

Characterization of the D-Glucuronyl C5-epimerase Involved in the Biosynthesis of Heparin and Heparan Sulfate*

Received for publication, December 29, 2000, and in revised form, March 22, 2001
Published, JBC Papers in Press, March 26, 2001, DOI 10.1074/jbc.M011783200

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The murine gene for the glucuronyl C5-epimerase involved in heparan sulfate biosynthesis was cloned, using a previously isolated bovine lung cDNA fragment (Li, J.-P., Hagner-McWhirter, Å., Kjellén, L., Palgi, J., Jalkanen, M., and Lindahl, U. (1997) *J. Biol. Chem.* 272, 28158–28163) as probe. The ~11-kilobase pair mouse gene contains 3 exons from the first ATG to stop codon and is localized to chromosome 9. Southern analysis of the genomic DNA and chromosome mapping suggested the occurrence of a single epimerase gene. Based on the genomic sequence, a mouse liver cDNA was isolated that encodes a 618-amino acid residue protein, thus extending by 174 N-terminal residues the sequence deduced from the (incomplete) bovine cDNA. Comparison of murine, bovine, and human epimerase cDNA structures indicated 96–99% identity at the amino acid level. A cDNA identical to the mouse liver species was demonstrated in mouse mast cells committed to heparin biosynthesis. These findings suggest that the iduronic acid residues in heparin and heparan sulfate, despite different structural contexts, are generated by the same C5-epimerase enzyme. The catalytic activity of the recombinant full-length mouse liver epimerase, expressed in insect cells, was found to be >2 orders of magnitude higher than that of the previously cloned, smaller bovine recombinant protein. The ~52-kDa, similarly highly active, enzyme originally purified from bovine liver (Campbell, P., Hansson, H. H., Sandbäck, D., Rodén, L., Lindahl, U., and Li, J.-P. (1994) *J. Biol. Chem.* 269, 26953–26958) was found to be associated with an ~22-kDa peptide generated by a single proteolytic cleavage of the full-sized protein.

Heparin and heparan sulfate (HS)¹ are both linear, sulfated glycosaminoglycans based on a common carbohydrate back-

bone of alternating D-glucosamine (GlcN) and hexuronic acid (D-glucuronic (GlcUA) or L-iduronic acid (IdoUA)) units. Both polymer types are synthesized as proteoglycans. Heparin occurs in connective tissue-type mast cells, whereas HS has a ubiquitous distribution and is produced by almost all mammalian cells. The biosynthesis of heparin and HS follows a common pathway that involves: (i) formation of a GlcUA-Gal-Gal-Xyl-Ser carbohydrate-protein linkage region; (ii) assembly of repeating -GlcUA-GlcNAc- disaccharide units; and (iii) modification of the [GlcUA-GlcNAc]_n polymers (1, 2). The latter process includes N-deacetylation and N-sulfation of GlcNAc units, C5-epimerization of GlcUA to IdoUA units, and O-sulfation at various sites of the sugar residues. Heparin is highly modified, heavily N- and O-sulfated and with more IdoUA than GlcUA units. Generally, a predominant proportion of heparin chains consists of trisulfated -IdoUA(2-OSO₃)-GlcNSO₂(6-OSO₃)- units. By comparison, HS has a more variable and heterogeneous structure, with highly modified, less modified, and unmodified sequences arranged in domain-type fashion (3, 4). The IdoUA units occur in essentially two types of domains, composed of contiguous N-sulfated, and of alternating N-sulfated and N-acetylated disaccharide units, respectively (5). The sequence variability of the chains is believed to reflect the functional role of HS glycosaminoglycans (GAGs) in specific interactions with different proteins (1–4, 6). IdoUA residues generally appear to promote protein binding due to their conformational flexibility and have been identified as invariable constituents of protein-binding HS domains (4). The reaction catalyzed by the C5-epimerase therefore is crucial for many biological functions of heparin and HS.

The mechanisms in control of the structural diversity of heparin and, in particular, of HS are only partly understood but clearly rely on the substrate specificities of the enzymes involved (2, 4). The enzymes required to synthesize a HS chain have all been cloned. Notably, several of these proteins, including species committed to polymer modification, occur in multiple forms that are encoded by different genes. Some of these species have been shown to differ with regard to kinetic properties and/or substrate specificity from the respective homologous forms (7–10).

The IdoUA units of heparin and HS chains occur in widely different structural contexts, which range from the minimally sulfated -GlcNSO₂-IdoUA-GlcNAc- sequence found in HS molecules to the extensively sulfated -GlcNSO₂(6-OSO₃)-IdoUA(2-OSO₃)-GlcNSO₂(6-OSO₃)- structure typical of heparin (4). These findings raise the question as to whether the C5-epimerase, similar to other enzymes in the same biosynthetic

* This work was supported by Swedish Medical Research Council Grant 3309, the European Commission Grants BIO4-CT95-0036 and QLK3-CT-1999-00536, and Polysackaridforskning AB (Uppsala, Sweden). The costs of publication of this article were defrayed in part by the payment of page charges. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

The nucleotide sequence(s) reported in this paper has been submitted to the GenBank™ (EBI Data Bank with accession number(s) AF230049 and AF000927.

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‡ The abbreviations used are: HS, heparan sulfate; GlcUA, D-glucuronic acid; IdoUA, L-iduronic acid; GAG, glycosaminoglycan; FISH, fluorescence in situ hybridization; DAPI, 4',6-diamidino-2-phenylindole; aMann, 2,5-anhydromannitol (formed by reduction of terminal 2,5-anhydromannose residues with NaBH₄); PAGE, polyacrylamide gel

electrophoresis; kb, kilobase pair; FCS, fetal calf serum; bp, base pair; ORF, open reading frame; PCR, polymerase chain reaction; RT-PCR, reverse transcriptase-PCR; NDeT, N-deacetylase/N-sulfotransferase.

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