Structure of O-Antigens

3

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3.1 Introduction

The lipopolysaccharide (LPS) is the major constituent of the outer leaflet of the outer membrane of Gram-negative bacteria. Its lipid A moiety is embedded in the membrane and serves as an anchor for the rest of the LPS molecule. The outermost repetitive glycan region of the LPS is linked to the lipid A through a core oligosaccharide (OS), and is designated as the O-specific polysaccharide (O-polysaccharide, OPS) or O-antigen. The O-antigen is the most variable portion of the LPS and provides serological specificity, which is used for bacterial serotyping. The OPS also provides protection to the microorganisms from host defenses such as complement mediated killing and phagocytosis, and is involved in interactions of bacteria with plants and bacteriophages. Studies of the OPSs ranging from the elucidation of their chemical structures and conformations to their biological and physicochemical properties help improving classification schemes of Gram-negative bacteria. Furthermore, these studies contributed to a better understanding of the mechanisms of pathogenesis of infectious diseases, as well as provided information to develop novel vaccines and diagnostic reagents.

Composition and structures of O-antigens have been surveyed repeatedly [1–7]. The number of OPSs with complete structural elucidation is rapidly growing and an annually updated Bacterial Carbohydrate Structure Database (BCSDB) is available online at http://www.glyco.ac.ru/bcsdb3/. The present chapter provides an updated collection of data on composition and structures of the OPSs published until the end of 2010. To avoid extensive citation of structures already reported, only earlier reviews are referenced. Whenever known OPS structures are presented in an earlier review or, in the case of *Escherichia coli*, in a permanently updated database, they

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are only briefly discussed in this chapter. Various OPS structures were established by older methods and required reinvestigation using new techniques. For structures already revised, only the publication reporting the final structure is cited.

Classification of Gram-negative bacteria is subject to change. In this review, the current names for bacterial classes, families, genera and species are used according to the NCBI Taxonomy Browser (http://www.ncbi.nlm.nih.gov/Taxonomy/). When an OPS structure was reported under a different bacterial name, the old name is indicated in parentheses.

3.2 Composition of O-Antigens

Typical components of the OPSs are both monosaccharides widely distributed in nature and uncommon sugars (Table 3.1), including those that have not been found elsewhere (here and below, the descriptor D in abbreviations of monosaccharides of the D series is omitted).

Most monosaccharides exist in the pyranose form (in the OPS structures below, the descriptor *p* for this form is omitted) but several are present as furanosides (Ara, Rib, L6dAlt, xylulose) or may occur in both forms (Gal, Fuc, paratose); in a few OPSs, Rib and L6dAlt are present as pyranosides and GalNAc as a furanoside.

From non-carbohydrate constituents (Table 3.2), commonly occurring are *N*-acetyl and *O*-acetyl groups. Less common is a methyl group, which is linked to hydroxyl or amino groups or esterifies a hexuronic acid. In various OPSs, hexuronic acids exist as a primary amide (this is indicated below by letter N, e.g. GalAN) or an amide with an amino compound like 2-amino-2-deoxyglycerol (GroN) or amino acids (in case of L-lysine and its N^{ε}-(1-carboxyethyl) derivatives hexuronic acids are linked to their α-amino group). Phosphate has been found only as diesters, including a cyclic phosphate.

3.3 Structures of O-Antigens

3.3.1 General Aspects

The OPS is the most variable LPS component in terms of composition and structure. The high diversity of O-antigens results mainly from genetic variations in the O-antigen gene clusters, and is further expanded by various prophage genes, which cause additional modifications such as lateral glycosylation or/and O-acetylation (see Chap. 11). The OPS is made of oligosaccharide repeats (O-units) consisting of two to eight different monosaccharide residues (heteroglycans) or, in some bacteria, of identical sugars (homoglycans). The O-unit is first assembled on a lipid carrier and then polymerized, whereas homoglycans and part of the heteroglycans with disaccharide O-units are synthesized by an alternative pathway including a sequential transfer of single monosaccharides to the growing chain (see Chap. 9). Lateral

Table 3.1 Monosaccharide components of OPSs

Pentoses, hexoses, heptoses and their deoxy derivatives	
D-arabinose (Ara)	D-glucose (Glc)
D-, L-xylose (Xyl, LXyl)	D-mannose (Man)
D-ribose (Rib)	D-galactose (Gal)
4-deoxy-D-*arabino*-hexose (4daraHex)	6-deoxy-D-gulose (6dGul)
6-deoxy-L-glucose (L-quinovose, LQui)	3,6-dideoxy-D-*arabino*-hexose (tyvelose, Tyv)
6-deoxy- D-, L-galactose (D-, L-fucose; Fuc, LFuc)	3,6-dideoxy-L-*arabino*-hexose (ascarylose, Asc)
6-deoxy-D-, L-mannose (D-, L-rhamnose; Rha, LRha)	3,6-dideoxy-D-*ribo*-hexose (paratose, Par)
6-deoxy-L-altrose (L6dAlt)	3,6-dideoxy-D-*xylo*-hexose (abequose, Abe)
6-deoxy-D-, L-talose (6dTal, L6dTal)	3,6-dideoxy-L-*xylo*-hexose (colitose, Col)
D-*glycero*-D-*manno*-heptose (DDmanHep)	L-*glycero*-D-*manno*-heptose (LDmanHep)
D-*glycero*-D-*galacto*-heptose (DDgalHep)	6-deoxy-D-*manno*-heptose (6dmanHep)
2-Amino-2-deoxyhexoses, amino and diamino 6-deoxyhexoses	
D-glucosamine (GlcN)	3-amino-3-deoxy-D-fucose (Fuc3N)
D-galactosamine (GalN)	4-amino-4-deoxy-D-quinovose (Qui4N)
D-mannosamine (ManN)	4-amino-4-deoxy-D-, L-rhamnose (Rha4N, LRha4N)
D-, L-quinovosamine (QuiN, LQuiN)	4-amino-4-deoxy-D-fucose (Fuc4N)
L-rhamnosamine (LRhaN)	2,3-diamino-2,3-dideoxy-L-rhamnose (LRhaN3N)
D-, L-fucosamine (FucN, LFucN)	2,4-diamino-2,4-dideoxy-D-quinovose (QuiN4N)
6-deoxy-L-talosamine (L6dTalN)	2,4-diamino-2,4-dideoxy-D-fucose (FucN4N)
3-amino-3-deoxy-D-, L-quinovose (Qui3N, LQui3N)	
Hexuronic acids, amino and diamino hexuronic acids	
D-glucuronic (GlcA)	D-glucosaminuronic (GlcNA)
D-mannuronic (ManA)	D-mannosaminuronic (ManNA)
D-galacturonic (GalA)	D-, L-galactosaminuronic (GalNA, LGalNA)
L-altruronic (LAltA)	L-altrosaminuronic (LAltNA)
L-iduronic (LIdoA)	L-gulosaminuronic (LGulNA)
3-amino-3-deoxy-D-glucuronic (Glc3NA)	2,3-diamino-2,3-dideoxy-D-glucuronic (GlcN3NA)
2,3-diamino-2,3-dideoxy-D-mannuronic (ManN3NA)	2,3-diamino-2,3-dideoxy-D-galacturonic (GalN3NA)
2,3-diamino-2,3-dideoxy-L-guluronic (LGulN3NA)	2,4-diamino-2,4-dideoxyglucuronic (GlcN4NA)
Keto sugars	
D-, L-*threo*-pent-2-ulose (D-, L-xylulose; Xlu, LXlu)	
2-amino-2,6-dideoxy-D-*xylo*-hexos-4-ulose	
3-deoxy-D-*manno*-oct-2-ulosonic acid (ketodeoxyoctonic acid, Kdo)	
5-amino-3,5-dideoxy-D-*glycero*-D-*galacto*-non-2-ulosonic acid (neuraminic acid, Neu)	

(*continued*)

Table 3.1 (continued)

5,7-diamino-5,7,9-trideoxynon-2-ulosonic acid[a]
5,7-diamino-3,5,7,9-tetradeoxy-L-*glycero*-L-*manno*-non-2-ulosonic (pseudaminic) acid (Pse)
5,7-diamino-3,5,7,9-tetradeoxy-D-*glycero*-D-*galacto*-non-2-ulosonic (legionaminic) acid (Leg)
5,7-diamino-3,5,7,9-tetradeoxy-D-*glycero*-D-*talo*-non-2-ulosonic (4-epilegionaminic) acid (4eLeg)
5,7-diamino-3,5,7,9-tetradeoxy-L-*glycero*-D-*galacto*-non-2-ulosonic (8-epilegionaminic) acid (8eLeg)
5,7,8-triamino-3,5,7,8,9-pentadeoxynon-2-ulosonic acid[b]
3-deoxy-D-*lyxo*-hept-2-ulosaric acid
Branched sugars[c]
3-*C*-methyl-D-mannose (Man3*C*Me)
3-*C*-methylrhamnose (Rha3*C*Me)[a]
3,6-dideoxy-4-*C*-[(*R*)-, (*S*)-1-hydroxyethyl]-D-*xylo*-hexose (yersiniose A, yersiniose B)
3,6,8-trideoxy-4-*C*-[(*R*)-1-hydroxyethyl]-D-*gulo*-octose (erwiniose)
3,6,10-trideoxy-4-*C*-[(*R*)-hydroxyethyl]-D-*erythro*-D-*gulo*-decose (caryophillose)
2-amino-4-*C*-(2-carbamoyl-2,2-dihydroxyethyl)-2,6-dideoxy-D-galactose (shewanellose)
4,8-cyclo-3,9-dideoxy-L-*erythro*-D-*ido*-nonose (caryose)

[a]The configuration of the monosaccharide remains unknown.
[b]The monosaccharide has the L-*glycero*-L-*manno* or D-*glycero*-L-*manno* configuration.
[c]For structures of branched monosaccharides see also review [7].

glycosyl groups and *O*-acetyl groups may be added to the growing OPS chain or after polymerization, and their content is often non-stoichiometric.

Some bacteria have LPS lacking OPS due to the absence or inactivation of the O-antigen gene cluster. When bacteria are able to assemble but unable to polymerize the O-unit, they elaborate LPS containing a single O-unit linked to the core OS. Several LPS forms may coexist in one strain. In some cases, LPS forms lacking O-antigen are designated as lipooligosaccharide. The length of the OPS chain varies considerably from one O-unit to more than 50 O-units. The chain length distribution is modal (except for bacteria which possess an S-layer) and is specific to each bacterial strain. It appears to be fine-tuned to give bacteria advantages in particular niches.

Most chemical data reported on OPSs are limited to the structure of the so-called chemical repeating unit, which may or may not agree with the structure of the biological O-unit that is based on the order of synthesis and that is the substrate for the O-antigen polymerization. Therefore, the monosaccharide sequence of the chemical repeating unit may be any cyclic permutation of the biological unit. Recently, it has been shown that in many heteroglycans, the first monosaccharide of the O-unit whose transfer to a lipid carrier initiates biosynthesis of the O-antigen, is a derivative of a 2-amino-2-deoxy-D-hexose (GlcN, GalN) or a 2-amino-2,6-dideoxy-D-hexose (QuiN, FucN, QuiN4N, FucN4N), all having the D-*gluco* or D-*galacto* configuration. One can assume that, when present, such an amino sugar is the first in other OPSs too. In several bacteria, e.g. *Salmonella enterica*, the first monosaccharide of the O-unit is Gal, whereas in many other species, the biological O-unit structure remains unknown.

Table 3.2 Non-carbohydrate components of OPSs

O-Linked (O-alkyl groups and acetals)	
(*R*)-, (*S*)-1-carboxyethyl (lactic acid ethers; *R*lac, *S*lac)	
(*1R,3R*)-, (*1S,3R*)-1-carboxy-3-hydroxybutyl (2,4-dihydroxypentanoic acid 2-ethers)	
(*R*)-, (*S*)-1-carboxyethylidene (pyruvic acid acetals; *R*pyr, *S*pyr)	
N-Linked (N-acyl groups)	
formyl (Fo)	acetimidoyl (Am)
(*R*)-, (*S*)-2-hydroxypropanoyl (*R*2Hp, *S*2Hp)	3-hydroxypropanoyl (3Hp)
(*R*)-, (*S*)-3-hydroxybutanoyl (*R*3Hb, *S*3Hb)	4-hydroxybutanoyl (4Hb)
L-glyceroyl (LGroA)	(*S*)-2,4-dihydroxybutanoyl
(*3S,5S*)-3,5-dihydroxyhexanoyl	malonyl
succinyl	(*R*)-, (*S*)-2-hydroxy-4-succinyl (4-D-malyl, 4-L-malyl)
(*S*)-2-hydroxy-5-glutaryl	glycyl (Gly)
D-, L-alanyl (DAla, LAla)	L-seryl (LSer)
D-homoseryl (DHse)	L-allothreonyl (LaThr)
D-, L-4-aspartyl (4DAsp, 4LAsp)	*N*-(1-carboxyethyl)alanyl[a]
(*2R,3R*)-3-hydroxy-3-methyl-5-oxoprolyl	3-hydroxy-2,3-dimethyl-5-oxoprolyl[a]
2,4-dihydroxy-3,3,4-trimethyl-5-oxoprolyl[a]	(*2R,3R,4S*)-3,4-dihydroxy-1,3-dimethyl-5-oxoprolyl
Carboxyl-linked (amides)	
2-amino-2-deoxyglycerol (GroN)	L-serine (LSer)
glycine (Gly)	L-threonine (LThr)
D-, L-alanine (DAla, LAla)	D-allothreonine (DaThr)
L-lysine (LLys)	
N^{ε}-[(*R*)-, (*S*)-1-carboxyethyl]-L-lysine ('alaninolysine'; *R*alaLys, *S*alaLys)	
Phosphate-linked (phosphodiesters)	
glycerol (Gro)	D-glyceric acid (DGroA)
ribitol (Rib-ol)	L-arabinitol (LAra-ol)
2-aminoethanol (ethanolamine, EtN)	2-[(*R*)-1-carboxyethylamino]ethanol
2-(trimethylammonio)ethanol (choline)	2-amino-2-deoxy-2-*C*-methylpentonic acid[a]

[a]The configuration of the amino acid remains unknown.

The core OS may carry a polysaccharide that is structurally different from the O-antigen and is encoded by a locus different from the O-antigen gene cluster. Examples of this are the enterobacterial common antigen produced by the Enterobacteriaceae [8] and the A-band O-antigen in *Pseudomonas aeruginosa* [9]. On the other hand, a repeat of the same structure as the O-unit may be employed as a building block for another surface polymer, e.g. a capsular polysaccharide [5] or a glycoprotein [10]. More than one structurally related or sometimes unrelated OPSs, may occur in one strain. In the latter case, one of the glycans may not be a part of the LPS but for example a capsular polysaccharide that is coextracted with the LPS [11].

The repetitive OPS structure is often masked by one or more non-stoichiometric modifications, including glycosylation, O-acetylation, methylation, phosphorylation or amidation (in the structures shown below, non-stoichiometric substituents are indicated in italics). Less common are epimerization at C-5 of hexuronic acids and alternative N-acylation of an amino group by different acyl groups. A rare reason for the lack of the strict regularity is a random or in another manner irregular distribution of α- and β-linked monosaccharide residues along the polymer chain.

Many LPSs, especially with homopolysaccharide O-chains, have additional nonrepetitive domains, which result from specific initiation and termination steps of the OPS biosynthesis. For instance, incorporation of an O-methylated sugar or a different monosaccharide to the non-reducing end is thought to be a signal for cessation of the OPS chain synthesis, which allows termination of the O-chain at a specific sugar residue rather than at any residue. Another non-repetitive domain may occur between the OPS and the core OS, such as a primer of a 2-*N*-acetylamino sugar whose transfer to a lipid carrier initiates the O-antigen synthesis. More complex reducing-end domains have been found in a few OPSs but they may be much more common than anticipated. Further information on OPS-associated non-repetitive structures is given in a recent review [7], whereas the present review focuses on the O-unit structures.

3.3.2 γ-Proteobacteria

3.3.2.1 Enterobacteriaceae

A majority of the bacteria, whose O-antigen structures have been elucidated, belong to the family Enterobacteriaceae.

Salmonella

Salmonella species, the agents of salmonellosis, are a leading cause of food-borne infections in many countries; several serovars are responsible for more severe diseases, such as typhoid fever. Currently, strains of *S. enterica* are combined into 46 O-serogroups, including former serogroups A–Z. Serovar names are used for strains of ssp. *enterica*, whereas Latin numbers are used to designate other subspecies: II for ssp. s*alamae,* IIIa for ssp. *arizonae*, IIIb for ssp. *diarizonae*, etc. The structures of the OPSs of *S. enterica* established by that time have been reviewed in 2006 [12], and more structures are shown below (Table 3.3).

Strains of serogroups A, B, D and E were the first bacteria whose O-antigen structures were elucidated in detail. They possess similar Man-L-Rha-Gal- main chains, in which the position of substitution of Man and the configuration of the linkages of Man and Gal vary both between and within O-serogroups. In serogroup D_3, α-Man- and β-Man-containing O-units coexist. In serogroups A, B and D, Man bears a 3,6-dideoxyhexose having D-*ribo* (paratose), D-*xylo* (abequose) or D-*arabino* (tyvelose) configuration, respectively, whereas in serogroup E, no 3,6-dideoxyhexose is present. Outside these serogroups, the OPSs display a variety of structures. Neutral sugars (Man, Glc, Gal, L-Rha, L-Fuc), GlcNAc and GalNAc

Table 3.3 Structures of *Salmonella* OPSs

O2 (A) Paratyphi [13,14]	2)Man(α1-4)LRha*2Ac*(α1-3)Gal(α1- Par(α1-3)┘ Glc(α1-4)┘
O4 (B) Typhimurium, Agona,[a] Abortusequi[a] [13,15-18]	2)Man(α1-4)LRha(α1-3)Gal(α1- Abe*2Ac*(α1-3)┘ *Glc(α1-4)*┘
O4 (B) Bredeney, Typhimurium SL3622[a] [13,16,19]	2)Man(α1-4)LRha(α1-3)Gal(α1- Abe*2Ac*(α1-3)┘ *Glc(α1-6)*┘
O6,7 (C_1) Livingstone [20]	2)Man(β1-2)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(β1- Glc(α1-3)┘
O6,7 (C_1) Thompson [21]	2)Man(β1-2)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(β1- and 2)Man(β1-2)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(β1- Glc(α1-3)┘
O6,7 (C_1) Ohio [22]	2)Man(β1-2)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(β1- Glc(α1-3)┘
O6,7 (C_4) Livingstone var. 14[+] (*S. eimsbuttel*) [23]	2)Man(β1-2)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(β1- Glc(α1-3)┘
O8 (C_2) Newport [13,24]	4)LRha*2Ac*(β1-2)Man(α1-2)Man(α1-3)Gal(β1- Abe(α1-3)┘ *Glc2Ac(α1-3)*┘
O8 (C_3) Kentucky I.S. 98 [13]	4)LRha(β1-2)Man(α1-2)Man(α1-3)Gal(β1- Abe(α1-3)┘ *Glc2Ac(α1-4)*┘
O8 (C_3) Kentucky 98/39 [25]	4)LRha(β1-2)Man(α1-2)Man(α1-3)Gal(β1- Abe(α1-3)┘ *Glc(α1-2)*┘
O9 (D_1) Typhi, Enteritidis SE6[a], Gallinarum bv. Pullorum 77[a] [26-28]	2)Man(α1-4)LRha(α1-3)Gal(α1- Tyv(α1-3)┘ *Glc2Ac(α1-4)*┘
O9 (D_1) Enteritidis I.S. 64, Gallinarum bv. Pullorum 11 [28,29]	2)Man(α1-4)LRha(α1-3)Gal(α1- Tyv(α1-3)┘
O9,46 (D_2) Strasbourg [13]	6)Man(β1-4)LRha(α1-3)Gal(α1- Tyv(α1-3)┘ *Glc(α1-4)*┘
O9,46 (D_2) II (*S. haarlem*) [30]	6)Man(β1-4)LRha(α1-3)Gal(α1- Tyv(α1-3)┘
O9,46,27 (D_3) II (*S. zuerich*) [31]	6)Man(α/β1-4)LRha(α1-3)Gal(α1- Tyv(α1-3)┘ *Glc(α1-6)*┘
O3,10 (E_1) Anatum [26,32]	6)Man(β1-4)LRha(α1-3)Gal*6Ac*(α1-
O3,10 (E_1) Muenster [13]	6)Man(β1-4)LRha(α1-3)Gal(α1- *Glc(α1-4)*┘
O3,10 (E_2) Anatum var. 15[+] (*S. newington*) [26]	6)Man(β1-4)LRha(α1-3)Gal(β1-
O3,10 (E_3) Lexington var. 15[+],34[+] (*S. illinois*) [26]	6)Man(β1-4)LRha(α1-3)Gal(β1- *Glc(α1-4)*┘
O1,3,19 (E_4) Senftenberg [13,26]	6)Man(β1-4)LRha(α1-3)Gal(α1- *Glc(α1-6)*┘
O11 (F) Aberdeen [33]	3)Gal(α1-4)LRha(α1-3)GlcNAc(β1- Man(β1-4)┘
O13 (G) [34]	2)LFuc(α1-2)Gal(β1-3)GalNAc(α1-3)GlcNAc(α1-

(*continued*)

Table 3.3 (continued)

O6,14 (H) Boecker, Carrau [35,36]	6)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(α1- and 6)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(α1- Glc(α1-3)┘
O6,14 (H) Madelia [37]	6)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(α1- and 6)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(α1- and Glc(α1-3)┘ 6)Man(α1-2)Man(α1-2)Man(β1-3)GlcNAc(α1- Glc(α1-4)┘
O16 (I) [38]	4)GalNAc(α1-6)Man*3Ac*(α1-3)LFuc(α1-3)GalNAc(β1- └(3-1α)LFuc *Glc(β1-4)*┘
O17 (J) [39]	2)Gal(α1-3)ManNAc(β1-6)Gal*f*2*Ac*(β1-3)GlcNAc(β1- └(4-1α)Gal*f*
O18 (K) Cerro [40]	4)Man(α1-2)Man(α1-2)Man(β1-3)GalNAc(α1-
O21 (L)[b] [41]	4)GalNAc(β1-3)Gal(α1-4)Gal(β1-3)GalNAc(β1- └(3-1α)GlcNAc
O28 (M, O28$_1$,28$_2$) Telaviv [42]	4)Qui3NAc(β1-3)Rib*f*(β1-4)Gal(β1-3)GalNAc(α1- *Gal(α1-3)*Gal(α1-3)┘ *Glc(α1-4)*┘
O28 (M, O28$_1$,28$_3$) Dakar [43]	4)Qui3NAc(α1-3)LRha(α1-4)Gal(β1-3)GalNAc(α1- Glc(β1-4)┘
O30 (N) Landau [44]	2)Rha4NAc(α1-3)LFuc(α1-4)Glc*6Ac*(β1-3)GalNAc(α1-
O30 (N) Urbana, Godesberg [45]	2)Rha4NAc(α1-3)LFuc(α1-4)Glc(β1-3)GalNAc(α1 Glc(β1-4)┘
O35 (O) Adelaide [46]	4)Glc(α1-4)Gal(α1-3)GlcNAc(β1- Col(α1-3)┘ └(6-1α)Col
O38 (P) [38]	3)Gal(β1-4)Glc(β1-3)GalNAc(β1- Gal(β1-4)┘ └(2-1β)GlcNAc
O39 (Q) Mara[c] [47]	2)Qui3NAc(α1-3)Man(α1-3)LFuc(α1-3)GalNAc(α1-
O40 (R) Riogrande [48]	4)GalNAc(α1-3)Man(β1-4)Glc(β1-3)GalNAc(α1- GlcNAc(β1-2)┘
O41 (S) [49]	2)Man(β1-4)Glc(α1-3)LQuiNAc(α1-3)GlcNAc(α1-
O42 (T) [50]	3)LRha(α1-2)LRha(α1-2)Gal(α1-3)GlcNAc(β1- └(2-1β)ManNAc
O43 (U) Milwaukee [51]	4)LFuc(α1-2)Gal(β1-3)GalNAc(α1-3)GlcNAc(β1- Gal(α1-3)┘
O44 (V) [52]	2)Glc(α1-6)Glc(α1-4)Gal(α1-3)GlcNAc(β1- GlcNAc(β1-3)┘
O45 (W) IIIa (*S. arizonae*) [53]	4)GlcA(β1-4)LFuc*3Ac*(α1-3)Rib*f*(β1-4)Gal(β1-3)GlcNAc(β1- LFuc(α1-2)┘
O47 (X) [54]	2)Rib-ol(5-*P*-6)Gal*4Ac*(α1-3)LFucNAm(α1-3)GlcNAc(α1-
O48 (Y) Toucra [55,56]	4)Neu5Ac*7,9Ac*(α2-3)LFucNAm(α1-3)GlcNAc(β1-
O50 (Z) II (*S. greenside*) [1,46]	6)GlcNAc(β1-3)Gal(α1-3)GalNAc(β1- └(3-1β)Gal(2-1α)Col
O50 IV (*S. arizonae*) [57]	6)GlcNAc(β1-3)Gal(α1-3)GlcNAc(β1- └(3-1β)Gal(2-1α)Col

(*continued*)

Table 3.3 (continued)

O51 [58]	6)Glc(α1-4)Gal(β1-3)GalNAc(α1-3)GlcNAc(β1- GlcNAc(β1-3)┘
O52 [50]	2)Rib*f*(β1-4)Gal(β1-4)GlcNAc(α1-4)Gal(β1-3)GlcNAc(α1-
O53 [59]	2)Gal*f*(α1-4)GalNAc(β1-4)LRha*2,3Ac*(α1-3)GlcNAc(β1-
O54 Borreze [60]	4)ManNAc(β1-3)ManNAc(β1-
O55 [61]	2)Glc(β1-2)Fuc3NAc(β1-6)Glc(α1-4)GalNAc(α1-3)GlcNAc(β1-
O56 [62]	3)Qui4N(LSerAc)(β1-3)Rib*f*(β1-4)GalNAc(α1-3)GlcNAc(α1-
O57 [63]	3)LRha(α1-2)LRha(α1-4)Glc(α1-3)GalNAc(β1- └(2-1β)GlcNAc
O58 [64]	3)Qui4N(DAlaS3Hb)(β1-6)GlcNAc(α1-3)LQuiNAc(α1-3)GlcNAc(α1-
O59[d] [65]	2)Gal(β1-3)GlcNAc(α1-4)LRha(α1-3)GlcNAc(β1-
O60 [66]	2)Man(β1-3)Glc(β1-3)GlcNAc(β1- Fuc3NFo(α1-3)┘
O61 IIIb (*S. arizonae*) [67]	8)8eLeg5(*R*3Hb)7Ac(α2-3)LFucNAm(α1-3)GlcNAc(α1-
O62 IIIa (*S. arizonae*)[e] [68]	3)LRha(α1-2)LRha(α1-3)LRha(α1-2)LRha(α1-3)GlcNAc(β1- └(2-1α)GalNAcAN
O63 IIIa (*S. arizonae*) [69]	3)Gal(β1-4)Glc(α1-4)GalNAc(α1-3)GalNAc(β1- └(4-1α)Fuc3NAc
O65 [50]	4)GlcNAc(β1-4)Man(β1-4)Man(α1-3)GlcNAc(β1-
O66 [70]	2)Gal(α1-6)Gal(α1-4)GalNAc(α1-3)GalNAc*6Ac*(β1- Glc(β1-3)┘

[a]The OPS lacks O-acetylation.
[b]This structure has been published erroneously as that of *S. enterica* ssp. *arizonae* O64 (*Arizona* 29) and *Citrobacter* O32 [71]. Earlier, another structure has been established for *S. enterica* ssp. *arizonae* O21 [72], which, in fact, may belong to *Citrobacter braakii* O37 [73].
[c]The absolute configuration of Qui3NAc has been revised from L to D [74].
[d]Earlier, another structure has been reported for *S. enterica* ssp. *arizonae* O59 [75], which, in fact, may belong to *Citrobacter braakii* O35 [76] or *E. coli* O15 [65].
[e]Amidation of GalNAcA has not been originally reported [68] but demonstrated later [50].

are common constituents, and ManNAc is present in three OPSs, including the O54 antigen, which is a homopolymer of ManNAc. There are present also 6-deoxyamino sugars, such as LQuiN, Qui3N, Qui4N, LFucN, Fuc3N and Rha4N, which often bear uncommon *N*-acyl groups, such as formyl, acetimidoyl, (*R*)-3-hydroxybutanoyl, *N*-[(*S*)-3-hydroxybutanoyl]-D-alanyl and *N*-acetyl-L-seryl. A few OPSs are acidic, from which the O48 and O61 antigens contain derivatives of higher acidic sugars: neuraminic acid (Neu) and 8-epilegionaminic acid (8eLeg), respectively. The O47 antigen is phosphorylated and has a ribitol teichoic acid-like structure. The O62 antigen contains GalNAcA but is neutral as the acid occurs in the amide form. Additional modifications by glucosylation or/and O-acetylation further extend the diversity of the O-antigen forms within several O-serogroups, including serogroups A-E. In serogroups B, C_1, D_3 and H, the glucosylated and non-glucosylated forms are discrete polymer chains. The O-polysaccharides of serovars

Telaviv ($O28_1,28_2$) and Dakar ($O28_1,28_3$) are significantly different in composition and structure of both main and side chains that is unusual for strains belonging to the same *Salmonella* serogroup.

A polysaccharide different from the O-antigen may be a part of the LPS of *Salmonella*. For instance, the T1-specificity of a transient form of *S. enterica* is defined by 6)Gal*f*(β1-3)Gal*f*(β1-3)Gal*f*(β1- and 2)Rib*f*(β1- homopolymers [1], whose synthesis is determined by the *rft* locus. The T1-antigen as well as the O54 antigen, which is encoded by genes located on a plasmid [60], can be co-expressed with various *S. enterica* O-antigens. Infection of a serovar Typhimurium strain with the ColIb drd2 plasmid suppressed the normal O-antigen synthesis and induced synthesis of an altered LPS O-chain, probably by activation of a chromosomal operon inactive in the wild strain [77]:

3)LRha(α1-6)Glc(α1-2)Man(α1-3)GlcNAc(β1-
└(2-1α)Gal*f*

Citrobacter, Edwardsiella

Bacteria of the genus *Citrobacter* are normal inhabitants of human and animal intestine but may cause gastrointestinal diseases, urinary tract infections and bacteremia. The OPS structures have been established for the majority of the existing 43 O-serogroups and several nontypable strains [78]. Many from them consist only of neutral monosaccharides, such as common hexoses, pentoses (Xyl, Rib) and deoxy sugars: both enantiomers of Rha and Fuc, a unique monosaccharide 4-deoxy-D-*arabino*-hexose (4daraHex) and abequose. A minority of the OPSs are acidic due to the occurrence of an acidic sugar (GlcA, Neu5Ac), glycerol phosphate or ethanolamine phosphate as a substituent or a glycosyl phosphate group in the main chain. Remarkably, in the O32 antigen, L-glyceric acid (LGroA) interlinks the Fuc3N residues being in each pair N-linked to one residue and glycosylated by the other. Another uncommon amino sugar, Rha4NAc, builds up various homopolysaccharides of serogroup O9 strains and is present also in the heteropolysaccharide of two nontypable strains (Table 3.4).

In the O12 and O41 antigens, GlcN and Fuc3N bear a (*R*)-3-hydroxybutanoyl group. The same OPS may be characteristic for more than one O-serogroup. For instance, a 4dAraHex homopolymer is present in serogroups O4, O36 and O27, and variations in the LPS core OS are the reason for classification of the corresponding strains in three different O-serogroups [78]. The O-antigens of serogroups O1-O3 and O7 possess similar 4)Sug(α1-3)Sug(β1-4)Sug(β1- main chains, where Sug indicates either Man or Rha. Two pairs of strains of serogroups O7 and O12 have quite different structures, and their classification to one O-serogroup is thus questioned.

Various *Citrobacter* O-antigens are identical with, or structurally related to, the O-antigens of other bacteria, including *S. enterica* (serogroups O21, O22, O24, O38), *E. coli* (O23, O35, *C. rodentium* ATCC 51459), *Klebsiella pneumoniae* (O28, O39), *Hafnia alvei* (O16, O41) and *Eubacterium sabbureum* (O32) [78]. The main

Table 3.4 Structures of *Citrobacter* OPSs

C. youngae O1 [79]	4)Rha(α1-3)Man(β1-4)Man(β1- Rib*f*(α1-4)┘
C. youngae O2, O25, *C. werkmanii* O20 [80]	4)Rha(α1-3)Man(β1-4)Rha(β1- Xyl*f*(α1-4)┘
C. youngae O3 [78]	4)Man(α1-3)Rha(β1-4)Rha(β1-
C. youngae O4, O36, *C. werkmanii* O27 [78]	2)4daraHex(β1-
C. braakii O5, *Citrobacter* sp. PCM 1487 [78]	6)GlcNAc(α1-4)GalNAc(α1- 4daraHex(β1-3)┘
C. braakii O6 [81]	3)Fuc(α1-3)LRha2Ac(β1-3)Fuc(α1 4daraHex(α1-4)┘
C. braakii O7 (PCM 1503) [82]	4)Man(α1-3)Rha(β1-4)Rha(β1- Glc(α1-2)┘
C. braakii O7 (PCM 1532) [78]	3)Man(α1-3)Man(α1-2)Man(α1-2)Man(α1-2)Man(α1- Glc(α1-3)┘
C. braakii O8 [78]	3)Rha(α1-3)Rha(α1-2)Rha(β1- Xyl*f*(α1-2)┘
C. gillenii O9 (PCM 1537) [78]	3)Rha4NAc(α1-2)Rha4NAc(α1-2)Rha4NAc(α1-3)Rha4NAc2Ac(α1- and 2)Rha4NAc(α1-
C. youngae O9 (PCM 1538) [83]	2)Rha4NAc(α1- and 3)Rha4NAc(α1-3)Rha4NAc(β1-
C. gillenii O11(PCM 1540) [84]	3)Man(β1-4)Glc*p*(β1-3)FucNAc4Ac(α1-4)GalNAc(α1- └(2-1β)GlcNAc Glc(α1-6)┘
C. gillenii O12 (PCM 1542) [78]	6)GlcN(*R*3Hb)(β1-3)GalNAc(α1-3)GalNAc(β1- Glc(α1-6)┘ └(4-1α)GlcNAc
C. gillenii O12 (PCM 1544) [78]	3)LRha2Ac(β1-4)GlcNAc(β1-6)Gal(α1- *GlcNAc(β1-3)*┘
C. werkmanii O14 [85]	4)Glc6(*P*1Gro)(β1-3)GlcNAc-(β1- GlcNAc(β1-2)┘ └(6-1α)Glc
C. youngae O16 [78]	6)Gal(β1-4)GalNAc3(*P*1Gro)(β1-4)Glc(β1-3)Gal*p*NAc(β1- Glc(α1-2)┘ └(6-1α)Gal
C. werkmanii O21 [78]	6)Man*3Ac*(α1-2)Man(α1-2)Man(α1-3)GlcNAc(α1- Glc(α1-3)┘
C. freundii O22 [86]	2)Man(α1-4)LRha(α1-3)Gal(α1- └(3-1α)Abe
C. freundii O23 [78]	4)Man(α1-2)Man(α1-2)Man(β1-3)GalNAc(α1-
C. werkmanii O24 [78]	4)GlcA(β1-4)LFuc*3Ac*(α1-3)Rib*f*(β1-4)Gal(β1-3)GlcNAc(β1- LFuc(α1-2)┘
C. werkmanii O26 [78]	3)ManNAc(β1-4)Glc(β1- Glc(α1-2)┘
C. braakii O28 [78]	2)Rib*f*(β1-3)LRha(α1-3)LRha(α1-
C. braakii O29, O30 [78]	3)ManNAc(β1-4)Glc(β1-
C. youngae O32 [78]	2)LGroA(1-3)Fuc3N*2Ac*(α1-
C. braakii O35 [78]	2)Gal(β1-3)LFucNAc(α1-3)GlcNAc(β1-
C. braakii O37 [73]	7)Neu5Ac(α2-3)LFucNAm(α1-3)GlcNAc*6Ac*(β1-

(*continued*)

Table 3.4 (continued)

C. werkmanii O38 [78]	4)L-Rha(β1-2)Man(α1-2)Man(α1-3)Gal(β1- └(3-1α)Abe4Ac Glc(α1-2)┘
C. freundii O39 [87]	3)Gal*6(PEtN)*(β1-3)Gal(α1- and 3)Gal*f*(β1-3)Gal(α1-
C. freundii O41 [78]	2)Glc(β1-2)Fuc3N(R3Hb)(β1-6)GlcNAc(α1-4)Gal(β1-3)GalNAc(β1- Glc(α1-2)┘
Citrobacter sp. 396[a] [78]	2)Man(β1-2)Man(β1-2)Man(β1-2)Man(β1-3)GlcNAc(α1- Abe2Ac(α1-3)┘ └(3-1α)Glc
C. sedlakii NRCC 6070, *C. freundii* OCU 158 [78]	2)Rha4NAc(α1-3)L-Fuc(α1-4)Glc(β1-3)GalNAc(α1-
C. freundii NRCC 6052 [78]	2)Rha(α1-3)Rha(β1-4)Glc(β1-
C. rodentium ATCC 51459 [78]	3)GlcNAc(α1-P-6)Glc(α1-2)Glc(β1-3)GlcNAc(β1- └(4-1β)L-Rha

[a]The structure was established by older methods and requires reinvestigation.

Table 3.5 Structures of *Edwardsiella* OPSs

E. ictaluri MT 104 [88]	4)Gal(β1-4)Glc(α1-4)GalNAc(α1-3)GalNAc(β1-
E. tarda MT 108 [89]	4)GalNAc(β1-3)Gal(α1-4)L-Rha(α1-3)GlcNAc(β1- └(3-1α)GalA6LThr
E. tarda 1145, 1151 [90]	2)Man(α1-4)L-Rha(α1-3)Gal(α1- └(3-1α)Abe*2Ac*
E. tarda 1153 [90]	4)GalA6(GroN)(α1-4)Gal(α1-3)GalA(α1-3)GlcNAc(β-

chain of *C. braakii* O7 (PCM 1532) has the same structure as the linear mannan of *E. coli* O9, *K. pneumoniae* O3, and *H. alvei* PCM 1223. *C. sedlakii* NRCC 6070 and *C. freundii* OCU 158 share the OPS with *S. enterica* O30 and *E. coli* O157, and are serologically related also to some other bacteria whose OPSs contain various *N*-acyl derivatives of Rha4N.

Edwardsiella are occasional pathogens of humans; *E. tarda* can cause gastroenteritis and extraintestinal infections. The acidic OPS of *E. tarda* MT 108 includes an amide of GalA with L-threonine, and that of strain 1153 contains both GalA and its amide with 2-amino-2-deoxyglycerol (GroN) (Table 3.5). The OPS of strains 1145 and 1151 has the same carbohydrate structure as those of *S. enterica* O4 and *C. freundii* O22.

Escherichia, Shigella

Escherichia coli is a common component of the normal gut flora but certain strains also cause diarrhea, gastroenteritis, urinary tract infections and neonatal meningitis. *E. coli* O157 and several other virulent strains cause hemorrhagic colitis and hemolytic uremic syndrome. Strains of *Shigella*, mainly *S. dysenteriae, S. flexneri*, and *S. sonnei*, are causative agents of shigellosis (bacillar dysentery). The two genera are closely related, and genetically most *Shigella* strains are clones of *E. coli*. The

complete O-antigen structures have been determined for all 46 *Shigella* serotypes and a majority of about 180 *E. coli* O-serogroups. Those of *S. dysenteriae, S. boydii* and *S. sonnei* [91] as well as most known *E. coli* OPS structures [92] have been summarized recently. The latter are also periodically updated in the *E. coli* O-antigens database (ECODAB) at http://www.casper.organ.su.se/ECODAB/. Therefore, the OPS structures of *E. coli* and *Shigella* species mentioned above are not shown here.

The OPSs of most *E. coli* and *Shigella* have linear or branched tri- to hexasaccharide O-units; less common are disaccharide O-units and homopolysaccharides. Almost all *Shigella* OPSs (except for most *S. flexneri* types, *S. boydii* type 18 and *S. dysenteriae* type 1) and many *E. coli* OPSs are acidic due to the presence of hexuronic acids, including such uncommon as L-IdoA (*E. coli* O112ab), L-AltNAcA (*S. sonnei*) and ManNAc3NAcA (*E. coli* O180), nonulosonic acids (Neu5Ac, *N*-acyl derivatives of 5,7-diamino-3,5,7,9-tetradeoxynon-2-ulosonic acids) and acidic non-sugar components, such as lactic, glyceric, pyruvic acids, amino acids or phosphate. Several OPSs possess glycerol or ribitol teichoic acid-like structures. Other constituent sugars rarely occurring in nature are colitose (*E. coli* O55 and O111), 6-deoxy-D-*manno*-heptose in *E. coli* O52, D-*threo*-pentulose (xylulose) in *E. coli* O97, *N*-acyl derivatives of various 6-deoxyamino and 6-deoxydiamino sugars, including L-RhaN3N (*E. coli* O109 and O119) and FucN4N (*S. sonnei*). In *S. sonnei* and all other OPSs where FucN4N is present, it is 2-N-acetylated and has a free amino group at position 4. About half of *Shigella* serotypes have identical or almost identical OPS structures with *E. coli* [91]. Many other *E. coli* strains share OPSs with various bacteria, such as *Salmonella, Citrobacter, Klebsiella, Serratia, Hafnia, Yersinia* (see published review [92] and the corresponding sections in this chapter).

The OPSs structures of two other *Escherichia* species, *E. hermannii* and *E. albertii*, have been established. A group of *E. hermannii* strains produce homopolymers of Rha4NAc differing in the position of substitution of one of the sugar residues in the pentasaccharide O-units (Table 3.6).

The neutral OPSs of *S. flexneri* types 1–5, X and Y as well as newly proposed types 7a and 7b possess a common basic structure, and a diversity of the O-antigen forms depends on prophage-encoded glucosylation or/and O-acetylation at different positions of the basic glycan (Table 3.7). These serotype-converting modifications add new and may mask existing antigenic determinants, and strains with

Table 3.6 Structures of *E. hermanii* and *E. albertii* OPSs

E. hermannii ATCC 33650, 33652 [93]	2)Rha(α1-3)Rha(β1-4)Glc(β1- └(3-1α)Gal
E. hermannii ATCC 33651 [94]	3)Rha*2Ac*(β1-
E. hermannii NRCC 4262 [95]	3)Rha4NAc(α1-2)Rha4NAc(α1-2)Rha4NAc(α1- 3)Rha4NAc(α1-2)Rha4NAc(α1-
E. hermannii NRCC 4297-4300 [95]	3)Rha4NAc(α1-2)Rha4NAc(α1-3)Rha4NAc(α1- 3)Rha4NAc(α1-2)Rha4NAc(α1-
E. albertii (former *Hafnia alvei* 10457) [96]	3)Gal(β1-6)Gal*f*(β1-3)GalNAc(β1- └(6-2α)Neu5Ac

Table 3.7 Structures of *S. flexneri* OPSs

1a [99]	2)-L-Rha*3,4Ac*(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc(β1- Glc(α1-4)-┘
1b [99]	2)-L-Rha*3,4Ac*(α1-2)-L-Rha(α1-3)-L-Rha*2Ac*(α1-3)-GlcNAc(β1- Glc(α1-4)-┘
2a [99]	2)-L-Rha*3,4Ac*(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc*6Ac*(β1- Glc(α1-4)-┘
2b [100]	2)-L-Rha(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc(β1- └(3-1α)-Glc Glc(α1-4)-┘
3a [74]	2)-L-Rha(α1-2)-L-Rha(α1-3)-L-Rha2Ac(α1-3)-GlcNAc*6Ac*(β1- └(3-1α)-Glc
3b [100]	2)-L-Rha(α1-2)-L-Rha(α1-3)-L-Rha2Ac(α1-3)-GlcNAc(β1-
4a[a] [101]	2)-L-Rha3(*P*EtN)(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc(β1- Glc(α1-6)-┘
4b [100]	2)-L-Rha(α1-2)-L-Rha(α1-3)-L-Rha2Ac(α1-3)-GlcNAc(β1- Glc(α1-6)-┘
5a [98]	2)-L-Rha*3,4Ac*(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc(β1- └(3-1α)-Glc
5b [102]	2)-L-Rha(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc(β1- └(3-1α)-Glc └(3-1α)-Glc
X [102]	2)-L-Rha(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc(β1- └(3-1α)-Glc
Y [74]	2)-L-Rha*3,4Ac*(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc*6Ac*(β1-
6, 6a[b] [74]	2)-L-Rha*3,4Ac*(α1-2)-L-Rha(α1-4)-Gal*p*A(β1-3)-GalNAc(β1-
7a [103]	2)-L-Rha(α1-2)-L-Rha(α1-3)-L-Rha(α1-3)-GlcNAc(β1- Glc(α1-2)-Glc(α1-4)-┘
7b [103]	2)-L-Rha(α1-2)-L-Rha(α1-3)-L-Rha*2Ac*(α1-3)-GlcNAc(β1- Glc(α1-2)-Glc(α1-4)-┘

[a]Type 4a strains may lack phosphorylation.
[b]Types 6 and 6a differ only in the degree of O-acetylation.

glycosylated O-antigens are increased in virulence [97]. *S. flexneri* types 6 and 6a have a distinct acidic OPSs but share a 2)-L-Rha(α1-2)-L-Rha(α1- disaccharide fragment with the other serotypes. Recently, a phosphorylated variant of the type 4a OPS has been found. The OPSs of *S. flexneri* types 4b and 5a are shared by *E. coli* O129 and O135, respectively [98].

Klebsiella, Raoultella, Serratia

Klebsiella pneumoniae is a common cause of nosocomial infections. Outside the hospital, these bacteria are often responsible of pneumonia and urinary tract

Table 3.8 Structures of *K. pneumoniae* OPSs

O1, O6 [1,104]	3)Gal(α1-3)Gal*f*(β1- and 3)Gal(β1-3)Gal(α1-
O2a, 2a,b [104,106]	3)Gal(α1-3)Gal*f*(β1-
O2a,c [104,106]	3)Gal(α1-3)Gal*f*(β1- and 5)Gal*f*(β1-3)GlcNAc(β1-
O2a,e, O2a,e,h, O9[a] [107,108]	3)Gal(α1-3)Gal*f*(β1- *Gal(α1-2)*┘
O2a,f,g [108]	3)Gal(α1-3)Gal*f*(β1- Gal(α1-4)┘
O3 [1,104]	2)Man(1-2)Man(1-2)Man(1-3)Man(1-3)Man(1-
O4, O11 [1,104]	4)Gal(α1-2)Rib*f*(β1-
O5 [1,104]	3)Man(β1-2)Man(α1-2)Man(α1-
O7 [1]	2)LRha(α1-2)Rib*f*(β1-3)LRha(α1-3)LRha(α1-
O8 [109]	3)Gal(α1-3)Gal*f2,6Ac*(β1- and 3)Gal(β1-3)Gal(α1-
O12 [1,104]	3)GlcNAc(β1-4)LRha(α1-
22535 [110]	3)LRha(1-3)LRha(1-2)LRha(1-2)LRha(1-2)LRha(1-
i28/94 [111]	4)Glc(α1-3)LRha(α1-

[a]Serotypes O2a,e, O2a,e,h and O9 differ in the degree of galactosylation and O-acetylation at unknown position.

infections. Their O-antigens are all neutral and many are linear. The OPSs of serogroups O1, O2 and O8 share a 3)Gal(α1-3)Gal*f*(β- chain called galactan I, and are serologically related (Table 3.8). The distal end of this chain may bear another homoglycan (galactan II in case of O1 and O8). The OPSs of some other serogroups are homopolysaccharides (mannans or an L-rhamnan) too. The O4 and O12 antigens are terminated with an α- or β-linked residue of 3-deoxy-D-*manno*-oct-2-ulosonic acid (Kdo) [104], and the O5-mannan with 3-O-methylated Man [1]. The terminating group in the O3-mannan is a methyl group too but it is linked presumably via a phosphate group rather than directly to a mannose residue [105]. The OPSs are linked to the core OS through a β-GlcNAc primer. In serogroups O3 and O5, a 3)Man(α1-3)Man(α1-3)- disaccharide bridge (so called adaptor) is located between the OPS and the primer [104]. The O-antigens of *K. pneumoniae* O3, O4 and O5 are shared by *E. coli* O9, O20a,b and O8, respectively [92]. The O5 antigen is shared by *Burkholderia cepacia* O2 and E (see below) and *S. marcescens* O28. *K. pneumoniae* O10 has been reclassified as *Enterobacter* sp.

Raoultella (former *Klebsiella*) are isolated from plants, soil and water. *R. terrigena* ATCC 33257 has the same OPS structure as *K. pneumoniae* O12 [112], and the OPS of another *R. terrigena* strain is acidic due to the presence of a pyruvic acid acetal and has a unique structure [113]:

2)Man4,6*S*pyr(β1-3)ManNAc(α1-3)LRha(β1-4)GlcNAc(α1-

Serratia marcescens is a widely distributed environmental bacterium, which can causes outbreaks of infection, and occasionally death, in hospitalized patients. Their OPSs are neutral and many of them are similar to each other (for structures

see review [114]). Rather common are disaccharide O-units containing usual sugars (Glc, Gal, L-Rha, GlcNAc, GalNAc), which are occasionally O-acetylated [114]. The O14 antigen has the same structure as that of *P. aeruginosa* O15 and *B. cepacia* O3, whereas the O2 antigen is shared by *H. alvei* 38. The O4 antigen is an O-acetylated variant of the OPS of *K. pneumoniae* i28/94. *S. marcescens* O19 antigen is composed of two separate blocks of disaccharide O-units; the shorter chain is proximal to the core OS and shares the O-unit with *K. pneumoniae* O12, and the longer distal chain differs in substitution of L-Rha (at position 3 rather than 4) and is terminated with β-Kdo [115]. The OPS of *S. plymuthica* S90/4625 consists of the same two galactan blocks as *K. pneumoniae* O1 but is O-acetylated at unknown position [116].

Hafnia

Strains of *H. alvei* are isolated from natural environments and also hospital specimens. A serotyping scheme including 39 O-groups has been proposed for *H. alvei* strains but not correlated with known O-antigen structures [117]. In addition to common monosaccharides, Rib, L-FucN, Qui3N, Qui4N are components of several *H. alvei* OPSs, and single OPSs include L-Fuc, 6dTal, ManN, Fuc3N and Neu. Amino sugars are usually N-acetylated but several bear an (*R*)-3-hydroxybutanoyl group; in strain 1204, Qui3NFo is present. Most OPSs are acidic, and many are phosphorylated. Several of the latter possess teichoic acid-like structures with glycerol or, in strain 1191, a unique L-arabinitol component; the others have a phosphate bridge between the O-units or are decorated with glycerol 1-phosphate or ethanolamine phosphate. The OPS of strain 1206 is the only known glycan that contains D-allotreonine amide-linked to GalA. The O-antigen of strain 2 has the largest octasaccharide O-unit, and that of strain 1189 consists of hexa-, hepta- and octasaccharde O-units owing to non-stoichiometric glucosylation at two sites.

There are two groups of strains with the O-antigens that are structurally and serologically related to strains 1187 and 1199 (Table 3.9). The OPSs of each group have the same main chain but differ in the patterns of glucosylation or/and O-acetylation. It has been suggested to combine these strains in two serogroups and to place the remaining strains having the strain-specific O-antigens to a separate serogroup each [117]. Several O-antigens of *H. alvei* are shared by other bacteria: the hexosaminoglycan of strain 38 by *S. marcescens* O2, the mannan of strain 1223 by *E. coli* O9 and *K. pneumoniae* O3, and two galactans of strain Y166/91 by *K. pneumoniae* O1.

Cronobacter, Enterobacter, Pantoea

Cronobacter species (former *Enterobacter sakazakii*) are food-borne pathogens causing bacteremia, necrotizing enterocolitis and neonatal meningitis. Most OPSs of the genus are acidic due to the presence of hexuronic acids or, in *C. malonaticus,* Kdo (Table 3.10). The latter is a common constituent of the LPS core OS and occur in other non-repetitive LPS domains but is uncommon in O-units. The only neutral OPS is that of *C. sakazakii* ZORB A 741, which contains a tyvelose side chain. The O-antigens of *C. sakazakii* O1 and HPB 3290 have the same composition, including

Table 3.9 Structures of *H. alvei* OPSs

1187 [117]	2)Glc(α1-*P*-6)GlcN(*R*3Hb)(α1-4)GalNAc(α1-3)GalNAc(β1-
744, 1194, 1219, 1221, 114/60 [117,118]	2)Glc(α1-*P*-6)GlcN(*R*3Hb)(α1-4)GalNAc(α1-3)GalNAc(β1- Glc(α1-6)┘
537 (ATCC 13337) [117]	2)Glc(α1-*P*-6)GlcN(*R*3Hb)*3Ac*(α1-4)GalNAc(α1-3)GalNAc(β1- Glc(α1-6)┘
1199 [117]	3)Qui4NAc(β1-3)Gro(1-*P*-3)Gal(β1-3)GlcNAc*6Ac*(α1- GlcNAc*6Ac*(β1-2)┘
1200, 1203, 1205[a] [117,119]	3)Qui4NAc(β1-3)Gro(1-*P*-3)Gal(β1-3)GlcNAc*6Ac*(α1- GlcNAc*3,6Ac*(β1-2)┘ └(4-1α)Glc
2 [117]	4)Neu5Ac(α2-6)Glc(α1-6)Gal(β1-3)GalNAc(β1- Glc(α1-4)Gal(β1-6)Glc(β1-3)┘ └(6-1α)Glc
23 [117]	3)Qui4NAc(β1-3)6dTal4Ac(α1-3)LFuc(α1-6)Glc(α1-*P*-3)GlcNAc(α1-
32 [120]	4)GalA*2,3Ac*(α1-2)LRha(α1-4)Gal(β1-3)GalNAc(β1-4)GlcNAc(α1-
38 [117]	4)ManNAc(β1-4)GlcNAc(α1-
39 [117]	3)Gal(β1-4)Glc(β1-3)GalNAc(β1- Gal(β1-4)┘ └(2-1β)GlcNAc
1185[b] [121]	2)Qui3N(*R*3Hb)(β1-6)Glc(α1-4)GlcA*2Ac*(β1-3)GlcNAc(α1- Glc(α1-4)┘
1188 [117]	4)GlcA(β1-2)Man(α1-4)Gal(β1-3)GlcNAc(β1- LRha*2,3,4Ac*(α1-3)┘
1189 [122]	6)Glc(α1-4)GlcA(β1-4)GalNAc(β1-3)Gal(α1-3)GalNAc(β1- └*(4-1α)Glc* └(6-1α)Glc*(2-1α)Glc*
1190 [117]	3)LRha(α1-2)Rib*f*(β1-4)GalA(α1-3)GlcNAc(β1- Gal*f*(α1-2)LRha(α1-2)┘ └(5-1α)Glc
1191[c] [123]	4)Glc(β1-1)LAra-ol*2Ac*(5-*P*-3)Gal(β1-3)GalNAc(β1- GlcNAc(β1-2)┘ └(4-1α)Glc
1192[b] [124]	3)LRha(α1-3)LRha(β1-4)LRha(α1-3)GlcNAc(β1- └(2-1α)GlcA*2Ac*(4-1β)Rib*f*
1195 [125]	3)LFucNAc(α1-4)Glc(α1-*P*-4)Glc(α1-3)LFucNAc(α1-3)GlcNAc(α1- GlcNAc(α1-4)┘
1196 [126]	2)Gal(β1-6)Glc(α1-6)GlcNAc(α1-4)GalA(α1-3)GlcNAc(β1-
1204[b] [127]	2)Qui3NFo(β1-3)GalNAc(α1-4)GlcA*3Ac*(α1-3)Man(α1-2)Man(α1-3)GlcNAc(β1-
1206 [117]	4)GalA6DaThr(α1-2)LRha(α1-2)Rib*f*(β1-4)Gal(β1-3)GalNAc(β1-
1207[b] [128]	4)GalNAc3(*P*1Gro)(β1-3)Gal(α1-4)Gal(β1-3)GalNAc(β1- Glc(α1-6)┘
1209 [117]	3)Gal(β1-4)Glc(α1-4)GlcA(β1-3)GalNAc(β1- └(4-1α)LRha
1210 [117]	3)GlcNAc(α1-*P*-6)Gal(α1-4)Gal(β1-3)GlcNAc(β1- └(4-1β)LRha
1211[d] [129]	2)Glc(β1-2)Fuc3N(*R*3Hb)4Ac(β1-6)GlcNAc(α1-4)GalNAc(α1-3)GlcNAc(β1- Glc(β1-3)┘
1216 [117]	4)Qui3N(*R*3Hb)(α1-4)Gal6Ac(β1-4)GlcNAc(β1-4)GlcA(β1-3)GlcNAc(β1-

(*continued*)

Table 3.9 (continued)

1220 [117]	3)Gro(1-*P*-6)Glc(β1-4)LFucNAc(α1-3)GlcNAc(β1- Glc(α1-6)Gal(α1-3)┘ Glc(α1-6)┘
1222 [130]	2)LRha(α1-2)LRha*3(PEtN)4Ac*(α1-2)Rif(β1-4)Gal(α1-3)GlcNAc(α1- └(3-1β)Gal*f*
1223 [131]	2)Man(α1-2)Man(α1-2)Man(α1-3)Man(α1-3)Man(α1-
1529 [132]	2)LRha(α1-3)LRha(α1-4)GalA(α1-3)GlcNAc*6Ac*(β1- └(3-1α)LRha
1546 [133]	6)Glc*3Ac*(α1-4)GlcA(β1-4)GalNAc3Ac(β1-3)Gal(α1-3)GalNAc(β1-
Y166/91 [134]	3)Gal(β1-3)Gal(α1- and 3)Gal(α1-3)Gal*f*(β1-
481-L [135]	4)GalNAc(α1-*P*-6)Gal(β1-3)GalNAc(β1-4)GlcNAc(α1- └(3-1β)Glc Glc(α1-4)┘

[a]The OPS lacks *O*-acetyl groups at position 6 of α-GlcNAc in strain 1205, position 6 of β-GlcNAc in strain 1203 or at both positions in strain 1200.
[b]The OPS is non-stoichiometrically O-acetylated at unknown position.
[c]Arabinitol may be partially replaced by xylitol (~3:1).
[d]In ~10% α-GlcN, the *N*-acetyl group is replaced by a 3-hydroxybutanoyl group.

Table 3.10 Structures of *Chronobacter* OPSs

C. malonaticus [136]	4)Kdo(β2-6)Glc(β1-6)Gal(β1-3)GalNAc(β1- GlcNAc(β1-2)┘
C. muytjensii [137]	4)Qui3NAc(α1-3)LRha(α1-6)GlcNAc(α1-4)GlcA(β1-3)GalNAc(α1-
C. sakazakii O1 [138]	2)Qui3N(LAlaAc)(β1-6)Glc(β1-3)GalNAc(α1- Glc(α1-4)GlcA(α1-4)┘
C. sakazakii HPB 3290 [139]	2)Qui3N(LAlaAc)(β1-6)Glc(α1-3)GlcA(β1-3)GalNAc(α1- Glc(α1-2)┘
C. sakazakii O2[a] [140], *C. sakazakii* HPB 2855 [141]	3)LRha4Ac(α1-4)Glc(α1-2)LRha(α1-3)GlcNAc(β1- └(2-1α)GalA(4-1α)LRha*2,3,4Ac*
C. sakazakii 767 [142]	3)LRha*4Ac*(α1-4)Glc(α1-2)LRha(α1-3)GlcNAc(β1- └(2-1α)GalA(4-1α)LRha └(4-1α)Glc
C. sakazakii ZORB A 741 [143]	3)LRha(α1-3)Gal6Ac(α1-3)Gal(α1- Tyv(α1-2)┘

[a]In the O2 antigen, LRha in the main chain is not acetylated.

an *N*-acetyl-L-alanyl derivative of Qui3N, but a different O-unit topology and sugar sequence. *C. sakazakii* O2 and two more strains possess the same main chain and a disaccharide side-chain but differ in the pattern of O-acetylation and the presence of a lateral Glc in strain 767.

Enterobacter cloacae is sometimes associated with urinary tract and respiratory tract infections. The structure has been established for the O10 antigen [144]:

6)Man(α1-2)Man(α1-2)Man(β1-3)FucNAc(α1-
Glc(α1-4)┘

Table 3.11 Structures of *P. agglomerans* OPSs

FL1 [145]	2)Rha(α1-2)Rha(β1-3)Rha(α1-2)Rha(α1-
62D1[a] [146]	2)Qui3NAc(β1-3)LRha(α1-3)Gal(β1-3)FucNAc(α1- Gal(α1-6)┘
CIP 55.49 [147]	3)LFucNAc(α1-3)LFucNAc(α1-3)GlcNAc(β1- Glc(α1-2)LRha(α1-6)┘

[a]Strain was originally classified as *E. coli,* then as *Erwinia herbicola.*

The OPS of an *Enterobacter* sp. strain, formerly classified as *K. pneumoniae* O10, is a linear riborhamnan terminated with 3-O-methylated LRha [1]:

3)LRha(α1-3)Rib*f*(β1-4)LRha(α1-3)Rib*f*(β1-4)LRha(α1-

Pantoea (former *Enterobacter*) *agglomerans* is commonly isolated from plant surfaces, seeds, fruits, animal or human feces, and is known to causing wound, blood, and urinary tract infections. The OPSs of this species studied are neutral and enriched in 6-deoxyhexoses (Table 3.11).

Proteus, Providencia, Morganella

O-antigen structures have been established for all 76 known *Proteus* O-serogroups and more than half of 61 *Providencia* O-serogroups. The former have been summarized in a recent review [148], and the OPS structures of *Providencia* are shown below. The O-antigens of both genera possess some peculiar features in common. Most of them are acidic due to the presence of hexuronic acids, including a rare isomer LAltA, nonulosonic acids: Kdo, pseudaminic acid (Pse) and 8-epilegionaminic acid (8eLeg), and non-sugar acids, such as carboxyl-linked amino acids, including stereoisomers of N^{ε}-(1-carboxyethyl)-L-lysine, N-linked dicarboxylic acids [malonic, succinic, aspartic acids, *N*-(1-carboxyethyl)alanine], ether-linked hydroxy acids (lactic and 2,4-dihydroxypentanoic acids) and a pyruvic acid acetal. Phosphate-linked non-sugar groups are both occurring in other bacterial OPS: ethanolamine, glycerol and ribitol, which are found mainly in *Proteus*, and unique: *N*-(1-carboxyethyl)ethanolamine, choline and D-glyceramide in *Proteus mirabilis* O14, O18 and *Providencia alcalifaciens* O22, respectively. Man and LFuc have been detected only in *Providencia* but some other monosaccharides (LRha, L6dTal, various 6-deoxyamino sugars) are common for both genera. LQui present in the OPS of *P. stuartii* O44 is a rare component of O-antigens. From diamino sugars, LRhaN3N has been found in *Proteus penneri* O66, whereas FucN4N in both *Proteus* and *Providencia*. The main chain of the OPS of *P. alcalifaciens* O6 has the same structure as hyaluronic acid. The O-unit of *P. alcalifaciens* O38 and O45 contains D-alanine linked to the carboxyl group of *N*-acetylmuramic acid and thus represents a fragment of the bacterial cell-wall peptidoglycan (Table 3.12).

Table 3.12 Structures of *Providencia* OPSs

P. stuartii O4 [149]	3)Gal(β1-6)GlcNAc(β1-6)Gal(β1-3)GlcNAc(β1- └(6-1β)Qui4N(4LAspAc)
P. alcalifaciens O5 [150]	4)Qui3NAc(β1-3)Gal(α1-3)Gal(β1-3)GlcNAc(β1-
P. alcalifaciens O6 [151]	4)GlcA(β1-3)GlcNAc(β1- Col(α1-2)Gal(β1-3)GlcNA(β1-6)┘
P. alcalifaciens O7 [152]	3)LRha2Ac(β1-4)GlcNAc(β1-3)GlcA(α1-4)GlcNAc(α1-
P. alcalifaciens O8[a] [153]	3)GlcNAc4R(β1-3)Gal(β1-2)Gro(1-*P*-3)FucNAc4N(β1-
P. alcalifaciens O9 [154]	2)Glc(β1-6)Gal(α1-6)GalNAc(α1-4)GalNAc(α1-3)GalNAc(α1- Glc(β1-3)┘
P. alcalifaciens O12 [155]	4)Gal(β1-3)GalNAc(α1-4)Gal(β1-3)GalNAc(β1- GlcNAc(β1-3)┘└(2-1β)Glc(2-1β)GlcNAc
P. rustigianii O14 [156,157]	3)GalA6(2*S*alaLys)(α1-4)GalNAc(α1-3)GlcNAc(α1-
P. rustigianii O16 [158]	6)GlcNAc3(*R*lac)(α1-3)LRha(β1-4)GlcNAc(β-
P. stuartii O18 [159]	4)Qui3NAc(β1-6)GlcNAc(α1-4)GlcA(β1-3)GalNAc(α1-
P. alcalifaciens O19 [160, 161]	2)Fuc3NAc4Ac(β1-3)GlcNAc4,6(*S*pyr)(α1-4)Gal(α1-4)Gal(β-3)GlcNAc(β1-
P. stuartii O20 [162]	8)8eLeg5Ac7Ac(α2-4)GlcA(β1-4)GlcA(β1-3)GlcNAc(α1-
P. alcalifaciens O21 [163]	3)GalA(α1-4)GalNAc(α1-4)GalNAc(α1-3)GalNAc(β1- └(4-1α)Fuc3NFo
P. alcalifaciens O22 [164]	4)GalNAc3(*P*2DGroAN) (β1-4)Gal(β1-3)FucNAc4N(β1-
P. alcalifaciens O23 [165]	4)GlcA6(2*R*alaLys)(β1-6)Gal(β1-6)Glc(β1-3)GalNAc(β1-
P. alcalifaciens O25 [166]	6)GalNAc(β1-4)GlcA(β1-3)GlcNAc(β1- └(4-1α)GalA(2*R*alaLys)
P. alcalifaciens O27 [167]	2)Qui4NFo(α1-4)GlcA(α1-4)Glc(β1-3)GalNAc*6Ac*(β1-
P. alcalifaciens O28 [168]	3)GlcNAc(β1-3)LFuc(α1-3)GlcNAc(β1- └(4-1α)LFuc(3-1α)GlcA
P. alcalifaciens O29 [169]	6)GlcNAc(α1-3)LFucNAc(α1-3)GlcNAc(α1- Glc(β1-4)┘
P. alcalifaciens O30 [170]	2)Qui4NFo(β1-2)Rib(β1-4)GlcA(β1-4)GlcA(β1-3)FucNAc4N(α1-
P. alcalifaciens O31[b] [171]	3)Gal(α1-4)GalNAc(β1-3)GalNAc(β1- Man4R(β1-4)┘
P. alcalifaciens O32 [172]	6)GlcNAc3(*S*lac)(α1-3)LFucNAc(α1-3)GlcNAc(α1- Glc(β1-4)┘
P. stuartii O33 [173]	3)Qui4N(4DAspAc)(β1-6)GlcNAc(α1-4)GalA(α1-3)GlcNAc(α1-
P. rustigianii O34 [174]	4)GlcA(β1-4)LFuc(α1-2)Man(α1-2)LFuc(α1-2)Glc(β1-3)GlcNAc(β1- GalNAc(α1-3)┘
P. alcalifaciens O35[c] [164]	4)GalNAc(α1-6)Glc(α1-4)GlcA(β1-3)GalNAc(β1 └(6-1β)Qui4NR
P. alcalifaciens O36 [175]	7)Kdo(β2-3)L6dTal2*Ac*(α1-3)GlcNAc(α1-
P. alcalifaciens O38, O45 [164]	4)GlcNAc3(*R*lac-DAla)(α1-4)GlcNAc(β1-
P. alcalifaciens O40 [164]	4)Qui3NFo(β1-3)Gal(α1-3)GlcA(β1-3)GalNAc(β1-
P. stuartii O43 [167]	2)Qui4NAc(α1-4)GlcA(β1-3)GalA6LSer(β1-3)GlcNAc(β1-

(*continued*)

Table 3.12 (continued)

P. stuartii O44 [176]	4)GalNAc(α1-3)LFuc(α1-3)Glc(α1-4)LQui(α1-3)GlcNAc(α1- GlcA(β1-4)┘
P. alcalifaciens O46 [177]	3)GlcA(β1-4)LFuc(α1-4)LFuc(α1-2)Glc(β1-3)GlcNAc6*Ac*(α1- Glc(α1-3)┘
P. stuartii O47 [178]	2)Gal(β1-4)Man6*Ac*(β1-3)Man(β1-4)GlcA(β1-3)GlcNAc(α1- LRha(α1-3)┘
P. alcalifaciens O48 [179]	3)Man(α1-2)LFuc(α1-2)GlcA4Ac(β1-3)GalNAc(α1-
P. stuartii O49 [180]	4)Gal(α1-6)Gal(β1-3)GalNAc(β1-
P. stuartii O57 [181]	2)Gal(α1-3)LRha2*Ac*(α1-4)Glc(α1-4)GalA6LAla(α1-3)GlcNAc(β1-
P. alcalifaciens O60 [182]	4)GlcA6LSer(β1-3)GalNAc(β1-4)Glc(β1-3)Gal(α1-4)GalNAc(β1-

[a]R indicates (*1S,3R*)-3-hydroxy-1-carboxybutyl. In the original publication [153], Gro(3-*P* has been shown in the structure erroneously.
[b]R indicates (*1R,3R*)-3-hydroxy-1-carboxybutyl.
[c]R indicates *N*-(1-carboxyethyl)alanine of unknown configuration.

Morganella morganii is commonly found in the environment and in the intestinal tract of humans, mammals and reptiles as normal flora. A remarkable feature of the OPS of *M. morganii* is the presence of two rare sugars: a 5-*N*-acetimidoyl-7-*N*-acetyl derivative of 8-epilegionaminic acid and a higher branched ketouronamide called shewanellose, which occurs in the pyranose form in some O-units or in the furanose form in the others [183] (Fig. 3.1).

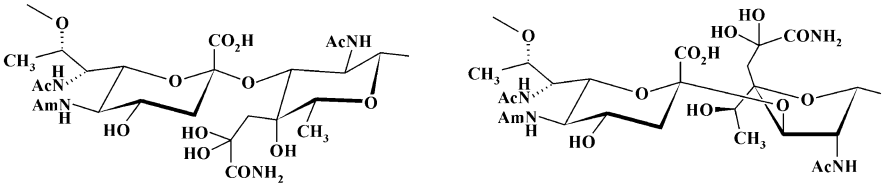


Fig. 3.1 Structures of the O-units of *Morganella morganii* [183]

A similar structure but with shewanellose exclusively in the pyranose form has been reported for a polysaccharide of *Shewanella putrefaciens* A6 [184].

Yersinia

Most important *Yersinia* species are *Yersinia pestis*, the cause of bubonic and pneumonic plague, *Yersinia pseudotuberculosis* and *Yersinia enterocolitica*, which cause less severe diseases usually restricted to gastrointestinal tract. *Y. pestis* has a cryptic O-antigen gene cluster and does not express any O-antigen [186]. Minireviews on the OPS structures of other *Yersinia* have been published [185–188].

Yersinia pseudotuberculosis is the only bacterium that produces all known natural 3,6-dideoxyhexose, and most of its OPSs have a side chain of one of the isomers. Paratose occurs as either pyranose (serogroup O3) or furanose (serogroup

O1); other 3,6-dideoxyhexoses are always pyranosidic. Two OPSs have an L6dAlt*f* side chain (Table 3.13). The 6-deoxy- and 3,6-dideoxy-hexoses are linked either directly to the main chain or through another uncommon monosaccharide: 6-deoxy-D-*manno*-heptose (6dmanHep) or, in serogroup O6, a branched sugar 3,6-dideoxy-4-*C*-[(*S*)-1-hydroxyethyl]-D-*xylo*-hexose (yersiniose A). When synthesis of 6dmanHep is impaired, its biosynthetic precursor, D-*glycero*-D-*manno*-heptose, is incorporated into the O-unit in place of 6dmanHep [189]. Between O-serogroups, the OPSs differ in the side chain or the main chain or both. Within complex O-serogroups, division to subgroups is based either on different side chains linked to the same main chain as in serogroup O5, or different main chains bearing the same side chain as in the other serogroups. The OPS of *Y. pseudotuberculosis* O10 is remarkably similar to that of *E. coli* O111 and *S. enterica* O35.

Many linear OPSs and main chains of branched OPSs of *Y. enterocolitica* and several other *Yersinia* species are homopolymers of Rha, LRha or L6dAlt (Table 3.14). The lateral monosaccharides are enantiomers of xylose and xylulose (Xlu), yersiniose A and its (*R*)-stereoisomer yersiniose B. The O-antigens of *Y. enterocolitica* O6,31 and O8 are the only known polysaccharides that contain 6dGul. The O5,27 and O10 antigens have comb-like structures with each rhamnose residue of the main chain substituted with a xylulose residue. The OPSs of two *Y. kristensenii* strains resemble glycerol teichoic acids. The *Y. ruckerii* OPSs are acidic due to the presence of *N*-acetylmuramic acid or a derivative of 8eLeg with a 4-hydroxybutanoyl group at N-5. An α1-2-linked homopolymer of Rha4NFo is shared by *Y. enterocolitica* O9 and *Brucella abortus* [203]. The OPS of *Y. ruckerii* O1 is remarkably similar to that of *Salmonella arizonae* O61, and those of *Y. enterocolitica* O5,27 and *Y. kristensenii* O11,23 are identical with the OPSs of *E. coli* O97 and O98, respectively.

Other Genera

Plesiomonas shigelloides, the only species in the genus, is a ubiquitous microorganism, which may cause water- and food-born gastrointestinal infections and illnesses in immunocompromised hosts and neonates. Its OPSs contains various unusual components, including D-*glycero*-D-*manno*-heptose (DDmanHep), 6dmanHep, L6dTalN, QuiN4N and GlcN3NA as well as *N*-acyl groups: acetimidoyl, (*S*)-3-hydroxybutanoyl or 3-hydroxy-2,3-dimethyl-5-oxoprolyl (Table 3.15). The O17 antigen possesses a disaccharide O-unit composed of two uncommon sugars: one acidic, LAltNAcA, and one basic, FucNAc4N. It has the same structure as the plasmid-encoded OPS of *Shigella sonnei* [91].

Yokenella regensburgei is recovered from wounds and knee fluid, respiratory tract, urine, sputum and stool. It is an opportunistic pathogen, especially under immunocompromised conditions. The OPSs of four strains studied have the same trisaccharide O-unit containing LDmanHep and 2-O-acetylated or, in one strain, 2,4-di-O-acetylated L6dTal [227]:

2)LDmanHep(α1-3)L6dTal2(4)Ac(α1-3)FucNAc(α1-

Table 3.13 Structures of *Y. pseudotuberculosis* OPSs

O1a [190]	3)Gal(α1-3)GlcNAc(β1- Par*f*(α1-3)6dmanHep(β1-4)┘
O1b [191]	2)Man(β1-4)Man(α1-3)LFuc(α1-3)GlcNAc(α1- Par*f*(β1-3)┘
O1c [192]	2)Man(α1-3)LFuc(α1-3)GalNAc(β1- Par*f*(β1-3)┘
O2a [189,193]	3)Gal(α1-3)GlcNAc(β1- Abe(α1-3)6dmanHep(β1-4)┘
O2b [194]	2)Man(α1-3)LFuc(α1-3)GalNAc(β1- Abe(α1-3)┘
O2c [195]	6)Man(α1-2)Man(α1-2)Man(β1-3)GalNAc(α1- Abe(α1-3)┘
O3 [186, 195]	2)Man(α1-3)LFuc(α1-3)GalNAc(α1- Par(β1-4)┘
O4a [196]	6)Man(α1-2)Man(α1-2)Man(β1-3)GalNAc(α1- Tyv(α1-3)┘
O4b [197]	3)Gal(α1-3)GlcNAc(β1- Tyv(α1-3)6dmanHep(β1-4)┘
O5a [185,186]	2)LFuc(α1-3)Man(α1-4)LFuc(α1-3)GalNAc(α1- Asc(α1-3)┘
O5b [185,186]	2)LFuc(α1-3)Man(α1-4)LFuc(α1-3)GalNAc(α1- L6dAlt*f*(α1-3)┘
O6[a] [185,186,198]	3)GlcNAc(β1-6)GalNAc(α1-3)GalNAc(β1- Col(α1-2)Sug(β1-3)┘
O7 [187]	6)Glc(β1-3)GalNAc(α1-3)GalNAc(β1- Col(α1-2)┘ Glc(α1-6)┘
O9 [199]	4)GlcNAc3Ac(β1-4)LFucNAm(α1-3)GlcNAc(α1- Gal(α1-3)┘
O10 [200]	4)Glc(α1-4)Gal(α1-3)GalNAc(β1- Col(α1-3)┘ └(6-1α)Col
O11 [201]	2)Man(β1-4)Man(α1-3)LFuc(α1-3)GlcNAc(α1- L6dAlt*f*(α1-3)┘
O15 [202]	2)LFuc(α1-3)Man(α1-4)LFuc(α1-3)GalNAc(α1- Par*f*(β1-3)┘

[a]Sug indicates yersiniose A.

Budvicia aquatica, Pragia fontium, Rahnella aquatilis are the only species in each of the three new genera of Enterobacteriaceae. They are isolated mainly from fresh water, water pipes and sometimes from clinical specimens but the

Table 3.14 Structures of other *Yersinia* sp. OPSs

Y. enterocolitica O1,2a,3[a], O2a,2b,3 [185,204]	2)L6dAlt*f3Ac*(β1-2)L6dAlt*f3Ac*(β1-3)L6dAlt*f*(β1-
Y. enterocolitica O2,3, O3 [185,204]	2)L6dAlt(β1-
Y. enterocolitica O4,32, *Y. intermedia* O4,33[a,b] [185,198]	3)GalNAc(α1-3)GalNAc(β1- Sug1'Ac(α1-4)┘
Y. enterocolitica O5,27[c] [185]	3)LRha(α1-3)LRha(β1- Xlu*f*(β2-2)┘ └(2-2β)Xlu*f*
Y. enterocolitica O6,31 [185]	2)Gal(β1-3)6dGul(α1-
Y. enterocolitica O8[d] [185]	4)Man(1-3)Gal(1-3)GalNAc(α1- 6dGul(1-3)┘ └(2-1)LFuc
Y. enterocolitica O9 [185]	2)Rha4NFo(α1-
Y. enterocolitica O10 [205]	3)Rha(α1- LXlu*f*(β2-2)┘
Y. kristensenii O11,23, O11,24[a] [206]	3)LQuiNAc(α1-4)GalNAcA3Ac(α1-3)LQuiNAc(α1-3)GlcNAc(β1-
Y. kristensenii O12,25 [207]	2)Gro(1-P-6)Glc(β1-4)LFucNAc(α1-3)GlcNAc(β1- Glc(α1-6)GalNAc(α1-3)┘ GlcNAc(β1-4)┘
Y. kristensenii O12,26 [208]	2)Gro(1-P-6)Glc(β1-6)GalNAc(α1-3)LFucNAc(α1-3)GlcNAc(β1- Glc(α1-2)┘ Glc(α1-4)┘
Y. frideriksenii O16,29[e] [209]	2)Rha(α1-3)Rha(β1-3)Rha(α1- *Sug(β1-2)*┘
Y. kristensenii O25,35 [210]	2)Gro(1-P-6)Glc(β1-4)LFucNAc(α1-3)GlcNAc(β1- Glc(α1-6)Gal(α1-3)┘ Glc(α1-4)┘
Y. kristensenii O28 [211]	3)LRha(α1-3)LRha(α1-3)LRha(α1-3)GlcNAc(β1- └(2-1α)GalNAcA(4-1α)LRha
Y. aldovae 6005 [212]	2)Glc(β1-2)Fuc3N(*R*3Hb)(β1-6)GlcNAc(α1-4)GalNAc(α1-3)GlcNAc(β1- Glc(β1-3)┘
Y. bercovieri O10[e] [213]	3)Rha(α1-3)Rha(α1- Sug(α1-2)┘
Y. mollarettii [214]	2)Gal(β1-3)6dGul(α1-
Y. rohdei WA 339 [215]	3)LRha(α1-3)LRha(α1-3)LRha(β1-
Y. ruckerii O1 [67, 216]	8)8eLegp5(4Hb)7Ac(α2-3)LFucNAm(α1-3)GlcNAc(α1- GlcNAc(β1-4)┘
Y. ruckerii O2[f] [217]	4)GlcNAc*6Ac*3(*R*lac)(α1-3)LQuiNAc(α1-3)GlcNAc(β1-

[a]The OPS lacks O-acetylation.
[b]Sug indicates yersiniose B.
[c]An alternative structure with one more LRha residue in the O-unit has been reported for the O5 and O5,27 antigens [218].
[d]The configurations of most glycosidic linkages have not been determined.
[e]Sug indicates yersiniose A.
[f]Details of the structure elucidation have not been reported.

Table 3.15 Structures of *P. shigelloides* OPSs

O1 [219,220]	3)L6dTalNAc*4Ac*(β1-4)LFucNAc(α1-4)LFucNAc(α1- 4) LFucNAc(α1-3)QuiNAc4N(S3Hb)(β1-
O17 [221]	-4)LAltNAcA(α1-3)FucNAc4N(β1-
O51 [222]	4)GlcNAc3N(S3Hb)A(β1-4)LFucNAm3Ac(α1-3)QuiNAc(α1-
O54 [223,224]	4)DDmanHep(β1-3)6dmanHep2Ac(β1-4)LRha(α1-3)GlcNAc(β1- └(3-1α)LRha(4-1β)Gal*f*
O74[a] [225]	2)Qui3NR(β1-3)LRha2Ac(α1-3)FucNAc(α1-
22074, 12254 [226]	3)LRha(α1-2)LRha(α1-2)LRha(α1-4)GalA(α1-3)GlcNAc(α1-

[a]R indicates 3-hydroxy-2,3-dimethyl-5-oxoprolyl of unknown configuration.

Table 3.16 Structures of *R. aquatilis* OPSs

33071[T] [231]	3)Man(α1-2)Man(α1-3)Gal(β1- and 4)Rha(α1-3)Rha(α1-3)Man(β1- └(2-1α)GlcA(4-1α)Gal(3-1β)Glc
1-95 [233]	3)Gal*f*(β1-3)Fuc(α1- Gal(α1-2)┘
3-95 [234]	2)Man(α1-3)Man(α1-6)Man(α1- and 6)Glc(α1-

medical significance of the three genera remains uncertain. The OPS of *B. aquatica* has a 1,3-poly(glycerol phosphate) main chain decorated with β1-2-linked Glc residues [228].

The OPS of *P. fontium* 27480 is acidic due to the presence of ManNAc3NAcA [229]:

4)ManNAc3NAcA(β1-2)LRha(α1-3)LRha(β1-4)GlcNAc(α1-

and that of *P. fontium* 97 U116 is neutral [230]:

2)Gal*f*(α1-3)LRha2Ac(α1-4)GlcNAc(α1-2)LRha(α1-3)GlcNAc(β1-

Both acidic and neutral OPSs have been found in *R. aquatilis* 33071[T] [231], the former being shared by strain 95 U003 [232]. In *R. aquatilis* 3–95, two neutral homoglycans, a mannan and a glycan, are present (Table 3.16).

Erwinia and *Pectobacterium* are pathogens of plants. The former causes wilts or blight diseases and the latter soft rot. The OPS of *E. amylovora* T is structurally similar to that of *R. aquatilis* 1–95 [233] but galactofuranose is replaced by glucofuranose [235]. The latter sugar has not been reported elsewhere in natural

carbohydrates, and the structure may need revision [1]. The OPS of *P. atrosepticum* ssp. *carotovora* (formerly *E. carotovora*) is enriched in deoxy sugars [236]:

3)LRha(β1-4)LRha(α1-3)Fuc(α1-
Glc(α1-3)┘

and a higher branched monosaccharide erwiniose has been identified in the OPS of *P. atrosepticum* ssp. *atroseptica* [237] (Fig. 3.2).

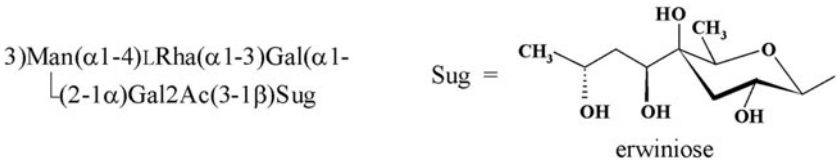


Fig. 3.2 Structure of the OPS of *Pectobacterium atrosepticum* ssp. *atroseptica* [237]

3.3.2.2 Aeromonadaceae

Aeromonas species are ubiquitous water-borne bacteria responsible for a wide spectrum of diseases in aquatic and terrestrial animals as well as in humans. *A. hydrophila* and *A. caviae* are often associated with gastrointestinal diseases in adults and acute gastroenteritis in children. Most OPSs of the genus studied so far are neutral. The O-unit of *A. hydrophila* O34 contains two L6dTal residues, one of which is randomly O-acetylated. The OPSs of various *A. salmonicida* types possess a main chain of 4)LRha(α1-3)ManNAc(β1- and differ in the modes of O-acetylation and glucosylation (Table 3.17). Under *in vivo* growth conditions, *A. salmonicida* type A strain A449 produces a different OPS with a side chain elongated by four more Glc residues and more sites of O-acetylation [238]. In encapsulated type A strain 80204-1, the OPS includes a partially amidated GalNAcA residue and an *N*-acetyl-L-alanyl derivative of Qui3N [239]. The OPSs of *A. caviae* are acidic due to the presence of GlcA or glycerol 1-phosphate. The O-antigen of *A. bestiarum* with an L-rhamnan backbone is shared by *Pseudomonas syringe* pv. *atrofaciens* [240, 241]. *A. trota*, *Vibrio cholerae* O22 and O139 and *Pseudoalteromonas tetraodonis* have a branched tetrasaccharide fragment in common, which represents a colitose (3-deoxy-L-fucose) analogue of the Le^b antigenic determinant.

3.3.2.3 Pseudoalteromonadaceae, Shewanellaceae, Idiomarinaceae

These families combine microorganisms of the marine origin, whose O-antigen structures have been summarized recently [251, 252]. The OPSs of obligatory marine bacteria *Pseudoalteromonas* (formerly *Alteromonas*) are neutral or acidic and contain various unusual components, such as LIdoA, amino and diamino hexuronic acids, their primary amides and amides with amino acids, keto sugars, including Kdo and Pse, an ether of Glc with (*R*)-lactic acid (glucolactilic acid) and glycerol phosphate; constituent amino sugars bear various N-linked hydroxy and amino acids (Table 3.18). An agarolytic strain *P. agarivorans* KMM 232 (former

Table 3.17 Structures of *Aeromonas* OPSs

A. bestiarum [242]	3)LRhap(α1-3)LRhap(α1-2)LRhap(α1-2)LRhap(α1- └(2-1β)GlcNAc
A. caviae 11212 [243]	6)ManNAc(β1-4)GlcA(β1-3)GalNAc(β1- LRha(α1-3)┘ └(4-1β)Gal
A. caviae ATCC 15468 [244]	4)GalNAc3(*P*1Gro)(β1-4)GlcNAc(β1-4)LRhap(α1-3)GalNAc(β1-
A. hydrophila SJ-44[a] [245]	4)LRha*2Ac*(α1-3)GlcNAc(β1-
A. hydrophila O34[b] [246]	4)Man(α1-3)L6dTal2Ac(α1-3)GalNAc(β1- └(3-1α)L6dTal*2,3,4Ac*
A. salmonicida type A [247,248]	4)LRha*2Ac*(α1-3)ManNAc(β1- Glc(α1-3)┘
A. salmonicida type B [248]	4)LRha(α1-3)ManNAc(β1-
A. salmonicida type C [248]	4)LRha*Ac*(α1-3)ManNAc(β1-
A. salmonicida SJ-15[c] [249]	4)LRha(α1-3)ManNAc*4Ac*(β1- Glc(α1-4)Glc(α1-3)┘
A. salmonicida 80204-1 [239]	4)Qui3N(LAlaAc)(β1-3)GalNAc*AN*(1-3)QuiNAc(β1-
A. trota [250]	3)Gal(β1-3)GlcNAc(β1-4)LRha(α1-3)GalNAc(α1- Col(α1-2)┘ └(4-1α)Col

[a]*A. hydrophila* O11 antigen has the same structure but, in addition to LRha2Ac, includes minor LRha3Ac [74].
[b]Lateral L6dTal carries no, one or two *O*-acetyl groups at any positions.
[c]The structure seems to need reinvestigation [248].

P. marinoglutinosa) synthesizes different polysaccharides in the S- and R-form colonies: a linear sulfated glycan, which is highly uncommon for O-antigens, or a branched OPS enriched in amino sugars, including an *N*-acetyl-L-threonyl derivative of FucN, respectively. The OPS of *P. rubra* has a similar structure to that of *Vibrio vulnificus* CECT 5198 [253] but the latter incorporates QuiNAc into the O-unit in place of its biosynthetic precursor 2-acetamido-2,6-dideoxy-D-*xylo*-hexos-4-ulose in *P. rubra*.

Bacteria of the genus *Shewanella* are responsible for spoilage of protein-rich foods and are opportunistic pathogens of marine animals and humans. All OPSs of *Shewanella* studied are acidic and many contain GlcA, GalA or amides of GalA with 2-amino-1,3-propanediol (GroN) or N^{ε}-[(*S*)-1-carboxyethyl]-L-lysine (*S*alaLys) (Table 3.19). The OPS of *S. japonica* KMM 3601 is one of a few O-antigens that contain a derivative of 4-epilegionaminic acid (4eLeg). In *S. algae* BrY, an LRha residue is linked to a neighbouring LFucN through O2 of an L-malyl group, which is the *N*-acyl substituent of the latter.

The OPS of *Idiomarina zobellii* is unique in the presence of two amino sugars, Qui4N and LGulNA, with free amino groups [258]:

3)Qui4N(α1-4)GlcA(α1-6)GlcNAc(α1-4)LGulNA(α1-3)FucNAc(β1-

Table 3.18 Structures of *Pseudoalteromonas* OPSs

Pseudoalteromonas sp. KMM 634 [251]	4)ManNAc3NAcA6LAla(β1-4)GlcNAc3NAcA(β1- 4)GlcA(β1-3)QuiNAc4N(*S*3Hb)(α1-
Pseudoalteromonas sp. KMM 637 [251]	4)Glc(β1-4)GalA(β1-4)Man(β1-
Pseudoalteromonas sp. KMM 639 [251]	3)LRha(α1-3)Gal6(*P*2Gro)(α1-
P. agarivorans (R-from) [254]	3)LRha(α1-3)FucN(LThrAc)(α1-3)GalNAc(α1- ManNAcA(β1-4)┘
P. agarivorans (S-from)[a] [251]	4)LRha2R(α1-3)Man(β1-
P. aliena [252]	3)GlcA6LSer(β1-4)GlcNAc(α1-4)ManNAcA6LSer(β1-4)GlcNAc(β1- └(4-1α)Qui4NAc
P. atlantica [255]	3)Gal(α1-6)GlcNAc(α1-4)GalA(α1-3)QuiNAc(β1- └(6-2β)Pse5Ac7Ac
P. distincta [251]	4)Pse5Ac7Fo(α2-4)QuiNAc(β1- GlcA(α1-4)GalNAc(β1-4)GalNAcA*3Ac*(α1-3)┘
P. elyakovii [251]	6)Glc(α1-2)Glc(α1-4)GalNAc(β1-3)Gal(α1-3)GalNAc(β1-
P. flavipulchra [251]	7)Kdo(α2-3)L6dTal4Ac(α1-3)Gal(1β-
P. haloplanktis ATCC 14393[T] [251]	2)Qui3N(DAlaAc)(β1-4)GalNAcA(α1-4)Gal*2,6Ac*(α1- 4)LGalNAcA(α1-3)QuiNAc4NAc(β1-
P. haloplanktis KMM 156 [251]	2)LRha(α1-3)LRha(β1-4)GlcNAc(β1- └(3-1α)Glc3*R*lac
P. haloplanktis KMM 223 [251]	2)LIdoA(α1-4)GlcA(β1-4)GlcA(β1-3)QuiNAc4N(*S*3Hb)(β1- └(4-1α)QuiNAc4N(*S*3Hb)
P. mariniglutinosa (*Alteromonas marinoglutinosa*) [256]	3)Gal(α1-3)GlcNAc(β1 └(4-1β)ManNAc
P. nigrifaciens [251]	3)Gal(α1-4)LGulNAcA(α1-4)GlcNAc3Ac(β1- └(4-1α)Fuc3N(4Hb)
P. rubra[b] [253]	4)GlcNAc3NRAN(β1-4)LGalNAmA3Ac(α1-3)Sug(α1-
P. tetraodonis [251], *P. carrageenovora* [252]	2)Col(α1-4)GlcNAc(β1-4)GlcA(β1-3)GalNAc(1β- └(3-1β)Gal(2-1α)Col

[a]R indicates sulfate.
[b]R indicates 4-L-malyl, and Sug indicates 2-acetamido-2,6-dideoxy-D-*xylo*-hexos-4-ulose.

Table 3.19 Structures of *Shewanella* OPSs

S. algae 48055 [251]	3)GalA6(GroN)(α1-4)Neu5Ac(α2-3)GalA6(GroN)(β1-3)GlcNAc(β1-
S. algae BrY[a] [251]	3)LRha(α1-2)LRha(α1-2)R(4-2)LFucN(α1-3)QuipNAc4N(*R*3Hb)(α1-
S. fidelis KMM 3582[T] [252]	2)GalA6(2*S*alaLys)(α1-3)GalNAc(β1-4)GlcA(β1-3)GalNAc(β1-
S. japonica KMM 3299[T] [252]	3)Fuc4NAc(α1-4)GalA(α1-3)LFucNAc(α1-3)QuiNAc4NAc(β1-
S. japonica KMM 3601 [257]	4)4eLeg5Ac7Ac(α2-4)GlcA3Ac-(β1-3)GalNAc(β1-

[a]R indicates 4-L-malyl.

3.3.2.4 Pasteurellaceae

Bacteria *Aggregatibacter* (former *Actinobacillus*) *actinomycetemcomitans* are associated with aggressively progressing periodontitis and also cause serious infections, such as endocarditis. The O-antigens of serotypes a-f are neutral polysaccharides with di- or tri-saccharide O-units enriched in 6-deoxy sugars (Table 3.20). In serotypes a and c, they are distinctly O-acetylated homopolymers of enantiomers of 6-deoxytalose.

Actinobacillus (*Haemophilus*) *pleuropneumoniae* is a primary swine pathogen that causes hemorrhagic necrotizing pneumonia. *A. pleuropneumoniae* O-antigens are neutral polysaccharides, including galactans and glucogalactans present in many serogroups (Table 3.21).

Actinobacillus suis is a pathogen of pigs too. The O1 antigen of *A. suis* is a β1-6-linked glucan [268]. The O2 antigen that occurs in the majority of isolates in sick animals is a heteropolysaccharide [269]:

3)Gal(β1-4)Glc(β1-6)GlcNAc(β1-
Gal(α1-6)┘

Mannheimia (*Pasteurella*) *haemolytica* is associated with several diseases of cattle and sheep. The OPSs of both biotypes A and T are neutral and as simple as the other O-antigens in the family Pasteurellaceae (Table 3.22). The OPS of serotypes T4 and T10 has the same structure as galactan I of *Klebsiella pneumoniae* present also in *S. marcescens* O20 and some other bacteria. Serotype T3 shares the OPS with *S. marcescens* O19.

Although *Haemophilus influenzae* is perceived to lack any O-antigen, it has been found that when grown on a solid medium enriched in sialic acid, a group of *H. influenzae* strains synthesize LPSs, in which a tetrasaccharide is attached *en bloc* to the core OS and may be considered thus as an O-unit in an SR-type LPS [273]. As in *S. enterica* serogroups A-E, the first sugar of the O-unit is Gal. Two glycofroms are coexpressed, which differ only in the terminal non-reducing sugar, which is either Neu5Ac or phosphoethanolamine-bearing GalNAc:

Neu5Ac(α2-3)Gal(β1-4)GlcNAc(β1-3)Gal(β1- and
GalNAc6*P*EtN(α1-6)Gal(β1-4)GlcNAc(β1-3)Gal(β1-

Table 3.20 Structures of *A. actinomycetemcomitans* OPSs

a [259]	3)6dTal2Ac(α1-2)6dTal(α1-	d [259]	3)Glc(β1-4)Man(β1-4)Man(α1- LRha(α1-3)┘
b [260]	3)Fuc(α1-2)LRha(α1- GalNAc(β1-3)┘	e [259]	4)GlcNAc(α1-3)LRha(α1-
c [259]	3)L6dTal4Ac(α1-2)L6dTal(α1-	f [261]	2)LRha(α1-3)LRha(α1- GalNAc(β1-2)┘

Table 3.21 Structures of *A. pleuropneumoniae* OPSs

1, 9,[a] 11 [262,263]	2)LRha(α1-2)LRha(α1-6)Glc(α1- GlcNAc(β1-3)┘
2 [262]	2)LRha(α1-2)Gal(α1-3)Glc(β1-4)Glc*6Ac*(α1-4)GalNAc(β1-
3, 8, 15 [262,264]	3)Glc(α1-2)Gal*f*(β1-6)Gal(α1-6)Glc(β1-3)Gal*f*(β1-
4 [262]	4)LRha(α1-3)Gal(β1-4)GalNAc(β1- Glc(β1-3)┘
5[b] [262]	6)Gal(β1-
6 [262]	3)Glc(α1-2)Gal*f*(β1-6)Glc(α1-6)Glc(β1-3)Gal*f*(β1-
7, 13 [262,265]	4)LRha(α1-3)Gal(β1-4)GalNAc(β1- Gal(β1-3)┘
10 [262]	2)Gal*f*(β1-
12 [266]	5)Gal*f*(β1-6)Gal*f*(β1- Gal(α1-6)┘
14 [267]	5)Gal*f*(β1- Gal(α1-2)┘

[a]In serotype 9, GlcNAc is present in a non-stoichiometric amount.
[b]In several strains, the polysaccharide is randomly O-acetylated.

Table 3.22 Structures of *M. haemolytica* OPSs

A1, A6, A9 [270]	4)Gal(β1-3)Gal(β1-3)GalNAc(β1-
T3 [271]	4)LRha(α1-3)GlcNAc(β1-
T4, T10 [272]	3)Gal(α1-3)Gal*f*(β1-

3.3.2.5 Pseudomonadaceae

Pseudomonas aeruginosa is an important opportunistic pathogen causing human infections, primarily in immunocompromized hosts and cystic fibrosis patients. O-antigen structures of this bacterium have been studied in detail and surveyed repeatedly [274–276]. In serogroups O1-O13, the OPSs have linear acidic tri- or tetra-saccharide O-units typically containing LRha, 6-deoxyamino sugars (QuiN, FucN, LFucN, QuiN4N) and acidic amino sugars, including GalNA, LGalNA, GlcN3NA, ManN3NA, LGulN3NA, Pse and 8eLeg. 2,3-Diamino-2,3-dideoxyhexuronic acids and both 5,7-diamino-3,5,7,9-tetradeoxynon-2-ulosonic acids have been found in *P. aeruginosa* for the first time in nature. Most amino sugars are N-acetylated but formyl, acetimidoyl, (*R*)- and (*S*)-3-hydroxybutanoyl occur as *N*-acyl groups too. Similar OPSs within complex O-serogroups differ in: (1) the pattern of O-acetylation, (2) an *N*-acyl group (acetyl *versus* 3-hydroxybutanoyl), (3) a monosaccharide (QuiN *versus* FucN, ManN3NA *versus* LGulN3NA, the presence of lateral Glc), and (4) a linkage (α1-3 *versus* α1-2 or β1-3, α1-4 *versus* β1-4).

Another bacterium well studied in respect to the O-antigen structure is *Pseudomonas syringae*, an important phytopathogen that infects a wide range of plants. The OPSs of *P. syringae* and related species are linear D- or L-rhamnan, a mixed D/L-rhamnan or branched polysaccharides with a rhamnan backbone and side chains of Rha, Fuc, GlcNAc or Fuc3NAc [240, 241, 277, 278]. In several D-rhamnan-based OPSs, Rha may be O-methylated. Characteristic features of the OPSs of this group are (1) irregularity owing to a non-stoichiometric glycosylation or O-methylation, (2) the presence of O-units of different types in one strain, (3) O-antigen diversity within one pathovar, and (4) sharing an OPS by different pathovars.

Structures of the OPSs have been determined also in an ubiquitous microorganism *P. fluorescens,* a phytopathogen *P. cichorii,* a mushroom pathogen *P. tolaasii,* a mushroom-associated bacterium *P. reactans,* a rhizosphere colonizer *P. putida* and several other *Pseudomonas* species. They are diverse in composition and include various 6-deoxyamino sugars (QuiN, LQuiN, FucN, Fuc3N, Fuc4N, QuiN4N), which may bear uncommon *N*-acyl groups, such as (*S*)-3-hydroxybutanoyl, *N*-acetyl-L-alanyl and 3-hydroxy-2,3-dimethyl-5-oxoprolyl. The last substituent resides on Qui3N in the OPSs of both *P. fluorescens* IMV 2366 and 361, which differ only in one monosaccharide (LRha *versus* L6dTal4Ac) (Table 3.23). The OPS of the type strain *P. fluorescens* ATCC 13525 is structurally related to that of several *P. syringae* strains [240, 241]. The OPS of *P. fluorescens* ATCC 49271 is a homoglycan composed of a partially 8-O-acetylated 5-*N*-acetimidoyl-7-*N*-acetyl derivative of Leg. Essentially the same homopolymer is the O-antigen of *Legionella pneumophila* serogroup 1 [67, 279]. The OPS of *P. corrugate* contains a derivative of a unique higher sugar 5,7-diamino-5,7,9-trideoxynon-2-ulosonic acid [280]; both OPS structure and configuration of the acid remain to be determined. *Pseudomonas* sp. (former *P. stutzeri*) OX1 has an OPS consisting of two 4-amino-4,6-dideoxyhexose derivatives, Rha4NAc and Fuc4NFo, but in the presence of the azo dye Orange II, it produces another, acidic OPS with such rarely occurring constituents as LGulNAcA and an amide of GalNAcA with L-serine. LGulNAcA in the amide form is present also in the OPS of *P. tolaasii*.

3.3.2.6 Moraxellaceae

Bacteria of the genus *Acinetobacter* are soil organisms, which participate in mineralization of various organic compounds. Several species are a key source of hospital infections in debilitated patients and are responsible for cases of community-acquired meningitis and pneumonia. The OPS structures have been studied in *A. baumanni* as well as several other species and unnamed DNA groups. A sugar pyruvic acid acetal is a component of the only known OPS of *A. calcoaceticus* (DNA group 1), whereas other strains of this species produce R-type LPSs. The OPSs of *A. haemolyticus* (DNA group 4) are similar in the presence of various 2-amino-2-deoxyhexuronic acids and derivatives of QuiN4N. The OPSs of *Acinetobacter* (DNA group 2) are either neutral or acidic due to the presence of hexuronic acids (GlcA, GalNAcA, GlcNAc3NAcA) or a derivative of Leg. The other OPSs studied, including those of *A. junii* and *A. lwoffii* (DNA groups 5 and 8,

Table 3.23 Structures of *Pseudomonas* OPSs

P. fluorescens A (ATCC 13525^T) [281]	3)LRha(α1-3)LRha(α1-2)LRha(α1- Fuc3NAc(α1-2)┘ └*(2-1α)Fuc3NAc*
P. fluorescens A (IMV 472) [282]	3)LRha2Ac(β1-4)LRha(α1-3)Fuc(α1- GlcNAc(β1-2)┘
P. fluorescens A (IMV 1152) [283]	3)Fuc4NAc(α1-4)LQuiNAc(α1-3)QuiNAc(β1-
P. fluorescens B (IMV 247) [284]	2)Qui3N(*S*3Hb)(β1-2)LRha(α1-4)GalNAcA(α1-3)QuiNAc4N(*S*3Hb)(α1-
P. fluorescens C[a] (IMV 2366) [285]	2)Qui3NR(β1-3)LRha(α1-3)FucNAc(α1-
P. fluorescens 361[a] [286,287]	4)Qui3NR(β1-3)L6dTal4Ac(α1-3)FucNAc(β1-
P. fluorescens G (IMV 2763)[b] [288]	4)Man(α1-2)Man(α1-3)GalNAc(βα1- L6dTal2Ac(α1-3)┘
P. fluorescens ATCC 49271 [67,289]	4)Leg5Am7Ac*8Ac*(α2-
P. chlororaphis ssp. aurantiaca (*P. aurantiaca*) [290]	3)LFucNAc(α1-3)LFucNAc(α1-3)QuiNAc4NAc(β1-
P. cichorii [291]	3)LFucNAc(α1-2)Qui3NAc(β1-3)LFucNAc(α1-3)QuiNAc(α1-
P. putida [292]	2)Rha(α1-3)Rha(α1-3)Man(β1-
P. reactans [293]	3)QuiN(LAlaAc)4N(LAlaAc)(β1-3)GlcNAm(α1-3)QuiNAc4NAc(α1-
P. tolaasii [294]	4)LGulNAcAN*3Ac*(α1-3)QuiNAc(β1-
Pseudomonas sp. OX1 [295]	2)Rha4NAc(α1- *Fuc4NFo(α1-3)*┘
Pseudomonas sp. OX1[c] [296]	4)GalNAcA6Ser(α1-4)ManNAcA(β1-4)LGulNAcA(α1-3)QuiNAc4N(*S*3Hb)(β1- └(3-1β)Glc

[a]R indicates 3-hydroxy-2,3-dimethyl-5-oxoprolyl of unknown configuration.
[b]Later, classification of this strain as *P. fluorescens* was questioned.
[c]Configuration of serine has not been determined.

respectively), are all neutral. In *A. lwoffii* EK30 and *Acinetobacter* sp. 4 (DNA group 11), Qui4N and Fuc3N bear uncommon *N*-acyl groups: D-homoseryl (DHse) and (*S*)-2-hydroxypropanoyl, respectively (Table 3.24). A peculiar feature of three *Acinetobacter* OPSs is alternating *N*-acetyl and *N*-[(*S*)-3-hydroxybutanoyl] groups on Leg, QuiN4N or DHse. The OPSs of *A. baumanni* O7 and O10 have the same main chain, and those of *A. haemolyticus* 57 and 61 differ only in the configuration of the linkage between the O-units.

3.3.2.7 Vibrionaceae

From about 200 *V. cholerae* O-serogroups, O1 and O139 strains cause Asiatic cholera, whereas others are opportunistic pathogens responsible for travel diarrhea and other enteric diseases. The OPS structures of both pathogenic and several non-O1, non-O139 serogroups have been established and most of them reviewed recently [322]. Homopolymers of (*R*)- and (*S*)-2-hydroxypropanoyl derivatives of LRha4N have been found in the O144 and O76 antigens, respectively, and the O1 antigen consists of an (*S*)-2,4-dihydroxybutanoyl derivative of Rha4N.

Table 3.24 Structures of *Acinetobacter* OPSs

A. calcoaceticus 7 [297]	2)Gal4,6*R*pyr3*Ac*(β1-3)GlcNAc(β1-4)GlcA(β1-3)GalNAc(β1-
A. baumanni O1 [298]	3)GlcNAc(α1-3)GalNAc(β1- Gal(α1-6)┘
A. baumanni O2 [299]	4)Gal(α1-6)Gal(β1-3)GalNAc(β1- └(3-1β)GalNAc(3-1α)GalNAc(3-1β)Fuc3N(*R*3Hb)
A. baumanni O5 [300,301]	3)GalNAcA(α1-3)LFucNAc(α1-3)GlcNAc(β1- └(4-1α)LFucNAc
A. baumanni O7 [302]	2)LRha(α1-2)LRha(α1-3)LRha(α1-3)GlcNAc(α1- └(3-1β)GlcNAc(4-1β)LRha
A. baumanni O10 [303]	2)LRha(α1-2)LRha(α1-3)LRha(α1-3)GlcNAc(α1- └(3-1α)ManNAc
A. baumanni O11[a] [304,305]	4)GalNAc(β1-3)Gal(α1-6)Gal(β1-3)GalNAc(α1- └(6-1β)Glc
A. baumanni O12[a] O23 [306]	3)GalNAc(β1-3)Gal(α1-3)GlcNAc(β1- └(4-1α)GlcNAc(6-1β)Qui3N(*R*3Hb)
A. baumanni O16 [305]	6)GlcNAc(α1-4)GalNAc(α1-3)GlcNAc(α1- Glc(β1-3)┘
A. baumanni O18 [307]	3)Gal(β1-3)GalNAc(β1- ManNAc(β1-4)Gal(α1-4)┘
A. baumanni O22 [308]	3)Glc(β1-3)GalNAc(β1- Gal(α1-6)┘
A. baumanni O24[b] [67,309]	4)Leg5R7Ac(β2-6)GlcNAc(α1-3)LFucNAc(α1-3)GlcNAc(α1-
A. baumanni ATCC 17961 [310]	3)Gal(α1-6)Glc(β1-3)GalNAc(β1- GlcNAc3NAcA(β1-4)┘└(6-1β)GlcNAc
A. baumanni [311]	3)Qui4NAc(β1-3)GalNAc(α1-4)GalNAc(α1-3)GalNAc(α1- Gal(α1-6)┘
A. baumanni 24[b] [312]	4)GlcNAc6*Ac*(α1-4)GalNAcA(α1-3)QuiNAc4NR(β1-
Acinetobacter sp. 44 (DNA group 3 [313]	3)LRha(α1-3)LRha(α1-2)LRha(α1-3)GlcNAc(β1- └(2-1α)LRha(2-1β)GlcA(4-1α)LRha
A. haemolyticus ATCC 17906 [314]	4)GalNAcA6DAla(α1-4)GalNAcA(α1-3)QuiNAc4NAc(β1-
A. haemolyticus 57 [315]	4)ManNAcA(β1-4)LGulNAcA3Ac(α1-3)QuiNAc4N(*S*3Hb)(α1-
A. haemolyticus 61 [315]	4)ManNAcA(β1-4)LGulNAcA3Ac(α1-3)QuiNAc4N(*S*3Hb)(β1-
A. junii 65 [316]	2)LRha(α1-3)LRha(α1-2)LRha(α1-3)LRha(α1-3)Gal(β1-
A. lwoffii EK30[b] [317]	3)Qui4N(DHseR)(β1-6)Gal(α1-4)GalNAc(α1-3)FucNAc(α1-
A. lwoffii EK67, *Acinetobacter* sp. VS-15 [318]	2)LRha(1-6)Gal(1-4)GalNAc(1-3)QuiNAc(1- GlcNAc(β1-3)┘
Acinetobacter sp. 90 (DNA group 10) [319]	3)Gal(α1-4)GalNAc(β1-3)Gal(α1-3)GlcNAc(β1- └(4-1α)Fuc4N(*R*3Hb)
Acinetobacter sp. 94 (DNA group 11) [320]	3)Gal(α1-3)GalNAc(β1- └(4-1β)GalNAc(4-1α)Fuc3N(*S*2Hp*Ac*)
Acinetobacter sp. 96 (DNA group 11) [321]	4)Man(β1-3)Man(α1-3)LFuc(α1-3)GlcNAc(β1- └(3-1α)LFuc
Acinetobacter sp. 108 (DNA group 13) [301]	4)Gal(α1-6)Gal(β1-3)GalNAc(β1- └(3-1β)GalNAc(3-1α)GalNAc(3-1β)Fuc3N(*R*3Hb)

[a]Another OPS having the same structure as the *A. baumanni* O16 antigen is also present.
[b]R indicates acetyl or (*S*)-3-hydroxybutanoyl.

2-O-Methylation of the terminal non-reducing Rha4N residue in the O1 antigen results in seroconversion from variant Inaba to Ogawa. There are present also other unusual monosaccharide components, such as ascarylose, DDmanHep and a 5-*N*-acetimidoyl-7-*N*-acetyl derivative of Pse. Several other unusual *N*-acyl groups present on amino sugars are 3,5-dihydroxyhexanoyl, (*2R,3R*)-3-hydroxy-3-methyl-5-oxoprolyl and *N*-acetyl-L-allothreonyl (Table 3.25). The O139 and O155 antigens, as well as that of *Vibrio mimicus* N-1990, include a cyclic phosphate group on Gal. The O22 and O139 antigens consist of only one O-unit with two colitose residues in each strain. The OPSs of *V. cholerae* O8, O10 and an unclassified strain H11 are similar to those of *Listonella anguillarum* O2a, *E. coli* O64 and *Shewanella algae* 48055, respectively.

Table 3.25 Structures of *V. cholerae* OPSs

O1[a] [322]	2)Rha4NR(α1-
O2 [323]	4)Qui*p*NAc(β1-4)Pse5Am7Ac(β2-4)Gal(β1-
O3[6] [324]	2)DDmanHep(α1-4)LFucNAc(α1-3)QuiNAc4NR(β1- └(3-1α)Asc
O5[c] [325]	4)ManNAcA(β1-3)QuiNAc4NAc(β1- Fuc3NR(α1-3)┘
O6 [326]	6)GlcNAc3Ac(α1-3)LRha2Ac(β1-4)GlcNAc(β1- └(4-1α)GlcA
O8 [327]	4)GlcNAc3N(LAlaFo)AN(β1-4)ManNAc3NAcAN(β1- 4)LGulNAc3NAcA(α1-3)QuiNAc4NAc(β1-
O9 [328]	4)Glc(α1-4)GalNAcA(α1-3)GalNAcA(α1-3)GlcNAc(α1- Glc(α1-4)┘
O10 [322]	3)ManNAc(α1-4)GlcA(β1-3)Gal(β1-3)GlcNAc(β1-
O21 [329]	7) DDmanHep(β1-3)GlcNAc(β1- LRha(α1-3)┘ └(4-1β)GalNAc
O22 [322]	GalA*3,4Ac*(β1-3)GlcNAc(α1-4)GalA(α1-3)QuiNAc(β1- └(2-1α)Col └(4-1α)Col
O43 [330]	3)Qui4N(LaThrAc)(β1-3)Gal*p*NAcA(α1-4)GalNAc(α1-3)QuiNAc(α1-
O76 [331]	2)LRha4N(*S*2Hp)(α1-
O139 [322]	Gal4,6*P*(β1-3)GlcNAc(β1-4)GalA(α1-3)QuiNAc(β1- Col(α1-2)┘ └(4-1α)Col
O140 (bioserogroup Hakata [332]	2)Rha4NAc(α1-
O144 [333]	2)LRha4N(*R*2Hp)(α1-
O155 [334]	4) LFuc(α1-3)FucNAc(β1- └(3-1α)GlcNAc(4-1α)LFuc(3-1α)Gal4,6*P*
H11 [335]	4)GalA6(GroN)(α1-4)NeuAc(α2-3)GalA6(GroN)(β1-3)QuiNAc(β1-

[a]R indicates (*S*)-2,4-dihydroxybutanoyl.
[b]R indicates 3,5-dihydroxyhexanoyl of unknown configuration.
[c]R indicates (*2R,3R*)-3-hydroxy-3-methyl-5-oxoprolyl.

Among non-cholerae vibrios, there are marine bacteria, including fish pathogens *V. vulnificus* and *V. ordalii*, as well as opportunistic pathogens of humans, such as *V. fluvialis* and *V. mimicus*. Their OPSs contain various unusual components too, e.g. a (*S*)-3-hydroxybutanoyl derivative of LRhaN3N, 2-acetamido-2,6-dideoxy-D-*xylo*-hexos-4-ulose, a 2-*N*-acetimidoyl derivative of LGalNA, a partially O-acetylated 4-D-malyl derivative of GlcN3N and 3-*O*-[(*R*)-1-hydroxyethyl]-L-rhamnose (rhamnolactilic acid). The OPS of *V. fluvialis* O19 and *Vibrio* bioserogroup 1875 is a homopolymer of a 3-hydroxypropanoyl derivative of Rha4N; in the latter bacterium, the monosaccharide at the non-reducing end is 2-O-methylated [336]. The SR-type LPS of *V. fluvialis* M-940 has a single heptasaccharide O-unit (Table 3.26). The OPS of *V. alginoluticus* includes di-*N*-acetyllegionaminic acid [67, 337] but the O-unit structure remains unknown.

In the OPSs of a fish pathogen *Listonella* (former *Vibrio*) *anguillarum,* derivatives of amino and diamino sugars and hexuronic acids are abundant (Table 3.27). In strain 1282, an *N*-formyl-L-alanyl derivative of GlcN3NAN at the non-reducing end of the OPS is 4-O-acetylated, and in an unnamed strain, the terminal LQui3NAc residue is 4-O-methylated. The discrimination of strains

Table 3.26 Structures of other *Vibrio* sp. OPSs

V. fluvialis sv. 3 [338]	4)LRha(α1-3)ManNAc(β1-
V. fluvialis OKA-82-708 [339]	2)LRha(α1-3)LRha(α1-3)LRha(α1-3)LRha(α1- GlcNAc(β1-2)┘
V. fluvialis AQ-0002B [340]	2)Man(β1-4)GalNAc(α1-4)GalA(α1-3)GlcNAc(α1- └(3-1α)LRha3*R*lac
V. fluvialis M-940 [341]	LRha(α1-2)LFuc(α1-2)Gal(α1-2)LFuc(α1-3)GlcA(β1- 4)LRha(α1-3)GlcNAc(β1-
V. fluvialis O19, *Vibrio* bioserogroup 1875 [342,343]	2)Rha4N(3Hp)(α1-
V. fluvialis AA-18239 [344]	4)GalNAc(α1-2)Rib*f*(β1-
V. mimicus N-1990 [345]	4)GalNAc(α1-3)GalNAc(β1-2)Gal4,6*P*(β1-3)GalNAc(α1-
V. mimicus W-26768 [346]	3)Qui3N(*R*3Hb)(β1- *GalNAc(α1-2)*┘
V. ordalii O2[a] [347,348]	4)GlcNAc3N(LAlaFo)AN(β1-4)GlcNAc3NAmA(β1- 4)LGulNAc3NAcA(α1-3)Sug-(β1-
V. vulnificus CECT 4602[b] [349]	4)GlcNAc(α1-3)LRha(α1-3)GlcNAc(β1- └(3-1β)LRhaNAc3N(*S*3Hb)
V. vulnificus YJ016 [350]	3)LGalNAmA(α1-3)QuiNAc4NAc(β1-3)LFuc(α1- 3)GlcNAc(α1- └(4-1β)GlcNAc*6Ac*
V. vulnificus CECT 5198[c] [253]	4)GlcNAc3NRAN(β1-4)LGalNAmA(α1-3)QuiNAc(α1-

[a]Sug indicates 2-acetamido-2,6-dideoxy-D-*xylo*-hexos-4-ulose.
[b]The presence of ~20% (*R*)-3-hydroxybutanoyl group reported [349] could be due to a partial racemization in the course of acid hydrolysis.
[c]R indicates 4-D-malyl or 2-*O*-acetyl-4-D-malyl.

Table 3.27 Structures of *L. anguillarum* OPSs

L. anguillarum O2a; O2b[a] [347,351,352]	4)GlcNAc3N(LAlaR)AN(β1-4)ManNAc3NAmA(β1- 4)LGulNAc3NAcA(α1-3)QuiNAc4NAc(β1-
L. anguillarum 1282 [352]	4)GlcNAc3N(LAlaFo)AN(β1-4)ManNAc3NAmA(β1- 4)Qui3NAc(β1-3)FucNAc4NAc-(α1-
L. anguillarum V-123[b] [353]	3)GalNAcAN(α1-4)GalNFoA(α1-3)QuiNAc(α1-3)Qui4NR(β1-
L. anguillarum[c] [354]	4)LQui3NAc(β1-4)LQui3NAc(β1- QuiNAc(α1-2)┘

[a]R indicates Fo in serotype O2a or Ac in serotype O2b [351].
[b]R indicates 2,4-dihydroxy-3,3,4-trimethyl-5-oxoprolyl of unknown configuration.
[c]Presumably, an *O*-propanoyl group is present at position 3 or 4 of QuiNAc.

of O2a and O2b serotypes is based on the nature of a 3-*N*-acyl group on GlcN3NAN, which is either *N*-formyl-L-alanyl or *N*-acetyl-L-alanyl, respectively.

3.3.2.8 Xanthomonadaceae

Xanthomonas campestris and related species cause several plant diseases. Their OPS structures have been examined [240, 278]. With a few exceptions, the OPSs have a D- or L-rhamnan backbone and many from them have Xyl or LXyl side chains. In *X. campestris* pv. *pruni,* there are three sites of non-stoichiometric xylosylation of the main chain, and totally 0 to 2 LXyl residues per O-unit are present (Table 3.28). The OPSs of *X. campestris* pv. *vitians* and *X. fragariae* have main chains of α1-3- and β1-3-linked LRha residues, which lack strict regularity.

Table 3.28 Structures of *Xanthomonas* OPSs

X. campestris pv. *begoniae* [240]	2)LRha(α1-3)LRha(α1-3)LRha(α1- LXyl(β1-2)┘ └*(4-1β)LXyl*
X. campestris pv. *campestris* 8004 [355]	3)Rha(α1-3)Rha(β1- Fuc3NAc(α1-2)┘
X. campestris pv. *malvacearum* [356]	2)Rha*3Me*(α1-3)Rha(α1-3)Rha(α1- Fuc*f*(α1-4)┘
X. campestris pv. *manihotis* [240]	2)LRha(α1-2)LRha(α1-3)LRha(β1- Xyl(β1-2)┘
X. campestris pv. *phaseoli* var. *fuscans* [356]	2)Rha(α1-3)Rha(α1-3)Rha(α1-
X. campestris pv. *pruni* [357]	2)LRha(α1-2)Glc(α1-3)LRha(α1- *LXyl(β1-4)*┘ *LXyl(β1-3)*┘ *LXyl(β1-4)*┘
X. campestris pv. *vignicola* [240]	2)Rha(α1-2)Rha(α1-3)Rha(β1- Rha(α1-3)┘ └*(3-1α)Rha*
X. campestris NCPPB 45 [240]	3)GalA(α1-2)LRha(α1-2)LRha(α1-3)LRha(α1-3)Gal(β1- └(4-1α)LRha
X. campestris 642 [240]	2)LRha(α1-3)LRha(α1-2)LRha(α1-3)LRha(α1-3)LRha(α1- Xyl(β1-2)┘ └(4-1β)Xyl
X. cassavae [278]	3)Rha(β1-3)Rha4NAc(α1- Xyl(β1-2)┘

In the former, parts of the polysaccharide chains are linear and the others bear α1-2-linked Fuc3NAc residues [240, 278], and in the latter, the rhamnan is decorated with α1-2-linked Fuc residues [240]. The OPS of *X. campestris* NCPPB 45 is exceptionally acidic due to the presence of GalA.

Stenotrophomonas (Xanthomonas or *Pseudomonas) maltophilia* is an emerging opportunist human pathogen, which can causes blood-stream infections and pneumonia with considerable morbidity in immunosuppressed patients. The OPSs of these bacteria are neutral, and most O-units are branched tri- and tetra-saccharides (Table 3.29). As in *X. campestris*, Xyl and Rha in both enantiomeric forms occur in many O-serogroups, and several xylorhamnans are structurally related in the two

Table 3.29 Structures of *S. maltophilia* OPSs

O1[a] [358]	3)LRha(α1-3)GlcNAc(β1- Araf(α1-6)┘
O2 [359]	4)Man(α1-3)LRha(α1- LXyl(β1-2)┘
O3 [360]	3)Fuc(α1-3)GlcNAc(β1- └(4-1α)Fuc4NAc
O4 [361]	2)Rha(α1-3)Rha(α1-3)Rha(α1- Xyl(β1-2)┘ └(4-1β)Xyl
O6 [362]	3)LRha(α1-3)GlcNAc(β1- Xyl(β1-4)┘
O7 [363]	2)Rha(α1-3)Rha(α1-3)Rha(α1-
O8 [364]	2)LRha(α1-3)LRha(α1-4)LRha(α1- LXyl3Me(β1-4)┘
O10 [365]	2)LRha(β1-2)LRha(α1-2)LRha(α1- LXyl(β1-3)┘
O12/O27 [366]	3)Rha(β1-3)Rha4NAc(α1-3)Rha4NAc(α1-3)Rha4NAc(α1- └(2-1α)Fuc3NAc
O16[b] [367]	3)ManNAc(β1-4)GlcNAc(β1- Ribf(α1-4)┘
O18 [361]	2)LRha(α1-3)LRha(α1-3)LRha(α1- LXyl(β1-2)┘ └*(4-1β)LXyl*
O19 [368]	3)LRha(β1-4)LRha(α1-3)Fuc(α1- Glc(α1-3)┘
O20 [369]	2)Man(α1-3)Rha(β1-2)Rha(α1-2)Rha(α1-
O21 [370]	6)GlcNAc(α1-4)GalNAc(α1- Araf(α1-3)┘
O25 [370]	6)GlcNAc(α1-4)GalNAc(α1-

[a]The location of the *O*-acetyl group is tentative.
[b]The OPS is non-stoichiometrically O-acetylated at unknown position.

species. The O4 and O18 antigens have the same structure but the constituent monosaccharides, Xyl and Rha, are either D or L, respectively. The O8 antigen contains 3-*O*-methyl-L-xylose as a component of each O-unit, and the O1 antigen is presumably terminated with 3-*O*-methyl-6-deoxytalose. Whereas Xyl is always pyranosidic, two other constituent pentoses, Ara and Rib, are present in the furanose form. Other uncommon monosaccharides, including L6dTal, Fuc3NAc, Fuc4NAc and Rha4NAc, are components of the OPSs. A linear D-rhamnan of serogroup O7 has the same structure as the common polysaccharide antigen of *P. aeruginosa* [9] and the O-antigen of several strains of *P. syringae* [240, 241, 277, 278] and *X. campestris* pv. *phaseoli*. A 6)GlcNAc(α1-4)GalNAc(α1- backbone of the O21 and O25 antigens is shared by several *Citrobacter* strains [78].

3.3.2.9 Other Families

Francisella tularensis from the family Francisellaceae is the etiologic agent of tularemia and one of the most virulent Gram-negative bacteria considered as a biological weapon or bioterrorist agent. From four subspecies, ssp. *tularensis* is the most infective and fatal for humans, whereas ssp. *novicida* is virulent for mice but not humans. The OPS common for *F. tularensis* ssp. *tularensis* and *holarctica* (types A and B) has a tetrasaccharide O-unit with two residues of GalNAcA, both in the amide form, and one residue each of QuiNAc and Qui4NFo [371]:

2)Qui4NFo(β1-4)GalNAcAN(α1-4)GalNAcAN(α1-3)QuiNAc(β1-

The 4)GalNAcAN(α1-4)GalNAcAN(α1- disaccharide fragment of this O-antigen is shared by *F. tularensis* ssp. *novicida,* in which QuiNAc is replaced by QuiNAc4NAc and Qui4NFo by the third GalNAcAN residue [371]:

4)GalNAcAN(α1-4)GalNAcAN(α1-4)GalNAcAN(α1-3)QuiNAc4NAc(α1-

A fish pathogen *Francisella victoria* possesses a non-repetitive polysaccharide part of the LPS containing 20 monosaccharides as well as alanyl, 3-aminobutanoyl and 4-acetamido-3-hydroxy-3-methyl-5-oxoprolyl on Qui3N, Qui4N and Fuc4N [372].

Legionella pneumophila from the family Legionellaceae is a facultative intracellular bacterium and the cause of legionellosis, pneumonia with sometimes-fatal progression. From 15 existing O-serogroups, strains of serogroup 1 are most often isolated from environmental samples and clinical specimens. Their O-antigen is polylegionaminic acid 4)Leg5Am7Ac(α2-, which is 8-O-acetylated in part of the strains and mostly nonacetylated in the others [67, 279]. Accordingly, serogroup 1 strains are divided into the Pontiac and non-Pontiac groups. The O-antigen of *L. pneumophila* serogroup 2 and most other non-1 serogroups, except for serogroups 7 and 13, is a homopolymer of a similar derivative of 4-epilegionaminic acid 4)4eLeg5Am7Ac(α2-, which is also 8-O-acetylated to a different extent (10–90%)

Table 3.30 Structures of *Halomonas* OPSs

H. alkaliantarctica [375]	3)LRha(β1-4)LRha(α1-3)LRha(α1-
H. magadiensis [376,377]	4)Glc(β1-3)Gal(β1- and Glc(α1-4)┘ 4)LGulNAcA(α1-4)LGulNAcA(α1-6)Glc(α1-
H. pantelleriensis [374]	2)GlcA4Slac(β1-4)GlcA(β1-4)GalNAcA(α1-3)LQuiNAc(β1-
H. stevensii [378]	4)Glc(β1-3)Gal(β1- Glc(α1-4)┘

[67, 373]. Both Leg and 4-eLeg have been found in *L. pneumophila* for the first time in nature.

The O-antigens have been studied in four species of halophilic bacteria of the genus *Halomonas* (family Halomonadaceae) (Table 3.30). The OPS of *H. alkaliantarctica* is an L-rhamnan, and that of *H. pantelleriensis* is highly acidic due to the presence of GlcA, GalNAcA and an ether of GlcA with (*S*)-lactic acid. The latter OPS is unusual in that an L-configurated monosaccharide, LQuiNAc, is the first sugar of the O-unit [374]. *H. magadiensis* (former *H. magadii*) produces two OPSs, one neutral (major) and one acidic enriched in LGulNAcA. The neutral OPS of *H. magadiensis* is shared by *H. stevensii*.

The OPS of the marine bacterium *Marinomonas communis* classified to the family Ocenospirillaceae is a 2)LRha(α1-3)LRha(α1-3)LRha(α1- rhamnan [379], which is shared by several *P. syringae* strains [241, 278].

The OPS of a mesophilic chemolithotroph *Acidithiobacillus* (*Thiobacillus*) *ferrooxidans* from the family Acidithiobacillaceae includes both rhamnose enantiomers and 3-*O*-methyl-L-rhamnose as a component of the O-unit [380]:

3)Glc(α1-3)Rha(α1-3)LRha(α1-3)Glc(β1-
LRha3Me(α1-4)┘

3.3.3 α-Proteobacteria

3.3.3.1 Rhizobiaceae, Xanthobacteraceae

Rhizobacteria are unique in their ability to interact with roots of legumes and to form nitrogen-fixing nodules. The OPSs of *Rhizobium, Mesorhizobium* and *Sinorhizobium* (both former *Rhizobium* too) from the family Rhizobiaceae have a lipophilic character due to the abundance of 6-deoxyhexoses (Rha, LRha, LFuc, 6dTal, L6dTal), *O*-methyl and *O*-acetyl groups [381, 382] (Table 3.31).

A short-chain OPS of *R. etli* consisting of five O-units is enriched in O-methylated sugars, including methyl ester of GlcA present in the majority of the O-units. It is increased in the content of 2-*O*-methyl-L-fucose in bacteroids isolated from root nodules of the host plant *Phaseolus vulgaris* or in bacterial cultures grown in the presence of anthocyanin as compared with cultures grown

Table 3.31 Structures of rhizobial OPSs

R. etli[a] [383,384]	4)GlcA6Me(β1-4)LFuc*2Me*(α1- 6dTal3Me(α1-3)┘
R. leguminosarum bv. *viciae* 3841 [387]	4)Glc3NAmA(β1-4)LFuc*2Ac*(α1-3)LQuiNAc(α1- 6dTal2Ac3Me*4Me*(α1-3)┘
R. leguminosarum bv. *viciae* 5523[a] [388]	4)Glc(α1-3)QuiNAc(α1-
R. leguminosarum bv. *trifolii* 4s [382]	3)LRha(α1-3)LRha(α1-3)LRha(α1-4)GlcNAc(β1- ManNAc(α1-2)┘
R. leguminosarium bv. *trifolii* 24[b] [389,390]	3)L6dTal(α1-2)LRha(α1-5)Sug(2-
R. leguminosarum bv. *viciae* [382]	3)LRha(α1-3)LFuc(α1-3)LFuc(α1- Man(α1-2)┘
R. tropici [382]	3)6dTal2Ac(α1-3)LFuc(α1-4)Glc(β1-
M. amorphae ATCC 19655, *M. loti* HAMBI 1148 [391]	3)Rha(α1-3)Rha(α1-3)Rha(α1-3)Rha(α1-2)Rha*3Me*(α1- └*(2-1β)GlcNAc4Me*
M. loti NZP2213 [392]	3)L6dTal2Ac(α1-
M. loti 2213.1[c] [385]	3)L6dTal*2R*(α1-
M. loti Mlo-13 [386]	2)L6dTal(α1-3)L6dTal4Ac(α1-2)LRha*3Me*(α1-
M. huakuii [382]	2)L6dTal(α1-3)L6dTal(α1-2)LRha(α1-
S. fredii[c] [393]	4)GalA(α1-3)LRha2Ac(α1-3)Man2Ac*6R*(α1-
Sinorhizobium sp. NGR234 [394]	3)LRha(α1-3)LRha(α1-2)LRha*3Me*(α1-

[a]The OPS is O-acetylated at unknown position.
[b]Sug indicates 3-deoxy-D-*lyxo*-hept-2-ulosaric acid. The configuration of its linkage remains unknown.
[c]R indicates Ac or Me.

under standard laboratory conditions [383]. 2,3,4-Tri-*O*-methylfucose or, in a minority of molecules, 2-*O*-methyl- and 2,3-di-*O*-methylfucose terminates the non-reducing end of the OPS, and a non-repetitive tetrasaccharide with a Kdo residue at the reducing end is located between the O-antigen and the core OS [384].

The OPS of *R. leguminosarium* 3841 is also short and is built up of three to four O-units. It is the only known O-antigen that contains a derivative of 3-amino-3-deoxyhexuronic acid (Glc3NAmA). Another unique components, a dicarboxylic 3-deoxyhept-2-ulosaric acid, is present in the OPS of *R. leguminosarium* bv. *trifolii* (*R. trifolii*) 24. A Fix$^-$ mutant of this bacterium has a totally different OPS that lacks L6dTal but is rich in heptose and *O*-methylheptose [384]. The OPS of *M. loti* NZP2213 is a homopolymer of 2-*O*-acetyl-6-deoxy-L-talose with a small content of 2-*O*-methyl-6-deoxy-L-talose, which is significantly higher in a Tn5 mutant 2213.1 with impaired effectiveness of symbiosis with the host plant *Lotus corniculatus* [385]. In contrast, another Tn5 mutant of the same *M. loti* strain, Mlo-13, is symbiotically enhanced [386]. It has structurally different OPS that makes it resistant to bacteriophage A1, which requires the 6-deoxytalan of the parent strain as receptor.

6-Deoxyhexoses are abundant also in the OPSs of the genus *Agrobacterium* from the same family Rhizobiaceae but non-sugar groups are less common (for the known structures of six strains of *A. tumefaciens* and *A. radiobacter* see review [382]). Three O-antigens are homoglycans: (1) a 6-deoxy-L-talan in *A. tumefaciens* C58, which shares the carbohydrate structure with *M. loti* NZP2213 but differs in the pattern of O-acetylation, (2) an L-rhamnan in a *A. radiobacter* strain having the same structure as the main chain in several *P. syringae* strains [240, 241], and (3) a unique α1-3-linked L-*glycero*-D-*manno*-heptan in *A. radiobacter* M2/1. Two OPSs are elaborated by *A. tumefaciens* TT9, one of which is a homopolymer of a 3-O-methylated derivative of Fuc4N, in which the monomers are linked through a 4-N-linked 3,4-dihydroxy-1,3-dimethyl-5-oxoprolyl group [382].

The OPS of *Azorhizobium caulinodans* from the family Xanthobacteraceae is composed of a rarely occurring branched monosaccharide 3-*C*-methylrhamnose, together with rhamnose and 2-*O*-methylrhamnose, whose absolute configurations are either all D or all L [395]:

3)Rha2Me(α1-2)Rha3*C*Me(β1-3)Rha(α1-2)Rha3*C*Me(β1-3)Rha(α1-

3.3.3.2 Other Families

Bacteria of the genus *Brucella* (family Brucellaceae) are facultative intracellular pathogens that cause brucellosis, a group of closely related zoonotic diseases. The bacteria are rather homogeneous in terms of the O-antigens, which are homopolymers of α1-2-linked Rha4NFo in A-dominant smooth *Brucella* strains but every fifth residue is α1,3-linked in M-dominant strains [203]. Biotype 1 *B. abortus* and *B. melitensis* carry exclusively A or M epitopes, respectively. The existence of various intermediate AM biotypes in these species and *B. suis* with a reduced proportion of the α-1,3 linkage suggests that the two OPSs are coexpressed. The A-type OPS is characteristic also for *Y. enterocolitica* O9 (Hy 128) [185] that accounts for false-positive serological reactions in the serodiagnostics of the diseases caused by the two bacteria.

Bacteria of the genus *Ohcrobactrum* are taxonomically related to *Brucella* but have no medical importance. The only known OPS structure of *O. anthropi*, 3)GlcNAc(α1-2)LRha(α1- [396], resembles those of several *S. marcescens* serogroups [114].

The OPS of *Pseudaminobacter defluvii* THI 051^T (former *Thiobacillus* sp. IFO 14570), the only representative of the family Phyllobacteriaceae studied, consists of three diamino sugars, one of which, 2,4-diamino-2,4-dideoxyglucuronic acid, has not been found elsewhere in nature (the absolute configurations of the monosaccharides have not been proven) [397]:

4)GlcNAc3NAcA(β1-3)GlcNAc4NAcA(β1-3)QuiNAm4NAc(α1-

The O-antigens of several strains of *Acidomonas methanolica* (former *Acetobacter methanolicus*) from the family Acetobacteraceae are homopolysacharides

Table 3.32 Structures of *Azospirillum* OPSs

A. brasilense S17 [278]	4)LRha2Me(α1-3)ManN(*S*3Hb)(α1- and GlcNAc(β1-4)┘ 3)LRha(α1-3)LRha(α1-2)LRha(α1-Glc(β1-3)┘
A. lipoferum SpBr17, SR65[a] [278,399]	3)LRha(α1-3)LRha2Ac(α1-2)LRha(α1-Glc(β1-3)┘
A. brasilense SR15 [400]	2)Rha(α1-2)Rha(β1-3)Rha(α1-2)Rha(α1-
A. brasilense Sp245, S27, *A. lipoferum* RG20a [278,400]	2)Rha(α1-2)Rha(β1-3)Rha(α1-3)Rha(α1-2)Rha(α1-
A. brasilense Sp245.5 [401]	6)GalNAc(α1-4)ManNAcA(β1-
A. irakense KBC1 [278]	4)LRha(α1-3)Gal(β1-└(3-1α)LRha(3-1β)Man(3-1α)LRha(2-1α)Gal*f*
A. lipoferum Sp59b [278]	3)Gal(α1-3)Gal(β1-└(4-1β)Man(3-1α)LRha(2-1α)LRha(3-1α)LRha

[a]The OPS of strain SR65 lacks O-acetylation.

of common hexoses (for the structures see review [4]). The OPS of another representative of the family, *Gluconacetobacter* (former *Acetobacter*) *diazotrophicus*, has the following structure [398]:

2)Rib*f*(β1-3)LRha(α1-3)LRha(α1-2)LRha(α1-
Glc(β1-2)┘

In the family Rhodospirillaceae, studied are nitrogen-fixing soil bacteria of the genus *Azospirillum*, which colonize roots and promote growth of a broad range of plants. In most strains, the OPSs are D-rhamnans or heteroglycans enriched in LRha [278] (Table 3.32). In *A. brasilense* S17, two OPSs have been observed, one of which includes 2-*O*-methyl-L-rhamnose and a (*S*)-3-hydroxybutanoyl derivative of ManN. The OPSs of *A. irakense* KBC1 and *A. lipoferum* Sp59b are built up of hexasaccharide O-units having the same composition but different structures. A spontaneous mutant Sp245.5 of *A. brasilense* with a changed plasmid switched from the production of a D-rhamnan to an acidic hexosaminoglycan.

The OPS of *Brevundimonas* (*Pseudomonas*) *diminuta* from the family Caulobacteraceae is a partially O-acetylated 4)Man*6Ac*(α1-2)Man(α1- mannan [402].

3.3.4 β-Proteobacteria

3.3.4.1 Burkholderiaceae

Bacteria classified as *Burkholderia* and *Ralstonia* were known formerly as *Pseudomonas* species. Emergent pathogens *B. mallei* and *B. pseudomallei* are the etiologic agents of glanders and melioidosis, respectively, whereas a closely related

bacterium *B. thailandensis* is avirulent. All these bacteria possess similar OPSs having a 3)L6dTal(α1-3)Glc(β1- backbone, where L6dTal may be non-modified or 2-O-acetylated (in all species), 2-O-methylated (in *B. mallei*) or 2-O-methylated and 4-O-acetylated (in *B. thailandensis* and *B. pseudomallei*) [403–406].

Microorganisms of the so-called *B. cepacia* complex (currently 17 species) including *B. cepacia, B. cenocepacia, B. vietnamiensis* and others are opportunistic pathogens in immunocompromised patients, especially in those with cystic fibrosis and chronic granulomatous disease. There are several O-serotyping schemes of these bacteria based on the O-antigens, whose structures have been reviewed earlier [407, 408] and are updated below. They are rather simple with linear di- or trisaccharide O-units consisting mainly of hexoses, 6-deoxyhexoses and *N*-acetylhexosamines (Table 3.33). In various strains, two structurally different OPSs coexist. The OPS of *B. cepacia* L is one of a few known O-antigens that contain L-*glycero*-D-*manno*-heptose, a common component of the LPS core OS of many bacteria (see Chap. 2). The OPS of *B. cepacia* O3 (CIP 8237) is shared by *P. aeruginosa* O15, *S. marcescens* O14 and *Vibrio fluvialis* AA-18239; that of *B. cepacia* O5 by *P. aeruginosa* O14, *Burkholderia plantarii* and *V. fluvialis* sv. 3.

Other representatives of *Burkholderia* with known OPS structures are phytopathogens, such as *B. gladioli* and *B. plantarii* [240], and plant growth-promoting bacteria (*B. phytofirmans*, *B. brasiliensis*) (Table 3.33). One of the OPS components of *B. brasiliensis* is yersiniose A, a branched monosaccharide found also in *Yersinia*.

Another phytopathogen, *Burkholderia caryophylli,* possesses two OPSs, which are homopolymers of unique higher monosaccharides caryophyllose and caryose (reviewed in ref. [240]). Caryophyllan is irregular owing to the presence of both α- (major) and β-linked monosaccharide units, and caryan is built up of blocks of O-acetylated and non-acetylated units. Caryan is linked to the core OS through a QuiNAc primer [416].

Phytopathogenic bacteria *Ralstonia solanacearum* cause wilt in tobacco and other plants. A large group of strains of this species have linear or branched OPSs with similar LRha-LRha-LRha-GlcNAc- main chains that differ in the configuration of the GlcNAc linkage, the position of substitution of a Rha residue and a lateral monosaccharide (L-xylose or L-rhamnose) (reviewed in ref. [240]). In many strains, more than one OPS of the sort occur [417]. The OPS of *Ralstonia pickettii* NCTC 11149 has a main chain of the same type [418]:

2)LRha(α1-2)LRha(β1-3)LRha2Ac(α1-3)GlcNAc(β1-

whereas that of another *R. pickettii* strain [419] resembles several OPSs of *P. aeruginosa* [276]:

4)Rha(α1-4)LGalNAcA(α1-3)QuiNAc4NAc(β1-

Table 3.33 Structures of *Burkholderia* OPSs

B. cepacia O1 [408]	4)Glc(α1-3)LGlcNAc(α1- and 4)Glc(α1-3)LRha(α1-
B. cepacia O2, E (McKevitt) [408]	2)Man(α1-2)Man(α1-4)Gal(β1- and 2)Man(α1-2)Man(α1-3)Man(β1-
B. cepacia O2, G (IMV 4137) [408]	2)LRha(α1-4)Gal(α1-
B. cepacia O2, G (IMV 598/2) [408]	2)LRha(α1-4)Gal(α1- and 4)Glc(β1-3)Man2Ac(β1-
B. cepacia O3 (CIP 8237) [408]	2)Rib*f*(β1-4)GalNAc(α1-
B. cepacia O3 (IMV 4176) [408]	4)GalNAc(α1-4)GalNAc(β1- and 2)Rib*f*(β1-4)GalNAc(α1-
B. cepacia O4, C, *B. vietnamiensis* LMG 6999 [408]	3)Gal(α1-3)Gal(β1-3)GalNAc(β1- and 4)LRha(α1-3)GalNAc(α1-3)GalNAc(β1-
B. cenocepacia K56-2 [409]	4)LRha(α1-3)GalNAc(α1-3)GalNAc(β1-
B. cepacia O5 [408]	4)LRha(α1-3)ManNAc(β1-
B.cepacia O6 [408]	3)Gal*f*6*Ac*(β1-3)Man(β1-
B. cepacia O7, A [408]	4)Glc(β1-3)Man2Ac(β1-
B. cepacia O9 [408]	4)Glc(α1-3)LRha(α1-
B. cepacia B [408]	3)Gal*f*(β1-3)Fuc(α1-
B. cepacia E [408]	3)Fuc(α1-3)GlcNAc(β1-
B. cepacia I [408]	3)Fuc(α1-4)GalNAc(β1- and 3)Fuc(α1-2)LRha(α1-
B. cepacia J [407]	3)LRha(α1-3)Man(β1-4)Man3Ac(α1-
B. vietnamiensis LMG 6998 [408]	3)LRha(α1-3)Man(β1-4)Man(α1-
B. cepacia K [408]	3)Rha(α1-3)Rha(α1-2)Rha(β1-
B. cepacia L [408]	3)Rha(α1-3)Rha(α1-2)LDmanHep(α1-
B. cepacia A (McKevitt) [408]	4)LRha(α1-3)GalNAc(α1-3)GalNAc(β1-
B. cepacia PVFi-5A [408]	3)Gal(α1-6)GlcNAc(α1-4)GalNAc(β1-
B. cepacia [410]	3)Rha(α1-3)Rha(α1-4)Gal(α1- and 3)Rha(α1-3)Rha(α1-2)Rha(α1-
B. cepacia ASP B 2D [278]	2)Rib*f*(β1-6)Glc(α1-
B. multivorans C1576 [411]	2)Man(α1-2)Rha(α1-3)Man(α1- and 2)Man(α1-2)Rha3Me(α1-3)Rha(α1-
B. vietnamiensis LMG 10926 [412]	4)LRha(α1-2)LRha(α1-3)LRha(β1- and 3)Fuc(α1-3)Fuc(α1-3)LRha(α1- LRha(α1-2)⌋
B. anthina LMG 20983 [413]	3)LRha(α1-2)LRha(α1-2)Gal(α1-
B. gladioli pv. gladioli [240]	3)Man2Ac(β1-4)LRha(α1-3)Gal(α1-
B. gladioli pv. *agaricicola* [414]	3)Man2Ac(α1-2)Rha(α1-4)Gal(β1-
B. gladioli pv. alliicola [240]	4)LRha(α1-3)Man2Ac(β1- └(2-1α)Fuc(3-1α)LRha
B. plantarii [240]	4)LRha(α1-3)ManNAc(β1-
B. phytofirmans [278]	3)L6dTal(α1-3)GalNAc(β1- *Xyl(β1-2)*⌋ └*(4-1β)Xyl*
B. brasiliensis[a] [415]	3)Rha(α1-3)Rha(α1-2)Rha(1- └(2-1α)Sug

[a]Sug indicates yersiniose A.

3.3.4.2 Alcaligenaceae

The genus *Bordetella* includes respiratory pathogens causing a variety of diseases in warm-blooded animals (*B. bronchiseptica, B. hinzii, B. avium*) and whooping cough in humans (*B. pertussis* and *B. parapertussis*). *B. trematum* has been found in human ear and blood infections. Except for *B. pertussis* having no long-chain O-antigen, the OPSs of *Bordetella* are homo- or hetero-glycans containing derivatives of various 2,3-diamino-2,3-dideoxyhexuronic acids (Table 3.34). These are fully amidated in *B. hinzii* or partially amidated in *B. bronchiseptica* and *B. parapertussis*. The OPSs of *B. hinzii* and *B. bronchiseptica* MO149 are rather short having not more than six O-units and that of *B. trematum* not more than two O-units.

The OPSs of *B. bronchiseptica* and *B. parapertussis* are terminated with various *N*-acyl derivatives of 2,3,4-triamino-2,3,4-trideoxygalacturonamide, which, together with variations in the amidation pattern of the uronic acids, confer clear serological distinctions between strains sharing the same LGalNAc3NAcA*N* homopolysaccharide [421]. The OPSs of *B. hinzii* and *B. bronchiseptica* MO149 are terminated with a 4-O-methylated GalNAc3NAcAN residue. In *B. bronchiseptica, B. parapertussis* and *B. hinzii,* the O-chain is linked to the core OS through a specific non-repetitive pentasaccharide domain enriched in 2,3-diamino-2,3-dideoxyhexuronic acid derivatives too [421, 423]. A portion of this domain proximal to the core OS, called A-band trisaccharide, is also present in the short-chain LPS of *B. pertussis* and synthesized by a pathway similar to that of an O-unit [425].

Taylorella equigenitalis is the cause of contagious equine metritis, a venereal disease of horses, whereas *Taylorella asinigenitali* is not pathogenic. They elaborate quite different acidic OPSs. That of *T. equigenitalis* consists of two partially amidated derivatives of 2,3-diamino-2,3-dideoxyhexuronic acids and is terminated with a 4-O-methylated LGulNAc3NAcA residue [426]:

4)LGulNAc3NAcA*N*(α1-4)ManNAc3NAcA*N*(β1-

The OPS of *T. asinigenitali* also has a disaccharide O-unit containing a unique *N*-acetimidoyl derivative of GlcNA [427]:

3)GlcNAmA(β1-3)QuiNAc4NAc(β1-

Alcaligenes faecalis shares the OPS structure with *S. maltophilia* O4 [428].

Table 3.34 Structures of *Bordetella* OPSs

B. avium[a] [420]	4)GlcNAm3N(3Hb)A(β1-
B. bronchiseptica, B. parapertussis [421]	4)LGalNAc3NAcA*N*(α1-
B. bronchiseptica MO149 [422]	4)GlcNAc3NAcA*N*(β1-4)LGalNAc3NAcA*N*(α1-
B. hinzii [422,423]	4)GlcNAc3NAcAN(β1-4)GlcNAc3NAcAN(β1-4)LGalNAc3NAcAN(α1-
B. trematum [424]	4)ManNAc3NAmA(β1-4)ManNAc3NAmA(β1-3)FucNAc(α1-

[a]The absolute configuration of the 3-hydroxybutanoyl group has not been determined.

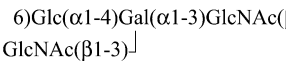
3.3.4.3 Other Families

The OPS structures have been established for several soil- or/and water-inhabiting β-proteobacteria, including *Naxibacter alkalitolerans* from the family Oxalobacteraceae, *Sphaerotilus natans,* a non-classified bacterium of the order Burkholderiales, and *Chromobacterium violaceum* from the family Neisseriaceae (Table 3.35). The last bacterium has the only known OPS that contains D-*glycero*-D-*galacto*-heptose (DDgalHep).

3.3.5 ε-Proteobacteria

3.3.5.1 Campylobacteraceae

Campylobacter jejuni is a common cause of human gastroenteritis and is associated with postinfection autoimmune arthritis and neuropathy (Guillain-Barré syndrome). Molecular mimicry between the R-type LPS of *C. jejuni* and gangliosides in peripheral nerves plays a crucial role in the pathogenesis. Structures of LPS-associated polysaccharides have been established in various *C. jejuni* serotypes but later found to be capsular polysaccharides not related to LPS [432], whereas LPS is of R-type. The only documented exception is *C. jejuni* 81116, which produces a neutral OPS of the following structure [433]:



Polysaccharides characterized in several *Campylobacter lari* and *Campylobacter coli* strains do not seem to be O-antigens too. *Campylobacter fetus,* a causative agent of abortion in cattle and sheep, can cause bacteremia and thrombophlebitis in humans. The OPS of serotype A is an α1-2-linked homopolymer of partially (80–90%) 2-O-acetylated Man [434] and that of serotype B is a 3)Rha(β1-2)Rha(α1- rhamnan terminated with 3-O-methylated Rha [435].

3.3.5.2 Helicobacteraceae

Helicobacter pylori is a prevalent gastroduodenal pathogen of humans, which colonizes gastric mucosa. Once established, infection may persist in the stomach for life and is associated with active inflammation of gastric mucosa leading to gastritis, gastric and duodenal ulcer and increasing risk of gastric cancer. The LPSs of *H. pylori* have generally a poly(*N*-acetyl-β-lactosamine) chain, which in most strains is L-fucosylated to various degrees (see reviews [436, 437]). In several

Table 3.35 Structures of OPSs from other families of β-proteobacteria

N. alkalitolerans [429]	3)FucNAc(α1-2)Qui3N(*S*3Hb)(β1-2)Rha(α1-4)Gal(β1-
S. natans[a] [430]	4)Glc(α1-3)Rha(α1-3)Rha(α1-3)Rha(α1-3)Rha(α1-
C. violaceum [431]	4)DDgalHep(α1-2)LRha(α1-4)DDgalHep(β1-3)GlcNAc(α1-

[a]The absolute configurations of the monosaccharides have not been determined.

strains, an additional non-stoichiometric decoration of the main chain with Glc or Gal (Sug) has been reported [436, 438]:

3)Gal(β1-4)GlcNAc(β1- or 3)Gal(β1-4)GlcNAc(β1- or 3)Gal(β1-4)GlcNAc(β1-
LFuc(α1-3)┘ LFuc(α1-3)┘└(6-1α)Sug

The terminal non-reducing unit usually carries one or two LFuc residues giving rise to Le^x trisaccharide or Le^y tetrasaccharide, respectively, which are interconvertible upon phase variation [438]. Less often, the OPS chain is terminated with another Lewis or related blood group antigenic determinant. In polylactosamine-lacking strains of *H. pylori* and several less studied non-human *Helicobacter* species, like *H. mustelae* from ferrets [436], the antigenic determinants may be expressed on the LPS core OS. These features have multiple biological effects on pathogenesis and disease outcome, including gastric adaptation due to molecular mimicry of Lewis antigens [437].

In *H. pylori* LPSs, there are also other core OS-linked polymers, such as heptans and glucans [436, 437]. Atypically of *H. pylori,* the O-antigen of strains D1, D3 and D6 is a 2)Man3*C*Me(α1-3)LRha(α1-3)Rha(α1- heteropolysaccharide composed of 3-*C*-methyl-D-mannose and both D- and L-rhamnose [439].

3.3.6 Flavobacteria

Flavobacteriaceae is the only family studied in the class Flavobacteria. Marine bacteria of the genus *Flavobacterium* are fish pathogens and are also associated with infectious diseases in humans. The OPSs of *F. columnare* A contains a keto amino sugar, namely 2-acetamido-2,6-dideoxy-D-*xylo*-hexos-4-ulose (Sug) [440] and is structurally related to the OPS of *Pseudoalteromonas rubra* [253]:

4)GlcNAcA3Ac(β1-4)LFucNAm3Ac(α1-3)Sug(α1-

An unusual 4-*N*-[(*3S,5S*)-3,5-dihydroxyhexanoyl] derivative of QuiN4N (QuiNAc4NR) is a component of the trisaccharide O-unit of *F. psychrophilum* [441]:

2)LRha(α1-4)LFucNAcA(α1-3)QuiNAc4NR(α1-

The OPS of another fish pathogen *Tenacibaculum maritimum* (former *Flexibacter maritimus*) includes a unique higher sugar 5-acetamido-8-amino-3,5,7,8,9-pentadeoxy-7-[(*S*)-3-hydroxybutanoylamino]non-2-ulosonic acid. The C-4—C-7 fragment of the acid has the β-L-*manno* configuration, whereas the configuration at C-8 is unknown. It is linked to the neighbouring QuiN4N residue through O-2 of a (*S*)-2-hydroxy-5-glutaryl group at the N-4 of the latter [442] (Fig. 3.3).

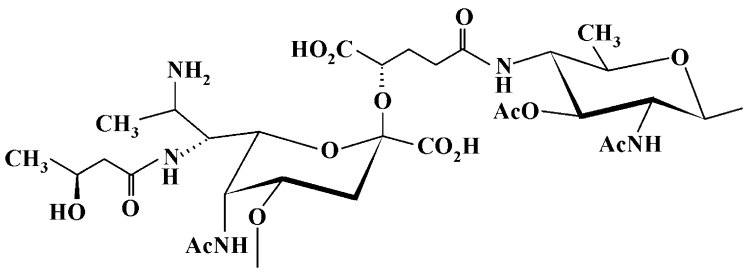


Fig. 3.3 Structure of the OPS of *Tenacibaculum maritimum* (former *Flexibacter maritimus*) [442]

The structures of the OPSs of two marine bacteria of the genus *Cellulophaga* have been established. That of *C. fucicola* contains a di-*N*-acetyl derivative of Pse [443]:

4)Pse5Ac7Ac(β2-4)Gal(β1-4)Glc(β1-

The OPS of *C. fucicola* is acidic too due to the presence of GlcA [444]:

2)Man(β1-3)Man*2Ac*(β1-4)GlcA(β1-3)GlcNAc(α1-

3.3.7 Other Classes

Fusobacterium necrophorum (class Fusobacteria, family Fusobacteriaceae) is an anaerobic bacterium associated with pyogenic infections in animals and humans. It has a teichoic acid-like O-antigen with a highly unusual polyalcohol, 2-amino-2-deoxy-2-*C*-methylpentonic acid (R), whose configuration remains unknown [445]:

4)R(5-*P*-4)Glc(α1-3)LFucNAm(α1-3)QuiNAc4N(*S*3Hb)(β1-

The genus *Pectinatus* from the family Veillonellaceae (class Clostridia) includes strictly anaerobic beer spoilage bacteria. The OPS of *P. frisingensis* consists of α- and β-linked L6dAlt, both in the furanose form [446]:

2)L6dAlt*f*(β1-3)L6dAlt*f*(β1-2)L6dAlt*f*(α1-
L6dAlt*f*(α1-2)┘

The OPS of *P. cerevisiiphilus* contains a fucofuranose residue as a component of the 2)Fuc*f*(β1-2)Glc(α1- discaccharide O-unit [446].

The genus *Porphyromonas* (class Bacteroidia, family Bacteroidaceae) includes etiologic agents for periodontal disease in adults (*P. gingivalis*) and animals: cats and dogs (*P. circumdentaria*). The OPS of *P. gingivalis* is distinguished by a non-stoichiometric phosphorylation of a rhamnose residue with phosphoethanolamine [447]:

3)Gal(α1-6)Glc(α1-4)LRha*2PEtN*(α1-3)GalNAc(β1-

The LPS of this bacterium has another phosphorylated branched α-mannan chain [448]. The OPS of *P. circumdentaria* consists of hexoses and *N*-acetylhexosamines only [449]:

6)Glc(β1-6)Gal(β1-6)Gal(β1-3)GlcNAc(β1-3)GalNAc(β1-

Bacteroides vulgatus from the same family is involved in the aggravation of colitis. It has a linear OPS with the 4)LRha(α1-3)Man(β1- disaccharide O-unit and a rhamnose residue at the non-reducing end [450].

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