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IUPAC-IUB Joint Commission on Biochemical Nomenclature (JCBN). Nomenclature of Glycoproteins, Glycopeptides and Peptidoglycans

JCBN Recommendations 1985

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These are recommendations of the IUPAC-IUB Joint Commission on Biochemical Nomenclature (JCBN). They have been approved for publication by the Executive Committee of IUB, and for publication as provisional recommendations by the Interdivisional Committee on Nomenclature and Symbols of IUPAC. The members of JCBN are HBF Dixon (Chairman), A Cornish-Bowden (Secretary), C Liébecq (representing the IUB Committee of Editors of Biochemical Journals), KL Loening, GP Moss, J Reedijk, SF Velick and JFG Vliegenthart. Comments may be sent to any member of the commission, or to its secretary: A Cornish-Bowden, Department of Biochemistry, University of Birmingham, P.O. Box 363, Birmingham, England, B15 2TT. JCBN thanks the following for comments on these recommendations: CE Ballou, E Buddecke, EA Davidson, RJ Doyle, D Duksin, JM Ghuysen, T Hardingham, VC Hascall, D Heinegård, FW Hemming, D Horton, RC Hughes, WB Jakoby, RW Jeanloz, O Kandler, T Laurent, YC Lee, U Lindahl, B Lindberg, H Lis, FG Loontiens, J Montreuil, H Muir, A Neuberger, EF Neufeld, T Osawa, L Rodén, H Schachter, R Schauer, K Schmid, GD Shockman, JE Silbert, CC Sweeley and I Yamashina, as well as members, associate members and former members of the Nomenclature Committee of IUB (NC-IUB), namely H Bielka, CR Cantor, P Karlson, N Sharon, EJ Van Lenten and EC Webb.

[a]This compound could more strictly be described as 5(α-D-galactopyranosyloxy)-L-lysine, but hydroxylysine is regarded as a trivial name [8], so names are based on it.

[b]Hydroxyproline is the trivial name for *trans*-4-hydroxy-L-proline.

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1.0 Introduction

Various types of compound consisting of carbohydrates covalently linked with other types of chemical constituent are classified under the general name of *glycoconjugates*. The major groups of glycoconjugates are the glycoproteins, glycopeptides, peptidoglycans, glycolipids and lipopolysaccharides. The first three of these are considered in the present document. The nomenclature of glycolipids has been the subject of an earlier document [1], which is now under revision.

As early as 1907, when very little was known about *glycoproteins*, they were defined by the Committees on Protein Nomenclature of the American Society of Biological Chemists and the American Physiological Society as "compounds of the protein molecule with a substance or substances containing a carbohydrate group other than a nucleic acid" [2]. In spite of the enormous progress in our knowledge of the occurrence, biosynthesis, properties and functions of the glycoproteins this definition remains appropriate.

Glycoproteins are widely distributed in all forms of life, with the possible exception of the eubacteria. They occur in cells, both in soluble and membrane-bound forms, as well as in the extracellular matrix and in extracellular fluids. The commonest glycoproteins are those in which the carbohydrate is linked to the protein by glycosyl linkages. Glycosylation represents one of the important co-translational and post-translational modifications of proteins.

The term "glycoprotein" should include *proteoglycans*, which in the past were considered as a separate class of compound. Proteoglycans are those glycoproteins whose carbohydrate moieties consist of long, unbranched chains of alternating residues of hexosamine and uronic acid or galactose, often sulfated. Such polysaccharides belong to the class of *glycosaminoglycans*. Proteoglycans were not considered as glycoproteins in the past because their carbohydrate seemed to differ so greatly from the comparatively small, branched, usually unsulfated carbohydrate units, devoid of repeating units, found in other glycoproteins. Another reason was their unique distribution: the proteoglycans are found mainly in connective tissues, where they contribute to the organization and physical properties of the extracellular matrix. It is known, however, that proteoglycans too are glycosylated proteins, synthesized by the action of glycosyltransferases, and that repeating disaccharide units are present in typical glycoproteins as well. Proteoglycans are therefore considered to be a subclass of glycoproteins.

The terms "protein glucosylation (or glycosylation)" and "glucosylated (or glycosylated) hemoglobin" have been used improperly to refer to the products of non-enzymic reactions between glucose or other sugars and free amino groups of proteins. Compounds formed in this manner are not glycosides, however, as they result from the formation of a Schiff base followed by Amadori rearrangement to 1-deoxyketosyl derivatives of the

proteins. For example, the product of the reaction between glucose and hemoglobin is not glycosylated hemoglobin but *N*-(1-deoxyfructosyl)hemoglobin. The term "glycation" is suggested for all reactions that link a sugar to a protein or peptide, whether or not catalysed by an enzyme. The product of glycation is a glycoprotein, or, in the special case of the reaction with hemoglobin, glycohemoglobin. When appropriate a more precise name such as deoxyfructosylhemoglobin may be used.

Peptidoglycans, sometimes referred to as *mureins*, are glycoconjugates found only in bacterial cell walls. Although they are also composed of carbohydrates and amino acids covalently linked together, they are a distinct class of compound as (a) they do not contain a protein portion; (b) they contain sugars not found elsewhere; and (c) they consist of linear polysaccharides (of the class of glycosaminoglycan) crosslinked by oligopeptides, thus forming a huge and rigid network.

No official nomenclature of glycoproteins, glycopeptides and peptidoglycans has been available hitherto. In drawing up the present document, we follow the general rules of biochemical nomenclature [3], especially the more recent ones on carbohydrates [4-7] and amino acids and peptides [8].

2.0 Nomenclature

2.1 Glycoproteins, Proteoglycans and Glycosaminoglycans

A *glycoprotein* is a compound containing carbohydrate (or glycan) covalently linked to protein. The carbohydrate may be in the form of monosaccharide(s), disaccharide(s), oligosaccharide(s), polysaccharide(s), or their derivatives (e.g. sulfo- or phospho-substituted). One, a few, or many carbohydrate units may be present. *Proteoglycans* are a subclass of glycoproteins in which the carbohydrate units are polysaccharides that contain amino sugars. Such polysaccharides are also known as *glycosaminoglycans.*

2.2 Glycopeptides, Glyco-amino-acids and Glycosyl-amino-acids

A *glycopeptide* is a compound consisting of carbohydrate linked to an oligopeptide composed of L- and/or D-amino acids. A *glyco-amino-acid* is a saccharide attached to a single amino acid by any kind of covalent bond. A *glycosyl-amino-acid* is a compound consisting of saccharide linked through a glycosyl linkage (*O*-, *N*- or *S*-) to an amino acid. (The hyphens are needed to avoid implying that the carbohydrate is necessarily linked to the amino group.)

2.3 Peptidoglycans

A *peptidoglycan* consists of glycosaminoglycan formed by alternating residues of D-glucosamine and either muramic acid (2-amino-3-*O*-[(*S*)-1-carboxyethyl]-2-deoxy-D-glucose) or L-talosaminuronic acid (2-amino-2-deoxy-L-taluronic acid) that are usually *N*-acetylated or *N*-glycoloylated. The carboxyl group of the muramic acid is commonly substituted by a peptide containing residues of both L- and D-amino acids, whereas that of L-talosaminuronic acid is substituted by a peptide consisting of L-amino acids only.

Table 1. Structure of glycosaminoglycans[a].

Name	Repeating disaccharide	Sulfation	Linkage region
Hyaluronic acid	GlcNAc(β1-4)GlcA(β1-3)	None	(Not proved to be linked to protein)
Chondroitin 4- and 6-sulfate	GalNAc(β1-4)GlcA(β1-3)	GalNAc-4-*O*-sulfate, 6-*O*-sulfate or hybrids	GlcA(β1-3)Gal(β1-3)Gal(β1-4)Xyl(β1-)Ser
Dermatan sulfate	GalNAc(β1-4)GlcA(β1-3) and GalNAc(β1-4)L-IdoA(α1-3)	GalNAc-4-O-sulfate, or 6-O-sulfate; L-iduronic acid may be sulfated at position 2	GlcA(β1-3)Gal(β1-3)Gal(β1-4)Xyl(β1-)Ser
Heparin and heparan sulfate	GlcNR(α1-4)GlcA(β1-4) and GlcNR(α1-4)L-IdoA(α1-4)	In heparin (highly sulfated), R mostly SO_3H, little acetyl; in heparan sulfate generally less SO_3H and more acetyl than in heparin. Some of the *N*-acetyl-D-glucosamine is 6-*O*-sulfated, and some of the L-iduronic acid is 2-*O*-sulfated.	GlcA(β1-3)Gal(β1-3)Gal(β1-4)Xyl(β1-)Ser
Keratan sulfate	GlcNAc(β1-3)Gal(β1-4)	GlcNAc-6-*O*-sulfate; Gal-6-*O*-sulfate	(See Fig. 1)

[a] Based mainly on Lindahl U, Höök M (1978) Ann Rev Biochem 47:385-417; and Rodén L (1980) in The Biochemistry of Glycoproteins and Proteoglycans, ed Lennarz WJ. Plenum Press, New York, p 267-371.

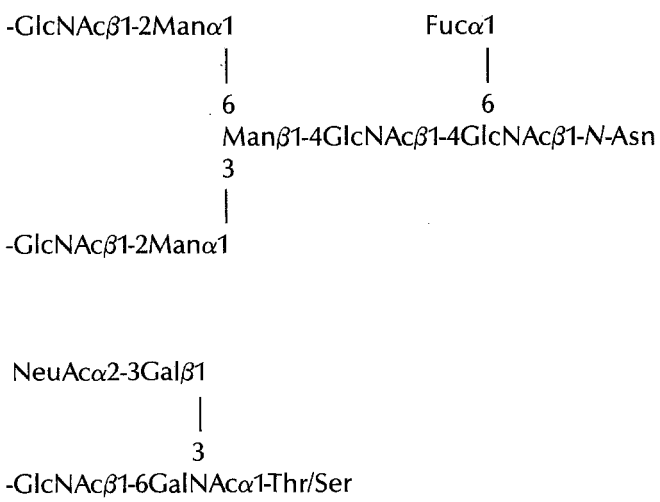


Figure 1. Linkage region of corneal and skeletal keratan sulfate. The upper structure shows the linkage region in keratan sulfate type I (corneal); the lower shows that in keratan sulfate type II (skeletal).

3.0 Comments

3.1 Form of Carbohydrate in Glycoproteins

In many glycoproteins (e.g. plasma glycoproteins such as human α_1-acid glycoprotein or fetuin) the carbohydrate is in the form of oligosaccharides, linear or branched, the latter containing up to about 20 monosaccharide residues; glycoproteins containing mono- or disaccharide units are also known [e.g. collagens, fish antifreeze glycoproteins, sheep submaxillary (or submandibular) glycoproteins], as well as those that contain oligosaccharides that consist of repeating units of *N*-acetyllactosamine (e.g. band 3 of the human erythrocyte membrane).

3.2 Proteoglycans

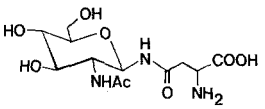
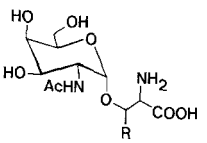
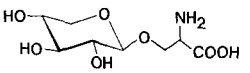
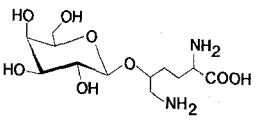
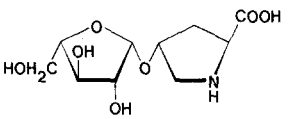
A *proteoglycan* is a protein glycosylated by one or more (up to about 100) glycosaminoglycans (Table 1). The glycosaminoglycans of the proteoglycans are linear polymers of up to about 200 repeating disaccharide units that consist of a hexosamine (D-glucosamine or D-galactosamine) alternating with a uronic acid (D-glucuronic or L-iduronic) or a neutral sugar (D-galactose). The hexosamines are usually *N*-acetylated, and in some of the glycosaminoglycans the D-glucosamine is *N*-sulfated. Varying degrees of sulfation occur in other positions of the hexosamines as well as on the L-iduronic acid. The chain of repeating units is linked to the protein by an oligosaccharide of a structure different from the repeating units. This *linkage region* (Table 1) is identical in most of the proteoglycans (chondroitin sulfates, dermatan sulfate, heparin, and heparan sulfate), but is different in keratan sulfate, (Fig. 1) This last glycosaminoglycan contains repeating units of *N*-acetyllactosamine that are *O*-sulfated. Because of their content of uronic acid and/or ester sulfate, the glycosaminoglycans of the proteoglycans are anionic polyelectrolytes and have been referred to as "acidic glycosaminoglycans" (equivalent to the older term "acid mucopolysaccharides"). Proteoglycans may also contain one or more oligosaccharide of structure similar to those found in other glycoproteins.

Several diseases of proteoglycan metabolism are recognized, including the Hunter and Hurler syndromes; they are referred to as mucopolysaccharidoses, but strictly speaking should go by the term "glycoproteinoses", which encompasses other diseases of glycoprotein metabolism such as mannosidosis and fucosidosis.

3.3 Microheterogeneity

A particular glycoprotein may occur in forms that differ in the structure of one or more of its carbohydrate units, a phenomenon known as *microheterogeneity*. Such differences may affect both the size and charge of individual glycoproteins; occasionally, the differences may be solely due to changes in linkage position in a carbohydrate unit. For example, chicken ovalbumin contains a single glycosylated amino acid residue (Asn-293), but more than a dozen different oligosaccharides have been identified at that site. In proteoglycans, individual glycosaminoglycan chains may differ in structure, e.g. the degree of sulfation, the ratio of D-glucuronic acid to L-iduronic acid, and chain length. Proteoglycans are therefore highly polydisperse, in contrast to typical glycoproteins, which, in spite of their microheterogeneity, are not markedly polydisperse in their molecular size.

Table 2. Commonly occurring glycosyl-amino-acids[a].

Example	Structure	Occurrence
N-GLYCOSIDE[b] β-*N*-Acetylglucosaminyl-asparagine, (GlcNAc-)Asn		Widely distributed in animals, plants and microorganisms
O-GLYCOSIDES α-*N*-Acetylgalactosaminyl--serine or -threonine, (GalNAc-)Ser, (GalNAc-)Thr		Glycoproteins of animal sources
β-Xylosyl-serine (Xyl-)Ser		Proteoglycans, human thyroglobulin
β-Galactosyl-hydroxylysine (Gal-)Hyl		Collagens
β-L-Arabinosyl-hydroxyproline, (L-Ara-)Hyp		Plant and algal glycoproteins

[a] Based on: Sharon N, Lis H (1982) in The Proteins, 3rd edn., eds. Neurath H, Hill L, vol 5, Academic Press, New York, p 1-144.

[b] Traditionally the term "glycoside" referred explicitly to *O*-linked compounds; we use the term "*N*-glycoside" rather than "nitrogen analog of glycoside", which is unnecessarily cumbersome.

3.4 Glycopeptides, etc.

Glycopeptides, *glyco-amino-acids*, *glycosyl-amino-acids* and *glycosylpeptides* are obtained by enzymic or chemical cleavage of glycoproteins, or by chemical or enzymic synthesis.

Examples of glycosyl-amino-acids that constitute the common linking compounds between the carbohydrate and protein in glycoproteins are as follows (Table 2): 2-acetamido-*N*-(L-aspart-4-yl)-2-deoxy-β-D-glucopyranosylamine, i.e. N^4-(*N*-acetyl-β-D-glucosaminyl)asparagine, which is abbreviated to (GlcNAc-)Asn (parentheses here around the carbohydrates placed next to the symbol for an amino-acid residue indicate

substitution on its side chain: see ref. 8, section 3AA-17.2); O^3-(*N*-acetyl-α-D-galactosaminyl)serine or threonine, (GalNAc-)Ser or (GalNAc-)Thr; *O*-β-D-xylosylserine, (Xyl-)Ser; O^5-α-D-galactosylhydroxylysine[a], (Gal-)Hyl; and β-L-arabinosylhydroxyproline[b], (L-Ara-)Hyp. Another example of a glyco-amino-acid is [Man_9-GlcNAc(β1-4)GlcNAc-]Asn, isolated from a proteolytic digest of soybean agglutinin. Such a compound may be referred to as an *oligosaccharylasparagine*.

Commonly occurring glycosyl-amino-acids are listed in Table 2.

3.5 N-,O-Glycoproteins

If desirable, the linkage between carbohydrate and protein may be indicated by the locants *N*- or *O*-. The locant *N*- is used for the *N*-glycosyl linkage to asparagine. *N*-Linked oligosaccharides are divided into two major classes: the *N-acetyllactosamine type* containing *N*-acetyl-D-glucosamine, D-mannose, D-galactose, L-fucose and sialic acid; and the *oligomannose type* containing *N*-acetyl-D-glucosamine and a variable number of D-mannose residues. Structures containing both oligomannose- and *N*-acetyllactosamine-type oligosaccharides are designated as *hybrid type*. Examples of *N*-glycoproteins (or *N*-glycosylproteins) are chicken ovalbumin, pig ribonuclease, human α_1-acid glycoprotein and soybean agglutinin.

The locant *O*- is used for the *O*-glycosyl linkage to serine, threonine, hydroxylysine or hydroxyproline. Sheep submaxillary glycoprotein, collagen, fish antifreeze glycoproteins and potato lectin are *O*-glycoproteins (or *O*-glycosylproteins).

Two types of carbohydrate-peptide linkage in the same protein or peptide chain may be indicated by a combination of the locants. Thus, calf fetuin, procollagen, human erythrocyte membrane glycophorin and human chorionic gonadotropin are *N*-,*O*-glycoproteins (or *N*-,*O*-glycosylproteins).

3.6 Asialoglycoproteins and Asialo-agalactoglycoproteins

Glycoproteins from which the sialic acid has been removed (by treatment with enzymes or mild acid) are designated by the prefix asialo-, e.g. asialo-α_1-acid glycoprotein and asialofetuin. Removal of both sialic acid and galactose results in asialo-agalactoglycoproteins.

3.7 Condensed Representation of Sugar Chains

For writing the structure of sugar chains, the non-reducing terminus of the carbohydrate chain should always be on the left-hand end. The following simplification might be suitable [6]. Current practice allows the use of either an *extended form* (a) or a *con-*

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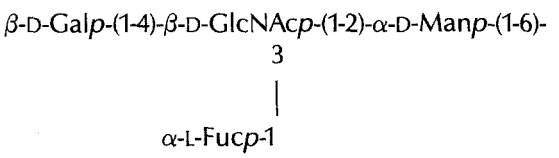
[a] This compound could more strictly be described as 5(α-D-galactopyranosyloxy)-L-lysine, but hydroxylysine is regarded as a trivial name [8], so names are based on it.

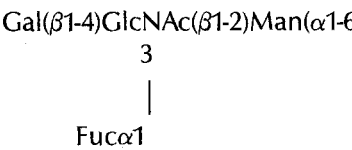
[b] Hydroxyproline is the trival name for *trans*-4-hydroxy-L-proline.

densed form (b), which allows structures to be shown in one line as well as in two or more, and in which the longest chain should always be the main chain:

(a)*extended form*



(b)*condensed form in two lines*



or *condensed form in one line*

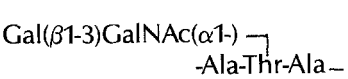
Gal(β1-4)[Fuc(α1-3)]GlcNAc(β1-2)Man(α1-6)-

The condensed form is still unnecessarily long, however, and there should be no serious loss if it is shortened further by (i) omitting locants of anomeric carbon atoms, (ii) omitting the parentheses around the specification of linkage, and (iii) omitting hyphens if desired. We therefore suggest a more condensed or *short form* of writing:

(c)*short form*

Galβ4(Fucα3)GlcNAcβ2Manα6-

Similarly a glycopeptide sequence, represented in the condensed form in two lines as:



or in the condensed form in one line as:

-Ala-[Gal(β1-3)Gal NAc (α1-)]Thr-Ala-

may be written in the short form in two lines as:

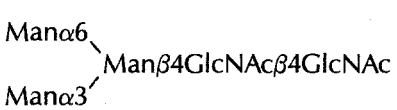
Galβ3GalNAcα-┐
-Ala-Thr-Ala-

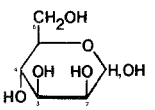
or in the short form in one line as:

-Ala-(Galβ3GalNAcα)Thr-Ala-

3.8 Representation of N-Linked Oligosaccharides

As a rule, *N*-linked oligosaccharides contain a common pentasaccharide core as follows:





For the sake of uniformity, the location of substitution should be written as above in accordance with Haworth's representation of the pyranose structure of monosaccharides, in analogy with the glycogen molecule.

3.9 Peptidoglycans

In peptidoglycans, peptide units of adjacent polysaccharides (glycosaminoglycans) may be cross-linked by a peptide bond between the C-terminal alanine residue of one peptide subunit and the ω-amino group of the diamino acid residue of the other (e.g. L-lysine or *meso*-diaminopimelic acid), thereby giving rise to a giant macromolecule forming the rigid cell wall ("sacculus"). This macromolecule is known to occur as a monomolecular layer between the inner and outer membrane in Gram-negative bacteria and as a multimolecular layer, often associated covalently or noncovalently with various additional compounds (teichoic acid, neutral polysaccharides, etc.) in Gram-positive bacteria.

Extensive investigations of peptidoglycans in thousands of bacterial strains demonstrated the existence of more than 100 chemotypes in the eubacteria [9]. The peptidoglycans of eubacteria have been classified into two major groups (A and B) and several subgroups according to the mode of cross-linkage. Within group A two main subgroups are recognized: one in which the C-terminal alanine residue is directly bound to the ω-amino group of the diamino acid at position 3 of the peptide subunit of an adjacent polysaccharide (glycosaminoglycan) and one in which the cross-linkage is mediated by an interpeptide bridge consisting of either one or up to five amino acid

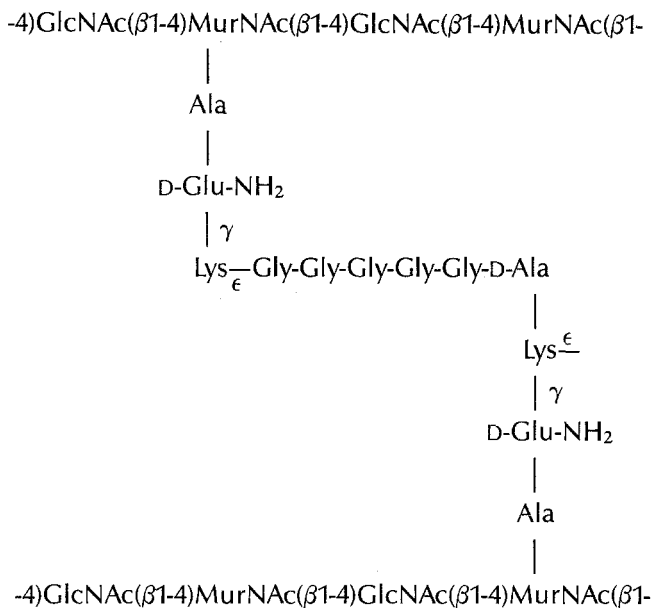


Figure 2. Primary structure of a peptidoglycan, in which the cross-linkage between adjacent peptide-substituted polysaccharides is mediated by an interpeptide bridge consisting of Lys-$[Gly]_5$.

residues (e.g. Lys-Gly_5-type, Fig. 2). Depending on the kind of diamino acid at position 3 and the amino acids serving as interpeptide bridges, many variations of these subgroups of murein are known. In the peptidoglycan types of group B, the cross-linkage does not occur at position 3 of the peptide subunit but at position 2, utilizing the α-carboxyl group of the D-glutamic residue. The interpeptide bridge must contain a diamino acid, which may be lysine, ornithine or diaminobutyric acid, in either L- or D-configuration. As a second special characteristic of the group B peptidoglycan types, the L-alanine residue at position 1 of the peptide subunit is replaced by either glycine or serine.

In the archaebacteria, several organisms contain a peptidoglycan that differs in certain respects from those described above, typical for the eubacteria [10, 11]. It consists of a polysaccharide formed by alternating (β1-3)-linked *N*-acetylated residues of D-glucosamine or D-galactosamine and (β1-3)-linked *N*-acetylated residues of L-talosaminuronic acid, and a peptide containing exclusively L-amino acids attached to the carboxyl group of L-talosaminuronic acid. The peptide units of adjacent polysaccharides may be cross-linked by a peptide bond between the γ-carboxyl group of the glutamic acid of one peptide subunit and the α-amino group of the lysine residue of the other, thus giving rise to a huge macromolecule that forms the rigid cell wall (or sacculus) of the methanogenic bacteria. This multimolecular layer is often associated covalently, but also non-covalently, with neutral polysaccharides. Only a few chemotypes of such peptidoglycans have so far been described.

4.0 References

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5.0 Appendix: Implied Configurations and Ring Sizes

In the condensed system of symbols for sugar residues the common configuration and ring size (usually pyranose) are implied in the symbol. Thus, Gal denotes D-galactopyranose; Man, D-mannopyranose; Fuc, L-fucopyranose; GlcNAc, 2-acetamido-2-deoxy-D-glucopyranose or D-glucosamine; Neu5Ac (which may be abbreviated to NeuAc), *N*-acetylneuraminic acid. The symbol Sia stands for sialic acid, a general term that can also be used when the exact structure is unknown.

Whenever the configuration or ring size is found to differ from the common one it must be indicated by using the appropriate symbols for the extended system. The configuration of amino acids is L unless otherwise noted. Although symbols such as Gal and Man are useful in representing oligosaccharide structures they should not be used in the text to represent monosaccharides.