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Structure and serology of O-antigens as the basis for classification of *Proteus* strains

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This review is devoted to structural and serological characteristics of the O-antigens (O-polysaccharides) of the lipopolysaccharides of various *Proteus* species, which provide the basis for classifying *Proteus* strains to O-serogroups. The antigenic relationships of *Proteus* strains within and beyond the genus as well as their O-antigen-related bioactivities are also discussed.

Keywords: Proteus, O-antigen, lipopolysaccharide, polysaccharide structure, immunospecificity, classification, serological cross-reactivity

INTRODUCTION

Gram-negative bacteria of the genus *Proteus* belong to the *Enterobacteriacea*e family. These micro-organisms were described by Hauser in 1885 and originally had two species – *P. mirabilis* and *P. vulgaris*. The biochemical classification of the genus *Proteus* has been changing. Currently, the genus consists of five species – *P. mirabilis*, *P. vulgaris*, *P. penneri*, *P. hauseri*, and *P. myxofaciens*, as well as three unnamed *Proteus* genomospecies 4, 5, and 6.[1] *Proteus myxofaciens*, isolated from living and dead larvae of the gypsy moth *Porthetia dispar*,[2] is the only *Proteus* species without any pathogenic significance to humans.

Proteus bacilli are widely distributed in the natural environment, where they are involved in decomposing organic matter of animal origin. They are also present in the intestines of humans and animals[3] and are opportunistic pathogens which, under favorable conditions, cause mainly wound and urinary tract infections (UTI).[4] Their importance in rheumatoid arthritis has also been shown.[5] *Proteus* rods are a frequent cause of UTI in patients with a urinary catheter in place or with structural and/or functional abnormalities in the urinary tract or who have had surgical intervention in the urogenital system. Strains of *P. mirabilis* cause UTI with the highest frequency among the *Proteus* species, including complicated infections and infections in long catheterized patients. In addition, *Proteus* bacteria may be associated with nosocomial infections[6] and can cause hematogenous and ascending infections, the latter being more common for these micro-organisms.

Proteus bacteria are dimorphic being able to display two types of behavior. When grown in liquid media they are motile, peritrichously flagellated short rods called 'swimmer cells'. When transferred to a solid medium, the short rods differentiate into elongated forms called 'swarmer cells', which are multinucleated, non-septated, and highly flagellated. Populations of swarmer cells can migrate in a co-ordinated way on solid media and then disintegrate into short rods. This process is cyclic and is known as the swarming phenomenon or swarming growth.[7] Both morphologically and physiologically, different short swimmer rods and swarmer cells are important for pathogenesis, although their significance in particular stages of infection remains to be clarified.

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Most probably, multiflagellated swarmer cells are suited in an ascending route of infection, whereas fimbriae-containing short rods are important for the colonization of the host mucosal surface.[8]

Proteus bacilli evolved a number of morphological and biochemical features which are considered as virulence factors. These are fimbriae, important for adhesion, flagella, crucial for bacterial ascent to the kidneys through the ureter, as well as enzymes (urease hydrolyzing urea to CO_2 and NH_3; antibody-degrading proteases, complement proteins, and tissue matrix proteins; α-keto acid-generating amino-acid deaminases which function as iron-binding siderophores), toxins, such as hemolysins, and endotoxin (lipopolysaccharide, LPS).[9]

Smooth(S)-form LPS consists of three parts: an O-specific polysaccharide (O-antigen, O-polysaccharide, OPS), a core oligosaccharide, and lipid A. The O-polysaccharide is built up of oligosaccharide repeating units (O-units), whereas the core is a large, non-repetitive oligosaccharide consisting of a structurally rather conserved inner region and a more variable outer region. Rough(R)-form LPS is devoid of any O-polysaccharide chain.

Proteus is an antigenically heterogeneous genus due to high structural diversity of both O-antigens and H-antigens (flagella). These serve as the basis for the serological classification of *Proteus* strains, which is important for serodiagnostics and epidemiological monitoring. The original classification scheme of Kauffmann and Perch[10] included 49 different *P. mirabilis* and *P. vulgaris* O-serogroups and 19 serologically distinct H-antigens. Later, it was supplemented with additional serogroups by Larsson[11] and Penner and Hennessy.[12] Our recent chemical and serological studies of *Proteus* O-antigens resulted in a further extension of the classification scheme by including new O-serogroups for strains of *P. penneri*, *P. hauseri*, *P. myxofaciens*, and those *P. mirabilis* and *P. vulgaris* strains which had not been classified earlier. Currently, it consists of 76 O-serogroups. In this paper, we summarize the chemical and serological characteristics of the *Proteus* O-antigens and their exploration as the molecular basis for the extended classification scheme of *Proteus* bacteria.

Composition of Proteus *O-polysaccharides*

Proteus OPSs have a characteristic composition of monosaccharide and non-sugar components (Table 1). All polysaccharides include amino sugars and, with one exception (*P. vulgaris* O53), all contain either D-glucosamine (GlcN) or D-galactosamine (GalN). GlcNAc and GalNAc are known as monosaccharides whose transfer to an undecaprenol carrier initiates the O-antigen biosynthesis in many Gram-negative bacteria.[13,14] Rather common are also D-glucose (Glc), D-galactose (Gal), D-glucuronic acid (GlcA), and D-galacturonic acid (GalA). Hereafter, members of this group of six monosaccharides will be called common sugars; the absolute configuration descriptor D- at the monosaccharide abbreviations will be omitted.

Other constituent monosaccharides are listed in Table 1. Among them are rarely occurring in nature amino and diamino sugars, such as 2-amino-2,6-dideoxy-L-mannose (L-RhaN), 2,3-diamino-2,3,6-trideoxy-L-mannose (L-RhaN3N), and 2,4-diamino-2,4,6-trideoxy-D-galactose (FucN4N), as well as uncommon acidic sugars, including L-altruronic acid (L-AltA), 2-amino-2-deoxy-D-galacturonic acid (GalNA), and 5,7-diamino-3,5,7,9-tetradeoxy-L-*glycero*-L-*manno*-non-2-ulosonic acid (Pse, pseudaminic acid). The frequencies of the occurrence of the sugar constituents in the *Proteus* OPSs are indicated in Table 1.

The pyranose form is characteristic for most monosaccharides, except for ribose, which always is present in the furanose form. The OPS of *P. penneri* O63 contains GalN in the furanose form, which is uncommon in natural carbohydrates.

The hexuronic acids GlcA and GalA either have a free carboxyl group or, less often, are amidated with the α-amino group of amino acids, including L-alanine, L-serine, L-threonine, and L-lysine (Fig. 1, compounds **1–6**). The most common is L-lysine, which confers a zwitterionic character to the polysaccharides. The OPSs of *P. myxofaciens* O60 and *P. mirabilis* O13 contain amides of GlcA and GalA with an unusual amino-acid derivative, N^{ε}-[(*R*)-1-carboxyethyl]-L-lysine (a regioisomer of lysopine; Fig. 1, compounds **7** and **8**, respectively).

The amino group(s) of most amino sugars is acetylated, but sometimes it bears another acyl substituent, such as (*R*)-3-hydroxybutanoyl group (*R*-3HOBu), a residue of malonic acid, succinic acid, or an amino acid, such as L- or D-alanine, *N*-(1-carboxyethyl)alanine (alanopine), and D-aspartic acid (Fig. 2, compounds **9–16**). The amino acids either have the free amino group or are *N*-acylated themselves with an acetyl group or (in *P. vulgaris* O4) an (*R*)-3-hydroxybutanoyl group (compound **12**). In *P. vulgaris* O53, the amino group at position 4 of FucN4N is free. Malonic, succinic, and *N*-acetyl-D-aspartic acids, all attached to a Qui4N residue (compounds **13–15**), confer a negative charge to the polysaccharides, L-alanine on GlcN (**9**) confers a positive charge, and the alanopine derivative of Qui4N (**16**) carries both negatively and positively charged groups.

Some *Proteus* OPSs are acidic due to the presence of (*R*)- or (*S*)-lactic acid, which is ether-linked to a residue of Glc or GlcNAc (Fig. 3, compounds **17–20**). In three *P. mirabilis* OPSs, a residue of Gal or GalNAc carries

Table 1. Composition of the O-polysaccharides of *Proteus*

Component	Abbreviation	Frequency of occurrence
Monosaccharide		
D-Ribose	D-Rib	4
D-Glucose	D-Glc	49
D-Galactose	D-Gal	48
L-Rhamnose	L-Rha	12
6-Deoxy-L-talose	L-6dTal	2
2-Amino-2-deoxy-D-glucose	D-GlcN	101
2-Amino-2-deoxy-D-galactose	D-GalN	60
2-Amino-2-deoxy-L-quinovose (2-amino-2,6-dideoxy-L-glucose)	L-QuiN	6
2-Amino-2-deoxy-L-fucose	L-FucN	12
2-Amino-2-deoxy-L-rhamnose	L-RhaN	1
3-Amino-3-deoxy-D-quinovose	D-Qui3N	3
3-Amino-3-deoxy-D-fucose	D-Fuc3N	5
4-Amino-4-deoxy-D-quinovose	D-Qui4N	6
2,3-Diamino-2,3-dideoxy-L-rhamnose	L-RhaN3N	1
2,4-Diamino-2,4-dideoxy-D-fucose	D-FucN4N	1
D-Glucuronic acid	D-GlcA	27
D-Galacturonic acid	D-GalA	35
L-Altruronic acid	L-AltA	1
2-Amino-2-deoxy-D-galacturonic acid	D-GalNA	1
5,7-Diamino-3,5,7,9-tetradeoxy-L-*glycero*-L-*manno*-non-2-ulosonic acid (pseudaminic acid)	Pse	1
Non-sugar constituent		
L-Alanine	L-Ala	6
D-Alanine	D-Ala	3
L-Serine	L-Ser	1
L-Threonine	L-Thr	2
L-Lysine	L-Lys	5
D-Aspartic acid	D-Asp	1
N-(1-Carboxyethyl)alanine (alanopine)	Cet-Ala	1
N^{ϵ}-[(*R*)-1-Carboxyethyl]-L-lysine	*R*-Cet-L-Lys	2
(*R*)-3-Hydroxybutanoic acid	*R*-3HOBu	5
Malonic acid (propandioic acid)	Mal	1
Succinic acid (butandioic acid)	Suc	1
(*R*)-Lactic acid [(*R*)-2-hydroxypropanoic acid]	*R*-Lac	3
(*S*)-Lactic acid [(*S*)-2-hydroxypropanoic acid]	*S*-Lac	4
Pyruvic acid (2-oxopropanoic acid), (*R*)- or (*S*)-acetal	Pyr	3
D-Glycerol 1-phosphate	D-Gro-1-*P*	5
D-Ribitol 5-phosphate	D-Rib-OL-5-*P*	7
Ethanolamine phosphate	Etn*P*	11
Choline phosphate	Cho*P*	1
N-[(*R*)-1-Carboxyethyl]ethanolamine phosphate	*R*-Cet-Etn*P*	2

a pyruvic acid acetal attached at positions either 3 and 4 or 4 and 6 (Fig. 3, compounds **21–23**).

Phosphorylation is rather common in *Proteus* OPSs. Glycerol and ribitol phosphates (*e.g*. Fig. 4, compounds **24** and **25**) are present either as lateral substituents or enter into the main polymer chain. Other phosphate-linked components are ethanolamine (*e.g*. Fig. 4, compound **26**) and its derivatives, such as *N*-acetylethanolamine, *N*-[(*R*)-1-carboxyethyl]ethanolamine, and choline (Fig. 4, compounds **27–29**). Whereas ethanolamine phosphate is present in the OPSs of a number of bacteria besides *Proteus*, to our knowledge, choline phosphate occurs only in *Proteus* OPSs and the derivatives *N*-acetylethanolamine and *N*-[(*R*)-1-carboxyethyl]ethanolamine (compounds **27** and **28**) are not found in other natural carbohydrates. Finally, a number of *Proteus* OPSs include a glycosyl phosphate in the main chain, which makes the polymers acid-labile.

In many OPSs (~40%), various monosaccharides carry an *O*-acetyl group (or groups), the *O*-acetylation

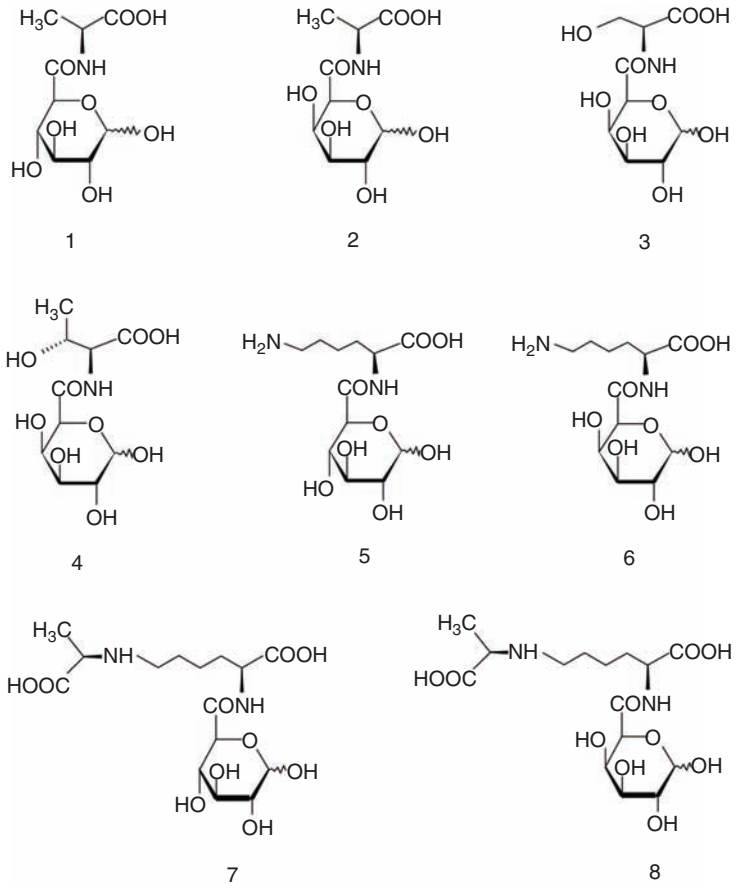

Fig. 1. Amides of hexuronic acids with amino acids. 1 *N*-(D-glucuronoyl)-L-alanine (*P. vulgaris* O44) 2 *N*-(D-galacturonoyl)-L-alanine (*P. mirabilis* O27, O59 and O74) 3 *N*-(D-galacturonoyl)-L-serine (*P. mirabilis* O28) 4 *N*-(D-galacturonoyl)-L-threonine (*P. mirabilis* O11 and O58) 5 N^{α}-(D-glucuronoyl)-L-lysine (*P. mirabilis* O27) 6 N^{α}-(D-galacturonoyl)-L-lysine (*P. mirabilis* O3, O26 and O28) 7 N^{ε}-[(*R*)-1-carboxyethyl]-N^{α}-(D-glucuronoyl)-L-lysine (*P. myxofaciens* O60) 8 N^{ε}-[(*R*)-1-carboxyethyl]-N^{α}-(D-galacturonoyl)-L-lysine (*P. mirabilis* O13).

usually being non-stoichiometric. In some OPSs, the degree of *O*-acetylation is so low that the exact location of the *O*-acetyl groups could be determined only tentatively, if at all.

Chemical structure of Proteus *O-polysaccharides*

All *Proteus* OPSs are heteropolymers consisting of linear or branched O-units, which contain from three to six monosaccharides (Table 2). The overwhelming majority of the OPSs (~90%) are acidic, and a number of them (~20%) possess both negatively and positively charged groups. The OPS structures of all *Proteus* O-serogroups from the extended classification scheme, which currently includes serogroups O1-O34, O36-O45 and O47-O78, are shown in Table 2 and discussed below.

Serogroup O1 (*P. vulgaris* OX19, ATCC 29905 = CCUG 1086-80, CCUG 4635 = CCUG 18984)

The acidic OPS of *P. vulgaris* O1 has a branched pentasaccharide O-unit containing two residues of L-QuiNAc, one residue each of GalNAc and GlcNAc, and galactose-1-phosphate.[15–17] A different OPS structure was ascribed first to *P. vulgaris* OX19[18] owing to a confusion of *P. vulgaris* OX2 and OX19 strains.[16]

Serogroup O2 (*P. vulgaris* OX2, PrK 5/57)

A linear tetrasaccharide O-unit of the neutral OPS of *P. vulgaris* O2 contains one residue each of Glc and L-QuiNAc and two residues of GlcNAc, one of which is non-stoichiometrically O-acetylated at position 6.[16,18,19]

Serogroup O3 (*P. mirabilis* G1, 1959, OXK)

Proteus mirabilis O3 serogroup is divided into two subgroups: O3a for strain G1, which was not included in the Kauffmann–Perch scheme,[10] and O3a,b (formerly O3) for strains 1959 and OXK. The O3a OPS has a branched tetrasaccharide O-unit containing one GlcA and two GalNAc residues in the main chain and an amide of GalA with L-lysine (Fig. 1, compound **6**) attached as a side chain.[20] The O3a,b OPS differs in the presence of an additional lateral Glc residue.[5,21–26]

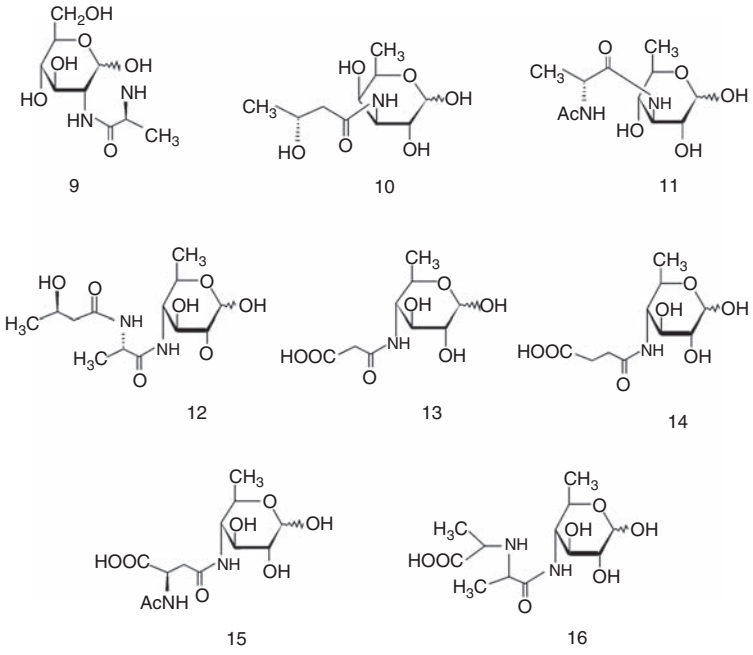

Fig. 2. *N*-Acyl derivatives of amino sugars. 9 2-(L-alanyl)amino-2-deoxy-D-glucose (*Proteus* O69) 10 3,6-dideoxy-3-[*N*-(*R*)-hydroxybutanoyl)]amino-D-galactose (*Proteus* O17) 11 3-(*N*-acetyl-D-alanyl)amino-3,6-dideoxy-D-glucose (*P. penneri* O59) 12 4,6-dideoxy-4-{*N*-[(*R*)-3-hydroxybutanoyl]-L-alanyl}amino-D-glucose (*P. vulgaris* O4) 13 4,6-Dideoxy-4-malonylamino-D-glucose (*P. mirabilis* O7) 14 4,6-dideoxy-4-succinylamino-D-glucose (*P. mirabilis* O49) 15 4-(*N*-acetyl-4-D-aspartyl)amino-4,6-dideoxy-D-glucose (*P. mirabilis* O38) 16 4-[*N*-(1-carboxyethyl)alanyl]amino-4,6-dideoxy-D-glucose (*P. vulgaris* O76).

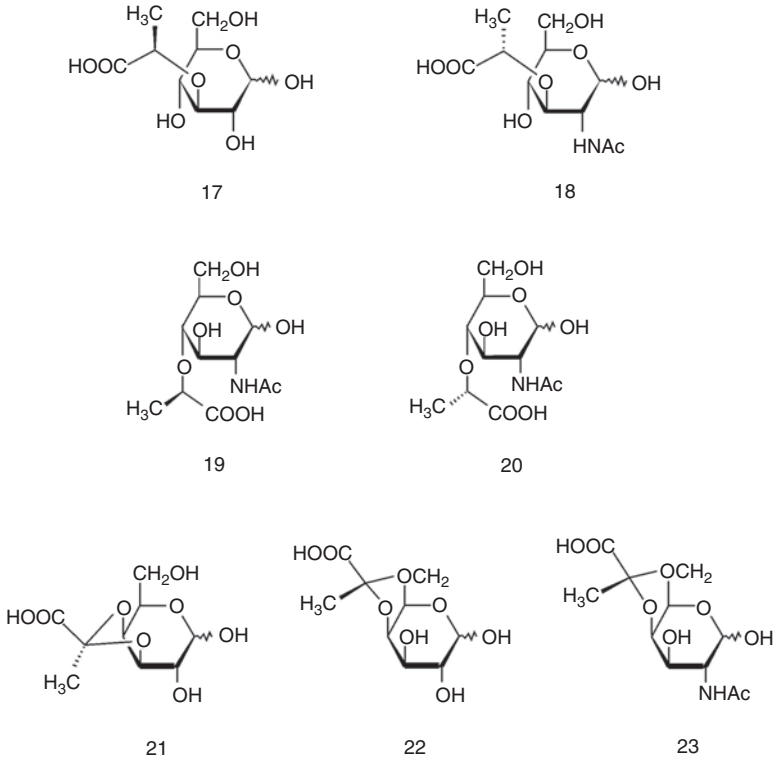

Fig. 3. Sugar ethers with lactic acid (17–20) and acetals with pyruvic acid (21–23). 17 3-*O*-[(*R*)-1-carboxyethyl]-D-glucose (*P. vulgaris* O25) 18 2-acetamido-3-*O*-[(*S*)-1-carboxyethyl]-2-deoxy-D-glucose (*N*-acetylisomuramic acid) (*P. penneri* O31 and O64) 19 2-acetamido-4-*O*-[(*R*)-1-carboxyethyl]-2-deoxy-D-glucose (*P. mirabilis* O15 and O40) 20 2-acetamido-4-*O*-[(*S*)-1-carboxyethyl]-2-deoxy-D-glucose (*P. penneri* O62) 21 3,4-*O*-[(*S*)-1-carboxyethylidene]-D-galactose (*P. mirabilis* O24) 22 4,6-*O*-[(*R*)-1-carboxyethylidene]-D-galactose (*P. mirabilis* O52) 23 2-acetamido-4,6-*O*-[(*R*)-1-carboxyethylidene]-2-deoxy-D-galactose (*P. mirabilis* O51).

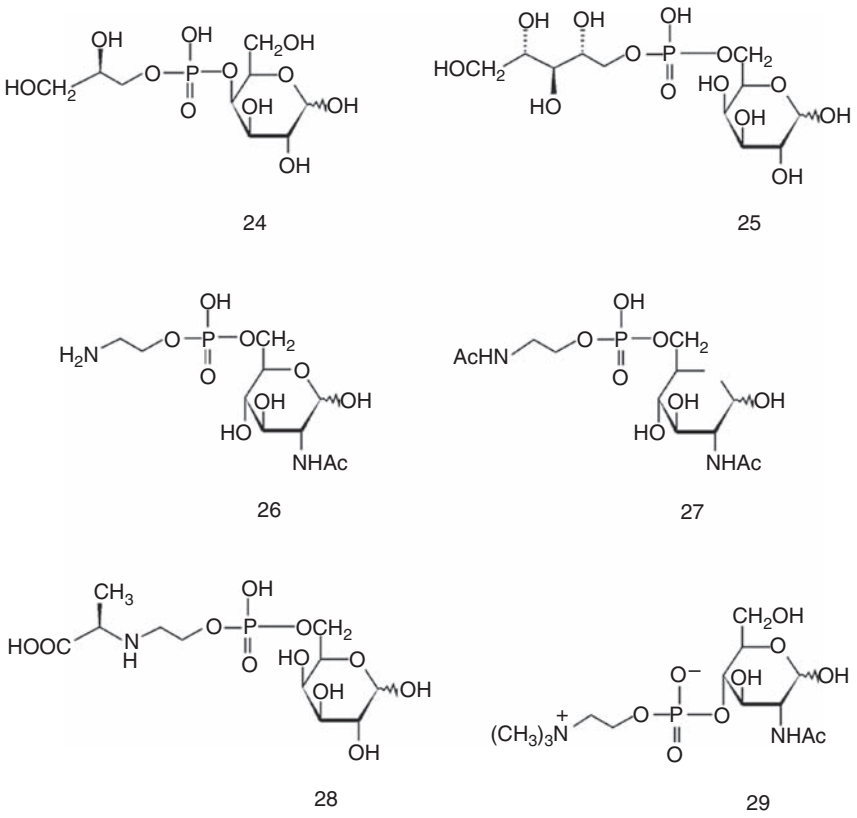

Fig. 4. Selected phosphorylated sugar derivatives. 24 D-galactose 4-(D-glycerol 1-phosphate) (*P. mirabilis* O54a,b) 25 D-galactose 6-(D-ribitol 5-phosphate) (*P. mirabilis* O41) 26 2-acetamido-2-deoxy-D-glucose 6-(ethanolamine phosphate) (*P. mirabilis* O16, O17, O27, *P. penneri* O19a,b, O67, O68) 27 2-acetamido-2-deoxy-D-glucose 6-(*N*-acetylethanolamine phosphate) (*P. mirabilis* O38) 28 D-galactose 6-{*N*-[(*R*)-1-carboxyethyl]ethanolamine phosphate} (*P. mirabilis* O14) 29 2-acetamido-2-deoxy-D-glucose 4-(choline phosphate) (*P. mirabilis* O18).

Serogroup O4 (*P. vulgaris* PrK 9/57)

The acidic OPS of *P. vulgaris* O4 has a linear tetrasaccharide O-unit containing common sugars and a unique monosaccharide derivative, Qui4N bearing an *N*-[(*R*)-3-hydroxybutanoyl]-L-alanyl group (Fig. 2, compound **12**), which has not been found elsewhere in nature.[27]

Serogroup O5 (*P. mirabilis* PrK 12/57)

A linear tetrasaccharide O-unit of the acidic OPS of *P. mirabilis* O5 is built up of two GalA and two GlcNAc residues. One of the GlcNAc residues is non-stoichiometrically (~70–80%) *O*-acetylated at positions 3 and 6.[28] This OPS is structurally related to the branched OPS of *P. mirabilis* O74.[29]

Serogroup O6 (*P. mirabilis* PrK 14/57, ATCC 49565)

The acidic OPS of *P. mirabilis* O6 is one of the simplest among the *Proteus* O-antigens. It has a branched trisaccharide O-unit containing one residue each of L-FucNAc, GlcNAc, and GlcA.[30,31]

Serogroup O7 (*P. mirabilis* PrK 15/57)

The acidic OPS of *P. mirabilis* O7 includes Qui4N bearing a malonic acid residue (Fig. 2, compound **13**), which is linked as a side chain to the main chain composed of common sugars.[32] This sugar derivative has been reported only once elsewhere as a component of a capsular polysaccharide of *Escherichia coli*.[33]

Serogroup O8 (*P. vulgaris* PrK 17/57, *P. mirabilis* TG 326, *P. penneri* 107, *Proteus* genomospecies 5)

The O8 serogroup includes strains of various *Proteus* species. The O8 OPS has a branched tetrasaccharide O-unit consisting of GlcA, GlcNAc and L-FucNAc in the main chain and Gal in the side chain.[34,35]

Serogroup O9 (*P. mirabilis* PrK 18/57)

The acidic OPS of *P. mirabilis* O9 is distinguished by the presence of Rib*f*, which is non-stoichiometrically (~70%) O-acetylated at position 3.[36] It has a β-Rib*f*-(1 → 4)-β-Gal*p*-(1 → 3)-Glc*p*NAc trisaccharide fragment in common with the OPS of *P. penneri* O59.[37]

Table 2. Structures of the O-polysaccharides of *Proteus*. In all O-serogroups, except for O53, GlcNAc or GalNAc is shown as the first monosaccharide of the repeating unit to indicate the most probable structure (or one of the most probable structures) of the biological O-unit

Serogroup[a]	Strains[b]	Structure of the repeating unit	References
O1	*P. vulgaris* OX19, ATCC 29905 = CCUG 1086-80, CCUG 4635 = CCUG 18984	α-L-Qui*p*NAc-(1→ 3 →4)-α-D-Gal*p*NAc-(1→4)-α-D-Gal*p*-1-*P*-(O→4)-α-L-Qui*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	15–17
O2	*P. vulgaris* OX2, PrK 5/57	→2)-β-D-Glc*p*-(1→6)-α-D-Glc*p*NAc-(1→3)-α-L-Qui*p*NAc-(1→3)-β-D-Glc*p*NAc6Ac-(1→	16, 18, 19
O3a	*P. mirabilis* G1	α-D-Gal*p*A6(L-Lys)-(1→ 4 →6)-β-D-Gal*p*NAc-(1→4)-β-D-Glc*p*A-(1→3)-β-D-Gal*p*NAc-(1→	20
O3a,b	*P. mirabilis* OXK, 1959	α-D-Gal*p*A6(L-Lys)-(1→ α-D-Glc*p*-(1→ 4 2 →6)-β-D-Gal*p*NAc-(1→4)-β-D-Glc*p*A-(1→3)-β-D-Gal*p*NAc-(1→	16, 21–26
O4	*P. vulgaris* PrK 9/57	→2)-β-D-Qui*p*4N(*R*-3HOBu-L-Ala)-(1→3)-α-D-Gal*p*-(1→4)-β-D-Glc*p*A-(1→3)-β-D-Glc*p*NAc-(1→	27
O5	*P. mirabilis* PrK 12/57	→4)-α-D-Glc*p*NAc3,6Ac_2-(1→4)-α-D-Gal*p*A-(1→3)-α-D-Gal*p*A-(1→3)-β-D-Glc*p*NAc-(1→	28
O6	*P. mirabilis* PrK 14/57, ATCC 49565	α-D-Glc*p*A-(1→ 3 →4)-α-L-Fuc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	30, 31
O7	*P. mirabilis* PrK 15/57	β-D-Qui*p*4NMal-(1→ 6 →2)-β-D-Gal*p*-(1→4)-β-D-Glc*p*-(1→3)-β-D-Glc*p*NAc-(1→	32
O8	*P. vulgaris* PrK 17/57 *P. mirabilis* TG 326 *P. penneri* 107 *P.* genomospiecies 5	α-D-Gal*p*-(1→ 3 →3)-β-D-Glc*p*A-(1→4)-α-L-Fuc*p*NAc-(1→3)-α-D-Glc*p*NAc-(1→	34, 35
O9	*P. mirabilis* PrK 18/57	→4)-α-D-Gal*p*A-(1→2)-β-D-Rib*f*3Ac-(1→4)-β-D-Gal*p*-(1→3)-α-D-Glc*p*NAc-(1→	36
O10	*P. mirabilis* PrK 19/57, PrK 20/57, HJ 4320	α-L-Alt*p*A-(1→ 3 →4)-α-D-Gal*p*NAc-(1→3)-α-D-Gal*p*A-(1→3)-α-D-Glc*p*NAc-(1→	39, 40
O11	*P. mirabilis* PrK 24/57	β-D-Glc*p*NAc-(1→ α-D-Glc*p*-(1→ 2 6 →4)-β-D-Glc*p*A-(1→3)-β-D-Gal*p*A6(L-Thr)-(1→3)-β-D-Glc*p*NAc-(1→	42
O12	*P. mirabilis* PrK 25/57	α-D-Glc*p*-(1→6)-α-D-Gal*p*NAc4Ac-(1→ 3 →3)-D-Gro-1-*P*-(O→6)-β-D-Glc*p*-(1→4)-α-L-Fuc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	44
O13	*P. mirabilis* PrK 26/57 *P. vulgaris* 8344	α-D-Gal*p*A6(*R*-Cet-L-Lys)-(1→ 4 →3)-α-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→	46–48
O14a,b	*P. mirabilis* PrK 28/57, PrK 29/57	*R*-Cet-Etn*P*→ 6 →4)-α-D-Gal*p*-(1→4)-β-D-Gal*p*NAc-(1→3)-α-D-Gal*p*6Ac-(1→3)-β-D-Gal*p*NAc-(1→	53–55

O14a,c	*P. mirabilis* EU313	*R*-Cet-Etn*P*¬ 6 →3)-α-D-Gal*p*-(1→6)-β-D-Glc*p*-(1→3)-β-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→	53
O15	*P. vulgaris* PrK 30/57	→3)-α-D-Glc*p*NAc4(*R*-Lac)6Ac-(1→2)-β-D-Glc*p*A-(1→3)-α-L-6dTal*p*2Ac-(1→3)-β-D-Glc*p*NAc-(1→	56
O16	*P. mirabilis* PrK 31/57	Etn*P*¬ 6 →2)-D-Rib-ol-5-*P*-(O→6)-β-D-Gal*p*NAc-(1→4)-α-D-Gal*p*NAc-(1→3)-α-D-Glc*p*NAc-(1→	59, 60
O17	*P. mirabilis* PrK 32/57	Etn*P*¬ 6 →2)-β-D-Fuc*p*3N(*R*-3HOBu)-(1→6)-α-D-Glc*p*-(1→4)-β-D-Glc*p*A-(1→3)-α-D-Glc*p*NAc-(1→	60–64
	P. penneri 10, 16, 18, 20	α-D-Glc*p*-(1¬ 2 →2)-β-D-Fuc*p*3N(*R*-3HOBu)-(1→6)-α-D-Glc*p*4Ac-(1→4)-β-D-Glc*p*A3Ac-(1→3)-α-D-Glc*p*NAc-(1→	
	P. vulgaris PrK 33/57	→2)-β-D-Fuc*p*3N(*R*-3HOBu)-(1→6)-α-D-Glc*p*3Ac-(1→4)-β-D-Glc*p*A-(1→3)-α-D-Glc*p*NAc-(1→	
	P. mirabilis PrK 61/57	→2)-β-D-Fuc*p*3N(*R*-3HOBu)4Ac-(1→6)-α-D-Glc*p*3Ac-(1→4)-β-D-Glc*p*A-(1→3)-α-D-Glc*p*NAc-(1→	
O18	*P. mirabilis* PrK 34/57	Cho*P*¬ α-D-Glc*p*-(1¬ 4 4 →3)-α-D-Glc*p*NAc-1-*P*-(O→6)-β-D-Glc*p*-(1→3)-β-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1 →	65
O19a	*P. vulgaris* PrK 37/57, CNCTC U349, CCUG 4654	→3)-α-D-Gal*p*-(1→4)-α-D-Gal*p*NAc-(1→3)-α-L-Fuc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	60, 66–68
O19a,b	*P. penneri* 31	Etn*P*¬ 6 →3)-α-D-Gal*p*-(1→4)-α-D-Gal*p*NAc-(1→3)-α-L-Fuc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	
O20	*P. mirabilis* PrK 38/57	α-D-Glc*p*-(1→2)-β-D-Gal*p*-(1¬ 4 →3)-α-D-Glc*p*NAc-(1→4)-β-D-Glc*p*-(1→3)-β-D-Glc*p*NAc-(1→	69
O21	*P. vulgaris* PrK 39/57	α-D-Glc*p*-(1¬ 6 →2)-α-D-Glc*p*-1-*P*-(O→6)-α-D-Glc*p*NAc-(1→4)-α-D-Gal*p*NAc-(1→3)-β-Gal*p*NAc-(1→	70
O22	*P. vulgaris* PrK 40/57	α-D-Qui*p*3NAc2,4Ac$_2$¬ 3 →2)-β-L-Rha*p*-(1→4)-α-L-Rha*p*-(1→4)-β-D-Glc*p*A-(1→3)-β-D-Glc*p*NAc-(1→	72
O23a,b,c	*P. mirabilis* PrK 41/57, TG 115, 7570, 71001	→2)-β-D-Gal*p*A-(1→3)-α-D-Gal*p*NAc-(1→4)-α-D-Gal*p*A-(1→3)-β-D-Glc*p*NAc-(1→	31, 73–77
	P. vulgaris CCUG 10701, OB	→2)-β-D-Gal*p*A4Ac-(1→3)-α-D-Gal*p*NAc-(1→4)-α-D-Gal*p*A-(1→3)-β-D-Glc*p*NAc6Ac-(1→	
O23a,b,d	*P. mirabilis* PrK 42/57 *P. vulgaris* PrK 43/57, PrK 44/57	β-D-Gal*p*A4Ac¬ 3 →4)-α-D-Gal*p*NAc-(1→4)-α-D-Gal*p*A-(1→3)-α-D-Glc*p*NAc-(1→	

(continued)

Table 2. Continued

Serogroup[a]	Strains[b]	Structure of the repeating unit	References
O24	*P. mirabilis* PrK 47/57	β-D-Gal*p*3,4(*S*-Pyr)¬ 3 →4)-β-D-Gal*p*NAc-(1→4)-β-D-Glc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	78–80
O25	*P. vulgaris* PrK 48/57	α-D-Glc*p*3(*R*-Lac)-(1¬ 3 →2)-α-L-Rha*p*-(1→2)-β-D-Rib*f*-(1→4)-β-D-Gal*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	38, 81
O26	*P. mirabilis* PrK 49/57	→4)-α-D-Gal*p*A6(L-Lys)-(1→4)-α-D-Gal*p*-(1→3)-β-D-Gal*p*A4Ac-(1→3)-β-D-Glc*p*NAc-(1→	83, 84
O27	*P. mirabilis* PrK 50/57	β-D-Glc*p*NAc-(1¬ Etn*P*¬ 4 6 →3)-β-D-Glc*p*A6(L-Lys)-(1→3)-α-D-Gal*p*A6(L-Ala)-(1→3)-β-D-Glc*p*NAc-(1→	85, 86
O28	*P. mirabilis* PrK 51/57	→4)-α-D-Gal*p*A6(L-Lys)-(1→4)-α-D-Gal*p*-(1→3)-α-D-Gal*p*A6(L-Ser)4Ac-(1→3)-β-D-Glc*p*NAc-(1→	87, 88
O29a	*P. mirabilis* PrK 52/57	α-D-Gal*p*NAc-(1¬ 3 →4)-β-D-Gal*p*NAc-(1→4)-β-D-Glc*p*A-(1→3)-β-D-Gal*p*NAc-(1→	79, 89
O29a,b	*P. mirabilis* 2002	α-D-Gal*p*NAc-(1¬ α-D-Glc*p*-(1¬ 3 2 →6)-β-D-Gal*p*NAc-(1→4)-β-D-Glc*p*A-(1→3)-β-D-Gal*p*NAc-(1→	90
O30	*P. mirabilis* PrK 53/57	→4)-β-D-Glc*p*A-(1→6)-α-D-Gal*p*NAc-(1→6)-β-D-Glc*p*NAc-(1→3)-β-D-Glc*p*NAc4Ac-(1→	84, 91
O31a	*P. penneri* 26	→6)-α-D-Glc*p*NAc-(1→3)-α-L-Qui*p*NAc-(1→3)-α-D-Glc*p*NAc-(1→	92–95
O31a,b	*P. vulgaris* PrK 55/57 *P. penneri* 28	→6)-α-D-Glc*p*NAc3(*S*-Lac)-(1→3)-α-L-Qui*p*NAc-(1→3)-α-D-Glc*p*NAc-(1→	
O32	*P. vulgaris* PrK 57/57	→4)-α-D-Gal*p*A-(1→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→4)-β-D-Gal*p*A-(1→3)-β-D-Glc*p*NAc-(1→	96
O33	*P. mirabilis* PrK 59/57, D52	D-Rib-ol-5-*P*¬ Etn*P*¬ 3 6 →2)-β-D-Gal*p*-(1→3)-α-D-Glc*p*NAc-(1→3)-β-D-Glc*p*-(1→3)-β-D-Glc*p*NAc-(1→	60, 98, 99
O34	*P. mirabilis* TG 276-90 *P. vulgaris* CCUG 4669	β-D-Glc*p*-(1¬ 2 →4)-α-D-Gal*p*NAc-1-*P*-(O→6)-β-D-Gal*p*-(1→3)-β-D-Gal*p*NAc-(1→	100, 101
O36	*P. mirabilis* PrK 62/57	→2)-β-D-Rib*f*-(1→4)-β-D-Gal*p*-(1→4)-α-D-Glc*p*NAc6Ac-(1→4)-β-D-Gal*p*-(1→3)-α-D-Glc*p*NAc-(1→	102
O37a,b	*P. vulgaris* PrK 63/57	→3)-β-D-Glc*p*A-(1→4)-α-D-Glc*p*-(1→3)-β-D-Glc*p*A-(1→3)-α-D-Glc*p*NAc6Ac-(1→	62, 104, 105
O37a,c	*P. vulgaris* PrK 72/57	→3)-β-D-Glc*p*A4Ac-(1→4)-α-D-Glc*p*6Ac-(1→3)-β-D-Glc*p*A4Ac-(1→3)-α-D-Glc*p*NAc-(1→	
O38	*P. mirabilis* PrK 64/57	AcEtn*P*¬ 6 →3)-β-D-Qui*p*4N(Ac-D-Asp)-(1→6)-α-D-Glc*p*-(1→3)-α-D-Gal*p*A-(1→4)-α-D-Glc*p*NAc-(1→	106, 107
O39	*P. vulgaris* PrK 65/57	→8)-β-Pse*p*5Ac7Ac-(2→3)-α-L-Fuc*p*NAc-(1→3)-α-D-Glc*p*NAc-(1→	110
O40	*P. mirabilis* PrK 66/57, CCUG 10703, OD	→3)-β-D-Glc*p*NAc4(*R*-Lac)-(1→3)-α-D-Gal*p*-(1→3)-D-Gro-1-*P*-(O→3)-β-D-Glc*p*NAc-(1→	57

O41	*P. mirabilis* PrK 67/57	Rib-ol-5-*P*→ 6 Etn*P*→ 6 Etn*P*→ 6 →3)-α-D-Gal*p*-(1→6)-β-D-Glc*p*NAc-(1→3)-β-D-Gal*p*-(1→3)-β-D-Gal*p*NAc-(1→	111
O42	*P. vulgaris* PrK 68/57, CCUG 4677	→3)-α-L-Fuc*p*NAc-(1→4)-α-D-Glc*p*-1-*P*-(O→4)-α-D-Glc*p*NAc-(1→3)-α-L-Fuc*p*NAc-(1→3)-α-D-Glc*p*NAc-(1→	112
O43	*P. mirabilis* PrK 69/57	→4)-α-D-Glc*p*-(1→4)-α-D-Gal*p*A-(1→3)-α-D-Gal*p*A-(1→3)-α-D-Glc*p*NAc-(1→	81, 113
O44	*P. vulgaris* PrK 70/57	→4)-β-D-Glc*p*-(1→3)-α-D-Gal*p*-(1→4)-β-D-Gal*p*NAc-(1→4)-β-D-Glc*p*A(L-Ala)-(1→3)-β-D-Gal*p*NAc-(1→	93, 114
O45	*P. vulgaris* PrK 73/57, CCUG 4680	→2)-β-Fuc*p*3NAc-(1→6)-α-Glc*p*NAc-(1→4)-α-Gal*p*NAc-(1→4)-α-Gal*p*A-(1→3)-β-Glc*p*NAc-(1→	115
O47	*P. vulgaris* PrK 71/57	β-D-Glc*p*A-(1→ 4 →3)-β-D-Gal*p*NAc-(1→4)-α-D-Gal*p*NAc3Ac-(1→3)-β-D-Gal*p*NAc-(1→	115, 116
O48	*P. mirabilis* 9615, NRCC 4420	→2)-α-D-Gal*p*-1-*P*-(O→6)-α-D-Glc*p*NAc3Ac-(1→4)-α-D-Gal*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	70
O49	*P. mirabilis* PrK 75/57	α-D-Quip4NSuc-(1→ 4 →2)-α-D-Gal*p*A-(1→3)-α-L-Rha*p*-(1→4)-α-D-Glc*p*-(1→2)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→	32
O50	*P. mirabilis* TG 332	β-D-Glc*p*-(1→ 4 →3)-β-D-Glc*p*A-(1→4)-β-D-Gal*p*NAc-(1→4)-β-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→	117
O51	*P. mirabilis* PrK 36/57, CCUG 19011	→3)-α-D-Gal*p*NAc4,6(*R*-Pyr)-(1→4)-α-D-Gal*p*A-(1→3)-α-L-Rha*p*2Ac-(1→3)-β-D-Glc*p*NAc-(1→	118
O52	*P. vulgaris* ATCC 49990 *P. penneri* 15, 49 *P. hauseri* 1086-80, 1732-80	→2)-α-D-Gal*p*4,6(*R*-Pyr)-(1→4)-β-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→	118–120
O53	*P. vulgaris* TG 276-1	→1)-D-Rib-ol-5-*P*-(O→1)-D-Rib-ol2/3/4Ac-5-*P*-(O→3)-β-D-Fuc*p*NAc4N-(1→	121
O54a,b	*P. mirabilis* CCUG 10704, OE	D-Gro-1-*P*–(1→ 4 →6)-α-D-Glc*p*NAc-(1→3)-β-D-Gal*p*-(1→3)-α-D-Gal*p*NAc-(1→	122
O54a,c	*P. vulgaris* TG 103	~50% D-Gro-1-*P*→ 4 →6)-α-D-Glc*p*NAc-(1→3)-β-D-Gal*p*-(1→3)-α-D-Gal*p*NAc6Ac-(1→	
O55	*P. vulgaris* TG 155	α-L-Rha*p*NAc-(1→ 4 →3)-α-D-Gal*p*NAcA-(1→3)-α-L-Qui*p*NAc-(1→4)-α-D-Glc*p*NAc-(1→	123
O56	*Proteus* genomospecies 4	α-D-Glc*p*-(1→ 2 →4)-β-D-Qui*p*3NAc-(1→6)-β-D-Glc*p*NAc-(1→4)-β-D-Gal*p*A-(1→3)-α-D-Gal*p*NAc-(1→	35

(continued)

Table 2. Continued

Serogroup[a]	Strains[b]	Structure of the repeating unit	References
O57	*P. mirabilis* TG 83, TG 319, ATCC 49995, CCUG 10700, OA	D-Gro-1-*P*¬ 3 α-D-Glc*p*-(1¬ 6 →4)-β-D-Gal*p*NAc-(1→3)-α-D-Gal*p*-(1→6)-β-D-Gal*p*-(1→3)-β-D-Gal*p*NAc-(1→	124, 125
O58	*P. penneri* 11, 12	α-D-Gal*p*A6(L-Thr)3Ac-(1¬ 3 →4)-β-D-Gal*p*NAc-(1→3)-β-L-Rha*p*-(1→4)-β-D-Glc*p*NAc6Ac-(1→	43, 81, 88
O59	*P. penneri* 3, 9, 14, 23	→2)-β-D-Qui*p*3N(Ac-D-Ala)-(1→4)-α-D-Gal*p*A6(L-Ala)-(1→2)-β-D-Rib*f*-(1→4)-β-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→	37, 126, 127
O60	*P. myxofaciens* ATCC 19692	→4)-β-D-Glc*p*A6(*S*-Cet-L-Lys)-(1→6)-α-D-Gal*p*NAc-(1→6)-β-D-Glc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	49
O61	*P. penneri* 21, 52, 104	β-D-Glc*p*NAc-1¬ 3 →4)-β-D-Gal*p*NAc-(1→3)-α-D-Gal*p*NAc-(1→4)-β-D-Gal*p*A-(1→3)-β-D-Glc*p*NAc-(1→	129
O62	*P. penneri* 41, 65, 74, 113	β-D-Glc*p*-(1→3)-β-D-Glc*p*NAc4(*S*-Lac)-(1¬ 2 →3)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→2)-α-D-Gal*p*6Ac-(1→3)-β-D-Glc*p*NAc-(1→	130
O63	*P. penneri* 22	α-D-Gal*f*NAc-(1→4)-β-D-Glc*p*A-(1¬ 4 →3)-α-D-Gal*p*-(1→4)-β-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→	132
O64a,b,c	*P. penneri* 19, 27, 35	→4)-β-D-Glc*p*NAc3(*S*-Lac)-(1→3)-α-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→	131, 133
O64a,b,d	*P. penneri* 29, 39, 40, 62	→6)-β-D-Glc*p*NAc3(*S*-Lac)-(1→3)-α-D-Gal*p*-(1→3)-β-D-Glc*p*NAc6Ac-(1→	134, 135
O64a,c,e	*P. penneri* 71	→4)-β-D-Glc*p*NAc-(1→3)-α-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→	136
O65	*P. vulgaris* TG 251 *P. penneri* 34	→4)-β-D-Gal*p*NAc-(1→4)-β-D-Gal*p*-(1→4)-β-D-Glc*p*-(1→3)-β-D-Gal*p*NAc-(1→	137
O66	*P. penneri* 2	β-L-Rha*p*NAc3NAc-(1¬ 3 →4)-α-D-Glc*p*-(1→3)-α-L-6dTal*p*2Ac-(1→3)-β-D-Glc*p*NAc-(1→	58
O67	*P. penneri* 8	α-D-Glc*p*-(1¬ 6 β-D-Glc*p*-(1¬ 4 Etn*P*¬ 6 →4)-β-D-Gal*p*A-(1→3)-α-D-Gal*p*NAc-(1→3)-α-L-Fuc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	138
O68	*P. penneri* 63	β-D-Glc*p*-(1¬ 4 Etn*P*¬ 6 →2)-β-D-Glc*p*-(1→6)-α-D-Glc*p*NAc-(1→3)-α-L-Fuc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	139
O69	*P. penneri* 25 *P. mirabilis* TG 277 *Proteus* genomospecies 6	α-D-Glc*p*A3/4Ac-(1¬ 4 →6)-β-D-Glc*p*N(L-Ala)3Ac-(1→4)-β-D-Glc*p*A-(1→3)-β-D-Glc*p*NAc6Ac-(1→	62, 140
O70	*P. penneri* 60	→3)-β-D-Qui*p*4NAc-(1→6)-α-D-Glc*p*-1-*P*-(O→6)-α-D-Gal*p*-(1→3)-α-L-Fuc*p*NAc-(1→3)-α-D-Glc*p*NAc-(1→	141

O71	*P. penneri* 42 *P. mirabilis* R14/1959	→4)-α-D-Gal*p*A-(1→2)-β-D-Glc*p*-(1→4)-β-D-Glc*p*-(1→3)-β-D-Glc*p*NAc-(1→	144, 145
O72a	*P. penneri* 1	β-D-Gal*p*NAc-(1→ 3 →4)-α-D-Gal*p*-(1→6)-β-D-Glc*p*-(1→3)-β-D-Gal*p*NAc-(1→	62, 146
O72a,b	*P. penneri* 4	β-D-Gal*p*NAc6Ac-(1→ α-D-Glc*p*-(1→ 3 6 →4)-α-D-Gal*p*-(1→6)-β-D-Glc*p*-(1→3)-β-D-Gal*p*NAc-(1→	
O73a,b	*P. penneri* 103	EtnP→ 6 →4)-Rib-ol-5-*P*-(O→4)-β-D-Glc*p*-(1→3)-β-D-Gal*p*-(1→3)-β-D-Gal*p*NAc-(1 →	60, 147
O73a,c	*P. penneri* 75	α-D-Glc*p*-(1→ 3 →4)-D-Rib-ol-5-*P*-(O→4)-β-D-Glc*p*-(1→3)-β-D-Gal*p*-(1→3)-β-D-Gal*p*NAc-(1 →	148
O74	*P. mirabilis* CCUG 10705, OF	α-D-Glc*p*NAc-(1→ 4 →3)-α-D-Gal*p*A2Ac-(1→3)-α-D-Gal*p*A6(L-Ala)-(1→3)-α-D-Glc*p*NAc-(1→	29
O75	*P. mirabilis* CCUG 10702, OC	β-D-Gal*p*NAc-(1→ 4 →3)-α-D-Gal*p*-(1→4)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→	149
O76	*P. vulgaris* HSC 438	→3)-β-D-Qui*p*4N(Cet-Ala)-(1→3)-α-D-Gal*p*6Ac-(1→6)-α-D-Glc*p*-(1→3)-α-L-Fuc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→	150
O77	*P. mirabilis* 3 B-m	→2)-β-D-Glc*p*-(1→3)-α-L-6dTal*p*2Ac-(1→3)-β-D-Glc*p*NAc-(1→	152
O78	*P. mirabilis* 1 B-m	Rib-ol1Ac-5-*P*→ ←1)-β-D-Gal*p*NAc 6 2 →3)-β-D-Gal*p*-(1→4)-β-D-Glc*p*-(1→3)-β-D-Glc*p*NAc-(1→	153

[a]Serogroups O35 and O46 that were in the original classification scheme of Kauffmann and Perch[10] were removed as the corresponding strains were reclassified into serogroups O17 and O37, respectively.
[b]Listed are strains for which the OPS structure is established by chemical methods.

A similar β-Rib*f*-(1 → 4)-β-Gal*p*NAc-(1 → 3)-Glc*p*NAc trisaccharide is present in the OPS of *P. vulgaris* O25.[38]

Serogroup O10 (*P. mirabilis* PrK 19/57, PrK 20/57, HJ 4320)

A branched tetrasaccharide O-unit of the OPS of *P. mirabilis* O10 has the main chain of GlcNAc, GalNAc, and GalA and an L-AltA side chain.[39,40] The last sugar has been reported only once elsewhere, namely in a capsular polysaccharide of *Aerococcus viridans* var. *homari*.[41]

Serogroup O11 (*P. mirabilis* PrK 24/57)

The OPS of *P. mirabilis* O11 is distinguished by the presence of an amide of GalA with L-threonine (Fig. 1, compound **4**) in the main chain of a doubly branched pentasaccharide O-unit.[42] The same amide **4** occupies the lateral position in the OPS of *P. penneri* O58.[43]

Serogroup O12 (*P. vulgaris* PrK 25/57)

A glycerol teichoic acid-like OPS of *P. vulgaris* O12 is composed of branched pentasaccharide O-units connected via a glycerophosphate group.[44] The OPS is similar to that of *E. coli* O29,[45] the only difference being the presence of a Gal residue in the latter in place of 4-O-acetylated GalNAc in the former.

Serogroup O13 (*P. mirabilis* PrK 26/57, *P. vulgaris* 8344)

The OPS of *P. mirabilis* O13 was historically the first bacterial polysaccharide found to contain N^{ε}-[(*R*)-1-carboxyethyl]-L-lysine.[46–48] This unusual amino acid forms an amide with GalA (Fig. 1, compound **8**), which is linked as a side chain. An amide of the same amino acid with GlcA (compound **7**) is a component of the OPSs of *Proteus myxofaciens* O60[49] and *Providencia alcalifaciens* O23,[50,51] whereas an amide of GalA with another stereoisomer, N^{ε}-[(*S*)-1-carboxyethyl]-L-lysine, is present in the OPS of *Providencia rustigianii* O14.[52]

Serogroup O14 (*P. mirabilis* PrK 28/57, 29/57, EU313)

Proteus mirabilis O14 consists of two subgroups: O14a,b (formerly O14) for strains PrK 28/57 and 29/57 and O14a,c (a new subgroup) for strain EU313. Linear tetrasaccharide O-units of the OPSs of the two subgroups are composed of common sugars only. The corresponding strains are combined into one O-serogroup based on the presence of a unique component, *N*-[(*R*)-1-carboxyethyl]ethanolamine phosphate, linked to a Gal residue (Fig. 4, compound **28**), whereas the rest of the O-units have different sugar compositions and different structures.[53–55] The O14a,b OPS structure was erroneously assigned first to the OPS of *P. mirabilis* O3.[54,55]

Serogroup O15 (*P. mirabilis* PrK 30/57)

A linear tetrasaccharide O-unit of the OPS of *P. mirabilis* O15 contains GlcNAc, GlcA, and two unusual components: 6-deoxy-L-talose and an ether of GlcNAc with (*R*)-lactic acid (Fig. 3, compound **19**), both being non-stoichiometrically (~80%) *O*-acetylated.[56] The same sugar ether GlcNAc4(*R*-Lac) is present also in the OPS of *P. mirabilis* O40,[57] which shares a β-GlcNAc-(1→3)-GlcNAc4(*R*-Lac) disaccharide fragment with *P. mirabilis* O15. The L-6dTal is a component of a α-L-6dTal-(1 → 3)-β-GlcNAc disaccharide fragment shared by *P. mirabilis* O15 and *P. penneri* O66.[58]

Serogoup O16 (*P. mirabilis* PrK 31/57)

A teichoic acid-like OPS of *P. mirabilis* O16 has two phosphate substituents: ribitol 5-phosphate in the main chain and ethanolamine phosphate (EtN*P*) linked to a part (~65%) of GlcNAc residues (Fig. 4, compound **26**).[59,60] The absolute configuration of ribitol 5-phosphate was first assigned erroneously[59] and later revised.[60]

Serogroup O17 (*P. mirabilis* PrK 32/57, PrK 61/57; *P. vulgaris* PrK 33/57; *P. penneri* 10, 16, 18, 20)

Proteus O17 is one of the most complex serogroups within the genus. The O-antigens of all O17 strains share the same linear backbone with a tetrasaccharide repeat containing common sugars and a *N*-(*R*)-3-hydroxybutanoyl derivative of Fuc3N (Fig. 2, compound **9**). The main chain is either non-substituted (*P. vulgaris* PrK 33/57 and *P. mirabilis* 61/57) or carries EtN*P* (*P. mirabilis* PrK 32/57) or Glc as a side chain (*P. penneri* 10, 16, 18, 20). The O17 OPSs differ also in non-stoichiometric *O*-acetylation of various monosaccharides.[60–64] In the Kauffmann–Perch scheme,[10] strain *P. mirabilis* PrK 61/57 was placed into serogroup O35 but later was reclassified to serogroup O17.[64]

Serogroup O18 (*P. mirabilis* PrK 34/57)

The OPS of *P. mirabilis* O18 has a branched pentasaccharide-phosphate O-unit composed of common sugars. This is the only *Proteus* OPS that includes GlcNAc 1-phosphate and, to our knowledge, the only bacterial O-antigen that contains choline phosphate (Cho*P*) (Fig. 4, compound **29**).[65]

Serogroup O19 (*P. vulgaris* PrK 37/57, CNCTC U349, CCUG 4654; *P. penneri* 31)

Proteus O19 serogroup is divided into two subgroups: O19a for strains of *P. vulgaris*[66,67] and O19a,b for *P. penneri* 31.[60,68] The O-antigens of both subgroups have a linear tetrasaccharide repeat composed of common sugars and L-FucNAc. The O19a,b OPS differs in the presence of EtN*P* at position 6 of GlcNAc (Fig. 4, compound **26**).

Serogroup O20 (*P. mirabilis* PrK 38/57)

The neutral OPS of *P. mirabilis* O20 has a branched pentasaccharide O-unit consisting of common sugars only.[69]

Serogroup O21 (*P. vulgaris* PrK 39/57)

A branched pentasaccharide O-unit of the OPS of *P. vulgaris* O21 is composed of common sugars and Glc 1-phosphate.[70] It resembles much that of *Hafnia alvei* 744 and PCM 1194,[71] the only difference being the N-substitution of GlcN with an (*R*)-3-hydroxybutanoyl group in *H. alvei* rather than an acetyl group in *P. vulgaris* O21. A similar OPS of *P. mirabilis* O48 lacks the lateral Glc residue and has a GlcNAc residue in place of one of the GalNAc residues in the main chain.[70]

Serogroup O22 (*P. vulgaris* PrK 40/57)

A branched pentasaccharide O-unit of the acidic OPS of *P. vulgaris* O22 contains two L-Rha residues in the main chain and a Qui3NAc residue in the side chain, which is *O*-acetylated stoichiometrically at position 3 and non-stoichiometrically (~65%) at position 2.[72]

Serogroup O23 (*P. mirabilis* PrK 41/57, PrK 42/57, TG 115, 7570, 71001; *P. vulgaris* PrK 43/57, PrK 44/57, CCUG 10701, OB)

Proteus O23 is a complex serogroup, which is divided into two subgroups: O23a,b,c for *P. mirabilis* PrK 41/57, TG 115, 7570, 71001, and *P. vulgaris* CCUG 10701 (OB) and O23a,b,d for *P. mirabilis* PrK 42/57, *P. vulgaris* PrK 43/57 and PrK 44/57.[73] The OPSs of both subgroups have the same tetrasaccharide O-unit composed of common sugars but differ in the mode of connection between the O-units giving rise to either branched or linear topology.[31,73–77] The O23 OPSs differ also in the patterns of non-stoichiometric *O*-acetylation. *P. vulgaris* CCUG 10701 (OB) was erroneously classified first into a new *Proteus* serogroup O74[77] but later was reclassified to serogroup O23.[73]

Serogroup O24 (*P. mirabilis* PrK 47/57)

The OPS of *P. mirabilis* O24 is distinguished by the presence of a pyruvic acid acetal of galactose (Fig. 3, compound **21**) linked as a lateral group to the main chain composed of common amino sugars.[78–80] The acidic acetal group was overlooked in an early study of the OPS[78] as it cleaved upon mild acid degradation of the LPS.

Serogroup O25 (*P. vulgaris* PrK 48/57)

The OPS of *P. vulgaris* O25 contains an ether of Glc with (*R*)-lactic acid (Fig. 3, compound **17**) attached as a lateral sugar residue and a β-Rib*f* residue in the main chain.[38,81] The O25 polysaccharide has a branched β-Glc*p*NAc-(1 → 2)[α-Glc*p*3(*R*-Lac)-(1 → 3)]-α-L-Rha*p* trisaccharide fragment in common with a capsular polysaccharide of the marine bacterium *Alteromonas haloplanktis* KMM 156.[82]

Serogroup O26 (*P. mirabilis* PrK 49/57)

A linear tetrasaccharide O-unit of the OPS of *P. mirabilis* O26 includes Gal, GlcNAc and two GalA residues, one of which is amidated with L-lysine (Fig. 1, compound **6**).[83,84] It shares a β-Glc*p*NAc-(1 → 4)-α-Gal*p*A6(L-Lys)-(1 → 4)-α-Gal*p*-(1 → 3)-Gal*p*A4Ac tetrasaccharide fragment with the OPS of *P. mirabilis* O28, which differs only in the configuration of the other, 4-*O*-acetylated GalA residue and its amidation with L-serine.

Serogroup O27 (*P. mirabilis* PrK 50/57)

The main chain of the OPS of *P. mirabilis* O27 includes amides of GalA with L-alanine and GlcA with L-lysine (Fig. 1, compounds **2** and **5**, respectively) as well as a GlcNAc residue, which in ~80% O-units bears Et*N*P (Fig. 4, compound **26**).[85,86] Having two amino acids, a phosphate group, and free amino groups of lysine and ethanolamine, this OPS is one of the most highly charged *Proteus* O-antigens.

Serogroup O28 (*P. mirabilis* PrK 51/57)

The linear OPS of *P. mirabilis* O28 is distinguished by the presence of two other amides of GalA: one with L-Ser and the other with L-lysine (Fig. 1, compounds **3** and **6**, respectively), the former being 4-*O*-acetylated[87,88] Sugar composition and structure of the O28 OPS are similar to those of the O26 OPS.

Serogroup O29 (*P. mirabilis* PrK 52/57, 2002)

Proteus mirabilis O29 is divided into two subgroups: O29a (formerly O29) for strain PrK 52/57 and O29a,b for a previously unclassified strain 2002. Branched O-units of both subgroups contain one GlcA and three GalNAc residues,[79,89,90] and the O-unit of subgroup O29a,b has an additional lateral Glc residue.

Serogroup O30 (*P. mirabilis* PrK 53/57)

The acidic linear OPS of *P. mirabilis* O30 is composed of common sugars only.[84,91] GlcNAc is non-stoichiometrically (~70%) *O*-acetylated.

Serogroup O31 (*P. penneri* 26, 28, S29, R15; *P. vulgaris* PrK 55/57)

The *Proteus* O31 serogroup is divided into two subgroups: O31a for *P. penneri* 2692 and O31a,b for *P. penneri* 28, S29, R15 and *P. vulgaris* PrK 55/57.[93–95] The OPSs of both subgroups are linear and have trisaccharide O-units containing one L-QuiNAc and two GlcNAc residues. The OPS of subgroup O31a,b is

distinguished by etherification of one of the GlcNAc residues with (*S*)-lactic acid giving rise to *N*-acetylisomuramic acid (Fig. 3, compound **18**).

Serogroup O32 (*P. vulgaris* PrK 57/57)

The OPS of *P. vulgaris* O32 has a linear pentasaccharide O-unit containing two residues each of L-Rha and GalA and one GlcNAc residue.[96] It shares an α-L-Rha*p*-(1 → 2)-α-L-Rha*p*-(1 → 4)-β-Gal*p*A trisaccharide fragment with the OPS of *Shigella flexneri* type 6.[97]

Serogroup O33 (*P. mirabilis* PrK 59/57, D52)

A tetrasaccharide O-unit of the OPS of *P. mirabilis* O33 consists of four common sugar residues, ribitol 5-phosphate and EtN*P*, the last component being present in ~75% O-units.[60,98,99]

Serogroup O34 (*P. mirabilis* TG 276-90; *P. vulgaris* CCUG 4669)

A branched tetrasaccharide O-unit of the acidic OPS of serogroup O34 is composed of common sugars, and the O-units are interlinked by the phosphodiester bond.[100,101] This OPS is the only *Proteus* O-antigen that contains GalNAc 1-phosphate.

Serogroup O35 (*P. mirabilis* PrK 61/57)

Based on structural and serological data of the O-antigens, *P. mirabilis* PrK 61/57 was reclassified from serogroup O35 to serogroup O17[64] (see above), and serogroup O35 was removed from the classification scheme.

Serogroup O36 (*P. mirabilis* PrK 62/57)

The neutral OPS of *P. mirabilis* O36 has a linear pentasaccharide O-unit containing common sugars and one Rib*f* residue; in ~70% O-units one of the GlcNAc residues is *O*-acetylated.[102] This OPS is structurally identical to that of *E. coli* O153, except that the latter is devoid of *O*-acetylation.[103]

Serogroup O37 (*P. vulgaris* PrK 63/57, PrK 72/57)

The OPSs of strain PrK 63/57[62,104] from serogroup O37 in the Kauffmann–Perch scheme[10] and strain PrK 72/57[104,105] belonging formerly to serogroup O46 both have a linear tetrasaccharide O-unit composed of common sugars only. However, the *O*-acetylation patterns of the OPSs are different: in strain PrK 63/57 (subgroup O37a,b), three of four monosaccharides are non-stoichiometrically *O*-acetylated, whereas in strain PrK 72/57 (subgroup O37a,c), an *O*-acetyl group is present only on GlcNAc, which is non-*O*-acetylated in the former strain.

Serogroup O38 (*P. mirabilis* PrK 64/57)

A linear tetrasaccharide O-unit of the acidic OPS of *P. mirabilis* O38 contains one residue each of Glc, GalA, GlcNAc, and Qui4N bearing *N*-acetyl-D-aspartic acid (Fig. 2, compound **15**).[106,107] Aspartic acid is a rarely occurring non-sugar component of bacterial polysaccharides; earlier, both D- and L-forms of this amino acid have been reported in the OPSs of *Providencia*.[107,109] Another peculiar feature of the O38 OPS is the presence of *N*-acetylethanolamine phosphate (Fig. 4, compound **27**).

Serogroup O39 (*P. vulgaris* PrK 65/57)

In addition to GlcNAc and L-FucNAc, a linear trisaccharide O-unit of the acidic OPS of *P. vulgaris* O39 contains a unique monosaccharide component, 5,7-diacetamido-3,5,7,9-tetradeoxy-L-*glycero*-L-*manno*-non-2-ulosonic acid (di-*N*-acetylpseudaminic acid) (Fig. 5),[110] which is the only higher sugar found in *Proteus* OPSs.

Serogroup O40 (*P. mirabilis* PrK 66/57, CCUG 10703, OD)

An O-unit of the linear teichoic acid-like OPS of *P. mirabilis* O40 is distinguished by the presence of a regio-isomer of *N*-acetylmuramic acid (Fig. 3, compound **19**) and glycerol 1-phosphate in the main chain.[57] The same regio-isomer is a component of the OPS of *P. vulgaris* O15.[56]

Serogroup O41 (*P. mirabilis* PrK 67/57)

The OPS of *P. mirabilis* O41 is the most highly phosphorylated *Proteus* O-antigen. Its linear tetrasaccharide O-unit consists of common sugars, which bear three phosphate substituents, including ribitol 5-phosphate and two EtN*P* groups, one of which is present in a non-stoichiometric amount (~65%).[111] The absolute configuration of ribitol 5-phosphate in the O41 OPS was assigned tentatively.

Serogroup O42 (*P. vulgaris* PrK 68/57, CCUG 4677)

The OPS of *P. vulgaris* O42 has a linear pentasaccharide-phosphate O-unit containing one residue of Glc

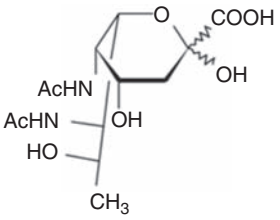

Fig. 5. 5,7-Diacetamido-3,5,7,9-tetradeoxy-L-*glycero*-L-*manno*-non-2-ulosonic (di-*N*-acetylpseudaminic) acid (*P. vulgaris* O39).

1-phosphate and two residues each of GlcNAc and L-FucNAc.[112]

Serogroup O43 (*P. mirabilis* PrK 69/57)

A tetrasaccharide O-unit of the linear acidic OPS of *P. mirabilis* O43 consists of common sugars only.[81,113]

Serogroup O44 (*P. vulgaris* PrK 70/57)

The acidic OPS of *P. vulgaris* O44 has a linear pentasaccharide O-unit containing common sugars and an amide of GlcA with L-alanine (Fig. 1, compound **1**).[93,114]

Serogroup O45 (*P. vulgaris* PrK 73/57, CCUG 4680)

A linear pentasaccharide O-unit of the OPS of *P. vulgaris* O45 is composed of common sugars and Fuc3NAc.[115] The OPS structure of *P. vulgaris* O47 was erroneously reported first as that of the O45 OPS.[116]

Serogroup O46 (*P. vulgaris* PrK 72/57)

In the Kauffmann–Perch classification scheme,[10] *P. vulgaris* PrK 72/57 was classified in serogroup O46. However, based on close structural[104,105] and serological[104] relatedness of the O46 and O37 O-antigens, strain PrK 72/57 was reclassified to serogroup O37.[104]

Serogroup O47 (*P. vulgaris* PrK 71/57)

A branched tetrasaccharide O-unit of the acidic OPS of *P. mirabilis* O47 contains a lateral GlcA residue and three GalNAc residues in the main chain, one of which is non-stoichiometrically (~75%) *O*-acetylated.[115,116]

Serogroup O48 (*P. mirabilis* 9615, NRCC 4420)

The acidic OPS of *P. mirabilis* O48 has a linear tetrasaccharide O-unit containing Gal 1-phosphate and common amino sugars, one of the GlcNAc residues being *O*-acetylated.[70]

Serogroup O49 (*P. mirabilis* PrK 75/57)

A branched hexasaccharide O-unit of the acidic OPS of *P. mirabilis* O49 contains a derivative of Qui4N with succinic acid (Fig. 2, compound **14**).[32] This derivative is attached as a side chain, whereas the main chain consists of common sugars and two L-Rha residues.

Serogroup O50 (*P. mirabilis* TG 332)

The acidic OPS of *P. mirabilis* O50 has a branched pentasaccharide O-unit consisting of common sugars only.[117] Serogroup O50 was the first from a number of new *Proteus* serogroups (O50–O78) that were not included in the original Kauffmann–Perch classification scheme.[10]

Serogroup O51 (*P. mirabilis* PrK 36/57, CCUG 19011)

A linear tetrasaccharide O-unit of the acidic OPS of *P. mirabilis* O51 contains one residue each of GlcNAc and GalA, 2-*O*-acetylated L-Rha and a pyruvic acid acetal of GalNAc (Fig. 3, compound **23**).[118] Being originally classified into *Proteus* O19 serogroup, strain PrK 36/57 was reclassified to a separate serogroup O51.[118]

Serogroup O52 (*P. vulgaris* ATCC 49990; *P. penneri* 15, 49, 76, 91, 110, 130; *P. hauseri* 1086-80, 1732-80)

The OPS of various *Proteus* species belonging to serogroup O52 has a trisaccharide O-unit containing one GalNAc and two Gal residues, one of which carries a pyruvic acid acetal (Fig. 3, compound **22**).[118–120]

Serogroup O53 (*P. vulgaris* TG 276-1)

The OPS of *P. vulgaris* O53 has an unusual teichoic acid-like structure with an O-unit containing one FucNAc4N and two ribitol 5-phosphate residues, one of which is randomly non-stoichiometrically *O*-acetylated.[121]

Serogroup O54 (*P. mirabilis* CCUG 10704, OE; *P. vulgaris* TG 103)

The acidic OPSs of both species are composed of common sugars and glycerol 1-phosphate.[122] They differ in the degree of phosphorylation, which is stoichiometric in *P. mirabilis* strains and does not exceed 50% in *P. vulgaris* TG 103, and in the *O*-acetylation of the latter OPS. The OPS similarity and differences are the basis for subdividing serogroup O54 into two subgroups: O54a,b for *P. mirabilis* strains and O54a,c for *P. vulgaris* TG 103.

Serogroup O55 (*P. vulgaris* TG 155)

The neutral OPS of *P. vulgaris* O55 has a branched tetrasaccharide O-unit containing only *N*-acetylated amino sugars, including GlcNAc, GalNAc, L-QuiNAc, and L-RhaNAc.[123]

Serogroup O56 (*Proteus* genomospecies 4)

The acidic branched OPS of *Proteus* genomospecies 4 contains common sugars and one residue of Qui3NAc.[35]

Serogroup O57 (*P. mirabilis* TG 83, TG 319, ATCC 49995, CCUG 10700, OA)

A branched pentasaccharide O-unit of the OPS of *P. mirabilis* O57 is composed of common sugars and glycerol 1-phosphate attached as a side chain.[124,125]

Serogroup O58 (*P. penneri* 6, 11, 12, 115, 125)

The acidic OPS of *P. penneri* O58 contains an amide of GalA with L-threonine (Fig. 1, compound **4**) attached as

a lateral sugar residue to the main chain composed of two common amino sugars and L-Rha.[43,81,88] The OPS has two sites of *O*-acetylation, one in the main chain and the other in the side chain.

Serogroup O59 (*P. penneri* 3, 5, 9, 14, 23, 47, 135)

The acidic OPS of *P. penneri* O59 has a linear pentasaccharide O-unit, which contains two amino acids. One of them, L-alanine, is amide-linked to the carboxyl group of GalA (Fig. 1, compound **2**), and the other, *N*-acetyl-D-alanine, is an *N*-acyl substituent on Qui3N (Fig. 2, compound **11**).[37,126,127] A derivative of Qui3N with L-serine has been found in the OPS of *E. coli* O:114, which has three more monosaccharides (GlcNAc, Gal and Rib) in common with *P. penneri* O59.[128]

Serogroup O60 (*P. myxofaciens* ATCC 19692)

A linear tetrasaccharide O-unit of the acidic OPS of *P. myxofaciens* O60 includes common amino sugars and an amide of GlcA with N^{ε}-[(*R*)-1-carboxyethyl]-L-lysine (Fig. 1, compound **7**).[49] The same amino-acid derivative is present in the OPS of *Providencia alcalifaciens* O23.[50,51]

Serogroup O61 (*P. penneri* 21, 33, 43, 50–55, 57, 58, 66–69, 72, 92, 104, 109, 116, 118, 127, 133, 136)

A branched pentasaccharide O-unit of the acidic OPS of *P. penneri* O61 consists of common sugars only.[129] Its structure was established by chemical methods in strain *P. penneri* 52 and confirmed in strains 21 and 54. Other *P. penneri* strains were classified in the O61 serogroup based on their serological identity.

Serogroup O62 (*P. penneri* 41, 56, 61, 64, 65, 70, 73, 74, 102, 113)

Another large group of serologically identical *P. penneri* strains were combined into serogroup O62. The acidic O62 OPS has a partially *O*-acetylated branched hexasaccharide O-unit containing two residues of L-Rha, one residue each of Glc, Gal, GlcNAc, and an isomer of *N*-acetylmuramic acid (Fig. 3, compound **20**), which was found in these bacteria for the first time in nature.[130] Originally, *P. penneri* 35 was erroneously placed in this group too,[131] but in fact it belongs to serogroup O64.

Serogroup O63 (*P. penneri* 22)

The OPS of *P. penneri* O63 has a branched pentasaccharide O-unit containing common sugars only. Its peculiar feature is the occurrence of GalNAc in the furanose form.[132]

Serogroup O64 (*P. penneri* 19, 24, 27, 29, 30, 35, 36, 38–40, 62, 71, 82, 83, 87, 94, 96, 100, 105, 114, 120, 122)

Proteus penneri O64 is divided into three subgroups: O64a,b,d for strains 29, 39, 40, and 62; O64a,c,e for strain 71; and O64a,b,c for the other strains. All OPSs of this group have the same linear carbohydrate backbone with a trisaccharide O-unit containing one residue of Gal and two GlcNAc residues.[133–136] In all strains, except for *P. penneri* 71 from subgroup O64a,c,e, one of the GlcNAc residues carries a lactic acid residue giving rise to *N*-acetylisomuramic acid (Fig. 3, compound **18**).[133,134] In strains of subgroups O64a,b,c and O64a,b,d, the O-units are interlinked differently by either β-(1 → 4)- or β-(1 → 6)-linkage, respectively. Only the OPS of subgroup O64a,b,d is *O*-acetylated.[134]

Serogroup O65 (*P. vulgaris* TG251; *P. penneri* 34, 78-81, 84-86, 88, 89, 95, 117, 119, 129)

The neutral OPS of serogroup O65 has a linear tetrasaccharide O-unit composed of common sugars only.[137]

Serogroup O66 (*P. penneri* 2)

A branched tetrasaccharide O-unit of the neutral OPS of *P. penneri* O66 contains Glc, GlcNAc and two rarely occurring sugars, L-6dTal and L-RhaNAc3NAc.[58] 6dTal is non-stoichiometrically *O*-acetylated at position 2. The O66 OPS is essentially identical to that of *E. coli* O109, which differs in the *O*-acetylation of L-RhaNAc3NAc only (authors' unpublished data).

Serogroup O67 (*P. penneri* 8, 93, 101)

The acidic OPS of *P. penneri* 8 has a branched hexasaccharide O-unit containing common sugars and L-FucNAc as well as Et*N*P on a GlcNAc residue (Fig. 4, compound **26**).[138]

Serogroup O68 (*P. penneri* 63)

The OPS of serogroup O68 has a branched pentasaccharide O-unit composed of GlcNAc, Glc and L-FucNAc in the ratio of 2:1:1. In addition, ethanolamine phosphate is present, which is typically linked at position 6 of GlcNAc.[139]

Serogroup O69 (*P. penneri* 25, 121, 123; *P. mirabilis* TG 277; *Proteus* genomospecies 6)

Strains of various *Proteus* species were classified in this serogroup. The acidic O69 OPS has a branched tetrasaccharide O-unit consisting of common sugars only but is distinguished by the presence of L-alanine with the free amino group as an *N*-acyl substituent of GlcN (Fig. 2, compound **10**).[62,140] The OPS of *P. penneri* 25 has three sites of non-stoichiometric O-acetylation, and that of *P. mirabilis* TG 277 possesses only one site.

Serogroup O70 (*P. penneri* 60)

The acidic OPS of *P. penneri* O70 has a linear O-unit composed of Glc 1-phosphate, Gal, GlcNAc, L-FucNAc and Qui4NAc.[141] Its structure resembles those of *P. vulgaris* O42,[112] *Shigella boydii* 13,[142] and *E. coli* O172,[143] which all have similar linear pentasaccharide-phosphate O-units.

Serogroup O71 (*P. penneri* 42; *P. mirabilis* R14/1959)

Serogroup O71 includes *P. penneri* 42[144] and *P. mirabilis* R14/1959, a mutant strain derived from *P. mirabilis* 1959 of serogroup O3.[145] The acidic OPS of both strains is composed of the same linear tetrasaccharide O-units containing common sugars only.

Serogroup O72 (*P. penneri* 1 and 4)

Proteus penneri strains 1 and 4 were classified in the complex serogroup O72 as two subgroups, O72a and O72a,b, respectively. Both OPSs have a branched tetrasaccharide O-unit consisting of common sugars and differ in decoration of the O72a,b OPS with lateral Glc and *O*-acetylation.[62,146] Both modifications are non-stoichiometric (~75% and ~55%, respectively).

Serogroup O73 (*P. penneri* 48, 75, 90, 103, 128)

Serogroup O73 is divided into two subgroups: O73a,b for strains 48, 90, and 103 and O73a,c for strains 75 and 128. The linear teichoic acid-like O73a,b OPS is composed of common sugars, ribitol 5-phosphate, and Et*N*P.[60,147] In the branched O73a,c OPS, a Glc residue in the main chain is glucosylated rather than phosphorylated.[148]

Serogroup O74 (*P. mirabilis* CCUG 10705, OF)

The acidic OPS of *P. mirabilis* O74 has a branched tetrasaccharide O-unit containing two residues each of GlcNAc and GalA. One of the GalA residues is amidated with L-alanine (Fig. 1, compound **2**) and the other is non-stoichiometrically (~50%) *O*-acetylated.[29] This OPS is related to the linear OPS of *P. mirabilis* O5,[28] in which the tetrasaccharide O-unit having the same carbohydrate backbone is polymerized differently. In addition, the OPS of *P. mirabilis* O5 is devoid of alanine and differs in the *O*-acetylation pattern. The O74 serogroup was formerly proposed for *P. mirabilis* CCUG 10701 (OB),[77] which was later reclassified into the *Proteus* O23 serogroup.[73]

Serogroup O75 (*P. mirabilis* CCUG 10702, OC)

A branched tetrasaccharide O-unit of the neutral OPS of *P. mirabilis* O75 consists of common sugars and L-Rha.[149]

Serogroup O76 (*P. vulgaris* HSC 438)

A peculiar feature of the OPS of *P. vulgaris* O76 is the presence of Qui4N bearing *N*-(1-carboxyethyl)alanine (alanopine) (Fig. 2, compound **16**), a rare component of bacterial carbohydrates.[150] Its configuration remains to be determined. An alanopine derivative of Qui4N is also present in the LPS core of *P. mirabilis* O6 and O57,[150] where it was originally misidentified as an alanine dipeptide derivative.[151] In addition to the Qui4N derivative, a linear pentasaccharide O-unit of *P. vulgaris* O76 contains neutral common sugars and L-FucNAc and has multiple *O*-acetylation sites (authors' unpublished data).

Serogroup O77 (*P. mirabilis* 3 B-m)

The neutral OPS of *P. mirabilis* O77 has a linear trisaccharide O-unit containing one residue each of L-6dTal, Glc and GlcNAc.[152] It resembles the backbone of the branched OPS of *P. penneri* O66.[58] As in other 6dTal-containing OPSs of *Proteus* (*P. vulgaris* O15 and *P. penneri* O66), this monosaccharide is *O*-acetylated at position 2.

Serogroup O78 (*P. mirabilis* 1 B-m)

The acidic OPS of *P. mirabilis* O78 has a branched tetrasaccharide O-unit containing common sugars and ribitol 5-phosphate, which is non-stoichiometrically (~50%) *O*-acetylated.[153]

Serology of Proteus *O-antigens*

Immunochemical characterization and serological classification of *Proteus* strains

The LPSs of representative strains of each of the existing *Proteus* O-serogroups and candidate strains for new O-serogroups were tested by various serological assays, including ELISA, passive immunohemolysis test, and immunoblotting with polyclonal rabbit O-antisera raised against heat-killed *Proteus* rods. Consideration of the serological results in view of the known O-antigen structures enabled recognition of domains that could be responsible for antibody binding (putative epitopes). In some cases, the homologous O-antigen was chemically modified and changes in the serospecificity were evaluated. In some other cases, partial synthetic O-antigen structures, for example amides of galacturonic acid with various amino acids,[25,43,87,96,145] were employed as inhibitors in serological reactions. As a number of *Proteus* epitopes are associated with the LPS core, the most informative test was immunoblotting as it showed directly which part of the LPS, the O-polysaccharide or the core, binds antibodies. In most cases, a decision on the classification of *Proteus* strains was made, and elucidation of epitope-associated partial

structures was performed, based on results of at least two serological assays.[154]

Polyclonal *Proteus* O-antisera contain several types of antibodies. The main antibody fraction usually recognizes the major O-antigen epitope, which defines the serogroup specificity, *i.e*. the classification of strains expressing the major epitope into the same serogroup. Other fractions are directed to minor epitopes on the O-antigen or, for example, as in *P. mirabilis* 1959 and OXK of serogroup O3a,3b,[155] on the LPS core. Strains having the same major epitopes but different minor O-antigen epitopes are classified in the same serogroup as subgroups. In most cases, major epitopes are associated with the same OPS carbohydrate backbone and their exact structures cannot be defined without extended immunochemical studies with synthetic antigens. In contrast, domains associated with minor O-antigen epitopes can usually be elucidated tentatively by a comparison of the structures of the cross-reactive antigens. They are often associated with a lateral glycosyl group or a non-sugar substituent, such as ethanolamine phosphate, choline phosphate or lactic acid.

In a few cases, the minor epitope structures remain unknown, whereas a partial structure associated with the major epitope could be clarified. An example is serogroup O14, in which the major epitope is associated with *N*-[(*R*)-1-carboxyethyl]ethanolamine phosphate linked to a galactose residue (epitope 14a), while minor epitopes 14b and 14c are associated with other parts of the O-units, which are significantly different.[53] Other examples are strains of *Proteus* serogroup O23, whose classification to the same serogroup is based on the identity of a terminal non-reducing tetrasaccharide fragment of the OPSs (major epitope 23a), whereas the minor epitopes are associated with the interior O-units having different (linear or branched) structures.[75] A similar situation occurs with *P. mirabilis* O5 and O74, which have the same terminal but different interior O-units. However, in this case, the serological cross-reactivity of the LPSs was weak (probably owing to amidation of one of the GalA residues with alanine in serogroup O74), and it was decided that combining the two strains into one serogroup is unreasonable.[29]

Serological cross-reactivity of *Proteus* O-antigens

One-way or two-way cross-reactivity of strains from different serogroups is common in *Proteus* and is due to sharing of minor epitopes on the O-antigen. In some cases, cross-reactive epitope are expressed by the LPS core, as, for example, in *P. mirabilis* O24 and O29.[79] Strains of *P. vulgaris* O45 and *P. penneri* O17 share an epitope associated with Fuc3N, which is located on the O-antigen of the former[115] and on the LPS core of the latter.[156] Similarly, the presence of an amide of L-lysine with GalA in the O-antigens of *P. mirabilis* 1959 (serogroup O3) and O28 and in the LPS core of *P. mirabilis* R14/1959 (serogroup O71) accounts for a serological relatedness of these strains.[145] Being only minor, cross-reactive core epitopes may not result in false serotyping to an O-serogroup.

Cross-reactive strains may belong to the same or different *Proteus* species, and strains of different *Proteus* species can be classified into the same serogroup. Although in some cases the chemical basis for the serological relatedness remains unknown, the associated partial O-antigen structures could be tentatively identified for many cross-reactive epitopes, as exemplified below.

As little OPS domain in common as a single 3-substituted β-D-Glc*p*NAc residue is sufficient for providing a cross-reactivity between *P. mirabilis* O23 antiserum and the LPSs of *P. mirabilis* O6,[31] as well as between *P. vulgaris* O22 antiserum and the LPS of *P. penneri* O59 and O61.[72] Cross-reactive minor epitopes are often associated with more complex monosaccharide derivatives, such as *N*-acetylisomuramic acid (O31 and O64a,b,d[92,94]), GlcNAc6*P*Etn (O16, O17 and O67[59,64]), an amide of GalA with L-lysine (O3, O26 and O28[84]), or ribitol 5-phosphate (O33 and O73a,73b[98,148]). A marked serological cross-reactivity of *P. mirabilis* O7 and O49 LPSs[32] was evidently due to the presence of similar negatively charged *N*-acyl derivatives of Qui4N with malonic and succinic acid, respectively.

A common chemical basis for cross-reactivity is sharing disaccharide fragments of O-antigens, from which occurring most frequently is an α-L-FucNAc-(1 → 3)-GlcNAc disaccharide. This fragment is evidently responsible for the serological relatedness of *P. mirabilis* O6, *P. vulgaris* O8, O12, and O39 as well as *P. vulgaris* O12, *P. penneri* O67, and O68.[34,44,110] A number of cross-reactive epitopes were assigned to other common disaccharides, as exemplified in Table 3. Strains may be serological related due to the occurrence of similar disaccharides, such as →2)-β-Fuc3NAc-(1 → 6)-α-GlcNAc-(1→ and →2)-β-Fuc3N(*R*-3HOBu)-(1 → 6)-α-GlcNAc-(1→ in the O-antigens of *P. vulgaris* O45 and strains of serogroup O17, respectively.[63]

Common trisaccharide fragments are characteristic of the O-antigens of a number of *Proteus* strains classified in different serogroups and often provide cross-reactivity of the LPSs; their examples are shown in Table 3. As in the case of disaccharide epitopes, the serological relatedness of strains may be due to the presence of only similar trisaccharide fragments of the OPSs, such as α-L-Rha-(1 → 4)-β-GlcA-(1 → 3)-β-GlcNAc and α-L-Rha-(1 → 4)-β-GalA-(1 → 3)-β-GlcNAc in *P. vulgaris* O22 and O32, respectively.[72,96] A significant similarity of the main chains of the O-antigens, which differs in the replacement of Glc and GalNAc with Gal and GlcNAc,

Table 3. Putative cross-reactive disaccharide and trisaccharide epitope structures

Common oligosaccharide	Cross-reactive strains	References
α-L-FucNAc-(1→3)-D-GlcNAc	*P. mirabilis* O6	34, 44, 110
	P. vulgaris O8, O12, O39	
	P. penneri O67, O68	
α-D-Glc*p*-(1→6)-D-Gal*p*NAc	*P. mirabilis* O57	125
	P. penneri O72a,72b	
β-D-Glc*p*-(1→3)-D-Glc*p*NAc	*P. mirabilis* O18, O20	69
β-D-Gal*p*-(1→3)-D-Glc*p*NAc	*P. mirabilis* O7, O20	69
β-D-Glc*p*A-(1→3)-D-Glc*p*NAc	*P. vulgaris* O4, O17, O37	27, 64
	P. penneri O17	
α-D-Gal*p*A-(1→3)-D-Glc*p*NAc	*P. mirabilis* O10, O43	40
β-D-Gal*p*A-(1→3)-D-Gal*p*NAc	*P. mirabilis* O23	73, 138
	P. vulgaris O23	
	Proteus O56	
	P. penneri O67	
β-D-Glc*p*NAc-(1→2)-D-Glc*p*	*P. vulgaris* O2	153
	P. penneri O68	
	P. mirabilis O77	
β-D-GalpNAc-(1→4)-D-Gal*p*	*P. mirabilis* O50	117
	P. penneri O65	
β-D-Glc*p*NAc-(1→4)-D-Gal*p*A	*P. vulgaris* O32	96
	P. mirabilis O71	
	P. penneri O71	
β-D-GlcNAc-(1→3)-D-GlcNAc	*P. vulgaris* O15	56
	P. mirabilis O30	
β-D-GlcNAc-(1→3)-D-GlcNAc4(*R*-Lac)	*P. vulgaris* O15	57
	P. mirabilis O40	
β-D-Glc*p*-(1→4)-α-L-Fuc*p*NAc-(1→3)-D-GlcpNAc	*P. vulgaris* O12	44, 139
	P. penneri O68	
α-D-Glc*p*NAc-(1→3)-α-L-Qui*p*NAc-(1→3)-D-Glc*p*NAc	*P. vulgaris* O2	92
	P. penneri O31a	
α-D-Glc*p*-(1→2)-β-D-Glc*p*A-(1→3)-D-Gal*p*NAc	*P. mirabilis* O3a,b, O29	90

respectively, is responsible for a marked serological cross-reactivity of *P. vulgaris* O21 and *P. mirabilis* O48.[70]

However, the presence in the O-antigens of common fragments may be sufficient for only a weak cross-reactivity or provide no cross-reactivity at all. A possible reason for the lack of cross-reactivity is that the corresponding common fragments are poorly accessible to antibodies and/or are masked by lateral glycosyl or non-sugar groups. Other explanations are that the conformations of the shared oligosaccharides may not be the same owing to different sizes of the O-units or that an epitope larger than a common fragment is necessary for antibody binding.

Antigenic relatedness between *Proteus* and other bacteria

Multiple antigenic relationships have been demonstrated between O-antigens of *Proteus* and some other bacterial genera, such as *Hafnia*, *Providencia*, and *Escherichia*. For instance, O-antisera against *P. mirabilis* O13 and *P. myxofaciens* O60 cross-reacted with the LPSs of *Providencia alcalifaciens* O14 and O23. Serological studies revealed an important role of amides of uronic acids with N^{ε}-(1-carboxyethyl)-L-lysine in manifesting the serospecificity of these strains.[48,49,51,52] Remarkably, the configuration of neither amino acid nor uronic acid was found to be significant for recognition by cross-reactive antibodies.

The serological relatedness of *P. mirabilis* O38 and *Providencia alcalifaciens* O4 and O33 is evidently due to the presence of a common epitope associated with a derivative of Qui4N with *N*-acetylaspartic acid.[108,109] Significant structural similarities of the OPSs have been shown for serologically related bacteria *P. vulgaris* O21, *P. mirabilis* O48, *Hafnia alvei* 744, and PCM 1194, all having oligosaccharide-phosphate O-units and differing only in *N*-acyl substituents on a GlcN residue.[71]

The two-way cross-reactivity of the LPSs of *Proteus* genomospecies 4 (serogroup O56) and *Providencia stuartii* O18 could be accounted for by sharing a β-Qui*p*3NAc-(1 → 6)-GlcNAc disaccharide fragment, which most likely occupies the non-reducing end of the OPS chain,

and/or a linear α-Gal*p*NAc-(1 → 4)-β-Qui*p*3NAc-(1 → 6)-GlcNAc trisaccharide fragment.[35,157]

Remarkable structural similarities are observed between the O-antigens of *P. vulgaris* O12[44] and *E. coli* O29,[45] *P. mirabilis* O36[102] and *E. coli* O153,[103] *P. penneri* O66[58] and *E. coli* O109 (authors' unpublished data). The O-antigens in each pair differ only in the O-acetylation patterns and in the first pair also in the replacement of an α-GalNAc residue in *P. vulgaris* O12 with an α-Gal residue in *E. coli* O29. Their cross-reactivity has not been tested but one can expect that these strains are, pair-wise, closely related serologically. This is also the case for *P. vulgaris* O25[38] and *Alteromonas haloplanktis* KMM 156,[82] whose O-antigens share a branched β-Glc*p*NAc-(1 → 2)[α-Glc*p*3(*R*-Lac)-(1 → 3)]-α-L-Rha*p* trisaccharide fragment.

Proteus mirabilis OXK is known to cross-react markedly with *Orientia tsutsugamushi* sera, as *P. vulgaris* OX19 of serogroup O1 and *P. vulgaris* OX2 of serogroup O2 do with sera against various *Rickettsia* species. Since 1916, this phenomenon has enabled employing *Proteus* OX strains in the unspecific Weil–Felix test for serodiagnostics of rickettsiosis.[158] Immunochemical studies revealed that the common epitopes reside on the *Proteus* OPSs,[16,17,19,25,155,159] but their exact structures, as well as the structures of the corresponding cross-reactive antigens of *Orientia* and *Rickettsia*, remain unknown.

Selected biological activities related to Proteus *O-antigens*

Lipopolysaccharides of Gram-negative bacteria, including *Proteus*, are able to trigger the activation of the human immune system via pathogen-associated pattern-recognition receptors, such as LPS-binding protein, CD14, MD2, and toll-like receptor (TLR)4. The activated immune cells release vasoactive substances and pro-inflammatory cytokines, such as tumor-necrosis factor (TNF)-α, interleukin (IL)-1, IL-6, IL-8, which promote and control early innate immune responses. An excessive cytokine production leads to septic shock, including severe pathophysiological derangements and multi-organ failure. The final outcome of moderate inflammatory responses is the induction of LPS-specific antibodies, which have a high diagnostic value.

Although the endotoxically active part of LPS is lipid A, the majority of anti-LPS antibodies are directed against the OPS part. In *Proteus* anti-LPS sera, antibodies to the core moiety are also abundant. The occurrence of O-antigen-specific antibodies in normal human sera is not uncommon. For instance, 25% of blood donors' sera contained a significantly elevated level of anti-*P. mirabilis* O36 antibodies.[102] The presence and a higher level of anti-*Proteus* antibodies correlate with the Thr399Ile TLR4 polymorphism,[102] which may predispose a susceptibility to Gram-negative septic shock.

Smooth-form LPS contributes significantly to the resistance of Gram-negative bacteria to the bactericidal action of normal serum. It was shown that the hydrophobic membrane attack complex of complement cannot pass the hydrophilic barrier provided by long-chain OPSs to gain access to the bacterial outer and inner membranes and form pores leading to bacterial lysis.[160] Studies of *Proteus* strains having different LPSs confirmed this hypothesis. It was found that *P. mirabilis* mutants with OPS-lacking R-form LPS are sensitive to the action of normal serum, whereas most wild-type *P. mirabilis* strains as well as about half of *P. vulgaris* and *P. penneri* strains are resistant.[161] The serum sensitivity of some *Proteus* strains with S-form LPS may result from an insufficient OPS length or/and a low concentration of OPS-containing LPS molecules on the cell surface.

As a surface antigen, OPS, together with the capsular polysaccharide, is involved in glycocalyx formation,[161] which enables bacteria to grow in biofilm. Glycocalyx binds bacterial cells together via lectins or cations and also makes possible their adhesion to epithelial cells or an artificial surface, for example urological catheters.[162] Being closed in a glycocalyx capsule, bacteria are protected against the action of antibodies and other antibacterial factors.[163]

Surface polysaccharides, including OPS, play a role in swarming phenomenon of *Proteus* bacteria[164] as they facilitate the migration of swarmer cells on solid media by reducing cell friction.[165] Indeed, whereas most *P. mirabilis*, *P. vulgaris*, and *P. penneri* strains having an S-form LPS can swarm intensively, the Re-mutant of *P. mirabilis* R45 with an LPS consisting of lipid A and a small core of 3-deoxy-D-*manno*-oct-2-ulosonic acid residues was unable to swarm and the Ra mutant of *P. mirabilis* R110 containing lipid A and the complete core region expressed only a limited ability to migrate on solid medium.[161]

The acidic character of *Proteus* O-antigens may significantly contribute to stone formation within the urinary tract. The negatively charge bacterial polysaccharides bind magnesium and calcium cations via electrostatic interactions and accelerate the supersaturation and crystallization of the salts. The structure and the anionic character of some *Proteus* capsular polysaccharides were shown to enhance struvite crystal formation.[166] It was demonstrated that the role of urease, the major factor involved in stone formation that is synthesized by *Proteus* bacteria, may be modified by OPS.[167] Particularly, it was found that variations in the sugar composition of *Proteus* LPS may either enhance or inhibit the crystallization of struvite and apatite depending on its chemical structure and the ability to bind cations.

The OPS of *P. vulgaris* O12 bound magnesium and calcium ions weakly but increased the crystallization rate, whereas the OPSs of *P. mirabilis* O28 and *P. vulgaris* O47, which are able to bind a large amount of the cations, inhibited the crystallization process.[167] It was hypothesized that Mg^{2+} and Ca^{2+} weakly bound to the OPSs could be easily released from the bacterial surface, giving rise to a local supersaturation of the solution and, as a result, to acceleration of crystallization and stone formation.

Conclusions

A characteristic feature of the *Proteus* O-polysaccharides is their acidic character due to the presence of hexuronic acids, non-sugar carboxylic acids, or phosphate groups. They are also enriched in *N*-acylated amino and diamino sugars, including rarely occurring 6-deoxy derivatives. From the non-sugar components, amino acids are rather common as either *N*-acyl groups of amino sugars or substituents of the carboxyl group of uronic acids. 1-Carboxyethyl derivatives of alanine and lysine were found in *Proteus* for the first time in bacterial polysaccharides. Phosphate-linked alcohols, such as ethanolamine and its *N*-substituted derivatives, choline, glycerol, and ribitol, are present in many *O*-polysaccharides as well.

The size of *Proteus* O-units varies from trisaccharide to hexasaccharide, tetrasaccharide O-units being most common. In some O-polysaccharides, the O-units are linked via a phosphate group and some others have glycerol 1-phosphate or ribitol 5-phosphate in the main chain and thus resemble teichoic acids. Therefore, the *Proteus* O-polysaccharides are highly diverse in structure, and the data presented in this review are useful as a basis for bioinformatics studies of bacterial glycosyl transferases.

In spite of the diversity of O-polysaccharide structures, antigenic relationships are common for *Proteus* strains due to sharing of structural domains in the LPS. Marked cross-reactions are observed due to the occurrence of common epitopes on the O-polysaccharides or on the LPS core or on the O-polysaccharide of one cross-reactive strain and the core of another strain. The cross-reactive epitopes may be limited to a single sugar or a non-sugar group or extended to a disaccharide or a trisaccharide. Depending on the degree of serological relatedness and O-antigen structure similarity, serologically related strains are either combined into one O-serogroup as subgroups or placed into different O-serogroups (Table 2). As a result, recently the Kauffmann–Perch serological classification scheme of *Proteus* strains[10,11] has been significantly modified by combining several existing serogroups, dividing some others to subgroups, and adding a number of new O-serogroups. It is not excluded that the scheme will be further extended, as serologically distinct *Proteus* strains are being constantly discovered by the serological screening of clinical and environmental isolates.

Some *Proteus* O-antigens are remarkably similar to those of other enteric bacteria, mostly *E. coli*, *Providencia*, and *Hafnia*. O-Antigen pairs of different genera may have the same carbohydrate backbone, the differences being restricted to the nature of *N*-acyl groups or *O*-acetylation pattern. These similarities indicate a role of horizontal gene transfer in the course of diversification of bacterial O-antigens.

Although the O-antigens are mainly discussed in the context of the immunospecificity of bacteria, they are important for bacterial virulence. As in some other enteric bacteria, the presence of a long-chain O-polysaccharide is important for the resistance of *Proteus* to normal serum. The *Proteus* O-polysaccharides are involved in the formation of protective glycocalyx and are important for swarming growth of the bacteria. The acidic character of *Proteus* O-antigens is suggested to play a crucial role in stone formation within the urinary tract.

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