for solutions of the preparations in 99.96% D<sub>2</sub>O at 30°C. Chemical shifts were calculated using TSP ( $\delta_{\text{H}}$  0.0) and acetone ( $\delta_{\text{C}}$  31.45) internal standards at 313 K. The two-dimensional NMR experiments were performed with the standard mathematical Bruker software (Bruker Optik GmbH, Germany). The spin-lock time in the <sup>1</sup>H, <sup>1</sup>H TOCSY experiments was 100 ms. The <sup>1</sup>H, <sup>13</sup>C HMBC experiments were optimized for coupling constants 8 Hz.

DNA isolation, amplification, sequencing, and the 16S rRNA gene sequence analysis of the strain VKM Ac-2576 were performed as described (Ryzhmanova et al., 2017).

## RESULTS AND DISCUSSION

Acid hydrolysates of cells walls of the studied strains (*P. aurescens* VKM Ac-1105<sup>T</sup>, *P. histidinovorans* VKM Ac-1978<sup>T</sup>, and *P. nicotinovorans* VKM Ac-1988<sup>T</sup>) and glycopolymer preparations isolated from these strains were shown to contain different ratios of galactose, glucose, arabinose, as well as glucosamine and galactosamine.

The phosphoric esters of glycerol and other polyols or sugars were not found, indicating the absence of teichoic acids and poly(glycosyl phosphates) and the presence of phosphate-free glycopolymers.

The preparations of glycopolymers from the cell walls of all three strains studied by the methods of NMR spectroscopy were completely identical. A detailed description of NMR-spectrometric analysis is given for the preparation of the strain *P. nicotinovorans* VKM Ac-1988<sup>T</sup>.

The NMR <sup>13</sup>C spectrum (Fig. 1) of the glycopolymer preparation from the strain VKM Ac-1988<sup>T</sup> contained three signals in the region of anomeric carbon resonance atoms at  $\delta_{\text{C}}$  109.1 ppm (minor), 107.3 ppm, and 97.3 ppm. The resonance region of N-linked carbon atoms had two signals at  $\delta_{\text{C}}$  53.6 and 53.1 ppm. Two signals of the methyl groups of N-acetates ( $\delta_{\text{C}}$  23.0 and 23.3 ppm) were identified in a high field; they corresponded to the two signals of carbonyl carbon atoms at  $\delta_{\text{C}}$  176.1 and 175.4 ppm. Signals for other carbon atoms were located at  $\delta_{\text{C}}$  88–62 ppm.

The <sup>1</sup>H NMR spectrum contained two intense signals in the anomeric region at  $\delta_{\text{H}}$  5.10 ppm (a broadened signal, <sup>3</sup>*J* < 2 Hz) and 5.02 ppm (a doublet, <sup>3</sup>*J* 4 Hz). In the high-field region of the spectrum, an intense signal was found at  $\delta_{\text{H}}$  1.98. Other signals were located at  $\delta_{\text{H}}$  3.5–4.2 ppm.

The signals in the <sup>1</sup>H and <sup>13</sup>C NMR spectra were assigned using 2D homonuclear <sup>1</sup>H, <sup>1</sup>H COSY, TOCSY and ROESY experiments and heteronuclear <sup>1</sup>H, <sup>13</sup>C HSQC and HMBC experiments.

The homonuclear spectra showed the presence of  $\beta$ -galactofuranose ( $\beta$ -Gal<sub>f</sub>, residues **A**, **A'**) and 2,3-diacetamide-2,3-dideoxy- $\alpha$ -glucopyranose ( $\alpha$ -D-Glc<sub>p</sub>Nac3Nac, residue **B**) residues in the polymer.

The <sup>1</sup>H, <sup>1</sup>H ROESY spectrum (Fig. 2, Table 1) contained, inter alia, correlation peaks H-1(**A**)/H-6,6'(**A**) (5.12/3.90; 3.64) and H-1(**B**)/H-1.2(**A**) (5.03/5.12; 4.20), indicating the (1→6)-bond between  $\beta$ -Gal<sub>f</sub>/residues and the substitution with  $\alpha$ -D-Glc<sub>p</sub>Nac3Nac residues at the C-2 hydroxyl group of  $\beta$ -Gal<sub>f</sub>.

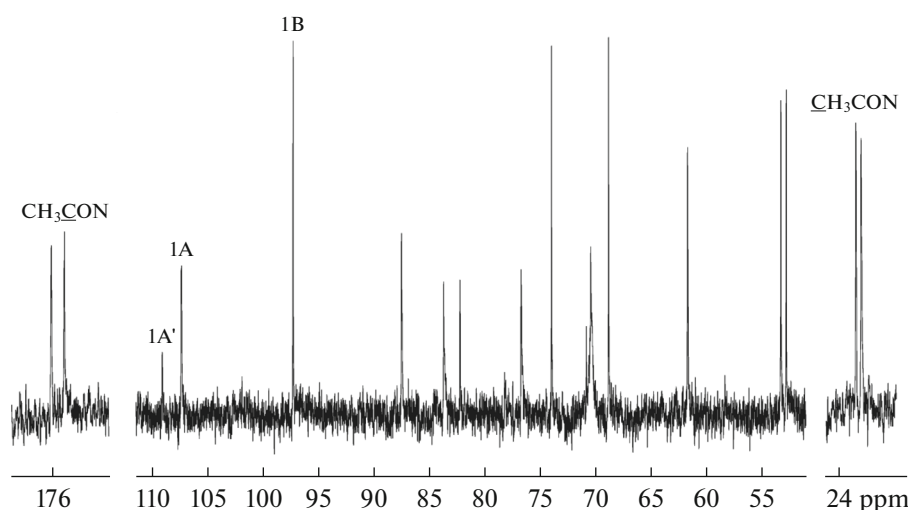


Fig. 1. The  $^{13}\text{C}$  NMR spectrum of galactofuranan from the cell wall of *P. nicotinevorans* VKM Ac-1988<sup>T</sup>. Arabic numerals are referred to the atoms in sugar residues designated by capital Latin letters as is shown in Table 1.

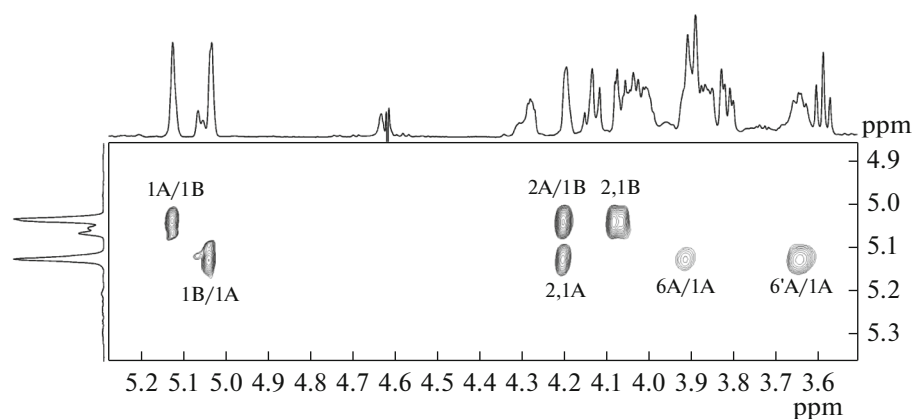


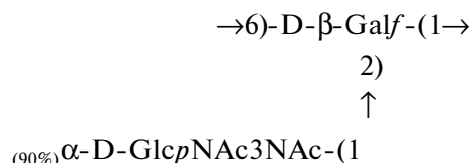
Fig. 2. A part of the  $^1\text{H}, ^1\text{H}$  ROESY spectrum of galactofuranan from the cell wall of *P. nicotinevorans* VKM Ac-1988<sup>T</sup>. The respective parts of the  $^1\text{H}$  NMR spectrum are shown along the axes. Arabic numerals are referred to the atoms in sugar residues designated by capital Latin letters as is shown in Table 1.

The large value of NOE H-1(**B**)/H-1(**A**) (5.03/5.12) in this disaccharide fragment points to identical D-configurations of pyranoses (Bock and Pedersen, 1983).

Signal assignment in the NMR  $^{13}\text{C}$  spectrum of the polymer was performed by analysis of the  $^1\text{H}, ^{13}\text{C}$  HSQC spectrum (Table 1). The downfield shift of C-2 and C-6 signals of the **A** residue compared to the respective signals in  $\beta$ -methyl-D-galactofuranoside (Lipkind et al., 1988) confirmed residue substitution at the hydroxyl groups of these atoms. Analysis of the two-dimensional spectra showed that the minor signals were from the  $\beta$ -Gal<sub>f</sub> residues unsubstituted at C-2 (residues **A'**; Table 1). The  $^1\text{H}, ^{13}\text{C}$  HMBC spectrum (Fig. 3, Table 1) confirmed the presence of the (1→6)-bond between  $\beta$ -Gal<sub>f</sub> residues (correlation peaks H-1(**A**)/C-6(**A**) (5.12/70.4) and H-6'(**A**)/C-

1(**A**) (3.64/107.3) and the (1→2)-bond between  $\alpha$ -D-Glc<sub>p</sub>NAc<sub>3</sub>NAc and  $\beta$ -Gal<sub>f</sub> residues (correlation peaks H-1(**B**)/C-2(**A**) (5.03/87.5) and H-2(**A**)/C-1(**B**) (4.20/97.3).

Thus, NMR experiments have shown that the preparation of glycopolymer of the strain VKM Ac-1988<sup>T</sup> contains a neutral polysaccharide – galactofuranan, which is almost completely (90%) substituted by diaminoglucose residues, with the following structure of the repeating unit:



**Table 1.** Chemical shifts in the  $^{13}\text{C}$  and  $^1\text{H}$  NMR spectra of galactofuranan from the cell wall of *P. nicotinovorans* VKM Ac-1988<sup>T</sup>

Residue	Chemical shifts $^{13}\text{C}$ ( $\delta_{\text{C}}$ acetone 31.45) and $^1\text{H}$ ( $\delta_{\text{H}}$ TSP 0.0)					
	C-1 H-1	C-2 H-2	C-3 H-3	C-4 H-4	C-5 H-5	C-6 H-6.6'
$\rightarrow 6$ -D- $\beta$ -Gal $f$ -(1 $\rightarrow$ 2) <b>A</b>	107.3 5.12	87.5 4.20	76.7 4.28	83.7 4.02	70.4 4.01	70.4 3.90, 3.64
$\uparrow$ $\alpha$ -D-Glc $p$ NAc3NAc-(1 <b>B</b>	97.3 5.03	52.8 <sup>a</sup> 4.06	53.3 <sup>b</sup> 4.13	68.9 3.58	74.0 3.86	61.7 3.86, 3.82
$\rightarrow 6$ -D- $\beta$ -Gal $f$ -(1 $\rightarrow$ <b>A'</b>	109.1 5.06	82.3 4.13	78.2 4.06	84.5 4.00	70.8 3.96	70.4 3.87, 3.81

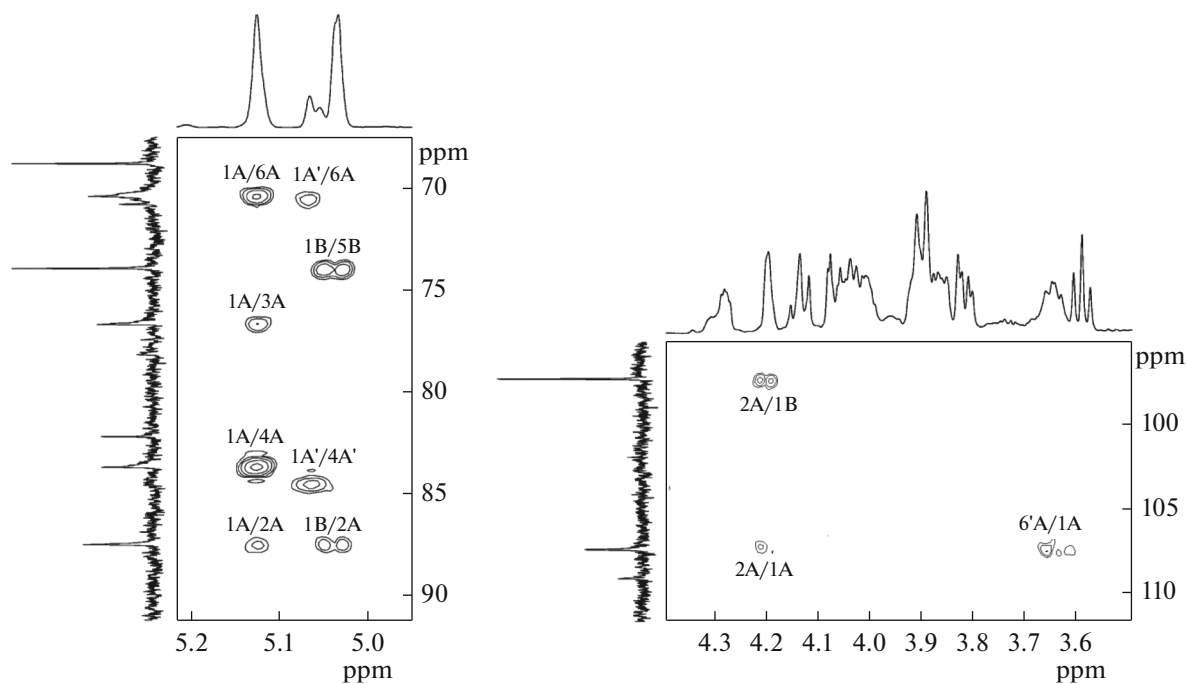
<sup>a</sup> NAc:  $\delta_{\text{C}}$  23.3; 176.1,  $\delta_{\text{H}}$  1.98.

<sup>b</sup> NAc:  $\delta_{\text{C}}$  23.0; 175.4,  $\delta_{\text{H}}$  1.98.

The identity of the spectra of glycopolymers of the strains *P. aureescens* VKM Ac-1105<sup>T</sup>, *P. histidinovorans* VKM Ac-1978<sup>T</sup> and the above-described strain VKM Ac-1988<sup>T</sup> indicated identity of the structures of galactofuranans in all three organisms.

Previously, a similar galactofuranan with diamino-glucose in the side chain has been described in the cell wall of *Arthrobacter* sp. VKM Ac-2576 (Shashkov et al., 2012). The taxonomic position of the strain

VKM Ac-2576 was determined more precisely by comparative study of the 16S rRNA gene sequences of this strain and the related organisms. It has been established that VKM Ac-2576 also belonged to the genus *Paenarthrobacter*. The 16S rRNA gene sequence of the strain VKM Ac-2576 has a 100% similarity with the sequence (BJMD01000050) of the strain *P. aureescens* NBRC 12136<sup>T</sup> (= *P. aureescens* VKM Ac-1105<sup>T</sup>) deposited in GenBank.



**Fig. 3.** A part of the  $^1\text{H}$ ,  $^{13}\text{C}$  HMBC spectrum of galactofuranan from the cell wall of *P. nicotinovorans* VKM Ac-1988<sup>T</sup>. The respective parts of the  $^1\text{H}$  and  $^{13}\text{C}$  NMR spectra are shown along the horizontal and vertical axes. Arabic numerals before and after the slash refer to protons and carbons, respectively, in the residues designated by capital Latin letters as is shown in Table 1.

Thus, all the studied *Paenarthrobacter* strains belonging to three species (*P. aurescens* (the type species of the genus), *P. histidinovorans*, and *P. nicotinovorans*) and the strain Ac-2576 similar in its 16S rRNA gene sequence to *P. aurescens* VKM Ac-1105<sup>T</sup> contain galactofuranan with  $\alpha$ -diaminoglucose in the side chain as a secondary cell wall glycopolymer. The structure of this polymer has so far been established only in representatives of *Paenarthrobacter* and has not been described in other prokaryotic microorganisms. At the same time, as was reported previously (Takeuchi and Yokota, 1989) and shown in the present work, strains of *Paenarthrobacter* species (*P. aurescens*, *P. histidinovorans*, *P. nicotinovorans*, and *P. ureafaciens*) have no teichoic acids or other phosphate-containing polymers.

It would be also interesting to note that the cell walls of other *Paenarthrobacter* species (*P. ilicis*, *P. nitroguajacolicus* and *P. ureafaciens*), as well as those of the strains studied in the present work, contain substantial amounts of galactose (Keddie and Cure, 1978; Takeuchi and Yokota, 1989). It may indicate that they contain either a similar galactofuranan or another galactose-containing polymer. Further investigation of representatives of these species will make it possible to elucidate whether the identified galactofuranan is typical for all species of the genus or only some of its species.

The few representatives of the revised genus *Arthrobacter* (*A. globiformis*, *A. pascens*, *A. ramosus*) that have been studied to date (Busse, 2016) and the species *Pseudarthrobacter oxydans* (previously *A. oxydans*) having peptidoglycan A3 $\alpha$  type similar to *Paenarthrobacter* are also characterized by the presence of phosphate-free polysaccharides (of unknown structure) (Naumova et al., 1988; Takeuchi and Yokota, 1989). The exception is *A. crystallopoietes*, which contains teichoic acids in its cell wall (Naumova et al., 1988; Takeuchi and Yokota, 1989). This species, however, phylogenetically is very distant from the type species of the genus, *A. globiformis*, and, according to Busse (2016), may be considered as a representative of a novel genus.

In contrast to the above-mentioned *Paenarthrobacter* and *Arthrobacter*, the studied representatives of the genera *Glutamicibacter* and *Paeniglutamicibacter* (previously assigned to *Arthrobacter*) have peptidoglycan A4 $\alpha$  type and contain teichoic acids and/or poly(glycosyl 1-phosphates) as secondary glycopolymers (*G. mysorens*, *G. nicotianae*, *G. uratoxydans*, *G. protophormiae*, *P. sulfureus*) (Naumova et al., 1988; Takeuchi and Yokota, 1989; Potekhina et al., 2012; Shashkov et al., 2020b).

Thus, our studies provide new data on the chemical composition of the cell walls of three *Paenarthrobacter* species. Members of this genus were shown to have galactofuranan with  $\alpha$ -diaminoglucose in the side chain, which has not been described previously in

other prokaryotic organisms. It was shown that this polymer and the set of sugars of acid hydrolysates of the cell walls (galactose, glucose, arabinose, glucosamine, and galactosamine), as well as the absence of teichoic acids and other phosphate-containing polymers, are typical of the above three species of *Paenarthrobacter*. These findings may be in demand for the systematics of prokaryotes in differentiation of actinobacterial genera at the level of phenotype.

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## COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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