CROSSREACTIONS OF *ESCHERICHIA COLI* K AND O
POLYSACCHARIDES IN ANTIPNEUMOCOCCAL AND
ANTI-SALMONELLA SERA

BY MICHAEL HEIDELBERGER,* KLAUS JANN,‡ AND BARBARA JANN‡

From the *New York University Medical Center, Department of Pathology, New York 10016;
and the ‡Max Planck Institut für Immunobiologie, 4800 Freiburg-Zähringen, Federal Republic
of Germany

The study of crossreactivity in relation to chemical structure of the microbial
polysaccharides has shown both theoretical and practical utility. In this paper,
we make use of recently determined structures of *E. coli* K and O polysaccharides
to derive new relationships of structure and specificity, and to update some of
the data in earlier work.

Materials and Methods

These have been described in earlier papers (1-3). Pneumococcal (Pn)$^A$ type-numbers
are given in Roman type to avoid confusion with those of *E. coli* and *Klebsiella*.

Results and Discussion

Data obtained are summarized in Table I.

*E. coli* K Polysaccharides. K2 has 1,4-linked D-galactose (D-gal) and 1,5-linked
D-galf (furan form of D-galactose; all sugars are pyranose form unless otherwise
stated) in addition to glycerophosphate residues in its repeating unit (4). Precip-
itation (+++) in anti-Pn XII (see Table I) may be caused by a loose fit of
glycerophosphate into antibody sites designed for the D-N-acetylmannosaminic
acid (D-ManNAcA) of Pn soluble specific capsular polysaccharide (PnS) XII (5,
6). PnS XXIX has two 1,6-linked D-galf residues in its repeating unit (7). Since
carbons 5 and 6 of galf are outside the furanose ring, it is possible that the 1,5-
D-galf of *E. coli* K2 would fit partially into antibody sites in anti-Pn XXIX
designed for 1,6-linked D-galf residues, to give the ++ precipitation found.
There was also ++ in anti-Pn XVI, but the structure of PnS XVI is not known.

K4 is omitted from Table I, as it gave only a single + reaction (on a scale of
− to ++++) in anti-Pn XXII serum.

K5 has the repeating unit $\rightarrow 4\)glcNAc-a-(1 \rightarrow 4)glcA-\beta-(1\rightarrow \frac{\alpha}{\beta}$ (glcNAc, N-
acetylglucosamine; glcA, glucuronic acid) (8). Its faint (+) crossprecipitations
were in anti-Pn III, IX, XII, XVI, and XXV.

K7 has the repeating unit $\rightarrow 3\)-D-manNAcA-\beta-(1 \rightarrow 4)-D-glc-\beta-(1\rightarrow \frac{\alpha}{\beta}$ (glc,
glucose) (9). It reacts with so many equine anti–Pn sera that at least some of the

$^A$Abbreviations used in this paper: f, furan form; Pn, pneumococcal; PnS, Pn soluble specific
capsular polysaccharide.
reactions might be due to previous or inapparent infections of the horses by strains of *E. coli* containing K7 or a crossreacting antigen such as the enterobacterial common antigen (ECA), which also contains D-mannosamine (D-mannosylamine) in its repeating unit (10), and has shown some unexpected crossreactions. Nevertheless, some of the precipitations appear to be correlated with known structural features of Pn polysaccharides. The 1,3-linked D-mannosamine of K7 probably reinforces a crossreaction in anti-Pn III due to 1,4-linked D-glc, since it would be expected to have some of the serological properties of the D-glcA of PnS III \(\rightarrow 3\)-D-GlcA-\(\rightarrow 4\)-D-GlcA (sugars are capitalized only when known to be immunodominant). For examples of the partial serological equivalence of D-glcA, D-glucosamine, and D-mannosamine, cf. previously published data (11-13). K7 precipitates 242 µg/ml of antibody nitrogen from anti-Pn III 792C, far more than the +++ in anti-Pn VIII 1008 of higher antibody content. The repeating unit of PnS VIII is half cellobiouronic acid (14), and the remainder is D-glc \(\rightarrow\) D-gal (galactose), but all linkages are 1,4, instead of the 1,3-linked D-glcA of PnS III \(\rightarrow 3\)-D-GlcA-\(\rightarrow 4\)-D-glc-B-(1 \(\rightarrow\) 4)-D-glc-B-(1 \(\rightarrow\) 4), so that the greater reactivity in anti-Pn III is in accord with the three structures.

PnS II, XIV, XV, XIX, XXII, and XXIII contain 1,4-linked D-glc in their repeating units: the crossprecipitations in antisera to these types appear due (16) to multiples of these residues, reinforced in the large reaction (99 µg/ml of antibody nitrogen) in anti-Pn XIX by 1,4-linked D-mannosamine, a determinant of PnS XIX (17). Precipitation in anti-Pn I, VI, IX, and X may be caused by inapparent crossreacting *E. coli* infections of the immunized horses, as indicated above.

K8 is made up of gal, D-glcA, D-galNAc, and D-glucosamine (glcN) (18). The reaction was only ++ in anti-Pn XXII, + in anti-*Salmonella typhi* and anti-*S. paratyphi* A, and ++ in anti-*S. paratyphi* B.

K9 (18, 19) contains gal, N-acetylneuraminic acid, and N-acetylgalactosamine (galNAc). It gave a + reaction in anti-Pn I, III, VIII, IX, XV, and XXV and +± in anti-Pn VI, VII, and X. In the last three, common linkages of D-gal and/or D-galNAc in the relevant polysaccharides probably give rise to antibodies producing the slight crossprecipitations.

K12 (20) showed a + reaction in anti-Pn V and XXVII.

K14 (21) and 17 were uniformly – to ± and, with K12, are not included in Table 1. Immunodominance of partially O-acetylated 2-keto-3-deoxymannosoctonic acid (KDO), which does not occur in PnS, may explain the lack of reactivity of K12 and 14 in anti-Pn sera.

K25 is made up of D-glcA, D-galNAc, and fucose (fuc) (18, 19). It crossreacts weakly in anti-Pn V and MMXXV. Possibly, 1,2-linked D-glcA will be found in K25, as it occurs in PnS V (22); the structure of PnS XXV is not known.

K26 contains D-glcA, gal, and rhamnose (rham) (18, 19). Strong crossprecipitation in anti-Pn II and XXIII indicates that its repeating units contain nonreducing lateral end groups of D-glcA, as in PnS II (23), and of L-rham, as in PnS XXIII (24-26). With these structural similarities to K85 (see below), there should be reciprocal crossreactivity between K26 and K85 and antisera to these, but this does not seem to have been looked for. The reaction in anti-Pn VI is
### Crossreactions of E. coli Polysaccharides in Antipneumococcal Antisera

| E. coli antigens | I 1924 | II 4000 | III 660 | IV 2390 | V 4060 | VI 724 | VII 893 | VIII 1288 | IX 1655 | X 864 | XI 792 | XII 1240 | XIV 1010 |
|------------------|-------|--------|-------|--------|-------|-------|-------|---------|--------|-------|-------|---------|---------|
|                  |       |       |       |        |       |       |       |         |        |       |       |         |         |
| K2               | - ±   | ± ±   | - ±   | ± ±    | - ±   | ± ±   | - ±   | ± ±     | - ±    | ± ±   | ±     | ± ±     | ± ±     |
| K7               | +±±   | ±±±   | +±±   | +±±    | +±±   | +±±   | +±±   | +±±     | +±±    | +±±   | +±±   | +±±     | +±±     |
| 9 (++)           | (-)   | (-)   | (-)   | (-)    | (+±)  | (+±)  | (+±)  | (+±)    | (+±)   | (+±)  | (+±)  | (+±)    | (+±)    |
| 25 (-)           | - -   | - -   | - -   | - -    | - -   | - -   | - -   | - -     | - -    | - -   | - -   | - -     | - -     |
| 26 -             | - 300 | - -   | - +±  | ++±    | - -   | - -   | - -   | - -     | - -    | - -   | - -   | - -     | - -     |
| 27 +±±           | - -   | - -   | - -   | - -    | - -   | - -   | - -   | - -     | - -    | - -   | - -   | - -     | - -     |
| 28 -             | +±±   | +±±   | +±±   | +±±    | +±±   | +±±   | +±±   | +±±     | +±±    | +±±   | +±±   | +±±     | +±±     |
| 30 505±1         | - ±   | +±±   | +±±   | +±±    | +±±   | +±±   | +±±   | +±±     | +±±    | +±±   | +±±   | +±±     | +±±     |
| 31 (-)           | (±)   | (±)   | (±)   | (±)    | (±)   | (±)   | (±)   | (±)     | (±)    | (±)   | (±)   | (±)     | (±)     |
| 32       |       |       |       |        |       |       |       |         |        |       |       |         |         |
| 34 (-)           | - (±) | - (±) | - (±) | - (±)  | - (±) | - (±) | - (±) | - (±)   | - (±)  | - (±) | - (±) | - (±)   | - (±)   |
| 36 +±±           | - -   | - -   | - -   | - -    | - -   | - -   | - -   | - -     | - -    | - -   | - -   | - -     | - -     |
| 37 (-)           | - -   | - -   | - -   | - -    | - -   | - -   | - -   | - -     | - -    | - -   | - -   | - -     | - -     |
| ( Of147 Ki) 100  | +±±   | +±±   | +±±   | +±±    | +±±   | +±±   | +±±   | +±±     | +±±    | +±±   | +±±   | +±±     | +±±     |
| O6PS (++)        | (+±)  | (+±)  | (+±)  | (+±)   | (+±)  | (+±)  | (+±)  | (+±)    | (+±)   | (+±)  | (+±)  | (+±)    | (+±)    |
| O8PS (++)        | +±±   | +±±   | +±±   | +±±    | +±±   | +±±   | +±±   | +±±     | +±±    | +±±   | +±±   | +±±     | +±±     |
| O9 (±)           | (±)   | (±)   | (±)   | (±)    | (±)   | (±)   | (±)   | (±)     | (±)    | (±)   | (±)   | (±)     | (±)     |
| O13H (++)        | (+±±) | (+±±) | (+±±) | (+±±)  | (+±±) | (+±±) | (+±±) | (+±±)   | (+±±)  | (+±±) | (+±±) | (+±±)   | (+±±)   |

* Readings in parentheses: tests made in two or more rows of antisera that were to ++ or ++++ with other polysaccharides.

† E. coli K26 precipitated Ranti-K47 Klebsiella. K1 47, like PnS XXIII, has lateral nonreducing end groups of 1-rham.

‡ From Heidelberger et al. (37).

§ ±±± in RXVII.

probably due to 1,3-L-rham and/or to 1,2-D-gal. The explanations of these crossreactivities in Ørskov et al. (18) are thus extended and modified.

K27 has the probable (27) structure:

$$\begin{align*}
\text{D-Gal(1 → 3)} & \text{D-glc(1 → 3)-D-glcA-β(1 → 3)-L-fuc(1 → 6) -OAc} \\
\end{align*}$$

Weak precipitation in anti-Pn I is difficult to explain. Failure to react in anti-Pn XIV may indicate that -OAc is on the gal. PnS X (28) and XX (29) have lateral nonreducing end groups of D-galf. Crossreactions in anti-Pn X and XX might indicate that the lateral gal of K27 is also galf, although gal (pyran) and galf are not necessarily noncrossreactive.

K28 has (30) the structure:

$$\begin{align*}
\text{D-gal-β(1 → 4)} & \text{D-glc-α(1 → 4)-D-glcA-β(1 → 4)-L-fuc-α(1)} \\
\end{align*}$$

L-fuc is acetylated at positions 2 or 3 in 70% of the repeating units. It is difficult to see why K28 should give even ++ in anti-Pn II or why, if reactivity in anti-Pn VII is due to the lateral D-gal, there is no definite precipitation in anti-Pn
Anticarbohydrate and Anti-Salmonella Sera

| Coccal Sera | Anti-Salmonella Sera |
|-------------|----------------------|
| XV 770      | Gryph | paratyphi A | paratyphi B |
| XVI 872 2200 | + + | + | + |
| XVII 2250 | + + | + | + |
| XIX 355 | + + | + | + |
| XX 878 | + + | + | + |
| XXI 420 | + + | + | + |
| XXII 620 | + + | + | + |
| XXIII 277 | + + | + | + |
| XXIV 785 | + + | + | + |
| XXV 380 | + + | + | + |

Tests with equine anti-Pn XXV 513C (New York City Department of Health).

** From Heidelberger et al. (37) table I, footnote d, (278 - 126 = 152).

± 27 µg after treatment with alkali.

† From G. Springer, Northwestern University School of Medicine, Evanston, IL.

‡ From A. Zweibaum, Hôpital Broussais, Paris.

XII or XIV; the +± reaction in anti-Pn X is probably for the reason given for K27.

K29 contains 1,3-linked glucosyl residues in its repeating unit (31). These are probably responsible for the ++ in anti-Pn VI. There should also be a heavy crossreaction with Klebsiella (KL) K31, which has the same pyruvyl (Py) 4,6-glc-(1 → 2)-D-man sidechain (32), and perhaps also with KL 36 (33) and KL 64 (34), which also have 4,6-Py-glc nonreducing lateral end groups.

Crossreactivity of K30 (35) and K85 (36) in anti-Pn II and V, and of K85 in anti-Pn XXIII was expected, found, measured, and discussed previously (37). It may now be added that, since K85 precipitates more antibody from anti-Pn V (PnS V has 1,2-linked D-glcA [22]) than from anti-Pn II, this would favor assignment of the 1,2-linkage to the nonterminal glcA of K85, rather than the 1,4-linked alternative also proposed (18, 37). Recent work (28) has shown that pure PnS X contains no glcNAc, so that the crossreaction of K85 in anti-Pn X cannot be attributed to this sugar, as was done previously (18, 37). Alternatively, the glcA residues of K85 might fit partially into combining sites of anti-Pn X designed for reception of the ribitolphosphate residues of PnS X.

Recently (38), Klebsiella K63 was found to contain the same sugars in the same linkages as E. coli K42 (39). Quantitative analyses (1), however, show that KI 63 precipitates 148 µg/ml of antibody nitrogen from anti-Pn I 1057C whereas E. coli K42 gives only 8 µg/ml (37). Although the primary structures of the two polysaccharides are the same, KI 63 is said to contain <0.2 residues of −OAc per...
repeating unit, while E. coli K42 has 0.5. Assuming that K42 has not been partially depolymerized or degraded, one might explain the analytical data as follows. If the -OAc of K42 were on galA, and antibodies in anti-Pn I were partly directed against unacetylated galA, the discrepancy would be accounted for. Alternatively, the three-dimensional form of the more highly acetylated K42 might differ from that of Kl K63. Strictly, then, E. coli K42 and Kl 63 are not identical.

K31 (described by K. Jann and B. Jann, unpublished results), with its only heavy crossreaction in anti-Pn XXIII, provides another instance of a 1,2-linked sugar acting serologically much like a nonreducing lateral end group. In the repeating unit of K31, it is the 1,2-linked L-rham that reacts like the L-rham in K26 (above).

K51 is omitted from Table I because the only significant reaction, (+ +) in anti-Pn XVIII, is not interpretable with the information at hand.

K52 is also omitted, as all tests showed little (+) or no (−) crossreactivity.

K54 has a unique repeating unit: \(\beta-3\)-D-glucA-l-threonylamide-\(\beta-(1 \rightarrow 3)\)-L-rham-\(\alpha-(1 \rightarrow \beta)\) (40) (occasional units have serine instead of threonine). From its crossprecipitation in anti-Pn III and not in anti-Pn VIII, predicted earlier that the glucA would be D-, and 1,3-linked, as in PnS III, and not 1,4-linked as in PnS VIII. Amidation of glucA seems not to have affected its specificity. 1,3-linked L-rham explains the crossreactivity in anti-Pn VI (41).

K57 contains gal, ribose, galA, and galNAc (18). Its only significant (+++) crossprecipitation, in anti-Pn I, appears due to D-galA in a 1,3- or 1,4-linkage, as in PnS I (42).

K87 has (43) the repeating unit,

\[
\begin{align*}
\text{4-D-glucA-β(1 \rightarrow 3)-L-fucNAc(1 \rightarrow 3)} & \quad \text{D-glucNac (1 \rightarrow 6)-D-gal(1 \rightarrow 4)} \\
\quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad \quad
bend the molecule into a shape different from that of O9, in which all linkages are α. The reaction of O9 in anti-Pn XII may be caused by its multiples of α-1,2 mannosyl residues. Since mannose is partially equivalent serologically to glucose (12), O9 could fit loosely into antibody sites designed to bind the kojibiosyl residues of PnS XII. The number of relatively weak crossprecipitations in anti-Pn sera may be due, as in other instances, to inapparent infection of the immunized horses with O8, O9, or to crossreacting strains.

Cells of E. coli O13 yield antisera in rabbits that precipitate heavily with glycogen (49). A glc-containing O13 polysaccharide also sent by Dr. A. Zweibaum (Hôpital Broussais, Paris, France) reacts to various extents with anti-Pn I–XX, so that it is questionable whether all of the precipitates involve type-specific antibodies.

O111 has the structure.

\[
\begin{align*}
&\text{Colitose } (1 \rightarrow 3)\alpha \\
&\text{Colitose } (1 \rightarrow 6)\beta \\
\rightarrow &4\text{-d-glc-α}(1 \rightarrow 4)\text{-d-gal-α}(1 \rightarrow 3)\text{-d-glcNAc-β}(1 \rightarrow 3)\alpha_n \\
\end{align*}
\]

(50, 51)

This polysaccharide, from Dr. O. Westphal (University of Freiburg, Federal Republic of Germany) contains colitose, glc, gal, and glcNAc. It was tested in all listed antisera, giving only very weak (+) to negative (−) reactions, and is therefore omitted from Table 1. After degradation with 1% acetic acid, at 100°C for 90 min, which removes both colitose residues from the glc, it precipitated 60 μg/ml of antibody nitrogen from anti-Pn VIII 1008, confirming the presence of 1,4-linked d-glc in O111.

Summary

Crossreactions of 24 K polysaccharides and 4 O polysaccharides of E. coli in antisera to 27 pneumococcal types, 3 anti-Salmonella sera, and anti-Klebsiella Kl serum are discussed in relation to structural features of the polysaccharides insofar as these are known. Predictions based on the crossprecipitations are also ventured for several instances in which structures are as yet undetermined.

Received for publication 24 June 1985.

References

1. Heidelberger, M., and W. Nimmich. 1976. Immunochemical relationships between bacteria belonging to two separate families: pneumococci and Klebsiella. Immunochemistry 13:67.
2. Heidelberger, M., and P. A. Rebers. 1958. Cross-reactions of polyglucoses in anti-pneumococcal sera. VI. J. Am. Chem. Soc. 80:116.
3. Heidelberger, M., and J. M. Tyler. 1964. Cross-reactions of pneumococcal types. Quantitative studies with the capsular polysaccharides. J. Exp. Med. 120:711.
4. Jann, K., B. Jann, M. A. Schmidt, and W. Vann. 1980. Structure of the Escherichia coli K2 capsular antigen, a teichoic acid–like polymer. J. Bacteriol. 143:1108.
5. Duke, J. L., I. J. Goldstein, and J. A. Cifonelli. 1974. Structural studies of capsular polysaccharide of type XII Diplococcus pneumoniae. Carbohydr. Res. 37:81.
6. Leontine, K., B. Lindberg, and J. Lönngren. 1981. Structural studies of the capsular polysaccharide from Streptococcus pneumoniae type 12 F. Can. J. Chem. 59:2081.
7. Rao, E. V., M. J. Watson, J. G. Buchanan, and J. Baddiley. 1969. Type-specific substance from Pneumococcus type 29. Biochim. J. 111:547.
8. Vann, W. F., M. A. Schmidt, B. Jann, and K. Jann. 1981. Structure of the capsular polysaccharide (K5 antigen) of urinary tract-infective Escherichia coli O10:K5:144. A polymer similar to desulfo-heparin. Eur. J. Biochem. 116:359.
9. Tsui, F. P., R. A. Boykins, and W. Egan. 1982. Studies of the Escherichia coli K7 (K56) capsular polysaccharide. Carbohydr. Res. 102:263.
10. Dell, A., J. Oates, C. Lugowski, E. Romanowska, L. Kenne, and B. Lindberg. 1984. Enterobacterial common antigen, a cyclic polysaccharide. Carbohydr. Res. 133:95.
11. Heidelberger, M., G. G. S. Dutton, J. Eriksen, W. Nimmich, and S. Stirn. 1982. Additional correlations of chemical structure and immunological specificity among cross-reactions of pneumococci and Klebsiella. Acta Pathol. Microbiol. Immunol. Scand. Sect. C. Immunol. 90:87.
12. Heidelberger, M., and M. E. Slodki. 1972. Cross-reactions of Lipomyces in antipneumococcal and other antisera. Carbohydr. Res. 24:401.
13. Robbins, J. B., R. L. Myerowitz, J. K. Whisnant, M. Argaman, R. Schneerson, Z. T. Handzell, and E. C. Gotschlich. 1972. Enteric bacteria cross-reactive with Neisseria meningitidis groups A and C and Diplococcus pneumoniae types I and III. Infect. Immun. 6:651.
14. Jones, J. K. N., and M. B. Perry. 1957. Structure of the type VIII pneumococcus specific polysaccharide. J. Am. Chem. Soc. 79:2787.
15. Reeves, R. E., and W. F. Goebel. 1941. Chemioimmunological studies on the soluble specific substance of pneumococcus: structure of type III polysaccharide. J. Biol. Chem. 139:511.
16. Heidelberger, M., and F. E. Kendall. 1934. Quantitative studies on the precipitin reaction. The role of multiple reactive groups in antigen-antibody union as illustrated by an instance of cross-precipitation. J. Exp. Med. 59:519.
17. Ohno, N., T. Yadomae, and T. Miyazaki. 1980. Structure of the type-specific polysaccharide of Pneumococcus type XIX. Carbohydr. Res. 80:297.
18. Örskov, I. F. Örskov, B. Jann, and K. Jann. 1977. Serology, chemistry, and genetics of O and K antigens of Escherichia coli. Bacteriol. Rev. 41:667.
19. Jann, K., and B. Jann. 1983. K antigens of Escherichia coli. Prog. Allergy. 33:53–79.
20. Schmidt, M. A., and K. Jann. 1983. Structure of the 2-keto-3-deoxy-D-manno-octonic acid–containing capsular polysaccharide (K 12 antigen) of the urinary tract–infective E. coli O4:K12:"H": Eur. J. Biochem. 131:509.
21. Jann, B., P. Hofmann, and K. Jann. 1983. Structure of 3-deoxy-D-manno-octulosonic acid (KDO)–containing capsular polysaccharide from Escherichia coli O6:K14:H31. Carbohydr. Res. 120:131.
22. Barker, S. A., S. M. Bick, J. S. Brimacombe, M. J. How, and M. Stacey. 1966. Structural studies on the capsular polysaccharide of pneumococcus type V. Carbohydr. Res. 2:224.
23. Kenne, L., B. Lindberg, and S. Svensson. 1975. Structure of the capsular polysaccharide of pneumococcus Type II. Carbohydr. Res. 40:69.
24. Heidelberger, M., M. Davie, and R. M. Krause. 1967. Cross-reactions of the group-specific polysaccharides of streptococcal groups B and G in antipneumococcal sera with special reference to type XXIII and its determinants. J. Immunol. 99:794.
25. Jones, C. 1985. Identification of the tetrasaccharide repeating unit of the Streptococcus pneumoniae type 23 polysaccharide by high-field proton NMR spectrography. Carbohydr. Res. 139:75.
26. Heidelberger, M. 1983. Precipitating cross-reactions among pneumococcal types. Infect. Immun. 41:1234.
27. Jann, K., B. Jann, K. F. Schneider, F. Ørskov, and L. Ørskov. 1968. Immunochemistry of K antigens of Escherichia coli. 5. K antigen of E. coli O8:K27(A):H+. Eur. J. Biochem. 5:456.
28. Perry, M. B., V. Daoust, and R. Lowe. 1980. Immunity, immunization, cerebrospinal meningitis. World Health Organization International Conference, Marburg. (Abstr.).
29. Richards, J. C., M. B. Perry, and D. J. Carlo. 1983. The specific capsular polysaccharide of Streptococcus pneumoniae type 20. Can. J. Biochem. Cell Biol. 61:178.
30. Altman, E., and G. G. S. Dutton. 1985. Capsular polysaccharide from Escherichia coli O9:K28(A):H) (K28 antigen). Carbohydr. Res. 138:293.
31. Choy, Y. M., F. Fenmel, N. Frank, and S. Stirm. 1975. Escherichia coli capsular bacteriophages. VI. Primary structure of the bacteriophage 29-receptor, E. coli serotype 29 capsular polysaccharide. J. Virol. 16:587.
32. Cheng, C.-C., S.-L. Wong, and Y.-M. Choy. 1979. Structure of the capsular polysaccharide of Klebsiella K type 31. Carbohydr. Res. 73:169.
33. Dutton, G. G. S., and K. L. Mackie. 1977. Structural investigation of Klebsiella serotype K56 polysaccharide. Carbohydr. Res. 55:49.
34. Merrifield, E. H., and A. M. Stephen. 1979. Structural studies on the capsular polysaccharide from Klebsiella serotype K 64. Carbohydr. Res. 74:241.
35. Chakraborty, A. K., H. Friebolin, and S. Stirm. 1980. Primary structure of the Escherichia coli serotype K30 capsular polysaccharide. J. Bacteriol. 141:971.
36. Jann, K., B. Jann, F. Ørskov, and L. Ørskov. 1966. Immunchemische Untersuchungen an K-Antigenen von Escherichia coli. III. Isolierung und Untersuchung der chemischen Struktur des sauren Polysaccharides aus E. coli O141:K85(B):H4(K85-Antigen). Biochem. Z. 346:368.
37. Heidelberger, M., K. Jann, B. Jann, F. Ørskov, L. Ørskov, and O. Westphal. 1968. Relations between structures of three K polysaccharides of Escherichia coli and cross-reactivity in antipneumococcal sera. J. Bacteriol. 95:2415.
38. Joseleau, J.-F., and M.-E. Marais. 1979. Structure of the capsular polysaccharide of Klebsiella K-type 63. Carbohydr. Res. 77:183.
39. Jann, K., and B., F. and I. Ørskov, and O. Westphal. 1966. Immunkiemische Untersuchungen an K-Antigenen von Escherichia coli. II. K-Antigen von E. coli O8:K42(A):H+. Biochem. Z. 342:1.
40. Hofmann, P., B. Jann, and K. Jann. 1985. Structure of the amino acid–containing capsular polysaccharide (K54 antigen) from Escherichia coli O6:K54:H10. Carbohydr. Res. 139:261.
41. Rebers, P. A., and M. Heidelberger. 1961. The specific polysaccharide of type VI pneumococci II. The repeating unit. J. Am. Chem. Soc. 83:3056.
42. Lindberg, B., B. Lindqvist, J. Lönngren, and D. A. Powell. 1980. Structural studies of the capsular polysaccharide from Streptococcus pneumoniae type 1. Carbohydr. Res. 78:111.
43. Tarcsay, L., Jann, B., and K. Jann. 1971. Immunochemistry of K antigens of Escherichia coli K 87 antigen from E. coli O8:K87(B):H19. Eur. J. Biochem. 23:505.
44. Robbins, J. B., R. Schneerson, J. C. Parke, T. Y. Lin, Z. T. Handzel, and F. Ørskov. 1976. E. coli O75:Kf147:H-5 cross-reactive with capsular polysaccharide of Haemophilus influenzae type b: immunochemical relationship and prospects for heteroimmunization on humans to H. influenzae b. In Role of Immunological Factors in Infections. R. F. Beers and E. G. Bassett, editors. Raven Press, New York. 103–120.
45. Branefors-Helander, P., C. Erbing, L. Kenne, and B. Lindberg. 1976. Structural
studies of the capsular antigen from Haemophilus influenzae type b. Acta Chem. Scand. Ser. B Org. Chem. Biochem. 30:276.

46. Reske, K., and K. Jann. 1972. O8 antigen of Escherichia coli. Structure of the polysaccharide chain. Eur. J. Biochem. 31:320.

47. Prehm, P., B. Jann, and K. Jann. 1976. O9 antigen of Escherichia coli. Structure of the polysaccharide chain. Eur. J. Biochem. 67:53.

48. Jann, K., B. Jann, V. Winter, and C. Wolf-Ullisch. 1979. Serological specificity of Escherichia coli O8 and O9 antigens. J. Gen. Microbiol. 110:203.

49. Zweibaum, A., M. Rousset, and S. Leon. 1976. Activite antiglycogene de serums de lapins immunises avec une souche d'Escherichia coli O13. Compt. Rend. Acad. Sci. (France) D 283:1815.

50. Edstrom, R. D., and Heath, E. C. 1967. Biosynthesis of cell wall lipopolysaccharides in Escherichia coli. VII. Studies on the O-antigenic polysaccharides. J. Biol. Chem. 242:4125.

51. Eklind, K., P. J. Garegg, L. Kenne, A. A. Lindberg, and B. Lindberg. 1978. Structural studies on the Escherichia coli O111 lipopolysaccharide. Internat. Symp. Carbohydr. Chem. 9:495a (Abstr.).