Oligosaccharides Produced by Acetolysis of Blood Group Active (A + H)sulfated Glycoproteins from Hog Gastric Mucin*

BRONISLAW L. SLOMIANY AND KARL MEYER

From the Department of Chemistry, Belfer Graduate School of Science, Yeshiva University, New York, New York 10033

SUMMARY

Blood group (A + H) sulfated glycoproteins containing oligosaccharides of 14 sugar residues have been purified from hog stomach mucosa, and the structure of the carbohydrate chains was investigated. Penta-, tetra-, tri-, and disaccharides were isolated from the products of acetolysis of this material, and their structures were studied by chemical, enzymatic, and immunological methods. Periodate oxidation of a reduced sulfated disaccharide composed of N-acetylglucosamine gave predominantly erythritol, indicating 1 → 4 linkage between the two glucosamine residues. Galactose and N-acetylglucosamine were obtained from the treatment of trisaccharide with β-galactosidase. Methylation analysis of the trisaccharide revealed equal amounts of acetates of 2,3,4,6-tetra-O-methylgalactitol and 2,4,6-tri-O-methylgalactitol in addition, 2,3,4-tri-O-methylfucitol and 3,6-di-O-methyl-N-methylglucosaminitol. These data are consistent with the structure Fuc α1-2 Gal β1-4 GlcNAc β1-4 Gal β1-6 Gal.

Methylation analyses of one of the two tetrasaccharides showed acetates of 2,3,4-tri-O-methylfucitol, 3,4,6-, 2,3,6-tri-O-methylgalactitol, and 3,6-di-O-methyl-N-methylglucosaminitol, and for the other acetates of 2,3,4-tri-O-methylfucitol, 3,4,6-, 2,3,6-tri-O-methylgalactitol, and 4,6-di-O-methyl-N-methylglucosaminitol. Those data are consistent with the structures Fuc α1-2 Gal β1-4 GlcNAc β1-4 Gal and Fuc α1-2 Gal β1-3 GlcNAc β1-4 Gal. The suggested structure of blood group (A + H)-sulfated glycoprotein presented below is further substantiated.

\[
\text{A} \quad \text{GalNAc} \quad \alpha1-2 \quad \text{Gal} \quad \beta1-3(4) > \text{GlcNAc} \quad \beta1-4 > \text{Gal} \\
\text{H} \quad \text{Gal} \quad \beta1-3(4) > \text{GlcNAc} \quad \beta1-4 > \text{Gal} \\
\]

addition to 3,6-di-O-methyl-N-methylglucosaminitol. This is consistent with the structure Gal β1-3, Gal β1-4, GlcNAc.

Blood group H-active monofucosyl penta- and tetrasaccharides were resistant to β-galactosidase, but were cleaved to the monosaccharides by a mixture of α1,2-L-fucosidase, β galactosidase, and β-N-acetylglucosaminidase. Analysis of the methylated pentasaccharide revealed the presence of acetates of 2,3,4-, 2,3,6-, and 3,4,6-tri-O-methylgalactitol in approximately equal amounts and, in addition, 2,3,4-tri-O-methylfucitol and 3,6-di-O-methyl-N-methylglucosaminitol. These compounds are characterized by the presence of fucose, galactose, glucosamine, galactosamine, sialic acid, and sulfate and differ from the acidic glycoproteins of mesodermal origin (except that of keratan sulfate) primarily by the absence of uronic acid.

The sulfated glycoproteins isolated from human (6, 9) and

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hogs (8) gastric mucosa were shown to possess blood group activity compatible with the blood type of the host. The structure of the carbohydrate portion of (A + H) blood group-active sulfated glycoproteins from hog stomach mucosa has been suggested recently (8).

The aims of the present investigation were to isolate and characterize the oligosaccharides produced by acetylation of the sulfated glycoproteins from hog stomach mucosa and to substantiate the suggested structure.

**EXPERIMENTAL PROCEDURE**

**Preparation of Sulfated Glycoproteins—**Sulfated glycoproteins were prepared from hog gastric mucin powder (Wilson Laboratories, batch #440) by digestion of mucin homogenate with trypsin, repeated alcohol precipitation and fractionation of the precipitate with cetylpyridinium chloride (8). The removal of nucleic acids, digestion with testicular hyaluronidase, and re-presentation with cetylpyridinium chloride was accomplished as described by Pamer et al. (5).

**Chromatography on DEAE-Sephadex A-50—**The crude sulfated glycoproteins dissolved in 0.2 N NaCl were applied in two portions to DEAE-Sephadex (Pharmacia) column (3.0 x 80 cm) equilibrated with 0.2 N NaCl. Initial elution with 0.2 N NaCl (800 ml) was followed by elution with a linear concentration gradient consisting of 1800 ml of 0.2 N NaCl in the mixing chamber and an equal volume of 1.0 N NaCl in the reservoir. Fractions (10 ml) were collected and the optical density at 231 nm and the hexose content of each was determined. Pooled fractions were dialyzed and lyophilized.

**Gel Filtration—**The major sulfated glycoprotein fraction from DEAE-Sephadex was dissolved in 0.5 N NaCl and applied to the column (3.6 x 220 cm) packed with Bio-Gel A-50m, 50 to 100 mesh (Bio-Rad Laboratories), equilibrated with 0.5 N NaCl. Fractions (15 ml) were collected, and the elution was monitored as described above. Pooled fractions were concentrated to one-third of their volumes, precipitated with 3 volumes of ethanol, dialyzed, and lyophilized.

**Final Fractionation—**The final fractionation of the sulfated glycoproteins obtained from Bio-Gel column was performed on DEAE-Sephadex A-50 equilibrated with 0.4 N NaCl. Sulfated glycoproteins (367 mg) dissolved in 0.4 N NaCl were applied to the column (3.0 x 80 cm), and the column was washed with 1000 ml of 0.4 N NaCl. The elution of the sulfated glycoprotein fraction was accomplished with a linear concentration gradient consisting of 1500 ml of 0.4 N NaCl in the mixing chamber and an equal volume of 0.8 N NaCl in the reservoir. Fractions (10 ml) were collected and monitored for optical density and hexose content as above. Pooled fractions were subjected to electrophoresis on cellulose acetate strips as previously described (8).

**Acetylation—**The sulfated glycoprotein fraction (220 mg) was dissolved in 5 ml of formamide, and 15 ml of acetic anhydride-pyridine (2:1, v/v) were added. The mixture was stirred at room temperature for 48 hours, and the acetylated product was recovered by dialysis.

**Acetylation—**The acetylated sulfated glycoprotein fraction was subjected to acetylation with 30 ml of the mixture of acetic anhydride-acetic acid-sulfuric acid (10:10:1, by volume) (10) at 40° for 6 hours. The reaction was terminated by addition of pyridine to the cooled solution. The mixture was poured on ice water, and the products were recovered by extraction with chloroform.

The optimum conditions for the oligosaccharide production by acetylation was determined with a 10-mg sample incubated at 40° for 1, 3, 5, 8, and 16 hours followed by thin layer chromatography (10).

**Deacetylation—**Deacetylation was carried out at room temperature by dissolving a sample in methanol and addition of one-third of the volume of 0.5% sodium methoxide in methanol. The reaction was terminated after 25 min by the addition of ethyl acetate, and the solvents removed by evaporation.

**Gel Filtration of Acetylation Products—**The fractionation of the deacetylated acetylation products as well as their desalting was performed on a Bio-Gel P-2, 50 to 100 mesh (Bio-Rad) column (1.7 x 215 cm) developed with 10% aqueous ethanol. Fractions (3 ml) were collected, and the optical density at 231 nm and the hexose content of each was determined. The pooled fractions were concentrated to a small volume and rechromatographed individually on the same column.

The material excluded from the Bio-Gel P-2 was subjected to gel filtration on a column (1.7 x 220 cm) packed with Bio-Gel P-100 and the column developed with 0.5 N NaCl. Fractions (5 ml) were collected and monitored as above.

The material excluded from this column was dialyzed, lyophilized, acetylated, and acetylated again under the conditions described above. The fraction retarded on Bio-Gel P-100 was desalted on Bio-Gel P-2 column and lyophilized.

**Paper Chromatography—**Descending paper chromatography (Systems A, B, and C) on Whatman No. 3 paper (previously washed with the solvent system used) was applied as a final step in the oligosaccharide purification. Whatman No. 1 was used for monosaccharide identification. The following solvent systems (by volume) were used: A, 1-butanol-acetic acid-water (5:1.5:3.5:0.5); B, 1-butanol-acetic acid-water (4:1:5); C, 1-butanol-pyridine-water (6:4:3); and D, ethyl acetate-acetic acid-water (6:3:2). Sugars were detected with alkaline silver nitrate or by the periodate benzidine staining technique. Ninhydrin spray was used for hexosamines.

**Thin Layer Chromatography—**Thin layer chromatography was performed on Silica Gel G plates with benzene-methanol mixtures containing 2 to 15% (v/v) methanol (11). The components were located either by ammonium bisulfate-charring technique or by the ferric hydroxamate reaction (11).

**Enzymatic Assays—**Sulfated glycoprotein fraction and the oligosaccharides derived from it by acetylation were incubated in the presence of tolune with β-galactosidase (EC 3.2.1.23, Worthington) under the conditions described previously (8). The galactose of the dialyzable fraction released from the sulfated glycoprotein was quantitated by gas-liquid chromatography. Sugars released from the oligosaccharides were determined by paper chromatography (Systems A and B).

Treatment of the sulfated glycoprotein fraction and the fucose containing oligosaccharides with α1,2-L-fucosidase (kindly provided by Dr. Bahl, State University of New York, Buffalo, N. Y.) was performed according to Bahl (12). The sugars released from the sulfated glycoproteins fraction were quantitated on a dialyzable fraction, and those released from the oligosaccharides were identified by paper chromatography (Systems A and B). Controls consisting only of substrates or enzymes accompanied each experiment.
Methylation—The oligosaccharides were methylated by the method of Hakomori (13). The samples dissolved in dimethyl sulfoxide were stirred at room temperature with methanesulfonic anhydride under nitrogen. After 6 hours methyl iodide was added and stirring continued for another 18 hours. This was followed by addition of dimethyl sulfoxide, methanesulfonic anhydride, stirring for 6 hours, addition of methyl iodide, and stirring for another 24 hours. Upon termination of the reaction with 4.0 M NaCl the methylated material was extracted into chloroform.

The permethylated oligosaccharide products were subjected to formylation and hydrolysis (14). The neutral sugars were separated from the methylated products of hexosamine on an AG 50W-X8 (H+) column (14).

Periodate Oxidation of Reduced Sulfated Disaccharide—The sulfated disaccharide obtained from the sulfated glycoprotein fraction by acetolysis, deacetylation of the aqueous portion of the acetolysis products, gel filtration on Bio-Gel P-2 column, and paper chromatography (System D) was reduced with sodium borohydride (16 hours at room temperature). Excess borohydride was destroyed with acetic acid and borate removed by evaporation with methanol. The residue was oxidized with excess 0.15 M sodium metaperiodate at room temperature for 50 hours. The periodate was destroyed with ethylene glycol and the residue reduced with sodium borohydride. The residue obtained after destruction of excess borohydride and removal of borate was hydrolyzed in 1.0 M sulfuric acid (16 hours at 100°C). The hydrolysate was neutralized with barium hydroxide, ten-fold excess, and then filtered through a mixed bed resin column. The eluate was concentrated to dryness and the residues derivatized by silylating reagents (15).

Gas-Liquid Chromatographic Analysis—Gas-liquid chromatography analyses were performed with a Hewlett-Packard Research chromatograph, model 5750 apparatus. Stainless steel columns (6 feet × ½ inch) packed with 3% ECNSS-M on Gaschrom Q, 100 to 120 mesh, or packed with 3% SE-30 on Gaschrom Q, 100 to 120 mesh, were used. Trimethylsilyl derivatives of methyl glycosides and reduced glycosides were analyzed on SE-30 columns developed for 6 min at 150°C and then programmed at 2°C per min to 200°C. Analysis of the trimethylsilyl derivatives of ethylene glycol, glycerol, and erythritol was performed on the same columns but developed at 65°C for 4 min and then programmed at 6°C per min to 170°C. The conditions for analysis of the alditol acetates on ECNSS-M columns were the same as described previously (8).

The methylated neutral sugars after reduction and acetylation were analyzed on ECNSS-M columns at 150°C and the similarly prepared amino sugar derivatives were analyzed on the same columns developed at 170°C for 3 min and then programmed at 2°C per min to 220°C.

The determination of the reducing end of oligosaccharides, their composition, and sugar ratios was performed as described previously (8). Individual sugar components were identified also by paper chromatography (Systems A, B, and D) following hydrolysis (2 N HCl, 100°C for 6 hours).

Infrared spectra were obtained with potassium bromide pellets in a Perkin-Elmer model 21 spectrophotometer with sodium chloride prism.

Hemagglutination and hemagglutination inhibition assays were performed with a Takata microtitrator.

The colorimetric analyses were the same as cited previously (16).

The 3,6-di-O-methyl-N-methyl-D-glucosamine, and the 3,4,6-

![Fig. 1. Chromatography on DEAE-Sephadex A-50 of crude sulfated glycoproteins from hog stomach. The sample (810 mg) was applied in 0.2 N NaCl to the column (3.0 × 80 cm) and eluted with a linear NaCl gradient as indicated.](https://www.jbc.org/content/229/5/2292/F1.large.jpg)
FIG. 2 (left). Gel filtration on Bio-Gel A-50m of sulfated glycoprotein Fraction III from DEAE-Sephadex. The sample (998 mg) was applied in 0.5 N NaCl to the column (3.6 X 220 cm) and eluted with the same salt solution.

FIG. 3 (left center). Chromatography on DEAE-Sephadex A-50 of sulfated glycoprotein Fraction IIIβ from Bio-Gel A-50m. The sample (367.4 mg) was applied in 0.2 N NaCl to the column and eluted with a linear NaCl gradient as indicated.

FIG. 4 (right center). Gel filtration on Bio-Gel P-2 column (1.75 X 215 cm) of deacylated products resulting from the acetolysis of sulfated glycoprotein Fraction IIIβ. From 220 mg of the sulfated glycoproteins subjected to two consecutive acetolysis procedures 61.0 mg were obtained in Fraction II and 15.0 mg in Fraction III. The yield of the monosaccharide fraction, Fraction IV, was not determined.

Fig. 5 (right). Gel filtration on Bio-Gel P-100 column (1.20 X 220 cm) of deacylated products excluded from P-2 column (Fraction I, Fig. 4). From 220 mg of the sulfated glycoproteins subjected to two consecutive acetolysis procedures 35.5 mg were obtained in glycoprotein Fraction I and 6.8 mg in Fraction II.

TABLE I
Composition of purified sulfated glycoprotein Fraction IIIβ from hog gastric mucin

| Component       | %   |
|-----------------|-----|
| Hexosamines     | 20.8|
| Hexose          | 42.4|
| Fucose          | 13.8|
| Sialic acid     | 9.2 |
| SO₄⁻            | 6.3 |
| Protein         | 2.5 |

TABLE II
Molar ratios of sugar components in purified sulfated glycoprotein Fraction IIIβ from hog gastric mucin

| Component   | Molar ratio |
|-------------|-------------|
| Galactose   | 5.72        |
| Fucose      | 1.84        |
| Glucosamine | 3.95        |
| Galactosamine| 2.00       |

16 hours incubation in acetolysis medium resulted in extensive monosaccharide production in addition to the oligosaccharides.

The 5-hour acetolysis appeared to be the most feasible for the oligosaccharide production from the acetylated sulfated glycoproteins.

Isolation of Oligosaccharides—The acetolysis products obtained by the chloroform extraction from the acetolysis medium were deacylated with sodium methoxide in methanol and fractionated on a Bio-Gel P-2 column. Four fractions were obtained (Fig. 4). The fraction, eluted from this column in the void volume, Fraction I, was chromatographed further on Bio-Gel P-100, to give two components (Fig. 5), one of which (I) was eluted in the void volume; this material was reacetylated and subjected once more to acetolysis and fractionation on Bio-Gel P-2 and P-100 columns. The fraction (II) retarded on a Bio-Gel P-100 column was concentrated, desalted on P-2 column, and lyophilized. The corresponding fractions obtained from the fractionation of the acetolysis products on Bio-Gel P-2 column were combined, rechromatographed individually on the same column, and lyophilized. The material eluted from P-2 column in the galactose region (Fraction IV, Fig. 4) was examined for the possible presence of components larger than monosaccharide by paper chromatography (Systems A and B). Since it contained only monosaccharides it was discarded.

The material remaining in the aqueous phase after chloroform extraction was deacylated and chromatographed on Bio-Gel P-2 column to give a single fraction in the region of Fraction III (Fig. 4). This fraction after rechromatography on the same column was concentrated and lyophilized to give 4.7 mg.

Paper Chromatography of Oligosaccharides—The oligosaccharide fractions obtained from fractionation of the deacylated acetolysis products and Bio-Gel P-2 and P-100 columns were purified further by preparative paper chromatography (Systems A, B, C). This procedure resulted in the isolation of a single component (oligosaccharide I) from the oligosaccharide fraction (II) retarded on P-100 (Fig. 5). From Fraction II (Fig. 4) two major components (oligosaccharides II and III), and from Fraction III (Fig. 4) a single component (oligosaccharide IV) were obtained.

The R_Gal values of these oligosaccharides are given in Table III.

Paper chromatography (System D) of the oligosaccharide fraction obtained from the aqueous portion of the acetolysis medium gave two spots. One of these (minor) corresponded to N-acetylglucosamine 6-sulfate standard in its migration in Sol-
of the oligosaccharides. Fucose, galactose, and \textit{\textalpha}'-acetylglucosamine were isolated from the deacylated aqueous phase of the acetolysis mixture. Fucose dialyzable. Similar treatment of the fucose-containing mixture of \textalpha,2-n-fucosidase, \textalpha-galactosidase, and \textbeta-N-acetylglucosaminidase (50 hours at 37\textdegree) rendered 98% of the deacylated products of chloroform extracts of the acetolysis mixture.

Four oligosaccharides in addition to the monosaccharides have given only galactose and \textbeta-N-acetylglucosamine in the chromatogram. Longer incubation produced mainly monosaccharides.

Identification of \textbeta-N-acetyllactosamine standard was demonstrated with a mixture of acetic anhydride-acetic acid-sulfuric acid (10) incubation (50 hours) of oligosaccharide IV with \textbeta-galactosidase incubation periods resulted in small yields of oligosaccharides. Gas-liquid chromatographic comparison of the retention values of alditol acetates obtained by formolysis and hydrolysis of the methylated oligosaccharides were performed by gas-liquid chromatography. The peaks were identified either by comparing their retention times with that of available or prepared standard compounds, or in some instances by comparing with the reported (17, 18) retention values.

The alditol acetates of the methylated neutral components of oligosaccharides I, II, and III revealed a peak which chromatographed with the acetates of 2,3,4-tri-0-methylfucitol and standard. Additionally by the same procedure about equal quantities of acetates of 2,3,6-, 2,4,6-, and 3,4,6-tri-0-methylgalactitol in oligosaccharide I, 2,3,6- and 3,1,6-0-methylgalactitol in oligosaccharides II and III, and 2,3,4,6-tetra-0-methylgalactitol and 2,4,6-tri-0-methylgalactitol in oligosaccharide IV were identified. Gas-liquid chromatographic comparison of the retention values of alditol acetates of the methylated hexosamine fractions permitted the identification of 3,6-di-0-methyl-N-methylgalactosaminitol in oligosaccharides I, III, and IV, and 4,6-di-0-methyl-N-methylgalactosaminitol in oligosaccharide II. These derivatives cochromatographed with the acetates of methylated galactosaminitol standards prepared from chitin and hyaluronic acid, respectively.

**DISCUSSION**

The preparation of the blood group (A + H)-active sulfated glycoproteins from the tryptic digests of hog gastric mucin was accomplished essentially as described previously (5, 8).

The blood group (A + H)-active sulfated glycoprotein corresponded in homogeneity, in blood group activity, carbohydrate composition, and its molar ratios (Table II) to the previously (8) characterized sulfated glycoprotein composed of 14 carbohydrate units.

The glycoprotein was resistant to the action of \textbeta-galactosidase and in this respect was also similar to the previously (8) characterized sulfated glycoprotein composed of 14 carbohydrate units.

Further evidence of the proposed structure of the carbohydrate chains of the blood group (A + H)-active sulfated glycoproteins was provided by the analysis of oligosaccharides produced by acetylation. The procedure was recently successfully used in the degradation of yeast mannan (10, 19).

Acetylation of the sulfated glycoproteins for 5 hours at 40\textdegree with a mixture of acetic anhydride-acetic acid-sulfuric acid (10) was found optimal for the production of oligosaccharides. Short incubation periods resulted in small yields of oligosaccharides whereas longer incubation produced mainly monosaccharides.

Four oligosaccharides in addition to the monosaccharides have been purified by gel filtration and paper chromatography from the deacylated products of chloroform extracts of the acetolysis mixture.

In addition by similar procedures \textbeta-N-acetyllactosamine 6-sulfate and sulfated disaccharide composed of glucosamine were isolated from the deacylated aqueous phase of the acetolysis mixture.

Identification of erythritol in addition to glycerol from the

| Table IV |
|----------------|
| **Molar ratios of carbohydrate components in oligosaccharides obtained by acetolysis of sulfated glycoproteins from hog stomach** |
| Oligosaccharide | Fucose | Galactose | GlcNAc |
|------------------|--------|-----------|--------|
| I                | 0.91   | 2.83      | 1.0    |
| II               | 0.90   | 2.08      | 1.0    |
| III              | 0.93   | 2.16      | 1.0    |
| IV               | 2.12   | 1.20      | 1.0    |

1 N. P. Bahl, personal communication.
hydrolysates of the reduced periodate-oxidized disaccharide suggests that the sulfated disaccharide is N-acetyllactosamine monosulfate, although the anomeric configuration of the linkage still remains to be determined. The presence of the two adjacent N-acetylgalactosamine residues in the blood group (A + H)-active carbohydrate chains of sulfated glycoproteins has been suggested previously (8). The occurrence of several adjacent glycosamine residues in the region close to the glycopeptide bond has been also reported in the (A + H)-active neutral glycoproteins from hog stomach (20). Adjacent glycosamine residues have been shown to be part of the carbohydrate structure of thyroglobulin (21), IgG immunoglobulins (22), fetuin (23), and ovalbumin (24).

On the basis of the molar ratios of sugar components and from the analysis of the reducing sugar it was established that oligosaccharide I is a pentasaccharide composed of fucose, galactose, and glucosamine with the galactose at the reducing end. Similarly it was found that oligosaccharides II and III are tetrasaccharides composed of fucose, galactose, and glucosamine with galactose at the reducing end, whereas oligosaccharide IV is a trisaccharide composed of galactose and glucosamine with the latter at the reducing end. The fucose containing oligosaccharides I, II, and III exhibit blood group H activity.

The results of immunological and enzymatic studies of the oligosaccharides I, II, and III indicate that the sugar units with the exception of the fucosyl residues are β linked and that the fucosyl group is a nonreducing end group in these oligosaccharides.

Susceptibility of trisaccharide (IV) to β-galactosidase and the data obtained by methylation establish the structure Gal β1-3(6)GalNAc β1-4 GlcNAc β1-4 GlcNAc β1-3 Gal. The results of immunological and enzymatic studies performed on oligosaccharides I, II, and III indicate that the sugar units with the exception of the fucosyl residues are β linked and that the fucosyl group is a nonreducing end group in these oligosaccharides.

The proposed structure of the carbohydrate chains of (A + H)-active sulfated glycoproteins is given in Fig. 6. The characterization of pentasaccharide chains and its sequence would support the results of sequential degradation with periodate obtained previously (8). The H-active tetrasaccharides II and III could be derived either from A- or H-determining chains, since both type of chains with 1 → 3 and 1 → 4 linkage to N-acetylgalactosamine may exist as branches on one main chain (25, 26). The characterized trisaccharide (IV) can be only derived from the branching point either from the side of the H or of the A determinant of the suggested structure (8). It is believed that the second galactose in this trisaccharide is the branching point for the A and H chains. The structure of this trisaccharide together with the structure of pentasaccharide, which also contains the branching point galactose as its terminal reducing end would indicate that the A and H chains are linked to the galactose at the branching point by β(1 → 3) or β(1 → 6) linkages, or both.

The 1 → 6 linkage was shown (10) to be readily cleaved by acetolysis. The relative low yield of the pentasaccharides compared to the yield of tetrasaccharides is additional evidence of the lability of such linkage to acetolysis.

The characterization of the isolated oligosaccharides lends further support for the suggested structure of the carbohydrate chains of blood group (A + H)-sulfated glycoproteins of hog stomach mucosa.

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