Carbohydrate Structure of Hamster Plasma Fibronectin

EVIDENCE FOR CHEMICAL DIVERSITY BETWEEN CELLULAR AND PLASMA FIBRONECTINS*

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The structure of the carbohydrate moiety of hamster plasma fibronectin was determined. The glycopeptides and oligosaccharides released by hydrazinolysis (Fukuda, M., Kondo, T., and Osawa, T. (1976) J. Biochem. (Tokyo) 80, 1223-1232) were analyzed by methylation and exoglycosidase digestion and the major oligosaccharide unit of hamster plasma fibronectin was shown to be

\[
\text{NeuGly} \rightarrow \text{6Gal} \rightarrow \text{4GlcNAc} \rightarrow 2\text{Man} \\
\]

\[
\begin{array}{c}
\text{6} \\
\text{Man} \rightarrow \text{4GlcNAc} \rightarrow \text{4GlcNAc} \rightarrow \text{Asn} \\
\text{3}
\end{array}
\]

\[
\text{NeuGly} \rightarrow \text{6Gal} \rightarrow \text{4GlcNAc} \rightarrow 2\text{Man} \\
\]

The structure of the carbohydrate moiety of plasma fibronectin shown above (NeuGly, N-glycolylneuraminic acid) and that of cellular fibronectin (Fukuda, M., and Hakomori, S. (1979) J. Biol. Chem. 254, 5451-5457) are distinctly different with respect to the linkage of sialic acid, the degree of sialylation and the absence or presence of fucose. These results, therefore, provide the evidence for chemical diversity between cellular (fibroblast) and plasma fibronectins.

Fibronectins are large glycoproteins present on the cell surface of fibroblasts and other types of cells and are decreased greatly after oncogenic transformation (1, 2). Fibronectin has adhesive properties and forms pericellular matrices and basement membranes together with collagens, glycosaminoglycans, laminin, and other components (3-8). Fibronectin is also present in plasma (9) and has been termed "cold insoluble globulin" (10). Cellular and plasma fibronectins share most of their chemical and biological properties (3-8, 11). Both forms also consist of several distinct functional domains which are connected by flexible, protease-sensitive polypeptide segments (12-18). Most of the carbohydrate chains are attached to a site near the gelatin-binding domain in both cellular (13) and plasma fibronectin (18).

Several lines of evidence, however, suggest that certain differences exist between these two forms. Cellular fibronectin is less soluble (11), has slightly larger apparent subunit size (11, 18-20), and is more active in inducing morphological change of transformed cells and agglutinating formalin-fixed sheep erythrocytes (11) than plasma fibronectin. More recently, differences in the polypeptide moieties of these two forms have been detected by immunochemical (21) and chemical (22) methods.

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In addition to these differences, it has been suggested that the carbohydrates of the two forms are different (23-26). We have determined the carbohydrate structure of cellular fibronectin from hamster (23), which has fucose linked to innermost N-acetylgalactosamine and sialic acid linked to galactose by α2 → 3 linkage. Takasaki et al., however, reported quite different structure for bovine plasma fibronectin (24). These differences could be due to species differences, since comparisons of carbohydrate structures of two forms of the same species have not been made.

In this paper, we describe the carbohydrate structure of plasma fibronectin from hamster and present the evidence that the structures of the carbohydrate moieties of cellular and plasma forms* from the same species are different. We also discuss some problems encountered in structural analysis of carbohydrate chains when hydrazinolysis (27) is used to release oligosaccharides from glycoproteins.

EXPERIMENTAL PROCEDURES

Materials—Glycopeptides from bovine IgG (28) and fetuin (29) were prepared as described using proteins purchased from Sigma. The core glycopeptide of IgM (30) was kindly donated by Dr. Tarantino, Albany, NY. Oligosaccharides from fetuin were prepared by hydrazinolysis (27) and reduced with NaBH4 as described (31).

Isolation of Hamster Plasma Fibronectin and Its “40K” and “150K-140K” Fragments from the Protein—Hamster plasma fibro-
neutri and the thermolysin fragments were prepared as described (18) and kindly supplied by Dr. K. Sekiguchi in this laboratory.

Isolation of Glycopeptides and Preparation of Oligosaccharides from Glycopeptides—Hamster plasma fibronectin (10 mg) was digested with pronase as described (32) and the digest was applied to a small column of Sephadex G-25 equilibrated with water. The fractions containing oligosaccharides, detected by orcinol-H_{2}SO_{4} reaction, were pooled and lyophilized. The glycopeptides were then subjected to hydrazinolysis, and the N-desacytelated oligosaccharides were isolated by Sephadex G-25 gel filtration and N-acetylated as described (27).

N-Acetylated oligosaccharides were then reduced with NaB\(^{3\text{H}}\)\(_{4}\) (31) and the reaction mixture was directly applied to a column of Bio-Gel P-4 (see below).

**Gel Filtration**—Glycopeptides or oligosaccharides were applied to a column (1.0 x 40 cm) of Sephadex G-25 (fine) equilibrated and eluted with water. They were subsequently applied to a column of Bio-Gel P-4 (200-400 mesh) equilibrated with water (33, 34) or to a column (1 x 94 cm) of Sephadex G-50 equilibrated with 0.2 M NaCl (35).

**Fractionation of Oligosaccharides by Quaternary Aminomethyl (QAE)-Sephadex Column Chromatography**—Oligosaccharides were applied to a column (1.0 x 40 cm) of QAE-Sephadex (36), equilibrated with 20 mM Tris, pH 7.0. After washing with 30 ml of the same solution, the elution was carried out with a linear gradient of 5 mM Tris solution, pH 8.0, to 100 mM sodium phosphate buffer, pH 7.0 (100 ml of each solution). The column was further washed with 200 mM sodium phosphate buffer, pH 7.0. Fractions of 1.2 ml were collected and aliquots were taken for radioactivity determination.

Standard Oligosaccharides—Standard \(^{18}\)O-labeled oligosaccharides were prepared from the glycopeptides from IgG and fetuin by hydrazinolysis followed by exoglycosidase digestion as follows; Gal\(\alpha\)1→4GlcNac\(\beta\)1→2Man\(\alpha\)1→6Gal\(\beta\)1→Gal\(\alpha\)1→GlcNac\(\beta\)1→2Man\(\alpha\)1→3Man\(\beta\)1→4GlcNAc\(\beta\)1→4Fuc\(\alpha\)1→9GlcNAcOH, and GlcNAc\(\beta\)1→2Man\(\alpha\)1→6GlcNAc\(\beta\)1→2Man\(\alpha\)1→3Man\(\beta\)1→4GlcNAc\(\beta\)1→4(Fuc\(\alpha\)1→6)GlcNAcOH from IgG, Man\(\alpha\)1→6Man\(\alpha\)1→3Man\(\beta\)1→4GlcNAc\(\beta\)1→4GlcNAcOH from fetuin glycopeptide. GlcNAc\(\beta\)1→2Man\(\alpha\)1→6GlcNAc\(\beta\)1→2Man\(\alpha\)1→3Man\(\beta\)1→4GlcNAc\(\beta\)1→4GlcNAc\(\beta\)1→4(Fuc\(\alpha\)1→6)GlcNAcOH.

**Exoglycosidase Treatment**—Glycopeptides and \(^{18}\)O-labeled oligosaccharides were hydrolyzed by exoglycosidases as described (23), except that \(\beta\)-galactosidase, \(\beta\)-N-acetylgalactosaminidase, and \(\alpha\)-mannosidase from jack bean (37) were purified and kindly supplied by Dr. Michiko N. Fukuda of our institute.

**Permethylation of Glycopeptides and Oligosaccharide Alcohols**—Glycopeptides and oligosaccharide alcohols were permethylated as described previously (23, 38). Permethylated materials were purified by an LH-20 column equilibrated with chloroform/methanol (1:1), and minor methylated sugars of hydrolysates were analyzed by gas chromatography-mass spectrometry (39) using capillary columns coated with OV-101.

**RESULTS**

Isolation of Glycopeptides and Preparation of Oligosaccharides by Hydrazinolysis—Purified fibronectin from hamster plasma was digested with pronase, and glycopeptides were then subjected to hydrazinolysis and oligosaccharides were isolated, N-acetylated, reduced with NaB\(^{3\text{H}}\)\(_{4}\), and applied to a column of Bio-Gel P-4. As shown in Fig. 1A, the majority of oligosaccharides eluted just after void volume, indicating the majority of oligosaccharide chains were sialylated and no neutral oligosaccharide with 4-20 sugar residues was present as the carbohydrate unit of fibronectin. The fractions indicated by the *bar* were pooled and then applied to a column of Sephadex G-50. The oligosaccharides eluted at the position corresponding to 10-12 sugar residues. When glycopeptides were labeled by periodate/NaB\(^{3\text{H}}\)\(_{4}\) as described (35) and applied to the same column, an almost identical elution pattern was obtained (Fig. 1B). These results suggest that the carbohydrate units of hamster plasma fibronectin are essentially composed of sialic acid containing oligosaccharides with 10-12 sugar residues.

**Methylation Analysis of Glycopeptides**—Glycopeptides eluted at the fractions in Fig. 1B were permethylated and analyzed by mass spectrometry as described previously (31). As shown in Fig. 2A, intact glycopeptide showed the characteristic peaks m/e 406 and 374 (406-32) which are derived from nonreducing terminal N-glycolylneuraminic acid residues. The absence of peaks m/e 376 and 344 indicates that sialic acid residues of hamster plasma fibronectin are exclusively the N-glycolylic form. When the desialylated glycopeptides were analyzed, peaks m/e 406 and 374 completely disappeared and peaks m/e 465 and 433 appeared. These results confirm the above conclusion and also indicate that the Gal\(\alpha\)1→GlcNAc structure is present only after the glycopeptide is subjected to neuraminidase treatment.

**Analysis of methylated monosaccharides after hydrazinolysis confirmed the above conclusion and gave further information concerning linkages. From the data in Table I, it is clear that sialic acid is linked to galactose through \(\alpha\)2→6 and N-acetylgalactosamine is exclusively substituted at the C-4 position and no di-O-substituted N-acetylgalactosamine is present. The presence of mass peak m/e 182 in Fig. 2A is consistent with this result, as this mass number is thought to be derived from the Gal\(\beta\)1→4GlcNAc structure (40). The data also suggest that carbohydrate chains are mostly of the di antennary type since no 2,4- or 2,6-disubstituted mannose was detected. As expected from the carbohydrate composition (18), no permethylated derivative of fucose was detected. It was also noteworthy that only a trace amount of 2,3,4,6-tetra-O-methylgalactose was detected in the permethylated derivatives of the intact glycopeptide (Table I).**

**Analysis of Oligosaccharides Released by Hydrazinolysis**—Oligosaccharides obtained by hydrazinolysis (fractions 30-38 in Fig. 1A) were then fractionated by QAE-Sephadex as shown in Fig. 3A. Chemical analysis indicated that the fraction eluted with the starting buffer contained only a trace

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2 The abbreviations used are: GlcNAcOH, N-acetylgalactosaminic acid; NeuGly, N-glycolylneuraminic acid; NeuAc, N-acetylneuraminic acid; 40K fragment, the fragment of \(M_{r} = 40,000\).

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**Fig. 1.** Gel filtration of glycopeptides and oligosaccharides obtained from hamster plasma fibronectin. A, Bio-Gel P-4 column chromatography of oligosaccharides from hamster plasma fibronectin. Oligosaccharides were released by hydrazinolysis, N-acetylated, reduced with NaB\(^{3\text{H}}\)\(_{4}\), and the solution was evaporated with methanol containing acetic acid and applied to a column (1.0 x 160 cm) of Bio-Gel P-4. The radioactive peak in fractions 68 to 83 is the inorganic tritium salt. B, Sephadex G-50 column chromatography of glycopeptides labeled by periodate/NaB\(^{3\text{H}}\)\(_{4}\). Oligosaccharides pooled as shown in A showed the similar elution pattern. Elution positions of the standard glycopeptides are a, asialo-glycopeptide from fetuin, and b, Man\(\alpha\)1→6Man\(\alpha\)1→3Man\(\beta\)1→4GlcNAc\(\beta\)1→4GlcNAcOH→Asn peptide from IgM.
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**Fig. 2.** Mass spectrum of the permethylated intact glycopeptides (A) and permethylated asialo-glycopeptides (B) from hamster plasma fibronectin. The permethylated glycopeptides were subjected to electron impact direct probe mass spectrometry in the same manner as described previously (31).

**FIG. 3.** QAE-Sephadex A-25 column chromatography of oligosaccharides. A, oligosaccharides from whole fibronectin; B, oligosaccharides from 40K fragment; C, oligosaccharides from 150K-140K fragment. The buffer was changed at fraction 25. Chemical analysis indicated that fractions outside peaks 1 and 2 contained negligible amounts of carbohydrates.

| Relative proportions of methylated sugars from glycopeptides and oligosaccharides | Methylated sugars | Intact glycopeptides | Asialo-glycopeptides | Oligosaccharide 1 | Oligosaccharide 2 |
|---|---|---|---|---|---|
| moles/mol* (integer) | 2,3,4,6-Gal | 0.16 | 1.78 (2.0) | 0.68 (1.0) | 0.16 (0) |
| 3,4,6-Man | 2.0 (2.0) | 2.0 (2.0) | 2.0 (2.0) | 2.0 (2.0) |
| 2,3,4-Gal | 1.61 | 0 | 0.84 (1.0) | 1.74 (2.0) |
| 1,3,5,6-GlcNAcMe | 0 | 0 | 0.50 (1.0) | 0.43 (1.0) |
| 2,4-Man | 1.06 (1.0) | 0.87 (1.0) | 1.26 (1.0) | 0.94 (1.0) |
| 3,6-GlcNAcMe | 3.69 (4.0) | 3.43 (4.0) |

*Numbers are expressed as molar ratios relative to 3,4,6-tri-O-methyl-1,2,5-tri-O-acetyl mannose.

The recovery of this derivative was less than 70% as described previously (25).

**Table I**

Relative proportions of methylated sugars from glycopeptides and oligosaccharides

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A significant amount of carbohydrate; therefore, no further analysis was done on this fraction.

Oligosaccharides 1 and 2 were first treated with neuraminidase and both asialo-oligosaccharides 1 and 2 were found to elute close to the position of Galβ1→4GlcNAcβ1→2Manα1→6Galβ1→4GlcNAcβ1→2Man1→3)Manβ1→4GlcNAcβ1→4GlcNAcOH on Bio-Gel P-4 column chromatography. The oligosaccharides were then digested sequentially with purified glycosidases as described (23) and analyzed by Bio-Gel P-4 gel filtration. After β-galactosidase treatment, oligosaccharides 1 and 2 eluted at the position of GlcNAcβ1→2Manα1→6(GlcNAcβ1→2Man1→3)Manβ1→4GlcNAcβ1→4GlcNAcOH. The resultant heptasaccharides were then converted to Manα1→6(Mana1→3)Manβ1→4GlcNAcβ1→4GlcNAcOH by β-N-acetylglucosaminidase and then to Manβ1→4GlcNAcβ1→4GlcNAcOH by α-mannosidase. The trisaccharide was identified further by exoglycosidase treatment and paper chromatography as described previously (23) (data not shown).

The methylation analysis (Table I) confirmed the above results and the combined results indicate that asialo-oligosaccharides 1 and 2 have the same structure: Galβ1→4GlcNAcβ1→2Manα1→6(Galβ1→4GlcNAcβ1→2Manα1→3)Manβ1→4GlcNAcβ1→4GlcNAcOH.
We have previously shown that three carbohydrate chains of plasma fibronectin are attached to the gelatin-binding domain and one to the 150-140K fragment as depicted in Fig. 4. Oligosaccharides were prepared from these purified fragments and fractionated by QAE-Sephadex column chromatography. As shown in Fig. 3, B and C, oligosaccharides produced from both fragments showed patterns that were similar to each other and to that derived from whole fibronectin (see also "Discussion").

**Structure of Major Carbohydrate Units of Hamster Plasma Fibronectin—** Based on the structural studies on glycopeptides and oligosaccharides, an overall structure for the major carbohydrate chain is shown in Fig. 5A. Although monosialosyl-oligosaccharide was also obtained after hydrazinolysis, the amount of this oligosaccharide should be minimal in the original fibronectin, because only trace amounts of nonreducing terminal galactose were detected in glycopeptide (Table I). Thus, the major oligosaccharide chain of hamster plasma fibronectin is disialoynonaccharide as shown in Fig. 5A.

**DISCUSSION**

The present paper describes the complete structure of the carbohydrate chains attached to hamster plasma fibronectin. Based on the carbohydrate compositions of intact fibronectin, the 40K fragment and 150K-140K fragment, we have shown that three carbohydrate chains are attached to 40K gelatin-binding domain and one to 150-140K fragment (18). The carbohydrate compositions of these fragments (Table II of Ref. 18) are consistent with the idea that each fibronectin subunit has four of the disialononaccharides shown in Fig. 5A, and that three of these are present in the 40K domain and one in the 150K-140K fragment (see also Fig. 4).

The carbohydrate structure of hamster plasma fibronectin is quite different from that of hamster cellular fibronectin in several aspects (Fig. 5, A and B). First, the plasma form has no fucose whereas the cellular form has fucose linked by α1 → 6 to the innermost N-acetylglucosamine. Secondly, sialic acid is linked through α2 → 6 in the plasma form while it is linked through α2 → 3 in the cellular form. Thirdly, the plasma form is mostly fully sialylated whereas the cellular form has asialo type as a major unit.

It is interesting to compare our results with those obtained by Takasaki and co-workers (24, 41) on fibronectins from bovine and human plasma. Bovine plasma fibronectin contains discretely different sets of structures and one of the structures is presented in Fig. 5C. This structure which contains both type 1 and type 2 chains as well as two types of sialic acid linkage, however, seems to be unique to bovine plasma proteins, as bovine prothrombin and coagulation factor X have similar sets of carbohydrate chains (42, 43). On the other hand, the carbohydrate structure of human plasma fibronectin (41) is almost identical with that of hamster plasma fibronectin. It might be interesting to know the carbohydrate structures of human and bovine cellular fibronectins.

It is noteworthy that hamster plasma fibronectin contains exclusively N-glycolyneuraminic acid (see Fig. 2). As fibrinolysis from the hamster have N-acetylneuraminic acid in gangliosides (44), it is possible that the cellular fibronectin differs from the plasma fibronectin also in that its sialic acid is the N-acetylated form. The identification of N-glycolyneuraminic acid has been accomplished by analyzing the permethylated glycopeptide. Since hydrazinolysis removes the N-acetyl group during the reaction, hydrazinolysed and N-acetylated oligosaccharide should always give N-acetylneuraminic acid, regardless of the original N-acetyl form of the sialic acid. In this respect, identifications of N-acetylneuraminic acid in asparagine-linked oligosaccharides in bovine thrombin (42) and coagulation factor X (43) need to be reexamined. In these cases, oligosaccharides obtained by hydrazinolysis and N-acetylation were found to have N-acetyl neuraminic acid as expected, but N-glycolyneuraminic acid has also been reported in bovine thrombin (45) and N-glycolyneuraminic acid has been found in alkali-labile oligosaccharides of factor X when these were released without hydrazinolysis (43).

We have previously shown that cellular fibronectin contains five oligosaccharide chains, whereas plasma fibronectin contains four, based on the chemical composition (13, 18). On the other hand, Takasaki and co-workers (24, 41) reported four oligosaccharide chains in human plasma fibronectin and three in bovine plasma fibronectin based on the incorporated radioactivity. However, it is difficult to determine the number of oligosaccharides by estimating radioactivity incorporated from NaB[3H], as these authors did since NaB[3H], is easily degraded and the specific activity of NaB[3H], may not remain the same once it is dissolved. We feel it is essential to estimate

![Fig. 4. Proposed model of the domain structure of hamster plasma fibronectin. Y indicates the carbohydrate chains. The 24K domain binds heparin and fibrin, the 150K-140K domain enhances cell spreading and binds heparin, the 21K domain binds fibrin, and the 40K domain binds collagen (gelatin) (18).](attachment)

**Fig. 5. Proposed structure of the major oligosaccharide units of fibronectins from various sources.** A, hamster plasma fibronectin (present study). B, hamster cellular fibronectin (23, 46). C, bovine plasma fibronectin (24).
the number of oligosaccharide chains from the chemical analysis.

The formation of monosialosyl-oligosaccharide after hydrazinolysis of hamster plasma fibronectin suggests that non-reducing terminal sialic acid can be degraded by hydrazinolysis in addition to the modification of reducing terminal N-acetylglucosamine which has been described (27). Although it is not clear why such degradation takes place, the result suggests that analysis of glycopeptides is also necessary for structural studies. Further studies aimed at minimizing the degradation of these sugar residues will be needed.

In conclusion, the present study clearly indicates that differences in carbohydrate structures exist between cellular and plasma forms of fibronectin from the same species. This is clear evidence for the existence of chemical diversity between plasma and cellular forms. It will be interesting to know whether these forms differ in functions in vivo and what kind of cells produce plasma fibronectin.

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