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Review Paper

Type-specific Carbohydrate Antigens of Pathogenic Bacteria. Part 1: Enterobacteriaceae

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ABSTRACT

This review summarises the recently elucidated structures of the carbohydrate O-antigens, and where present, the K-antigens from the gram-negative Enterobacteriaceae Escherichia coli, Klebsiella, Salmonella *and* Shigella.

INTRODUCTION

The continued prevalence of serious bacterial infections, despite the development of antimicrobial agents, has led to a renewed interest in the structure and immunogenicity of bacterial polysaccharides. The number of structurally determined bacterial polysaccharides has increased dramatically in recent years. This review (in two parts) summarises the recently elucidated structures of type-specific polysaccharides as such information is central to the development of an understanding of the relationship between structure, conformation and the immunological properties of these carbohydrates. This first part of the review deals with the gram-negative Enterobacteriaceae. The second part (appearing in the next issue of Carbohydrate Polymers) will cover other pathogenic gram-negative bacteria and pathogenic gram-positive bacteria.

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A number of earlier reviews of bacterial polysaccharides exist (Stacey & Barker, 1960; Jann & Westphal, 1975; Jennings, 1983; Kenne & Lindberg, 1983) and additional information on less recently reported structures can be obtained from these sources.

GRAM-NEGATIVE BACTERIA

The cell envelope of a gram-negative bacterium is made up of an inner cytoplasmic membrane, the periplasm, the peptido-glycan layer and a lipopolysaccharide-containing outer membrane. The lipopolysaccharide consists of three parts: lipid A, a 'core' region and the O-chain (O-antigen). Lipid A is highly conserved and has a similar structure in many bacteria. Some variation exists within the core region, but most variability is within the O-antigen. For example, only one Lipid A moiety and five oligosaccharide core structures are expressed in *Escherichia coli.* This contrasts with over 150 O-specific polysaccharides. Additionally, there may be a polysaccharide capsule (K-antigen) surrounding the bacterium.

The surface location of the O- and K-antigens means that they are important agents in bacterial pathogenesis. When a polysaccharide capsule is present, covering the cell wall antigens, the dominant immunological properties are those of the capsular polysaccharide. In bacteria where a polysaccharide capsule is not usually produced (i.e. most types of *Salmonella*) the O-chain of the lipopolysaccharide covers the cell surface and assumes a similar function. Some pathogenic bacteria which are covered by polysaccharide capsules, such as *Neisseria meningitidis* and *Haemophilus influenzae*, are devoid of O-chains (Nikaido, 1988).

ENTEROBACTERIACEAE

Escherichia coli

E. Coli strains make up part of the normal adult intestinal flora. They can also be important pathogens causing urinary tract infections, diarrhoea and neonatal septicaemia and meningitis. Diarrhoea, caused by toxin-producing *E. coli*, is a major cause of infant mortality in the third world. The non-toxic nature of the K-antigens makes them an attractive target for vaccine development. However, a large number of *E. coli* cannot be typed with respect to a capsular antigen. A further

problem is that the K1 and K5 antigens, which are expressed by one-quarter of K-typeable isolates, are poorly immunogenic in man; this is thought to be due to the structural similarity they show to mammalian glycosaminoglycans (Cryz, 1987). Although many O-antigens are expressed by *E. coli*, the majority of O-typeable strains responsible for serious infections are represented by 11 serotypes. These are O1, O2, O4, O6, O7, O8, O15, O16, O18, O25 and O75 (McCabe *et al.*, 1978; Cross *et al.*, 1984*a*). Conjugation of the O-antigens of these serotypes with carrier proteins is being attempted (Cryz, 1987).

O-Antigens (Table 1)

Approximately 90% of bacteraemic *E. coli* isolates can be O-serotyped (Cryz, 1987). *E. coli* can lose O-specificity in a mutation from smooth (s) to rough (r) form. Smooth forms express all three components of a lipopolysaccharide whereas R mutants express lipid A and core oligosaccharide only and show an R specificity (Jann & Jann, 1987).

E. coli expresses both neutral and acidic O-antigens, in contrast to *Salmonella* and *Klebsiella*, which produce only neutral O-antigens. The acidic components are generally hexuronic acids. The antigen O149 contains a pyruvic acid acetal as its acidic component. Antigens O58 and O124 contain lactyl-substituted residues which resemble muramic acid (*O*-lactyl-*N*-acetyl glucosamine) which is found in cell wall peptidoglycan. The similarity of *E. coli* to other genera is evident in the structural identity that exists between some O-antigens for *E. coli* and those from, for example, *Klebsiella* and *Shigella dysenteriae*. Some of the known structures of *E. coli* O-antigens are shown in Table 1.

K-Antigens (Tables 2, 3, 4)

K-antigens are expressed by many strains of *E. coli*, particularly the invasive strains (Jann & Jann, 1987). However, only ~60% of bacteraemic isolates can be typed with respect to these antigens (Cryz, 1987). They can be divided into two groups (Jann & Jann, 1983, 1987) (Table 2). Group I polysaccharides (Table 3) resemble the capsular antigens of *Klebsiella* and group II (Table 4) those of *Neisseria meningitidis* and *Haemophilus influenzae*. In some instances a polysaccharide may occur as a group I K-antigen (co-expressed with the neutral O8 or O9 antigen) or as the sole acidic O-antigen (e.g. O32 and K87). KDO (3-deoxy-D-manno-2-octulosonic acid) is a major constituent of the group II antigens. It exists most frequently in the pyranose form, β configuration, and linked at O-5 (K12, K14 and K15) or O-7 (K6, K13, K20 and K23). In the K95 antigen the KDO is in the β-configuration and furanose form (Dengler *et al.*, 1988).

TABLE 1
Neutral and Acidic O-Specific Polysaccharides of *Escherichia coli*

O-antigen	*Structural identity with*	*Repeating unit*[a]	*Reference*
2		→4)-β-D-Glc*p*NAc-(1→3)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-β-L-Rha*p*-(1→ 2 ↑ 1 α-D-Fuc*p*3NAc	Jansson *et al.* (1987*b*)
4		→3)-β-D-GlcNAc-(1→2)-α-L-Rha-(1→6)-α-D-Glc*p*-(1→3)-α-L-FucNAc-(1→ 3 ↑ 1 α-D-Glc	Jansson *et al.* (1984*c*)
6		→3)-β-D-Man*p*-(1→4)-β-D-Man*p*-(1→3)-α-D-Glc*p*NAc-(1→4)-α-D-Gal*p*NAc-(1→ 2 ↑ 1 β-D-Glc*p*	Jansson *et al.* (1984*a*)
7		→3)-α-D-Glc*p*NAc-(1→3)-β-D-Qui*p*4NAc-(1→2)-α-D-Man*p*-(1→4)-β-D-Gal*p*-(1→ 3 ↑ 1 α-L-Rha*p*	L'vov *et al.* (1984)
8	*Klebsiella* O5	→3)-β-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→	Jansson *et al.* (1985)
9	*Klebsiella* O3	→3)-α-D-Man*p*-(1→3)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→	Prehm *et al.* (1976)

9a → 3)-α-D-Man*p*-(1 → 3)-α-D-Man*p*-(1 → 2)-α-D-Man*p*-(1 → 2)-α-D-Man*p*-(1 → — Parolis *et al.* (1986*b*)

10 → 3)-β-D-Glc*p*NAc-(1 → 3)-α-L-Rha*p*-(1 → 3)-α-L-Rha*p*-(1 → 3)-α-D-Gal*p*-(1 → — Kenne *et al.* (1986)

2
↑
1
α-D-Fuc*p*4NAcyl Acyl = −COCH$_3$ (60%) or −COCH$_2$CHOHCH$_3$ (40%)

18 → 2)-α-L-Rha-(1 → 4)-α-Gal-(1 → 6)-α-Glc-(1 → 3)-α-GlcNAc-(1 → — Gupta *et al.* (1984)

3
↑
1
β-GlcNAc

α-L-Rha*p*
1
↓
3

25 → 3)-α-L-Fuc*p*NAc-(1 → 3)-β-D-Glc*p*NAc-(1 → 4)-α-D-Glc*p*-(1 → — Kenne *et al.* (1983*a*)

6
↑
1
β-D-Glc*p*

32 → 4)-β-GlcA-(1 → 3)-L-Fuc-(1 → 3)-β-GlcNAc-(1 → 6)-Gal-(1 → — Jann and Jann (1987)

4 |
↑ OAc
1
OAc-β-Glc

TABLE 1 — *contd.*

O-antigen	*Structural identity with*	*Repeating unit*[a]	*Reference*
58	*Shigella dysenteriae* 5	→3)-α-Glc*p*NAc-(1→4)-α-Man*p*-(1→4)-β-Man*p*-(1→ 3 ↑ 1 Rha*p*LA	Jann and Jann (1987)
78		→3)-β-D-Glc*p*NAc-(1→4)-β-D-Glc*p*NAc-(1→4)-β-D-Man*p*-(1→4)-α-D-Man*p*-(1→	Jansson *et al.* (1987*c*)
86		→4)-α-L-Fuc*p*-(1→2)-β-D-Gal*p*-(1→3)-α-D-Gal*p*NAc-(1→3)-β-D-Gal*p*NAc(1→ 3 ↑ 1 α-D-Gal*p*	Andersson *et al.* (1989)
111	*Salmonella adelaide*	α-Col*p* 1 ↓ 3 →4)-α-D-Glc*p*-(1→4)-α-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→ 6 ↑ 1 α-Col*p*	Kenne *et al.* (1983*b*)

124	*Shigella dysenteriae* 3	→3)-β-GalNAc-(1→3)-α-Gal-(1→6)-β-Gal-(1→ 4 ↑ 1 Glc*p*LA-α-Glc	Jann and Jann (1987)
149		→4)-β-D-Glc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→3)-β-L-Rha*p*(1→ 4 6 H_3C CO_2H (*S*)	Adeyeye *et al.* (1988)

[a]Col = 3,6-dideoxy-L-galactose (colitose); FucNAc = 2-acetamido-2,6-dideoxy-galactose; Fuc3NAc = 3-acetamido-3,6-dideoxy-D-galactose; Fuc4NAc = 4-acetamido-4,6-dideoxy-D-galactose; GalNAc = *N*-acetylgalactosamine; GlcLA = 3-glucolactylic acid; GlcNAc = *N*-acetylglucosamine; Qui4NAc = 4-acetamido-4,6-dideoxy-D-glucose; RhaLA = 4-rhamnolactylic acid.

TABLE 2
General Properties of the Two Types of *K*-Antigens Produced by *Escherichia coli*[a]

Properties	*I*	*II*
Molecular weight	> 100 K	< 50 K
Acidic component	HexA, pyruvate	GlcA, phosphate, KDO, NeuNAc
Stability at pH6, 100°C	All stable	Most labile
O-Antigens co-expressed with	8, 9, 20, 101	Many
Chromosomal determination	His	SerA
Expressed at 17–20°C	Yes	No

[a]From Jann and Jann (1987) and Parolis *et al.* (1988*a*).

The six most commonly isolated K-antigens are K1, K2, K5, K12, K52 and K95 (Cross *et al.*, 1984*a*). The K1 antigen (colominic acid) is the most frequently isolated bacterial antigen from the blood of patients with *E. coli* infections. Systemic infection of neonates with K1-encapsulated organisms results in a high mortality rate (Cross *et al.*, 1984*b*). The antigen can occur both with and without *O*-acetylation, the *O*-acetyl groups being randomly distributed between the 7 and 9 positions (McGuire & Binkley, 1964; Orskov *et al.*, 1979).

Klebsiella

Klebsiellae are opportunistic gram-negative pathogens that are frequently involved in outbreaks of nosocomial infections. They are one of the most common causes of primary bacteraemia. Serious *Klebsiella* infections, such as bacteraemia and pneumonia, have associated mortality rates which can exceed 50%. *Klebsiellae* are also often the cause of urinary tract, wound, soft-tissue and respiratory tract infections (Cryz *et al.*, 1985).

Klebsiellae characteristically produce well-defined polysaccharide capsules and immunity to experimental *Klebsiella* infections are mediated by serospecific anticapsular antibodies (Cryz, 1987). Vaccine development has therefore concentrated on K-antigen-containing preparations. Six and 24 valent vaccines containing the K-antigens most commonly found in *Klebsiella* bacteraemic isolates (2, 3, 10, 21, 30, 55 and additionally 5, 9, 15, 16, 17, 18, 22, 25, 28, 35, 43, 52, 53, 60, 61, 62, 63, 64 in the latter) have undergone clinical studies (Cryz *et al.*, 1986, 1988; Lee, 1987).

O-Antigens (Table 5)

Nine chemically distinct O-antigens have been identified (O1, O3, O4, O5, O7, O8, O9, O10 and O12). Strains classified as *Klebsiella* sero-

TABLE 3
Group I Capsular Polysaccharides from *Escherichia coli*

K-antigen	*Structural identity with*	*Repeating unit*[a]	*Reference*
27		→4)-α-D-Glc*p*-(1→4)-α-D-Glc*p*A-(1→3)-α-L-Fuc*p*-(1→ 3 ↑ 1 α-D-Gal*p*	Chakraborty (1982)
28		→3)-α-D-Glc*p*(1→4)-β-D-Glc*p*A-(1→4)-α-L-Fuc*p*-(1→ 4 2/3 ↑ | 1 OAc β-D-Gal*p*	Altman and Dutton (1985)
30	*Klebsiella* K20	→2)-α-D-Man*p*-(1→3)-β-D-Gal*p*-(1→ 3 ↑ 1 β-D-Glc*p*A-(1→3)-α-D-Gal*p* OAc | 2	Jann and Jann (1983)
32(A)	*Klebsiella* K55	→4)-α-L-Rha*p*-(1→3)-β-D-Glc*p*-(1→ 3 ↑ 1 α-D-Glc*p*A(1→3)α-D-Gal*p*	Annison *et al.* (1987)

TABLE 3 — *contd.*

K-antigen	*Structural identity with*	*Repeating unit*[a]	*Reference*
34		→2)-β-D-Glc*p*A-(1→4)-β-D-Gal*p*-(1→3)-β-D-Gal*p*(1→ 3 ↑ 1 α-D-Glc*p*-(1→4)-β-D-Gal*p*	Dutton and Kuma-Mintah (1987)
36	*Klebsiella* K57	→3)-β-D-Gal*p*-(1→3)-α-D-Gal*p*A-(1→2)-α-D-Man*p*-(1→ 4 ↑ 1 α-D-Man*p*	Parolis *et al.* (1988*a*)
37		→3)-β-D-Glc*p*-(1→3)-α-D-Gal*p*-(1→ 4 ↑ 1 α-D-Gal*p* 4 6 H_3C CO_2H (*R*)	Anderson *et al.* (1987*b*)
39	*Klebsiella* K61	→6)-α-D-Glc*p*-(1→4)-β-D-Glc*p*A-(1→2)-α-D-Man*p*-(1→3)-β-D-Glc*p*-(1→ 3 ↑ 1 α-D-Gal*p*	Parolis *et al.* (1989)

40		→4)-β-GlcA-(1→4)-α-GlcNAc-(1→6)-α-GlcNAc-(1→ | CO—NH-serine	Dengler *et al.* (1986)
42	*Klebsiella* K63	→3)-α-D-Gal*p*-(1→3)-α-D-Gal*p*A-(1→3)-α-L-Fuc*p*(1→	Niemann *et al.* (1978)
44		→4)-β-D-Glc*p*A-(1→3)-α-L-Rha*p*-(1→4)-α-D-Glc*p*NAc-(1→6)-β-D-Gal*p*NAc-(1→	Dutton *et al.* (1988)
54		→3)-β-D-GlcA-(1→3)-α-L-Rha-(1→ | 85% CO—NH-threonine (90%) -serine (10%)	Hofmann *et al.* (1985*a*)
87		→4)-β-GlcA-(1→3)-FucNAc-(1→3)-GlcNAc-(1→6)-Gal-(1→ 4 | ↑ OAc 1 OAc-Glc	Jann and Jann (1983)

[a]FucNAc = *N*-acetylfucosamine; GalNAc = *N*-acetylgalactosamine; GlcNAc = *N*-acetylglucosamine.

TABLE 4
Group II Capsular Polysaccharides of *Escherichia coli*

K-antigen	*Repeating unit*[a]	*Reference*
12	→3)-α-L-Rha*p*-(1→2)-α-L-Rha*p*(1→5)-β-KDO*p*-(2→ 7/8 | OAc	Schmidt and Jann (1983)
6	→2)-β-D-Rib*f*-(1→2)-β-D-Rib*f*-(1→7)-α-D-KDO-(2→	Jennings *et al.* (1982)
74	→3)-β-D-Rib*f*-(1→2)-β-D-Rib*f*-(1→6)-β-KDO*f*-(2→ | OAc (65%)	Ahrens *et al.* (1988)
19	→3)-β-Rib*f*-(1→4)-β-KDO*p*-(2→ 8 | OAc (33%)	Jann *et al.* (1988)
13	→3)-β-D-Rib*f*-(1→7)-β-KDO*p*-(2→ 4 | OAc	Vann *et al.* (1983)
20	→3)-β-D-Rib*f*-(1→7)-β-KDO*p*-(2→ 5 | OAc	Vann *et al.* (1983)
23	→3)-β-D-Rib*f*-(1→7)-β-KDO*p*-(2→	Vann *et al.* (1983)

95	→3)-β-D-Rib-(1→8)-KDO*f*-(2→	Dengler *et al.* (1985)
14	→6)-α-GalNAc-(1→5)-β-KDO$^{\pm}$(2→	Jann *et al.* (1983)
15	→4)-α-GlcNAc-(1→5)-β-KDO$^{\pm}$(2→	Jann and Jann (1987)
1	→8)-α-Neu*p*5Ac-(2→	McGuire and Binkley (1964)
92	→8)-α-Neu*p*5Ac-(2→9)-α-Neu*p*5Ac-(2→	Lifely *et al.* (1985)
9	→4)-α-Neu*p*5Ac-(2→3)-β-D-Gal*p*-(1→3)-β-D-Gal*p*NAc(1→4)-α-D-Gal*p*-(1→ | OAc	Dutton *et al.* (1987)
2	-4)-α-Gal-(1→2)-Gro-(3-Ⓟ-	Jann and Jann (1987)
18	-2)-β-Rib-(1→2)-RibOH-(5-Ⓟ- 3 | OAc	Rodriguez *et al.* (1988*a*)
22	-2)-β-Rib-(1→2)-RibOH-(5-Ⓟ-	Rodriguez *et al.* (1988*a*)
100	-3)-β-D-Rib*f*-(1→2)-D-RibOH-(5-Ⓟ-	Tsui *et al.* (1988); Rodriguez *et al.* (1988*a*)

TABLE 4 — *contd.*

K-antigen	*Repeating unit*[a]	*Reference*
51	-3)-α-GlcNAc*(1-Ⓟ-	Jann *et al.* (1985)
52	OAc (80%) | 4 -3)-β-Gal-(1-Ⓟ- 2 ↑ 2 β-Fru*f**	Hofmann *et al.* (1985*b*)
5	→4-β-D-GlcA-(1→4)-α-D-GlcNAc-(1→	Vann *et al.* (1981)
4	→4)-β-D-GlcA-(1→3)-β-D-GalNAc-(1→ 3 ↑ 2 β-Fru*f*	Rodriguez *et al.* (1988*b*)

[a]GalNAc = *N*-acetylgalactosamine; GlcNAc = *N*-acetylglucosamine; Gro = glycerol; KDO = 2-keto-3-deoxy-D-mannooctulonic acid; Neu5Ac = *N*-acetyl-neuraminic acid; RibOH = ribitol; *Constituent is *O*-acetylated.

TABLE 5
O-Antigens of *Klebsiella*

O-antigen	*Repeating unit*[a]	*Reference*
1	→3)-α-D-Gal*p*-(1→3)-β-D-Gal*f*-(1→	Kenne and Lindberg (1983)
3	→3)-α-D-Man*p*-(1→3)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→	Curvall *et al.* (1973*a*)
4	→2)-β-D-Rib*f*-(1→4)-α-D-Gal*p*-(1→	Kenne and Lindberg (1983)
5	→3)-β-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→	Jansson *et al.* (1985)
7	→2)-α-L-Rha*p*-(1→2)-β-D-Rib*f*-(1→3)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→	Lindberg *et al.* (1973)
8	→3)-α-D-Gal*p*-(1→3)-β-D-Gal*f*-(1→3)-α-D-Gal*p*-(1→ 2/6 2 2/6 | | | OAc OAc OAc	Curvall *et al.* (1973*b*)
9	OAc-6-α-D-Gal*p* 1 ↓ 3 →3)-β-D-Gal*f*-(1→3)-α-D-Gal*p*-(1→3)-β-D-Gal*f*-(1→2)-α-D-Gal*p*-(1→ 2/6 6 2/6 6 | | | | OAc OAc OAc OAc	Lindberg *et al.* (1972)

TABLE 5 — *contd.*

O-antigen	*Repeating unit*[a]	*Reference*
10	→3)-α-L-Rha*p*-(1→3)-β-D-Rib*f*-(1→4)-α-L-Rha*p*-(1→3)-β-D-Rib*f*-(1→4)-α-L-Rha*p*-(1→	Björndal *et al.* (1970)
12	→3)-β-D-Glc*p*NAc-(1→3)-α-L-Rha*p*-(1→	Erbing *et al.* (1977)

[a]GlcNAc = *N*-acetylglucosamine.

TABLE 6
K-Antigens of *Klebsiella*

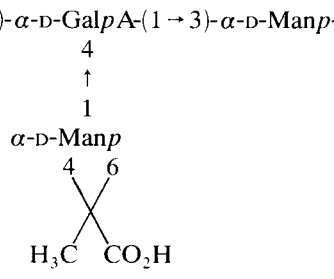
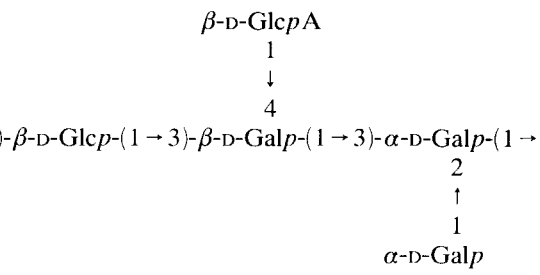
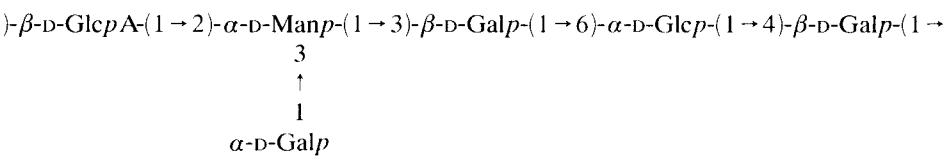
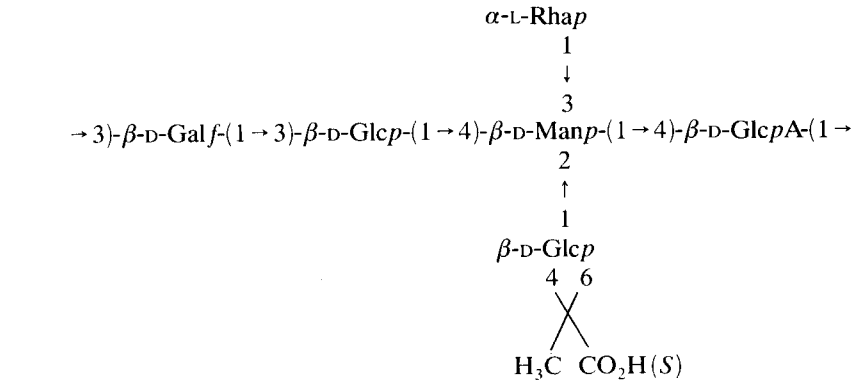
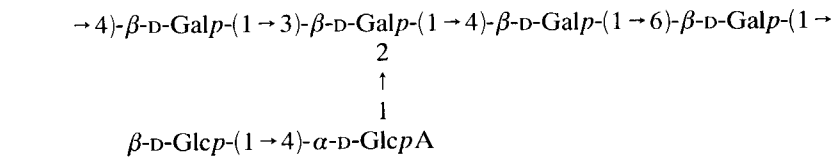
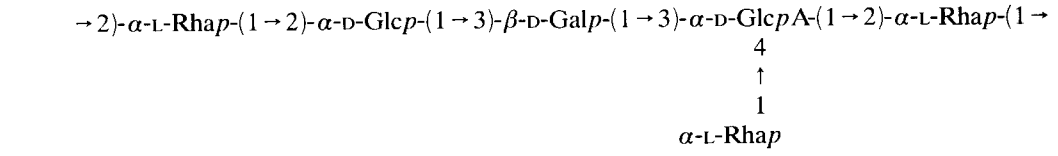
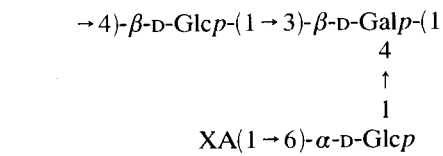
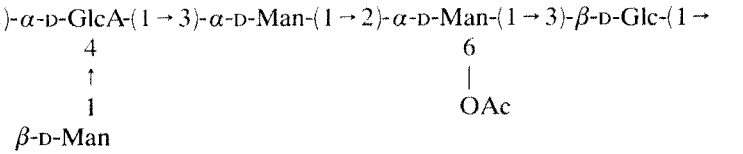
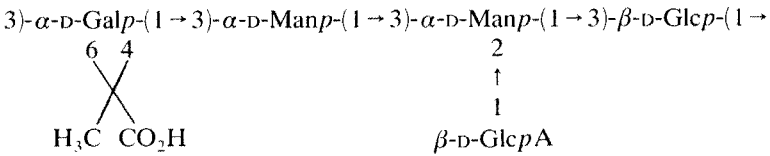
K-antigen	*Repeating unit*[a]	*Reference*
3		Dutton *et al.* (1986*a*)
8		Jansson *et al.* (1988*a*)
10		Sarkar and Roy (1986)

TABLE 6 — *contd.*

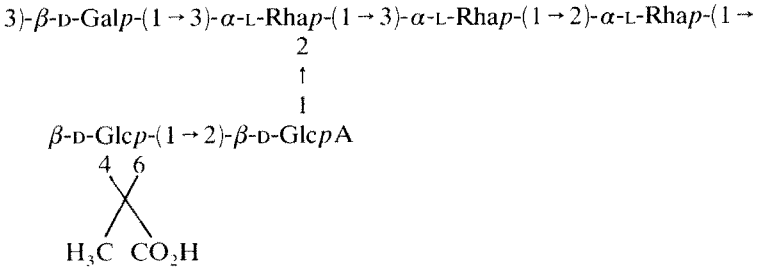
K-antigen	*Repeating unit*[a]	*Reference*
14		Parolis *et al.* (1988*c*)
15		Nath and Chakraborty (1987*a*)
19		Beurret *et al.* (1986)
22		Parolis *et al.* (1988*b*)

24 

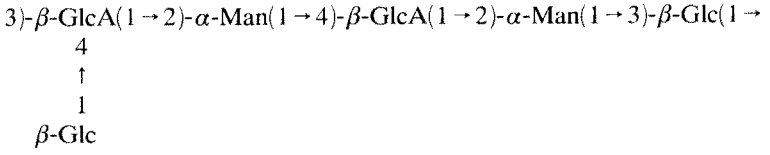
Annison *et al.* (1988)

35 

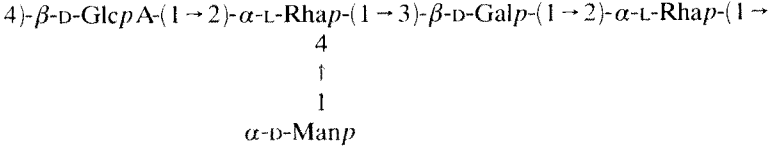
Dutton and Lim (1985)

36 

Ravenscroft *et al.* (1988)

39 

Anderson *et al.* (1987*a*)

40 

Nath and Chakraborty (1987*b*)

TABLE 6 — *contd.*

K-antigen	*Repeating unit*[a]		*Reference*
48	→3)-β-D-Glc*p*-(1→3)-α-L-Rha*p*-(1→4)-α-D-Glc*p*-(1→2)-α-L-Rha*p*-(1→ 2 ↑ 1 α-D-Gal*p*A		Joseleau and Marais (1988)
49	→3)-α-D-Gal*p*-(1→2)-α-D-Man*p*-(1→3)-α-D-Gal*p*-(1→ 3 ↑ 1 OAc-α-D-Gal*p*A		Joseleau (1985)
50	→3)-β-D-Gal*p*-(1→3)-α-D-Glc*p*-(1→4)-α-D-Glc*p*A-(1→3)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→ 6 ↑ 1 β-D-Gal*p*(1→6)-α-D-Glc*p*		Altman and Dutton (1983)
54	→6)-β-D-Glc*p*-(1→4)-α-D-Glc*p*A-(1→3)-α-L-Fuc*p*-(1→ 4 2 ↑ | 1 OAc β-D-Glc*p*	(50%)	Colquhoun *et al.* (1989)
66	→3)-α-D-Man*p*-(1→3)-α-D-Gal*p*-(1→2)-α-D-Glc*p*A-(1→3)-α-D-Man*p*-(1→ 3 ↑ 1 4-*O*-Lac-β-D-Glc*p*		Jansson *et al.* (1984*b*)

67 → 3)-α-L-Rha-(1 → 3)-α-D-Man-(1 → 3)-α-D-Man-(1 → 3)-β-D-Glc-(1 →
2
↑
1
β-D-Gal-(1 → 3)-β-D-GlcA
4
↑
1
α-L-Rha

Dutton and Karunaratne (1983)

68 → 2)-α-D-Gal*p*A-(1 → 2)-α-D-Man*p*-(1 → 3)-β-D-Gal*p*-(1 →
4
↑
1
α-D-Man*p*
4 6
H_3C CO_2H

H_3C CO_2H (R)
4 6
β-D-Gal*p*
1
↓
6

Dutton *et al.* (1986*b*); Parolis *et al.* (1986*a*)

69 → 4)-β-D-Glc*p*-(1 → 4)-β-D-Man*p*-(1 → 4)-β-D-Man*p*-(1 →
3 6
↑ |
1 OAc (33%)
α-D-Glc*p*A

Hackland *et al.* (1988*a*, *b*)

TABLE 6 — *contd.*

K-antigen	*Repeating unit*[a]	*Reference*
80	→3)-β-D-Gal-(1→2)-α-D-Man-(1→2)-α-D-Man-(1→ 3 ↑ 1 α-D-GlcA 4 ↑ 1 β-L-Rha 4 3 H_3C CO_2H β-D-Glc*p*A-(6-N)-L-Glu 1 ↓ 4	Dutton and Karunaratne (1984)
82	→3)-β-D-Glc*p*-(1→3)-β-D-Gal*p*-(1→3)-α-D-Gal*p*-(1→ 2 | OAc	Jansson *et al.* (1988*a*)

[a](6-N)-L-Glu = L-glutamic acid linked as amide; 4-*O*-Lac-D-Glc = 4-*O*-[(*R*)-1-carboxyethyl]-D-glucose.
XA = hex-4-enuronic acid.

TABLE 7
O-Antigens of *Salmonella*

O-antigen	*Repeating unit*[a]	*Reference*
A	→2)-α-D-Man*p*-(1→4)-α-L-Rha*p*-(1→3)-α-D-Gal*p*-(1→ 3 ↑ 1 α-Par*p*	Jann and Jann (1984)
B	→2)-α-D-Man*p*-(1→4)-α-L-Rha*p*-(1→3)-α-D-Gal*p*-(1→ 3 ↑ 1 α-Abe*p*	Jann and Jann (1984)
S. thompson (C_1)	→2)-β-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-β-D-Man*p*-(1→3)-β-D-Glc*p*NAc-(1→ 3 ↑ R R = H or α-D-Glc*p*	Lindberg *et al.* (1988)
S. boecker	→6)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-β-D-Man*p*-(1→3)-α-D-Glc*p*NAc-(1→ 3 ↑ R R = H or α-D-Glc*p*	Brisson and Perry (1988)
S. eimsbuttel	→2)-β-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-β-D-Man*p*-(1→3)-β-D-Glc*p*NAc*p*-(1→ 3 ↑ 1 α-D-Glc*p*	DiFabio *et al.* (1988*b*)

TABLE 7 — *contd.*

O-antigen	*Repeating unit*[a]	*Reference*
S. madelia PS1	→6)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-β-D-Man*p*-(1→3)-α-D-Glc*p*NAc-(1→	DiFabio *et al.* (1989)
PS11	→6)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-β-D-Man*p*-(1→3)-α-D-Glc*p*NAc-(1→ 3 ↑ 1 α-D-Glc*p*	
PS111	→6)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→2)-β-D-Man*p*-(1→3)-α-D-Glc*p*NAc-(1→ 4 ↑ 1 α-D-Glc*p*	
D	→2)-α-D-Man*p*-(1→4)-α-L-Rha*p*-(1→3)-α-D-Gal*p*-(1→ 3 ↑ 1 α-Tyv*p*	Jann and Jann (1984)
S. typhi	→2)-α-D-Man*p*-(1→4)-α-L-Rha*p*-(1→3)-α-D-Gal*p*-(1→ 3 4 ↑ ↑ 1 1 α-Tyv*p* α-D-Glc*p* (strain 1S59 100%) (strain 253Ty random)	Hellerquist *et al.* (1969); Weintraub *et al.* (1988)
E_1	→6)-β-D-Man*p*-(1→4)-α-L-Rha*p*-(1→3)-α-D-Gal*p*-(1→	Garegg *et al.* (1983)

E_2	→6)-β-D-Man*p*-(1→4)-α-L-Rha*p*-(1→3)-β-D-Gal*p*-(1→	Garegg *et al.* (1983)
S. carrau (H)	→2)-α-D-Man*p*-(1/2)-β-D-Man*p*-(1/3)-α-D-Glc*p*NAc-(1/6)-α-D-Man*p*-(1→ 3 ↑ 1 α-D-Glc*p*	DiFabio *et al.* (1988*a*)
S. godesberg, *S. urbana* (N)	→2)-α-D-Per*p*NAc-(1→3)-α-L-Fuc*p*-(1→4)-β-D-Glc*p*-(1→3)-α-D-Gal*p*NAc-(1→ 4 ↑ 1 β-D-Glc*p*	Perry *et al.* (1986)
S. landau (N)	→2)-α-D-Per*p*NAc-(1→3)-α-L-Fuc*p*-(1→4)-β-D-Glc*p*-(1→3)-α-D-Gal*p*NAc(1→ α-Col*p* 1 ↓ 3	Bundle *et al.* (1986)
S. adelaide (O)	→4)-α-D-Glc*p*-(1→4)-α-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→ 6 ↑ 1 α-Col*p*	Kenne *et al.* (1983*b*)
S. greenside (Z)	→6)-β-D-Glc*p*NAc-(1→3)-α-D-Gal*p*-(1→3)-β-D-Gal*p*NAc-(1→ 3 ↑ 1 α-Col*p*-(1→3)-β-D-Gal*p*	Kenne *et al.* (1983*b*)
S. arizonae 059	→3)α-L-Fuc*p*NAc-(1→3)-β-D-Glc*p*NAc-(1→2)-β-D-Gal*p*-(1→	Vinogradov *et al.* (1987*a*)

TABLE 7 — *contd.*

O-antigen	*Repeating unit*[a]	*Reference*
S. arizonae 063	→4)-α-D-Gal*p*NAc-(1→3)-β-D-Gal*p*NAc-(1→3)-β-D-Gal*p*-(1→4)-α-D-Glc*p*-(1→ 4 ↑ 1 α-D-Fuc*p*3NAc (contains OAc)	Vinogradov *et al.* (1987*b*)
S. arizonae 064	→4)-β-D-Gal*p*NAc-(1→4)-β-D-Gal*p*NAc-(1→3)-α-D-Gal*p*-(1→4)-β-D-Gal*p*-(1→ 3 ↑ 1 α-D-Glc*p*NAc	Kocharova *et al.* (1988)

[a]Abe = 3,6-dideoxy-D-xylo-hexose (abequose); Col = 3,6-dideoxy-L-xylo-hexose (colitose); FucNAc = *N*-acetylfucosamine; Fuc3NAc = 3-acetamido-3,6-dideoxy galactose; GalNAc = *N*-acetylgalactosamine; GlcNAc = *N*-acetylglucosamine; Par = 3,6-dideoxy-D-Ribo-hexose (paratose); Tyv = 3,6-dideoxy-D-arabino-hexose (tyvelose); PerNAc = *N*-acetylperosamine.

TABLE 8
O-Antigens of *Shigella flexneri*

O-antigen	*Repeating unit*[a]	*Reference*
Y	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→	Jansson *et al.* (1987*a*, 1988*b*)
X	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→ 3 ↑ 1 α-D-Glc*p*	Jansson *et al.* (1987*a*, 1988*b*)
3a	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→ 3 2 ↑ | 1 OAc α-D-Glc*p*	Jansson *et al.* (1987*a*, 1988*b*)
3b	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→ 2 | OAc	Jansson *et al.* (1987*a*, 1988*b*)
4a	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→ 6 ↑ 1 α-D-Glc*p*	Jansson *et al.* (1987*a*, 1988*b*)

TABLE 8 — *contd.*

O-antigen	*Repeating unit*[a]	*Reference*
4b	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→ 2 6 | ↑ OAc 1 α-D-Glc*p*	Jansson *et al.* (1987*a*, 1988*b*)
5a	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→ 3 ↑ 1 α-D-Glc*p*	Jansson *et al.* (1987*a*, 1988*b*)
6	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→4)-β-D-Gal*p*A-(1→3)-β-D-Gal*p*NAc-(1→ 3 | OAc	Dmitriev *et al.* (1979)
NPS	→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→3)-β-D-Glc*p*NAc-(1→ 4 ↑ 1 α-D-Glc*p*-(1→2)-α-D-Glc*p*	Wehler and Carlin (1988)

[a]GalNAc = *N*-acetylgalactosamine; GlcNAc = *N*-acetylglucosamine; NPS = new provisional serotype.

TABLE 9
O-Antigens of *Shigella dysenteriae*

O-antigen	*Repeating unit*[a]	*Reference*
1	→3)-α-L-Rha*p*-(1→3)-α-L-Rha*p*-(1→2)-α-D-Gal*p*-(1→3)-α-D-Glc*p*NAc-(1→	Dmitriev *et al.* (1976)
2	→3)-α-D-Gal*p*NAc-(1→3)-α-D-Gal*p*NAc-(1→4)-α-D-Glc*p*-(1→4)-α-D-Gal*p*-(1→ 4 ↑ 1 AcO-3/4α-D-Glc*p*NAc	Dmitriev *et al.* (1977*a*)
3	→3)-β-D-Gal*p*NAc-(1→3)-α-D-Gal*p*-(1→6)-β-D-Gal*f*-(1→ 4 ↑ 1 β-Glc*p*LA-(1→6)-α-D-Glc*p*	Dmitriev *et al.* (1977*b*)
4	→3)-α-D-Glc*p*NAc-(1→3)-α-D-Glc*p*NAc-(1→4)-α-D-Glc*p*A(1→3)-α-L-Fuc*p*-(1→ 4 ↑ 1 AcO-α-L-Fuc*p*	Dmitriev *et al.* (1977*c*)
5	→3)-β-D-Glc*p*NAc-(1→4)-α-D-Man*p*-(1→4)-α-D-Man*p*-(1→ 3 2/3 ↑ | 1 OAc α-Rha*p*LA	Dmitriev *et al.* (1977*d*)
6	→3)-β-D-Gal*p*NAc-(1→3)-α-D-Gal*p*-(1→6)-α-D-Glc*p*-(1→ 4 | X	Dmitriev *et al.* (1975*a*)

TABLE 9 — *contd.*

O-antigen	*Repeating unit*[a]	*Reference*
7	→4)-α-D-GalNAcAN-(1→4)-α-D-GalNAcA-(1→3)-α-D-GlcNAc-(1→3)-β-D-Qui4N(AcGly)-(1→ 3 | OAc	Knirel *et al.* (1988)
8	→4)-β-D-Glc*p*A-(1→3)-β-D-Gal*p*NAc-(1→3)-β-D-Gal*p*NAc-(1→ 4 ↑ 1 β-D-Glc*p*NAc-(1→4)-β-D-Glc*p*	Dmitriev *et al.* (1978*a*)
9	→4)-α-D-Gal*p*-(1→3)-β-D-Glc*p*NAc-(1→3)-β-D-Gal*p*-(1→4)-β-D-Man*p*-(1→ 2/3 4 6 | \ / OAc X H_3C CO_2H	Dmitriev *et al.* (1978*b*); Pal *et al.* (1983)
10	→2)-β-D-Man*p*-(1→3)-α-D-Man*p*NAc-(1→3)-β-L-Rha*p*-(1→4)-α-D-Glc*p*NAc-(1→	Dmitriev *et al.* (1977*e*)

[a]GalNAc = *N*-acetylgalactosamine; GalNAcAN = 2-acetamido-2-deoxy-galacturonamide; GlcNAc = *N*-acetylglucosamine; Glc*p*LA = 3-glucolactylic acid; Qui4N(AcGly) = 4-(*N*-acetylglycyl)amino-4,6-dideoxy-glucose; Rha*p*LA = 4-rhamnolactylic acid; X = unknown acidic component.

TABLE 10
O-Antigens of *Shigella boydii* and *Shigella sonnei*

O-antigen	*Repeating unit*[a]	*Reference*
Sh. boydii		
2	→2)-β-D-Rib*f*-(1→4)-α-D-Gal*p*A-(1→3)-α-D-Glc*p*NAc-(1→2)-α-L-Rha*p*-(1→2)-α-L-Rha*p*-(1→ 3 ↑ 1 β-D-Gal*f*	L'vov *et al.* (1983)
4	→4)-β-D-Glc*p*A-(1→3)-β-L-Rha*p*-(1→4)-β-D-Glc*p*NAc-(1→3)-α-L-Rha*p*-(1→ 2 ↑ 1 α-D-Glc*p*	L'vov *et al.* (1980)
6	→3)-β-D-Gal*p*NAc-(1→3)-α-D-Gal*p*-(1→6)-α-D-Man*p*-(1→2)-α-D-Man*p*-(1→ 4 ↑ 1 α-D-Glc*p*A	Dmitriev *et al.* (1975*b*)
7	Pseudaminic acid derivative	Knirel *et al.* (1988)
9	→4)-α-D-Glc*p*-(1→4)-β-D-Glc*p*A-(1→3)-α-D-Glc*p*NAc-(1→3)-α-L-Rha*p*-(1→	L'vov *et al.* (1987*a*)
14	→6)-α-D-Gal*p*(1→4)-β-D-Glc*p*A-(1→6)-β-D-Gal*p*-(1→4)-β-D-Gal*p*-(1→4)-GlcNAc(1→	L'vov *et al.* (1987*b*)

TABLE 10 — *contd.*

O-antigen	*Repeating unit*[a]	*Reference*
Sh. sonnei phase one	→4)-α-L-Alt*p*NAcA-(1→3)-β-D-Gal*p*NAcN-(1→	Gamian and Romanowska (1982)

[a]AltNAcA = 2-acetamido-2-deoxy-altruronic acid; GalNAc = *N*-acetylgalactosamine; GalNAcN = 2-acetamido-4-amino-2,4,6-trideoxy-galactose; GlcNAc = *N*-acetylglucosamine.

group O2 have the same O-antigen as either O8 or O9. Serogroups 1 and 6 have identical O-antigens, as do serogroups 4 and 11.

K-Antigens (Table 6)
There are more than 80 types of *Klebsiella* K-antigens and the structures of the majority of these have been determined. All are acidic and, in most, the acidity is attributable to the presence of glucuronic or galacturonic acid residues. Pyruvic acid acetals (e.g. K3, K14, K36 and K68) and some less-common acidic sugars (e.g. K22 and K66) also occur. There are no amino sugars or phosphate esters. Some of the recently reported or revised structures are summarised in Table 6.

Salmonella

Salmonellae cause enteritis (inflammation of the small intestine) and septicaemia. These conditions can occur either together or independently of each other. Certain species cause specific types of septicaemia. Typhoid fever is caused by *Salmonella typhi* and paratyphoid fever by *Salmonella paratyphi* (A, B and C) and *Salmonella cholerae suis*. The most frequent agents of enteritis are *Salmonella typhimurium* (group B), *Salmonella enteritidis* (group D), *Salmonella newport* (group C_2), *Salmonella heidelberg* (group B) and *Salmonella infantis* (group C_1). Transmission occurs mainly through infected foodstuffs and occurs most frequently during the summer months. Differentiation of types on the basis of O-antigens, flagellar (H)-antigens and capsular (Vi)-antigens (where present) has lead to over 1400 serotypes being identified (Graevenitz, 1987). Types with similar O-antigens are sero-grouped (A to Z).

O-Antigens (Table 7)
The serogroups most injurious to humans are A, B, C_1 and D. The O-antigens from groups A, B and D are closely related, each containing a different 3,6-dideoxy-α-D-hexopyranosyl residue, in otherwise identical repeating units.

Salmonella madelia produces three different homogeneous O-antigens which share the same tetrasaccharide repeating unit backbone but which differ through the substitution of α-D-glucopyranosyl residues. Similarly, *Salmonella boecker* and *Salmonella thompson* each produce two O-antigens, which differ from each other through the presence or absence of an α-D-glucopyranosyl substitutent.

The O-antigens from *Salmonella greenside* (group Z) and *Salmonella adelaide* (Group O) are identical to those from *E. coli* O55 and *E. coli* O111, respectively.

Shigella

Shigellae cause the enteric disease bacterial dysentry. The primary site of infection is the small intestine, although some may subsequently invade other body tissues. The four recognised species (*Shigella boydii, Shigella dysenteriae, Shigella flexneri* and *Shigella sonnei*) are distinguished on the basis of their O-antigens. *Sh. sonnei* and *Sh. flexneri* occur most frequently in Western Europe and the USA, the other species being found in tropical and subtropical regions.

O-Antigens (Tables 8, 9, 10)
The O-antigens of *Sh. flexneri* (Table 8) have, with the exceptions of O6 and NPS (new provisional serotype), the same basic tetrasaccharide repeating unit. Variation exists in the presence of an additional α-D-glucopyranosyl residue and/or *O*-acetyl groups.

Partial or complete structures have been determined for all of the 10 serotypes of *Sh. dysenteriae*. A number of unusual component sugars exist as part of the lipopolysaccharide repeating units. These included lactic acid derivatives (types 3 and 5) and an unknown acidic component in type 6.

Sh. boydii (Table 10) has been divided into 15 serogroups. Several of these have uronic acids (usually glucuronic acid) as the acidic function of their O-antigen. *Sh. sonnei* lipopolysaccharide (Table 10) contains the unusual sugars 2-acetamido-2-deoxy-L-altruronic acid and 2-acetamido-4-amino-2,4,4-trideoxy-D-galactose.

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REFERENCES

Adeyeye, A., Jansson, P.-E., Lindberg, B., Abaas, S. & Svenson, S. B. (1988). *Carbohydr. Res.*, **176**, 231–6.

Ahrens, R., Jann, B., Jann, K. & Brade, H. (1988). *Carbohydr. Res.*, **179**, 223–32.
Altman, E. & Dutton, G. G. S. (1983). *Carbohydr. Res.*, **118**, 183–94.
Altman, E. & Dutton, G. G. S. (1985). *Carbohydr. Res.*, **138**, 293–303.
Anderson, A. N., Parolis, H., Dutton, G. G. S. & Leek, D. M. (1987*a*). *Carbohydr. Res.*, **167**, 279–90.
Anderson, A. N., Parolis, H. & Parolis, L. A. S. (1987*b*). *Carbohydr. Res.*, **163**, 81–90.
Andersson, M., Carlin, N., Leontein, K., Lindquist, U. & Slettengren, K. (1989). *Carbohydr. Res.*, **185**, 211–23.
Annison, G., Dutton, G. G. S. & Altman, E. (1987). *Carbohydr. Res.*, **168**, 89–102.
Annison, G., Dutton, G. G. S. & Mandal, P. K. (1988). *Carbohydr. Res.*, **177**, 278–84.
Beurret, M., Vignon, M. & Joseleau, J.-P. (1986). *Carbohydr. Res.*, **157**, 13–25.
Björndal, H., Lindberg, B. & Nimmich, W. (1970). *Acta Chem. Scand.*, **24**, 3414–15.
Brisson, J.-R. & Perry, M. B. (1988). *Biochem. Cell. Biol.*, **66**, 1066–77.
Bundle, D. R., Gerken, M. & Perry, M. B. (1986). *Can. J. Chem.*, **64**, 255–64.
Chakraborty, A. K. (1982). *Macromol. Chem.*, **183**, 2881–7.
Colquhoun, I. J., Morris, V. J. & Sutherland, I. W. (1989). *Carbohydr. Res.*, **187**, 103–15.
Cross, A. S., Gemstik, P., Sadoff, J. C., Orskov, F. & Orskov, I. (1984*a*). *J. Infect. Dis.*, **149**, 184–93.
Cross, A., Orskov, I., Orskov, F., Sadoff, J. & Gemski, P. (1984*b*). *J. Clin. Microbiol.*, **20**, 302–4.
Cryz, S. J., Jr (1987). *Vaccine*, **5**, 261–5.
Cryz, S. J., Jr, Fürer, E. & Germanier, R. (1985). *Infect. Immun.*, **50**, 225–30.
Cryz, S. J., Jr, Mortimer, P. M., Mansfield, V. & Germanier, R. (1986). *J. Clin. Microbiol.*, **23**, 687–90.
Cryz, S. J., Jr, Cross, A. S., Sadoff, G. C. & Que, J. U. (1988). *Eur. J. Immunol.*, **18**, 2073–5.
Curvall, M., Lindberg, B., Lonngren, J. & Nimmich, W. (1973*a*). *Acta Chem. Scand.*, **27**, 2645–9.
Curvall, M., Lindberg, B., Lonngren, J., Ruden, U. & Nimmich, W. (1973*b*). *Acta Chem. Scand.*, **27**, 4019–21.
Dengler, T., Jann, B. & Jann, K. (1985). *Carbohydr. Res.*, **142**, 269–76.
Dengler, T., Jann, B. & Jann, K. (1986). *Carbohydr. Res.*, **150**, 233–40.
Dengler, T., Himmelspach, K., Jann, B. & Jann, K. (1988). *Carbohydr. Res.*, **178**, 191–201.
DiFabio, J. L., Brisson, J.-R. & Perry, M. B. (1988*a*). *Carbohydr. Res.*, **199**, 233–44.
DiFabio, J. L., Perry, M. B. & Brisson, J.-R. (1988*b*). *Biochem. Cell. Biol.*, **66**, 107–15.
DiFabio, J. L., Brisson, J.-R. & Perry, M. B. (1989). *Biochem. Cell. Biol.*, **67**, 78–85.
Dmitriev, B. A., Knirel, Y. A., Kochetkov, N. K. & Hofman, I. L. (1975*a*). *Carbohydr. Res.*, **44**, 77–85.
Dmitriev, B. A., Backinowsky, L. V., L'vov, V.-L., Knirel, Y. A., Kochetkov, N. K. & Khomenko, N. A. (1975*b*). *Carbohydr. Res.*, **41**, 329–33.

Dmitriev, B. A., Knirel, Y. A., Kochetkov, N. K. & Hofman, I. L. (1976). *Eur. J. Biochem.*, **66**, 559–66.
Dmitriev, B. A., Knirel, Y. A., Kochetkov, N. K., Hofman, I. L. & Capek, K. (1977*a*). *Eur. J. Biochem.*, **76**, 433–40.
Dmitriev, B. A., L'vov, V.-L. & Kochetkov, N. K. (1977*b*). *Carbohydr. Res.*, **56**, 207–9.
Dmitriev, B. A., L'vov, V.-L., Kochetkov, N. K. & Hofman, I. L. (1977*c*). *Bioorg. Khim.*, **3**, 1226–33.
Dmitriev, B.A., Backinowsky, L. V., Knirel, Y. A., Kochetkov, N. K. & Hofman, I. L. (1977*d*). *Eur. J. Biochem.*, **78**, 381–7.
Dmitriev, B. A., Knirel, Y. A., Sheremet, O. K., Kochetkov, N. K. & Hofman, I. L. (1977*e*). *Bioorg.-Khim.*, **3**, 1219–25.
Dmitriev, B. A., L'vov, V.-L., Ramos, E. L., Kochetkov, N. K. & Hofman, I. L. (1978*a*). *Bioorg. Khim.*, **4**, 760–6.
Dmitriev, B. A., Knirel, Y. A., Vinogradov, E. V., Kochetkov, N. K. & Hofman, I. L. (1978*b*). *Bioorg.-Khim.*, **4**, 40–6.
Dmitriev, B. A., Knirel, Y. A., Sheremet, O. K., Shashkov, A. A.,Kochetkov, N. K. & Hofman, I. L. (1979). *Eur. J. Biochem.*, **98**, 309–16.
Dutton, G. G. S. & Karunaratne, D. N. (1983). *Carbohydr. Res.*, **119**, 157–69.
Dutton, G. G. S. & Karunaratne, D. N. (1984). *Carbohydr. Res.*, **134**, 103–14.
Dutton, G. G. S. & Kuma-Mintah, A. (1987). *Carbohydr. Res.*, **169**, 213–20.
Dutton, G. G. S. & Lim, A. V. S. (1985). *Carbohydr. Res.*, **145**, 67–80.
Dutton, G. G. S., Karunaratne, D. N. & Lim, A. V. S. (1988). *Carbohydr. Res.*, **183**, 111–22.
Dutton, G. G. S., Parolis, H., Joseleau, J.-P. & Marais, M.-F. (1986*a*). *Carbohydr. Res.*, **149**, 411–23.
Dutton, G. G. S., Parolis, H. & Parolis, L. A. S. (1986*b*). *Carbohydr. Res.*, **152**, 249–59.
Dutton, G. G. S., Parolis, H. & Parolis, L. A. S. (1987). *Carbohydr. Res.*, **170**, 193–206.
Erbing, C., Lindberg, B., Lonngren, J. & Nimmich, W. (1977). *Carbohydr. Res.*, **56**, 377–81.
Gamian, A. & Romanowska, E. (1982). *Eur. J. Biochem.*, **129**, 105–9.
Garegg, P. J., Henrichson, C., Norberg, T. & Ossowski, P. (1983). *Carbohydr. Res.*, **119**, 95–100.
Graevenitz, A. (1987). In *McGraw-Hill Encyclopedia of Science and Technology*, 6th edn, Vol. 16. McGraw-Hill, pp. 17–18.
Gupta, D. S., Jann, B. & Jann, K. (1984). *Infect. Immun.*, **45**, 203–9.
Hackland, P. L., Parolis, H., Dell, A. & Tiller, P. R. (1988*a*). *Carbohydr. Res.*, **181**, 153–62.
Hackland, P. L., Parolis, H. & Parolis, L. A. S. (1988*b*). *Carbohydr. Res.*, **172**, 209–16.
Hellerquist, C. G., Lindberg, B., Svensson, S., Holme, T. & Lindberg, A. A. (1969). *Carbohydr. Res.*, **8**, 43–55.
Hofmann, P., Jann, B. & Jann, K. (1985*a*). *Carbohydr. Res.*, **139**, 261–71.
Hofmann, P., Jann, B. & Jann, K. (1985*b*). *Eur. J. Biochem.*, **147**, 601–9.
Jann, K. & Jann, B. (1983). *Prog. Allergy*, **33**, 53–79.
Jann, K. & Jann, B. (1984). Structure and biosynthesis of O Antigens. In *Handbook of Endotoxin*, Vol. 1, ed. Reitschel, E. T. Elsevier Scientific Publications, Amsterdam, pp. 138–86.

Jann, K. & Jann, B. (1987). *Rev. Infect. Dis.*, **9**, S517–26.
Jann, K. & Westphal, O. (1975). In *The Antigens*, Vol. 3, ed. Sela, M. Academic Press, London, pp. 1–125.
Jann, B., Hofmann, P. & Jann, K. (1983). *Carbohydr. Res.*, **120**, 131–41.
Jann, B., Dengler, T. & Jann, K. (1985). *FEMS Microbiol. Lett.*, **29**, 257–61.
Jann, B., Ahrens, R., Dengler, T. & Jann, K. (1988). *Carbohydr. Res.*, **177**, 273–7.
Jansson, P.-E., Lindberg, B., Lonngren, J., Ortega, C. & Svenson, S. B. (1984*a*). *Carbohydr. Res.*, **131**, 277–83.
Jansson, P.-E., Lindberg, B., Lonngren, J., Ortega, C. & Nimmich, W. (1984*b*). *Carbohydr. Res.*, **132**, 297–305.
Jansson, P.-E., Lindberg, B., Ogunlesi, M., Svenson, S. B. & Wrangsell, G. (1984*c*). *Carbohydr. Res.*, **134**, 283–91.
Jansson, P.-E., Lonngren, J., Widmalm, G., Leontein, K., Slettengren, K., Svenson, S. B., Wrangsell, G., Dell, A. & Tiller, P. R. (1985). *Carbohydr. Res.*, **145**, 59–66.
Jansson, P.-E., Kenne, L. & Wehler, T. (1987*a*). *Carbohydr. Res.*, **166**, 271–82.
Jansson, P.-E., Lennholm, H., Lindberg, B., Lindquist, U. & Svenson, S. B. (1987*b*). *Carbohydr. Res.*, **161**, 273–9.
Jansson, P.-E., Lindberg, B., Widmalm, G. & Leontein, K. (1987*c*). *Carbohydr. Res.*, **165**, 87–92.
Jansson, P.-E., Lindberg, B., Widmalm, G., Dutton, G. G. S., Lim, A. V. S. & Sutherland, I. W. (1988*a*). *Carbohydr. Res.*, **175**, 103–9.
Jansson, P.-E., Kenne, L. & Wehler, T. (1988*b*). *Carbohydr. Res.*, **179**, 359–68.
Jennings, H. J. (1983). *Adv. Carbohydr. Chem. Biochem.*, **41**, 155–208.
Jennings, H. J., Rosell, K.-G. & Johnson, K. G. (1982). *Carbohydr. Res.*, **105**, 45–6.
Joseleau, J.-P. (1985). *Carbohydr. Res.*, **142**, 85–92.
Joseleau, J.-P. & Marais, M.-F. (1988). *Carbohydr. Res.*, **179**, 321–6.
Kenne, L. & Lindberg, B. (1983). In *The Polysaccharides*, Vol. 2, ed. Aspinall, G. O. Academic Press Inc., New York. pp. 282–363.
Kenne, L., Lindberg, B. & Madden, J. K. (1983*a*). *Carbohydr. Res.*, **122**, 249–56.
Kenne, L., Lindberg, B., Söderholm, E., Bundle, D. R. & Griffith, D. W. (1983*b*). *Carbohydr. Res.*, **111**, 289–96.
Kenne, L., Lindberg, B., Lugowski, C. & Svenson, S. B. (1986). *Carbohydr. Res.*, **151**, 349–58.
Knirel, Y.A., Dashunin, V. V., Shashkov, A. S., Kochetkov, N. K., Dmitriev, B.-A. & Hofman, I. L. (1988). *Carbohydr. Res.*, **179**, 51–60.
Kocharova, N. A., Vinogradov, E. V., Knirel, Y. A., Shashkov, A. S., Kochetkov, N. K., Stanislavskii, E. S. & Kholodkova, E. V. (1988). *Bioorg. Khim.*, **14**, 697–700.
Lee, C.-J. (1987). *Molec. Immun.*, **24**, 1005–19.
Lifely, M. R., Lindon, J. C., Williams, J. M. & Moreno, C. (1985). *Carbohydr. Res.*, **143**, 191–205.
Lindberg, B., Lonngren, J. & Nimmich, W. (1972). *Carbohydr. Res.*, **23**, 47–55.
Lindberg, B., Lonngren, J., Nimmich, W. & Ruden, U. (1973). *Acta Chem. Scand.*, **27**, 4019–21.
Lindberg, B., Leonstein, K., Lindquist, U., Svenson, S. B. & Wangsell, G. (1988). *Carbohydr. Res.*, **174**, 313–22.

L'vov, V.-L., Tochtamysheva, N. V., Dmitriev, B. A., Kochetkov, N. K. & Hofman, I. L. (1980). *Bioorg. Khim.*, **6**, 1842–50.
L'vov, V.-L., Dashunin, V. M., Ramos, E. L., Shashkov, A. S., Dmitriev, B. A. & Kochetkov, N. K. (1983). *Carbohydr. Res.*, **124**, 141–9.
L'vov, V.-L., Shashkov, A. S., Dmitriev, B. A., Kochetkov, N. K., Jann, B. & Jann, K. (1984). *Carbohydr. Res.*, **126**, 249–59.
L'vov, V.-L., Musina, L. Y., Shashkov, A. S., Ermakov, G. A. & Dmitriev, B. A. (1987*a*). *Soviet J. Bioorg. Chem.*, **13**, 679–88.
L'vov, V.-L., Yakovleu, A. P., Pluzhnikova, G. N., Lapina, E. B., Shashkov, A. S. & Dmitriev, B. A. (1987*b*). *Bioorg. Khim.*, **13**, 1256–65.
McCabe, W. R., Kayser, B., Olling, S., Uwaydah, M. & Hanson, L. A. (1978). *J. Infect. Dis.*, **138**, 33–41.
McGuire, E. J. & Binkley, S. B. (1964). *Biochemistry*, **3**, 247–51.
Nath, R. K. & Chakraborty, A. K. (1987*a*). *Carbohydr. Res.*, **161**, 91–6.
Nath, R. K. & Chakraborty, A. K. (1987*b*). *Eur. J. Biochem.*, **162**, 439–43.
Niemann, H., Chakraborty, A. K., Friebolin, H. & Stirm, S. (1978). *J. Bacteriol.*, **133**, 390–91.
Nikaido, H. (1988). *Rev. Infect. Diseases*, **10**, S279–81.
Orskov, F., Orskov, I., Sutton, A., Schneerson, R., Liu, T.-Y., Egan, W., Hoff, O. E. & Robbins, J. B. (1979). *J. Exp. Med.*, **149**, 669–85.
Pal, J., Basu, S. & Rao, C. V. N. (1983). *Carbohydr. Res.*, **114**, 123–35.
Parolis, H., Parolis, L. A. S. & Dutton, G. G. S. (1986*a*). *Carbohydr. Res.*, **152**, 249–59.
Parolis, L. A. S., Parolis, H. & Dutton, G. G. S. (1986*b*). *Carbohydr. Res.*, **155**, 272–6.
Parolis, H., Parolis, L. A. S. & Stanley, S. M. R. (1988*a*). *Carbohydr. Res.*, **175**, 77–83.
Parolis, H., Parolis, L. A. S. & Dutton, G. G. S. (1988*b*). *Carbohydr. Res.*, **182**, 127–34.
Parolis, L. A. S., Parolis, H., Niemann, H. & Stirm, S. (1988*c*). *Carbohydr. Res.*, **179**, 301–14.
Parolis, H., Parolis, L. A. S. & Venter, R. D. (1989). *Carbohydr. Res.*, **185**, 225–32.
Perry, M. B., Bundle, D. R., Maclean, L., Perry, J. A. & Griffith, D. W. (1986). *Carbohydr. Res.*, **156**, 107–22.
Prehm, P., Jann, B. & Jann, K. (1976). *Eur. J. Biochem.*, **67**, 53–6.
Ravenscroft, N., Jackson, G. E., Joao, H. & Stephen, A. M. (1988). *S. Afr. J. Chem.*, **41**, 42–7.
Rodriguez, M.-L., Jann, B. & Jann, K. (1988*a*). *Carbohydr. Res.*, **173**, 243–53.
Rodriguez, M.-L., Jann, B. & Jann, K. (1988*b*). *Eur. J. Biochem.*, **177**, 117–24.
Sarkar, A. K. & Roy, N. (1986). *Carbohydr. Res.*, **152**, 205–15.
Schmidt, M. A. & Jann, K. (1983). *Eur. J. Biochem.*, **131**, 508–17.
Stacey, M. & Barker, S. A. (1960). *Polysaccharides of Microorganisms*, Oxford University Press, London.
Tsui, F.-P., Egan, W., Summers, M. F., Byrd, R. A., Schneerson, R. & Robbins, J. B. (1988). *Carbohydr. Res.*, **173**, 65–74.
Vann, W. F., Schmidt, M. A., Jann, B. & Jann, K. (1981). *Eur. J. Biochem.*, **116**, 359–64.
Vann, W. F., Soderstrom, T., Egan, W., Tsui, F.-P., Schneerson, R., Orskov, I. & Orskov, F. (1983). *Infect. Immun.*, **139**, 623–9.

Vinogradov, E. V., Knirel, Y. A., Lipkind, G. M., Shashkov, A. S., Kochetkov, N. K., Stanislavskii, E. S. & Kholodkova, E. V. (1987*a*). *Bioorg. Khim.*, **13**, 1275–81.

Vinogradov, E. V., Knirel, Y. A., Lipkind, G. M., Shashkov, A. S., Kochetkov, N. K., Stanislavskii, E. S. & Kholodkova, E. V. (1987*b*). *Soviet J. Bioorg. Chem.*, **13**, 760–5.

Wehler, T. & Carlin, N. I. A. (1988). *Eur. J. Biochem.*, **176**, 471–6.

Weintraub, A., Lindberg, A. A., Lipiunas, P. & Nilsson, B. (1988). *Glycoconjugate J.*, **5**, 207–13.