Structural Studies of the Major High Mannose Oligosaccharide Units from Chinese Hamster Ovary Cell Glycoproteins*

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The major high mannose-type glycopeptides present in Chinese hamster ovary cells have the compositions (Man)α(GlcNAc)2-Asn, (Man)α(GlcNAc)2-Asn, and (Man)α(GlcNAc)2-Asn. The structures of these glycopeptides were determined by the combination of methylation analysis, acetylation, Smith periodate degradation, and α- and β-mannosidase digestion. Their complete structures are: Manα1→2Manα1→6(Manα1→2Manα1→3)Manβ1→4GlcNAcβ1→4GlcNAc-Asn, Manα1→2Manα1→3Manα1→6(Manα1→2Manα1→3)Manβ1→4GlcNAcβ1→4GlcNAc-Asn, and Manα1→6(Manα1→3)Manα1→6(Manα1→2Manα1→3)Manβ1→4GlcNAcβ1→4GlcNAc-Asn. These structures are compared with the structures of the peptide-bound oligosaccharide intermediates that are processed to form complex-type oligosaccharides. From these results, it is proposed that the high mannose-type oligosaccharides are a product of "incomplete" processing of the protein-bound oligosaccharide along the same pathway which leads ultimately to the formation of a complex-type oligosaccharide.

The carbohydrate moieties of glycoproteins from cultured cells have been the subject of extensive studies; however, there is still little known about the detailed structures of these molecules. The need for further information has been made more evident by recent observations concerning the biosynthesis of asparagine-linked oligosaccharides. Workers from several laboratories, including this one (1-3), have recently demonstrated that the synthesis of complex-type chains involves the en bloc transfer of a high molecular weight, glucose-containing, mannose-rich oligosaccharide from a lipid carrier to the protein. The peptide-bound oligosaccharide is then processed to form a complex-type oligosaccharide (1-3). This pathway is blocked in a variant line of Chinese hamster ovary cells, termed clone 15B, which is deficient in a specific mannosidase activity (4), and which forms an oligosaccharide with the structure,

\[
\text{M} \quad \alpha,6 \\
\text{M} \quad \alpha,6 \\
\text{M} \quad \alpha,3 \\
\text{M} \quad \beta,4 \\
\text{M} \quad \beta,4 \\
\text{M} \quad \beta,4
\]

instead of the complex-type chains (2). Structural analysis of the cellular glycopeptides from wild type and clone 15B cells revealed that this oligosaccharide is the major oligosaccharide found in clone 15B cells, whereas wild type cells contain only small amounts of this oligosaccharide (5). Both cell lines, however, were shown to contain several other high mannose-type oligosaccharides of larger molecular weight (5).

The observations concerning the biosynthesis of complex asparagine-linked oligosaccharides (1-3) and the finding that only a single, very large lipid-linked oligosaccharide is present in several tissues and cell lines (1, 6) have led to the concept that high mannose and complex-type oligosaccharides are derived from the same lipid-linked oligosaccharide. This concept can now be tested by elucidating the structures of the asparagine-linked high mannose oligosaccharides isolated from total cellular glycopeptides and comparing them with the structures of the major lipid-linked oligosaccharide and the peptide-bound processing intermediates in the biosynthesis of complex-type chains, which have been previously determined (7, 8).

EXPERIMENTAL PROCEDURES

RESULTS

Isolation and Composition of the Major High Mannose Oligosaccharide Species—The isolation of the high mannose oligosaccharides, which were released from the glycopeptides by endo-β-N-acetylgalactosaminidase C1 has been described in a previous paper (5). The oligosaccharides were fractionated into three groups (A, B, and C) by gel filtration through a Bio-Gel P-4 column (5). Fraction C from clone 15B cells was further separated into three components termed C-1, C-2, and C-3 by descending paper chromatography with component C-2 representing the major oligosaccharide present in clone 15B. The complete structures of this oligosaccharide and of the two oligosaccharides in Fraction C-3 were described previously (5). Fraction C from parent cells, however, contained a single oligosaccharide C-1 (5). Fraction B from both clone 15B cells and parent cells contained two major components, termed B-1 and B-2, which were separated by descending paper chromatography.

1 Portions of this paper (including "Experimental Procedures," Figs. 1, 5, and 6, and Tables I to IV) are presented in miniprint at the end of this paper. Miniprint is easily read with the aid of a standard magnifying glass. Full size photocopies are available from the Journal of Biological Chemistry, 9650 Rockville Pike, Bethesda, Md. 20014. Request Document No. 78M-1395, cite author(s), and include a check or money order for $1.00 per set of photocopies.
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Fig. 2. (a) scheme for the characterization of \((\text{Man})_n\text{GlcNAc}\) (oligosaccharide Fraction C-1) with the expected products of the structural studies. * indicates radiolabeling with \(^{3}H\). (b) paper chromatography (developed in ethyl acetate/pyridine/acetic acid/water (5/5/1/3) for 19 h) of the products of (b) \(\alpha\)-mannosidase digestion. (c) chromatography (see Fig. 1). Fraction A, which represented a minor fraction of the total oligosaccharides, was extremely heterogeneous and was not further characterized. Fractions B-1, B-2, and C-1 were identified as \((\text{Man})_9\text{GlcNAc}, (\text{Man})_8\text{GlcNAc},\) and \((\text{Man})_7\text{GlcNAc},\) respectively, on the basis of their carbohydrate compositions (see Table I). The N-acetylglucosamine content was previously determined to be \(1 \text{ mol/mol of oligosaccharide}\) since all of the N-acetylglucosamine was converted to N-acetylglucosaminitol after reduction of the oligosaccharide with \(\text{NaBH}_4\) (5). These three oligosaccharides represent the three most abundant high mannose oligosaccharides in Chinese hamster ovary cells. The recovery from approximately 100 ml of frozen packed cells was \(0.4 \text{ pmol of } (\text{Man})_9\text{GlcNAc}, 0.3 \text{ pmol of } (\text{Man})_8\text{GlcNAc},\) and \(0.4 \text{ pmol of } (\text{Man})_7\text{GlcNAc}.\)

Although \((\text{Man})_9\text{GlcNAc}\) was by far the most abundant oligosaccharide in clone 15B cells, \((\text{Man})_8\text{GlcNAc}, (\text{Man})_7\text{GlcNAc},\) and \((\text{Man})_6\text{GlcNAc}\) were also present in significant amounts. The recovery from approximately 50 ml of packed cells was \(0.3 \text{ pmol of } (\text{Man})_9\text{GlcNAc}, 0.3 \text{ pmol of } (\text{Man})_8\text{GlcNAc},\) and \(0.4 \text{ pmol of } (\text{Man})_7\text{GlcNAc}.\)

Structural studies were performed on these three high mannose oligosaccharides. To aid the reader in following the discussion, an outline of the structural studies together with the expected products of each procedure are shown in Figs. 2a, 3a, and 4a. Since the same results were obtained for the oligosaccharides obtained from parent cells and from clone 15B cells, no distinction will be made on the source of the oligosaccharides.

\(\alpha\)-Mannosidase Digestion—Reduction of the oligosaccharides \((\text{Man})_9\text{GlcNAc}, (\text{Man})_8\text{GlcNAc},\) and \((\text{Man})_7\text{GlcNAc},\) with \(\text{NaBH}_4\), resulted in the oligosaccharide alcohol derivatives, \((\text{Man})_9\text{GlcNAc}, (\text{Man})_8\text{GlcNAc},\) and \((\text{Man})_7\text{GlcNAc},\) respectively. Digestion of the oligosaccharide alcohols with \(\alpha\)-mannosidase resulted in a single radioactive product that chromatographed with \(\text{ManPl + 4N-acetylglucosaminitol}\) (see Figs. 2b, 3b, and 4b). Subsequent digestion with hen oviduct \(\beta\)-mannosidase resulted in 20 to 33% hydrolysis of the disaccharide to yield N-acetylglucosaminitol (data not shown). These results indicate that all three oligosaccharides contain mannose residues linked \(\alpha\) to the disaccharide unit. 

\(\beta\)-Mannosidase works poorly on \(\text{ManPl + 4N-acetylglucosaminitol}\) relative to \(\text{Man} \rightarrow 4\text{GlcNAc}\). E. Li and S. Kornfeld, unpublished observation.
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**Fig. 3.** 
*a,* scheme for the characterization of (Man)$_n$GlcNAc (oligosaccharide Fraction B-2) with the expected products of the structural studies. * indicates radiolabeling with $^3$H. 
*b,* paper chromatogram (developed in ethyl acetate/pyridine/acetic acid/water (5/5/1/3) for 19 h) of the products of (b) $\alpha$-mannosidase digestion, (c) acetolysis, (d) acetolysis and reduction with $[^3H]$NaBH$_4$, (e) Smith periodate degradation of (Man)$_n[^3H]N$-acetylglucosaminitol. Ordinate: full scale = 1200 cpm. Arrows indicate the positions of the standards: 1, Man$_1$ + 3Man$_1$ + 4 GlcNAc; 2, Man$_1$ + 4N-acetylglucosaminitol; 3, mannitol; 4, N-acetylglucosaminitol. 

Disubstituted. The Smith periodate degradation was repeated on larger quantities of each of the unreduced oligosaccharides in order to obtain a methylation analysis of the fragment. The results indicate that the 2 mannose residues in the tritol are linked 1-6 (see Table III), since 2,3,4-tri-O-Me-mannose but not 2,4,6-tri-O-Me-mannose was detected. The presence of 3,4,6-tri-O-Me, and 2,4-di-O-Me-Man was probably due to incomplete hydrolysis of the oxidized oligosaccharide. The appearance of two methylated amino sugar alcohol derivatives can be attributed to partial N-demethylation during the acetolysis-acid hydrolysis step in the procedure, reported previously by Finne and Rauvala (9). All three oligosaccharides contain, therefore, a (Man)$_n$GlcNAc core with the structure, 

\[
\text{Man} \alpha 1,6 \quad \text{Man} \alpha 1,3 \quad \text{Man} \beta 1,4 \quad \text{GlcNAc} 
\]

This structure is identical with the structure of the major oligosaccharide in clone 15B cells (5).

The position of the remaining mannose residues, which are linked to the (Man)$_n$GlcNAc core via 1,2 linkages, was determined by subjecting the tritiated alcohol derivatives of each of the oligosaccharides to acetolysis, a procedure which cleaves Man$_1$ \rightarrow 6 Man linkages preferentially (10). The resulting fragments were separated by descending paper chromatography and identified.

**Acetolysis of (Man)$_n[^3H]N$-Acetylglucosaminitol**—Acetolysis of (Man)$_n[^3H]N$-acetylglucosaminitol resulted in a single radioactive product that migrated as a tetritol (see Fig. 2c). Methylation analysis (see Table IV), together with the Smith periodate degradation experiment (which indicated that the mannose linked to the N-acetylglucosamine residue was resistant to periodate oxidation), established the structure of the tetritol to be Man$_1$ \rightarrow 2Man$_1$ \rightarrow 3Man$_1$ \rightarrow 4N-acetylglucosaminitol. The complete structure of the oligosaccharide must therefore be 

\[
\text{Man} \alpha 1,6 \quad \text{Man} \alpha 1,3 \quad \text{Man} \beta 1,4 \quad \text{GlcNAc} 
\]
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Fig. 4. a, scheme for the characterization of (Man)$_n$GlcNAc (oligosaccharide Fraction B-1) with the expected products of the structural studies. * indicates radiolabeling with [$^3$H]. b, c, d, e, paper chromatogram (developed in ethyl acetate/pyridine/acetate acid/water (5/5/1/3) for 19 h) of the products of (b) $\alpha$-mannosidase digestion, (c) acetolysis, (d) acetolysis and reduction with [$^3$H]NaBH$_4$. (e) Smith periodate degradation of (Man)$_n$[3H]N-acetylglucosaminitol.

Acetolysis of (Man)$_n$[3H]N-acetylglucosaminitol resulted in a major radioactive product that migrated as a pentaitol and a minor radioactive product that migrated as a tetraitol (see Fig. 3c). Methylation analysis (see Table IV), together with the Smith periodate degradation experiment (which indicated that the mannose linked to the N-acetylglucosamine residue was resistant to periodate oxidation), established the structure of the pentaitol to be Man$_1$+2Man$_1$+2Man$_1$+3Man$_1$+4N-acetylglucosaminitol. The amount of tetraitol varied from experiment to experiment. The quantity recovered from the acetolysate was too low for detailed structural analysis. The appearance of this fragment is most likely due to overdegradation of the pentaitol (11).

In order to assign the position of the remaining mannose residue, the acetolysate was subjected to high voltage paper electrophoresis in 0.1 M sodium molybdate, pH 5.0 (see Fig. 5). The radioactivity distributed into two peaks termed a and b, in the ratio of 55 to 45 (see Fig. 5, upper panel). Peak a was identified as Man$_1$->2mannitol on the basis of its mobility on electrophoresis in sodium molybdate, pH 5.0 (16). Peak a was identified as Man$_1$->3mannitol on the basis of its methylation pattern (see Table IV) and on the basis of its chromatographic properties (12).

The only structure compatible with this acetylation fragmentation pattern is

\[
\begin{align*}
\text{Man}_1 & \rightarrow \text{Man} \rightarrow \text{Man} + \text{Man} + \text{Man} / \text{GlcNAc}, \\
\text{Man}_1 & \rightarrow \text{Man}_1 \rightarrow \text{Man} + \text{Man} + \text{Man} / \text{GlcNAc}.
\end{align*}
\]

Acetolysis of (Man)$_m$[3H]N-Acetylglucosaminitol — The major radioactive product, observed after acetolysis of (Man)$_m$[3H]N-acetylglucosaminitol, was identified as Man$_1$->2Man$_1$->2Man$_1$->3Man$_1$->4N-acetylglucosaminitol on the basis of its methylation pattern (see Table IV) and the Smith periodate degradation experiment. The tetraitol was present in relatively minor quantities and is most likely a product of overdegradation of the pentaitol (11).

In order to assign the position of the remaining 2 mannose residues, the acetolysate was reduced with [$^3$H]NaBH$_4$, of the same specific activity that was used to reduce the intact oligosaccharide. The paper chromatogram of the acetolysate after reduction (see Fig. 3d) revealed the appearance of a major radioactive fragment that migrated as a diitol.

The diitol was eluted from paper and subjected to high voltage paper electrophoresis in 0.1 M sodium molybdate, pH 5.0 (see Fig. 5). The radioactivity distributed into two peaks termed a and b, in the ratio of 55 to 45 (see Fig. 5, upper panel). Peak a was identified as Man$_1$->2mannitol on the basis of its mobility on electrophoresis in sodium molybdate, pH 5.0 (16). The only structure compatible with this acetylation fragmentation pattern is

\[
\begin{align*}
\text{Man}_1 & \rightarrow \text{Man} \rightarrow \text{Man} + \text{Man} + \text{Man} / \text{GlcNAc}, \\
\text{Man}_1 & \rightarrow \text{Man}_1 \rightarrow \text{Man} + \text{Man} + \text{Man} / \text{GlcNAc}.
\end{align*}
\]
oligosaccharide. The paper chromatogram of the acetyloside after reduction (see Fig. 4d), revealed the appearance of two major radioactive fragments that migrated as a triitol and a diitol, respectively.

The triitol was identified as Man$_1$ + 2Man$_1$ + 3mannitol on the basis of its methylation pattern (see Table IV). High voltage paper electrophoresis of the diitol in 0.1 M sodium molybdate, pH 5.0, revealed that virtually all of the radioactive fragments that migrated as a triitol and a diitol was confirmed by methylation analysis (see Table IV).

The only structure compatible with this acetylosis fragmentation pattern is

\[
\text{Man} \rightarrow \text{Man}_{1,2} \rightarrow \text{Man}_{1,3} \rightarrow \text{GlcNAc} \beta_{1,4}
\]

**DISCUSSION**

The structures of the three major high mannose oligosaccharides are shown in Fig. 6. The evidence for the di-N-acetylchitobiose unit has been presented previously (5). All three structures contain a $(\text{Man})_1(\text{GlcNAc})_2$ unit identical with the structure of the major oligosaccharide found in clone 15B cells. They differ only in the number of outer mannoses linked $\alpha_{1,2}$ to the $(\text{Man})_1(\text{GlcNAc})_2$ core. Furthermore, the arrangement of these outer mannoses is extremely specific since each of the oligosaccharide fractions, B-1, B-2, and C-1, consists of a single structure out of a number of possible isomers.

*Most of the high mannose oligosaccharides, which were isolated from whole cells, originate from membrane-bound glycoproteins, since virtually all of the cellular glycoproteins are found in the particulate fraction of the cells.*

However, as far as we are aware, this is the first description of the complete structures of the high mannose oligosaccharides isolated from cellular glycoproteins, which are, for the most part, membrane-bound.

The finding that only a limited number of high mannose oligosaccharide structures exist in Chinese hamster ovary cells is intriguing in view of recent observations concerning the biosynthesis of asparagine-linked oligosaccharides. Based on the structural analysis of the lipid-linked oligosaccharide and the protein-bound oligosaccharide intermediates from in vivo processing systems, a scheme for the synthesis of complex oligosaccharides has been suggested (8). The structures of the $(\text{Man})_1(\text{GlcNAc})_2$ (Fraction B-1) and $(\text{Man})_1(\text{GlcNAc})_2$ (Fraction B-2) oligosaccharides are identical with the structures of two of the processing intermediates. There was too little of the processing intermediate, identified as containing 5 mannose residues, to characterize. However, this intermediate is probably identical with the $(\text{Man})_1(\text{GlcNAc})_2$ (Fraction C-1) oligosaccharide, based on the structures worked out for the intermediate containing 7 mannose residues and the intermediate containing 5 mannose residues. The structural identity between the high mannose-type oligosaccharides and the processing intermediates provides support for the concept that high mannose-type oligosaccharides arise by “incomplete” processing of the protein-bound oligosaccharide along the same pathway which leads ultimately to the formation of a complex-type oligosaccharide and that the sequence in which the mannose residues are removed in this pathway is extremely specific. The regulation of this pathway is of great interest, especially since the relative proportion of complex and high mannose oligosaccharides on the cell surface of cultured fibroblasts has been shown to be both growth-dependent and transformation-dependent (14, 15).

Other lines of evidence also indicate that the synthesis of complex- and high mannose-type asparagine-linked oligosaccharides are closely linked. Only a single, major lipid-linked oligosaccharide, similar to the lipid-linked oligosaccharide involved in the synthesis of complex chains, has been isolated in a number of tissues (1, 6), suggesting that both types of oligosaccharides are derived from a single lipid-linked intermediate. Oligosaccharides with structures that are a hybrid of the high mannose- and complex-type chains have been isolated from ovomucoid (16, 17). One cannot, however, rule out the possibility that the high mannose-type oligosaccharides are made via a separate biosynthetic pathway and may arise by addition of mannose residues onto a protein-bound oligosaccharide core. Our current experiments are designed to investigate these possibilities.

Oligosaccharides with structures identical with the ones reported here have been found in soluble glycoproteins. The major oligosaccharide isolated from the Unit A glycopeptide of thyroglobulin is identical with the structure reported here for the $(\text{Man})_1(\text{GlcNAc})_2$ (Fraction B-1) oligosaccharide (11). Oligosaccharides with the structure of the $(\text{Man})_1(\text{GlcNAc})_2$ (Fraction C-1) oligosaccharide have been isolated from Taka-amylase (18) and ovomucoid (19). A specific series of high mannose oligosaccharides with structures including those reported here, have been found at a single glycosylation site in human IgM (20, 21). The isolation of these oligosaccharide structures from such a variety of sources indicate that they are highly conserved.

**REFERENCES**


*E. Li and S. Kornfeld, unpublished observation.*
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SULFAMIDE

Structural Studies of the Major High Mannose Oligosaccharide Units from Chinese Hamster Ovary Cell Glycosaminoglycans

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EXPERIMENTAL PROCEDURE

The methods and conditions are the same as described previously (1) with the following exceptions: High voltage paper electrophoreses were performed on Whatman 3MM paper in 0.1 M sodium acetate buffer, pH 5.0 (buffered with MOPS) at 60°C for 1 h., using a constant voltage of 200 V flat plate electrophoresis system.

Figure 1 - Paper chromatogram of 14C-mannose-labeled oligosaccharide from a functional fraction of the diol column. The 14C-mannose-labeled oligosaccharide, obtained after the reaction with glucose, was eluted as the major components. The oligosaccharide was then separated by the column chromatography. (Upper panel) oligosaccharides from parental cells. (Lower panel) oligosaccharides from clone 15B cells.

Table I

<table>
<thead>
<tr>
<th>Mannose Content</th>
<th>Relative Oligosaccharide a</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td></td>
</tr>
<tr>
<td>Parent</td>
<td>3.3 ± 0.1</td>
</tr>
<tr>
<td>15B</td>
<td>5.1 ± 0.1</td>
</tr>
<tr>
<td>1C</td>
<td>6.9 ± 0.1</td>
</tr>
<tr>
<td>Clone 15B</td>
<td>4.8 ± 0.5</td>
</tr>
<tr>
<td>15B</td>
<td>7.5 ± 0.5</td>
</tr>
<tr>
<td>1C</td>
<td>5.8 ± 0.3</td>
</tr>
</tbody>
</table>

The values shown are means of three to four determinations and are expressed ± S.D. error.

Table II

<table>
<thead>
<tr>
<th>Methylated Sugar</th>
<th>Methylated Methylglucosyl</th>
<th>Methylated Mannosyl</th>
<th>Methylated Glucosyl</th>
</tr>
</thead>
<tbody>
<tr>
<td>Methylated Glucosyl</td>
<td>3.8 ± 0.1</td>
<td>3.4 ± 0.1</td>
<td>3.2 ± 0.1</td>
</tr>
<tr>
<td>3,4,6-tri-O-Me</td>
<td>1.4 ± 0.1</td>
<td>1.3 ± 0.1</td>
<td>1.0 ± 0.1</td>
</tr>
<tr>
<td>2,4,6-tri-O-methyl</td>
<td>1.0 ± 0.1</td>
<td>1.0 ± 0.1</td>
<td>1.0 ± 0.1</td>
</tr>
</tbody>
</table>

The values were calculated relative to the amount of the acetylated 2,3,4,6-tetra-O-methylglucosyl.

Table III

<table>
<thead>
<tr>
<th>Methylated Sugar</th>
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<td>1.0 ± 0.1</td>
</tr>
<tr>
<td>2,4,6-tri-O-methyl</td>
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<td>1.0 ± 0.1</td>
<td>1.0 ± 0.1</td>
</tr>
</tbody>
</table>

The values were calculated relative to the amount of the acetylated 2,3,4,6-tetra-O-methylglucosyl.

Table IV

<table>
<thead>
<tr>
<th>Methylated Sugar</th>
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<th>Methylated Mannosyl</th>
<th>Methylated Glucosyl</th>
</tr>
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<tbody>
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<td>3.2 ± 0.1</td>
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<td>1.3 ± 0.1</td>
<td>1.0 ± 0.1</td>
</tr>
<tr>
<td>2,4,6-tri-O-methyl</td>
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<td>1.0 ± 0.1</td>
<td>1.0 ± 0.1</td>
</tr>
</tbody>
</table>

The values were calculated relative to the amount of the acetylated 2,3,4,6-tetra-O-methylglucosyl.

2 * The values shown are means of three to four determinations and are expressed ± S.D. error.
3 * The values were calculated relative to the amount of the acetylated 2,3,4,6-tetra-O-methylglucosyl.
4 * The values were calculated relative to the amount of the acetylated 2,3,4,6-tetra-O-methylglucosyl.
5 * The values were calculated relative to the amount of the acetylated 2,3,4,6-tetra-O-methylglucosyl.
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