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Coding and classification of D-galactose, *N*-acetyl-D-galactosamine, and β-D-Gal*p*-[1→3(4)]-β-D-Glc*p*NAc, specificities of applied lectins*,†

Albert M. Wu
Glyco-Immunochemistry Laboratory, Chang-Gung Medical College, Kwei-San, Tao-Yuan 33332 (Taiwan)

and Shunji Sugii
Department of Serology and Immunology, School of Medical Technology, Kitasato University, 1-15-1 Kitasato, Sagamihara, Kanagawa 228 (Japan)

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ABSTRACT

Grouping of lectin-binding properties, based on determinant structure rather than monosaccharide-inhibition pattern, should facilitate the selection of lectins as structural probes for glycans, as well as for the interpretation of the distribution and the properties of the carbohydrate chains on the cell surface. Based on the binding specificities studied with glycan by precipitin-inhibition, competitive-binding, and hemagglutinin-inhibition assays, twenty D-galactose-or *N*-acetyl-D-galactosamine-(or both)-specific lectins have been divided into six classes according to their specificity for a disaccharide unit, as all or part of the determinants, and the α-D-Gal*p*NAc-(1→3)-Ser(Thr) unit of the glycopeptide chain. A scheme of classification is shown as follows: (a) F-specific lectins [α-D-Gal*p*NAc-(1→3)-D-GalNAc, Forssman specific disaccharide]: *Dolichos biflorus* (DBL), *Helix pomatia* (HPL), hog peanut (ABL, *Amphicarpaea bracteata*), and *Wistaria floribunda* (WFL) lectins. (b) A-specific lectins [α-D-Gal*p*NAc-(1→3)-D-Gal blood group A-specific disaccharide]: *Griffonia (Bandeiraea) simplicifolia-A*$_4$ (GSI-A$_4$), lima bean (LBL), soy bean (SBL), *Vicia villosa* (VVL), *Wistaria floribunda* (WFL), *Dolichos biflorus* (DBL), and *Helix pomatia* (HPL) lectins. (c) Tn-specific lectins [α-D-Gal*p*NAc-(1→3)-Ser(Thr) of the protein core]: *Vicia villosa* B$_4$ (VVL-B$_4$), *Salvia sclarea* (SSL), *Maclura pomifera* (MPL), *Bauhinia purpurea alba* (BPL), HPL, and WFL, lectins. (d) T-specific lectins [β-D-Gal*p*-(1→3)-D-GalNAc, the mucin-type sugar sequences on human erythrocyte membrane and T antigen, or the terminal, nonreducing disaccharide end-groups of the gangliosides]: Peanut (PNA), *Bauhinia purpurea alba* (BPL), *Maclura pomifera* (MPL), *Sophora japonica* (SJL), *Artocarpus integrifolia* (Jacalin, AIL), and *Artocarpus lakoocha* (Artocarpin) lectins. (e) Type I and II specific lectins [β-D-Gal*p*-(1→3 or 4)-D-GlCNAc, the disaccharide residues at the nonreducing end of the carbohydrate chains derived from either *N*- or *O*-glycans]: *Ricinus communis* agglutinin (RCA1), *Datura stramonium* (TAL, Thorn apple), *Erythrina cristagalli* (ECL, Coral tree), and *Geodia cydonium* (GCL), lectins. (f) B-specific lectin [α-D-Gal*p*-(1→3)-β-D-Gal*p*, human blood group B-specific disaccharide]: *Griffonia* (Bandeiraea) *simplicifolia* B$_4$ (GSI-B$_4$) lectin. Many other GalNAc- or Gal-(or both)-specific lectins that can be used as tools are also described.

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INTRODUCTION

Lectins have been widely used to study the structural and functional role of cell surface carbohydrates[1-6], to detect sugar components on normal and neoplastic cell surfaces[1], to isolate mutants resistant to the cytotoxic action of some lectins[7-10], and to isolate and characterize glycoconjugates[5,11-14]. They require configurational and structural complementarity of sugars for interaction to occur. All lectin molecules have more than two carbohydrate-binding sites, a property resulting in their ability to agglutinate cells or to precipitate complex carbohydrates[1,4,15,16]. By the early eighties, the carbohydrate specificities of many lectins were grouped by the ability of monosaccharides or their glycosides to inhibit lectin-induced hemagglutination[2,15,17,18]. Even lectins of the same apparent monosaccharide specificity were found to demonstrate different reactivities toward different oligosaccharide chains, and differential affinities to animal cells and glycoproteins, which implies that they have their own binding specificity extending beyond the monosaccharide unit[1-4,15,18]. Today, the concept of the combining sites of many lectins extending to five or more sugars has been accepted, and the fact that multibranched oligosaccharides exhibit a significant increment in their lectin-binding reactivites as compared with the linear counterparts has also been recognized. For example, *Datura stramonium* (TAL, Thorn apple) lectin shows a specificity for a biantennary pentasaccharide, which contains two branches, β-D-Gal*p*-(1→4)-β-D-GlcNAc-(1→6)-D-Man and β-D-Gal*p*-(1→4)-β-D-GlcNAc-(1→2)-D-Man as nonreducing end-groups, 480-fold higher than for that of its branch trisaccharides[19]. Furthermore, some lectins having broad spectra of binding properties possess dual or multiple affinities to various disaccharides. Such lectins as *Wistaria floribunda* is specific for α-D-Gal*p*NAc-(1→3)-D-GalNAc, α-D-Gal*p*NAc-(1→3)-D-Gal, α-D-Gal*p*NAc-(1→3)-Ser(Thr), and β-D-Gal-(1→4 or 3)-D-GlcNAc units; *Bauhinia purpurea alba* for β-D-Gal-(1→3)-D-GalNAc, α-D-Gal*p*NAc-(1→3)-Ser(Thr), and β-D-Gal*p*-(1→4 or 3)-D-GlcNAc units, and *Datura stramonium* for *N*-acetyllactosamine *and* N-acetylchitobiose units[2,19]. Thus, organizing and grouping binding properties of lectins, based on disaccharide determinants and α-D-Gal*p*NAc-(1→3)-Ser(Thr) sequence, rather than monosaccharide-inhibition pattern, should facilitate the selection of lectins as structural probes for glycans, as well as the interpretation of the distribution and properties of the carbohydrate chains on the cell surface. From the information provided by inhibition assays (Tables I and II)*, the lectins selected in this paper were divided into six classes according to their specificity for the α-D-Gal*p*NAc-(1→3)-Ser(Thr) unit of the glycopeptide backbone and for the disaccharide units that are commonly found in mammalian glycoconjugates. The abbreviations and codes of the lectin determinants presented in Table III will be useful for the classification of the Gal and GalNAc lectins that can be used for the study of the sugar component(s) of complex carbohydrates.

* All sugars mentioned in the tables have the D configuration (except for fucose in the L configuration), are in the pyranose form, and are linked at C-1 (except for *N*-acetylneuraminic acid linked at C-2), unless specifically noted.

TABLE I

Comparison of the reactivities of GalNAc-specific lectins[a]

Carbohydrate residues or groups capable of reacting	*Class*[b]	*DBL*[20,21]	*HPL*[20,21]	*ABrL*[2,22]	*WFL*[20,23,c]	*SBA*[21,24]	*LBL*[25,26c]	*GSI*[27,c] (*A*$_4$)	VVL[28] (*A* & *B*)	*VVL*[29] (*B*$_4$)	*MPL*[30]	*BPL*[31]	*SSL*[32,c]
αGalNAc→3GalNAc	F	3+	3+	4+	2+	[d]	–	[d]	2+	[d]	–	–	[d]
αGalNAc→3βGalNAc →3αGal→4βGal→4Glc	F	4+	4+	[d]	3+	[d]	[d]	[d]	[d]	[d]	–	–	[d]
αGalNAc→3Gal	A	+	[d]	3+	3+	3+	[e]	3+	4+	[d]	–	2+	[d]
αGalNAc→3βGal→3GlcNAc	A	+	2+	[d]	3+	4+	[e]	3+	2+	[d]	–	3+	[d]
αGalNAc→3(αFuc→2) βGal→4βGlcNAc→6R[h]	A$_F$	2+	–	[d]	+	+	2+	+	2+	[d]	–	3+	[d]
βGal→3αGalNAc→Ser or Thr[f]	T	[d]	[d]	[d]	[d]	[d]	[d]	[d]	[d]	+	4+	4+	[d]
αGalNAc→Ser or Thr[g]	Tn	–	+	+	3+	2+	[d]	[d]	2+	4+	3+	3+	2+
βGal→3GlcNAc→R[h]	I	–	–	[d]	[d]	+	[d]	[d]	[d]	[d]	–	3+	[d]
βGal→4GlcNAc→R[h]	II	–	–	[d]	+	+	[d]	[d]	[d]	[d]	–	3+	[d]

[a] Based mainly on the results obtained from precipitin-inhibition assays: 4+, best inhibitor; 3+, about 1/2 of the best; 2+, about 1/10 of the best; +, about 1/100 of the best; –, less than 1/100 or no inhibition. [b] See Table III for structures. [c] The best inhibitors are αGalNAc→6Gal and αGalNAc$C_6H_4NO_2$(*o,p*) for WFL and GSI (A$_4$), respectively; αGalNAc→Ser(αGalNAc→)Thr for SSL; and αGalNAc→3(αFuc→2)βGal→3βGlcNAc→3βGal→4Glc, an A active hexasaccharide[25] for LBL. [d] Not determined. [e] From the results of αGalNAc→3(Fuc→2)βGal→4GlcNAc (*A* active, tetra-); 3+ and αGal→3(αFuc→2)Gal, 2+, it can be concluded that Fuc is important for binding[25]. [f] Values obtained from βGal→3GalNAc related inhibitors. [g] Values obtained from αGalNAc glycosides and also interact well with desialyted ovine salivary mucus glycoprotein, and mild acid treated armadillo salivary glycoprotein [αGalNAc→Ser(Thr) of the protein core] (unpublished data). [h] R; related carbohydrate residues.

TABLE II

Comparison of the reactivities of βGal→linked-specific lectins[a]

Carbohydrate residues or groups capable of reaction	*Class of lectin*[b]	*βGal →3GalNAc*							*βGal →3(4) GlcNAc*				*αGal→3Gal*
		PNA[46]	*MPL*[30]	*BPL*[31]	*SJL*[33,c]	*RCa*$_2$[34]	AIL[35,d]	ALL[36]	*RCA*$_I$[37]	*ECL*[38]	*GCL*[39]	*TAL*[19]	*GSI-B*$_4$[27]
βGal→3αGal-NAc→O	T	4+	4+	4+	4+	4+[d]	4+[d]	4+	[e]	[e]	[e]	[e]	[e]
αGalNAc→Ser (Thr)	Tn	−	4+	3+	?	2+[d]	2+[d]	2+	[e]	+	+	[e]	−
βGal→4 βGlcNAc →R	II	2+	−	3+	2+	2+[d]	±[d]	4+	3+	3+	4+	+[g]	[e]
βGal→3 βGlcNAc →R	I	+	−	3+	2+	[e]	±[d]	3+	2+	4+	4+	[e]	[e]
αGal→3Gal αGalNAc →3βGal→R	B	+	−	2+	−	[e]	[e]	[e]	2+	+	[e]	[e]	4+
	A	−	−	2+	−	[e]	[e]	[e]	[e]	[e]	[e]	[e]	−

[a] Based mainly on the results obtained from precipitin-inhibition assays: 4+, best inhibitors; 3+, about 1/2 the best; 2+, about 1/10 of the best; +, about 1/100 of the best; ±, less than 1/100; −, no inhibition. [b] Representive structures shown in Table III. [c] The best inhibitor for SJL is βGal→3βGalNAc-*N*-tosyl-L-serine. [d] Based on association constant[35]. [e] Not determined. [f] The specificity for αGalNac→3Ser or Thr is estimated from the results of precipitin-inhibition assays; the inhibitory potency of GalNAc for PNA, that of αGalNAc-linked glycosides for MPL and BPL, and that of methyl αGalNAc for ECL. The reactivity of SJL towards this residue is questionable. [g] The best inhibitor for TAL was a biantennary saccharide with two βGal→4βGlcNAc residues (see structure **1**) at the nonreducing end[19] as 4+.

TABLE III

Classification of 2-acetamido-2-deoxy-D-galactose- and D-galactose-specific lectins

	Determinant		
	Class	*Structure*	*Source and others*
1	F	αGalNAc→3GalNAc	Forssman specific disaccharide
2	A	αGalNAc→3Gal	Human blood group A specific disaccharide
	A_F	αGalNAc→3(αFuc→2)Gal	
3	Tn	αGalNAc→3Ser/Thr of protein core	Tn antigen
4	T	βGal→3αGalNAc→3Ser/Thr of protein core	The mucin-type sugar sequence on the human erythrocyte membrane
		βGal→3βGalNAc...ceramide	Gangliosides
5	I	βGal→3(4)GlcNAc	Human blood group type I
	II	βGal→4GlcNAc	and II carbohydrate sequences[40]. Most of the lectins reactive to II are also reactive to I. Lectin I(II) determinants can be found at the nonreducing end of the carbohydrate chains derived from either *N* or *O*-glycans.
6	B	αGal→3Gal	Human blood group B specific disaccharide

The source and structural relationship of the lectin determinants are shown in Scheme 1. Most of the lectin F determinants are found in glycosphingolipids[41–43], and the other determinants are present in mammalian glycoconjugates, especially in the human blood groups A, B, H, Le^a, Le^b, and Ii-active glycoproteins prepared from human ovarian cyst fluid[44,45]. The reactivities of lectin determinants (lectin-active disaccharides) represent a combination of the binding of two individual sugars. The contribution of each sugar to the binding is not necessarily equal, and is different among lectins. For example, both *Maclura pomifera* (MPL) and peanut (PNA) lectins are βGal→3GalNAc specific[30,46]; however, the inhibitory profile of the monosaccharide with these two lectins is quite different; GalNAc > Gal in MPL and Gal > > GalNAc (inactive) in PNA. From the data available in Tables I and II, a novel system to express the relationship among the carbohydrate specifities of Gal and GalNAc lectins is illustrated in Table IV.

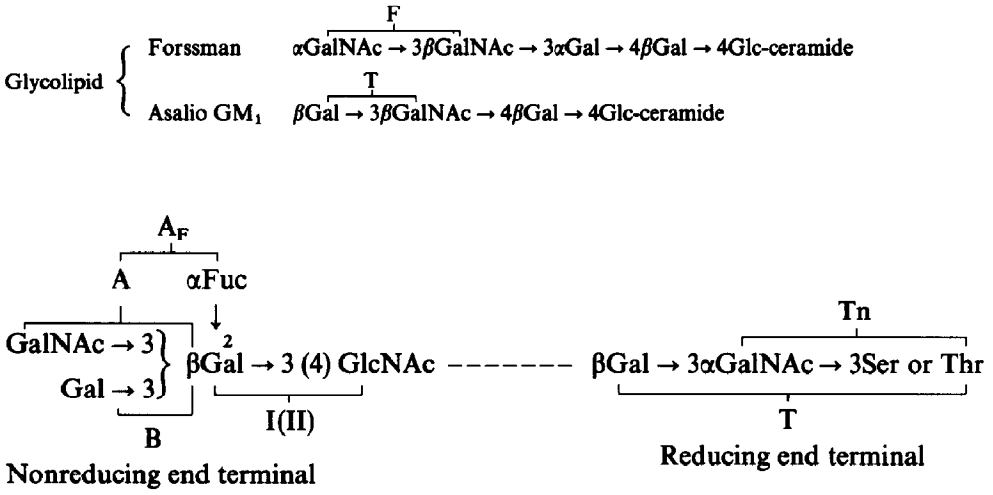
TABLE IV

Gal/GalNAc-specific lectins

Class (specificity)	*Name*	*Determinants (Active carbohydrate sequence)*
F/A	*Dolichos biflorus* (DBL)	F > A_T^a > A > Tn
	Helix pomatia (HPL)	F > *A* (> A_T^b) ≥ Tn, T
	Hog peanut (ABL, *Amphicarpaea bracteata*)	F > A > Tn
	Wistaria floribunda (WFL)	A(A_T^b, F > Tn, I(II)
A	Lima bean (LBL)	Hexa-A_T^a > A_T^b > > B
	Griffonia (Bandeiraea) simplicifolia-A_4 (GSI-A_4)	A > A_T^b > > B
	Soy bean (SBL)	A(> A_T^b), Tn and I(II)
	Vicia villosa (VVL) (A mixture of A_4, A_2B_2, and B_4)	A(> A_T^b) and Tn mainly
Tn	*Vicia villosa* B4 (VVL-B4)	Two Tn > > one Tn > > one or two T
	Salvia sclarea (SSL)	Two Tn > single or three sequential Tn structures
T	Peanut (*Arachis hypogaea*, PNA)	T > > I(II)
	Maclura pomifera (MPL)	T > Tn
	Bauhinia purpurea alba (BPL)	T > I(II) and Tn
	Sophora japonica (SJL)[c]	T and I(II)
	Artocarpus integrifolia (jacalin, AIL)	T > Tn > > > I(II)
	Ricinus communis toxin (ricin, RCA2)	T > I(II) and Tn
I(II)	*Ricinus communis* agglutinin (RCA_1)	I(II) > T and B
	Datura stramonium (TAL, thorn apple)	Biantennary I(II) (Penta-2,6) > > C[d]
	Erythrina cristagalli (coral tree, ECL)	Multiple antennary
	Geodia cydonium (GLC)	I(II) and Tn
B	*Griffonia (Bandeiraea) simplicifolia*-B_4 (GSI-B_4)	B

[a] Substitution of αFuc→2 to subterminal Gal is an important factor for binding. [b] Substitution of αFuc→2 to subterminal Gal blocks binding. [c] Some helping factor is required for precipitation of the lectin. [d] C, chitin oligosaccharide.

On this bais, the lectins determined by other methods and the lectins that require more information for classification can be included. Thus, the GalNAc-specific lectins could be subgrouped as shown in Tables V–VIII and the Gal-specific lectins in Tables IX–XII.



Scheme 1. Proposed Gal- and GalNAc-specific lectin determinants. Lectin F determinant is found in glycosphingolipid (the principal glycolipid of mammalian tissues) of the tissues of the guinea pig, horse, cat, and chicken. It can also be found on the surface of some bacteria, viruses, human gastric carcinoma, and colon tumors[41–43]. All (F, A/Af, B, I/II, T, and Tn) determinants are found in human blood groups A, B, H, Le^a, Le^b, and Ii active glycoproteins, prepared from human ovarian cyst fluid[44,45]. The βGal→3βGalNAc group at the nonreducing end of asialo-GM_1 is also considered as a lectin T determinant. Determinants of lectins I and II discussed in this article are equivalent to human blood group type I (Lacto-*N*-biose, βGal→3GlcNAc) and type II (*N*-acetyllactosamine) carbohydrate sequences[40].

TABLE V

I-1. αGalNAc→3GalNAc (Forssman, F) and αGalNAc→3Gal (human blood group A)-specific lectins

DBL, *Dolichos biflorus* lectin (horse Gram)[20a].
αGalNAc→3βGalNAc→3αGal→4βGal→4Glc (Forssman-specific pentasaccharide) > > αGalNAc→3GalNAc > > αGalNAc→3[αFuc→2]βGal→4βGlcNAc→6R (Blood group A active pentasaccharide, R_{LAC}, 0.52[a]) > αGalNAc→3βGal→3GlcNAc (A_5II)[a] and αGalNAc→3Gal (R_{LAC}, 1.85[a]) > GalNAc.

HPL, *Helix pomatia* lectin (edible snail)[20a,21].
αGalNAc→3βGalNAc→3αGal→4βGal→4Glc (Forssman-specific pentasaccharide) > αGalNAc→3Gal > αGalNAc→3βGalNAc→3GlcNAc (A_5II^a) > GalNAc.

ABrL, *Amphicarpaea bracteata* lectin (hog-peanut)[22].
αGalNAc→3GalNAc > αGalNAc→3Gal > GalNAc.

WFL, *Wistaria floribunda* lectin[20a,23].
αGalNAc→6Gal > αGalNAc→3Gal (R_{LAC}, 1.85[a]), αGalNAc→3βGalNAc→3αGal→4βGal→4Glc (Forssman-specific pentasaccharide) and αGalNAc→3βGal→3GlcNAc (A_5II^a) > βGalNAc→3αGal→4βGal→4Glc (Globoside) > αGalNAc→3GalNAc > GalNAc and αGalNAc→3(αFuc→2)βGal→4βGlcNAc→6R (R_{LAC}, 0.52[a]) > βGal→4GlcNAc (*N*-acetyllactosamine) > Lactose.

SBL, *Glycine max* lectin (soy bean) see Table VI.

[a] Coded for the source or properties of oligosaccharides tested.

TABLE VI

I-2. αGalNAc→3Gal (human blood group A)-specific lectins

GSI-A_4, *Griffonia (Bandeiraea) simplicifolia* A_4[20a,27].
αGalNAc→3βGal→3GlcNAc (A_5II^a), αGalNAc→3Gal (R_{LAC}, 1.85[a]), and αGalNAc→6Gal, αGalNAc→R > αGal→3Gal, αGal→6Glc, and raffinose > Gal.

LBL, *Phaseolus lunatus* lectin (lima bean)[20a,21,25].
αGalNAc→3(αFuc→2)βGal→3βGlcNAc→3βGal→4Glc > αGalNAc→3(αFuc→2)βGal→4Glc > αGalNAc→3(αFuc→2)βGal→4βGlcNAc→6R (R_{LAC}, 0.56[a]) > αGalNAc→3(αFuc→2)Gal > > GalNAc > > Gal. αFuc→2 to subterminal Gal is an important factor for binding.

SBL, *Glycine max* lectin (soy bean)[20a,24,47].
α- or β-GalNAc, αGalNAc→3βGal→3GlcNAc (A_5II^a) and αGalNAc→3Gal (R_{LAC} 1.85[a]) > > αGalNAc→3(αFuc→2)βGal→4βGlcNAc→6R (R_{LAC} 0.52[a]), αGal→6Glc (melibiose), βGal→6Glc, raffinose, stachyose, βGal→4Glc (lactose), and αFuc→2βGal→4βGlcNAc→6R (human blood H active oligosaccharide, JS, R_{LAC} 0.75[a]) > Gal. αFuc→2 to subterminal Gal blocks Gal for binding.

PT4, *Psophocarpus tetragonolobus* lectin[24a].

SN4, *Sambucas nigra* lectin[24b].

PTL, *Psophocarpus tetragonolobus* lectin[24a].
αGalNAc→3 [αLFuc→2]βGal→4 [αLFuc→3] Glc (A-penta) αGalNAc→3 [αLFuc→2] βGal→4Glc (A-tetra), and αGalNAc→3βGal→3GlcNAc > αGalNAc→3[αLFuc→2]Gal (A-tri), αGalNAc→3Gal (A-di), αGal→3 [αLFuc→2] βGal→4 [αLFuc→2] Glc (B-penta) αGalNAc→3βGalNAc→3αGalO $(CH_2)_8COOMe$ (Forssman trisaccharide), and GalNAc > αGal→3Gal (B–Di) > Gal.

SNA-II, *Sambucus nigra* lectin[24b].
αGalNAc→3Gal and αGalNAc→6Gal > βGalNAc→6Gal > GalNAc > di-(structure **1**), tri, -tetra, -antennary oligosaccharides containing βGal→4GlcNAc at nonreducing end > βGal→3GalNAc (**T**) > > βGal→4GlcNAc > Gal.

VVL, *Vicia villosa* lectin (hairy vetch; it is assumed that the lectin used to study the following determinant is a mixture of three isolectins: A_4-minor, B_4-major, and A_2B_2-minor[28,29].
αGalNAc→3Gal (R_{LAC}, 1.85[a]) > αGalNAc→6Gal > αGalNAc→3βGal→3GlcNAc (A_5II^a) and αGalNAc→3GalNAc > > αGalNAc→3(αFuc→2)βGal→4βGlcNAc→6R (R_{LAC} 0.52[a]) > αGal→3Gal.

WFL, *Wistaria floribunda* lectin (see Forssman-specific lectins, Table V, I-1).

DBL, *Dolichos biflorus* lectin (see Forssman-specific lectins, Table V, I-1).

HPL, *Helix pomatia* lectin (see Forssman-specific lectins, Table V, I-1).

[a] Coded for the source or properties of oligosaccharides tested.

TABLE VII

I-3. αGalNAc→3Ser or Thr (Tn)-specific lectins

VVL-B_4, *Vicia villosa* B_4 lectin (hairy vetch)[48,49].
A fetuin glycopeptide containing two αGalNAc→Ser(Thr) of the peptide chains (two Tn structures) > > single Tn structure > > a fetuin glycopeptide containing one or two βGal→3αGalNAc→Ser(Thr) of the peptide chain(s) (T structure) > αNeuNAc→3βGal→3αGalNAc→Ser(Thr) of the peptide chain.

SSL, *Salvia sclarea* lectin[50].
Glycopeptides containing two Tn structures > glycopeptides containing one Tn structure or glycopeptides containing three sequential Tn structures.

MPL, *Maclura pomifera* lecin.
(see βGal→3GalNAc-specific lectins, Table IX, II-1).

BPL, *Bauhinia purpurea alba* lectin.
(see βGal→3GalNAc-specific lectins, Table IX, II-1).

TABLE VIII

I-4. Other GalNAc-specific lectins requiring further characterization

APL, *Aegopodium podagraria* lectin[51].
GalNAc > lactose > Gal > melibiose > raffinose > Ara.
BDL, *Bryonia dioica* lectin[52].
GalNAc > lactose > melibiose > raffinose > stachyose.
CAL, *Caragana arborescens* lectin (pea tree)[53].
GalNAc > Gal > lactose and raffinose > stachyose > Ara > rhamnose.
CTL, *Clerodendron trichotomum* lectin[54].
GalNac > lactose > melibiose > Gal.
CNL, *Clitocycle nebularis* lectin[55].
GalNAc and Gal.
DDL-I, *Dictyostelium discoideum* I lectin (Discoidin I)[56,57].
GalNAc > D-Fuc > melibiose > lactose > Gal > L-Fuc.
EHy, L, *Eranthis hyemalis* lectin (winter aconite root tubers)[58].
GalNAc > lactose > Gal > melibiose > L-Fuc > Ara > raffinose.
EHe, L, *Euphorbia heterophylla* lectin[59].
GalNAc > lactose > Gal > melibiose > Fuc.
FFL, *Fomes fomentarius* lectin[55].
GalNAc > raffinose > Gal.
FJL, *Falcata japonica* lectin[55a].
GalNAc.
HCL, *Hura crepitans* seed lectin[60].
GalNAc > Gal > melibiose and D-Fuc > raffinose.
MAL, *Macrotyloma axillare* anti-A lectin[61].
GalNAc.
MCL, *Momordica charantia* lectin (bitter pear melon)[62,63].
GalNAc > D-Fuc > Gal > raffinose and stachyose > melibiose and L-Ara.
OHL, *Ononis hircina Jacq* lectin[64].
GalNAc > lactose > Gal > GlcNAc > Ara.
PTL, *Psophocarpus tetragonolobus* lectin (winged bean)[65-67,24a].
GalNAc > Gal and melibiose > raffinose > D-Fuc > lactose.
RPL, *Robinia pseudacacia* lectin[68].
GalNAc.
TML, *Tridacna maxima* lectin (Röding clam)[69].
GalNAc > βGal→6Gal, lactose and Gal > melibiose, raffinose, and stachyose.
VCL, *Vicia cracca* anti-A lectin[70].
GalNAc.
VAL-II & III, *Viscum album*-II & III lectins (mistletoe)
GalNAc > Gal[71].

TABLE IX

II-1. βGal→3GalNAc (T)-specific lectins

PNA, *Arachis hypogaea* lectin (peanut)[46,72].
βGal→3GalNAc > > βGal→4GlcNAc (*N*-acetyllactosamine) > Gal and βGal→3GlcNAc > > > GalNAc (inactive).
BPL, *Bauhinia purpurea alba* lectin[31,73].
βGal→3GalNAc > αGalNAc→6Gal > GalNAc. βGal→3βGlcNAc→3βGal→4Glc (lacto-*N*-tetraose) > βGal→3GlcNAc, βGal→6GlcNAc and αGalNAc→3βGal→3GlcNAc (A_3II^a) > αGalNAc→3Gal > βGal→4GlcNAc (*N*-acetyllactosamine) and βGal→3(αFuc→4)βGlcNAc→3βGal→4Glc (lacto-*N*-fucopentaose II) > βGal→4βGlcNAc→6Gal and lactose > Gal.
MPL, *Maclura pomifera* lectin (osage orange tree, hedge apple tree)[30].
βGal→3GalNAc > > αGalNAc→6Gal > αGal→6Glc (melibiose), stachyose > GalNAc > Gal.

TABLE IX (continued)

SJL, *Sophora japonica* lectin (Japanese pagoda tree)[33].
βGal→3βGalNAc→*N*-tosyl-L-serine > βGal→3GlcNAc > βGal→3βGlcNAc→3βGal→4Glc (lacto-*N*-tetraose) > βGal→3βGlcNAc→6Gal > βGal→4βGlcNAc→6Gal (blood group I Ma-active trisaccharide) and βGal→4GlcNAc > GalNAc > > lactose > Gal and melibiose.
Some unknown mild acid sensitive compound near, the terminal group at the nonreducing end plays an important role in binding or precipitating this lectin.

RCA_2, ricin[34,47,74].
(βGal→3αGalNAc→Ser or Thr)$_4$ glycopeptide > > triantennary oligosaccharides containing βGal→4GlcNAc at nonreducing end > (βGal→3αGalNAc→Ser or Thr)$_2$ glycopeptide with space between carbohydrate side-chains, βGal→3αGalNAc→βSer or Thr > > αGalNAc→Ser or Thr[34].
The ability of RCA_2 to bind to βGal→3GalNAc disaccharides appears to be markedly influenced by the relative locations of the disaccharides along the peptide backbone.
Biantennary oligosaccharides containing βGal→4GlcNAc at nonreducing end > lactose > GalNAc > melibiose and Gal[34,47] (≥ GalNAc, see ref. 74).

VGL, *Vicia graminea* lectin (blood group N-specific)[75,76].
βGal→3αGalNAc-linked in clusters and desialylated blood group N glycopeptide > untreated N glycopeptide and desialylated M glycopeptide.

ABiL, *Agaricus bisporus* lectin (mushroom)[77,78].
βGal→3GalNAc-*N*-tosyl-L-serine.

ACL, *Amaranthus caudatus* lectin[78a].
βGal→3αGalNAc → Ser/Thr > > GalNAc > > > Gal, βGal→3(4)GlcNAc (inactive).

ARL, *Agropyrum repens* lectin (couch grass)[79].
βGal→3GalNAc > GalNAc and chitin oligosaccharides (with type A cells).

AIL, *Artocarpus integrifolia* lectin (jacalin)[80,81,81a].
β-Gal→3GalNAc > αGalNAc→Ser/Thr > > > βGal→3GlcNAc, βGal→4GlcNac, and βGal→4Glc.

ALL, *Artocarpus lakoocha* lectin[36,82].
βGal→3GalNAc > αGalNAc→3Ser/Thr > melibiose > raffinose > Gal.

TABLE X

II-2. βGal→3(4)GlcNAc (human blood group type I and type II carbohydrate sequences; I & II)-specific lectins

AIDL-II, Allo L-II, *Allomyrina dichotoma* lectin II (hemolyph of a beetle)[82a,b].
βGal→4GlcNAc, substitution of their terminal Gal residues by αNeu5Ac→6 will enhance their affinity to this lectin.

RCA_1, *Ricinus communis* agglutinin (castor bean)[34,37,47,83].
Biantennary oligosaccharides containing βGal→4GlcNAc-linked units at nonreducing end > βGal→4βGlcNAc→6Gal (blood group I Ma specific) > βGal→4GlcNAc > βGal→3GlcNAc > lactose > αGal→3Gal > raffinose.
RCA_1 is also specific for βGal→3αGalNAc→3Ser (Thr). For further information, see ref. 34.

TAL, *Datura stramonium* lectin (DSL, thorn apple)[47,84-87].
Penta-2,6 (1) > > Penta-2,4 (2) > (βGlcNAc→4)$_4$ > (βGlcNAc→4)$_3$ > βGal→4GlcNAc (*N*-acetyllactosamine), βGlcNAc→4GlcNAc, and βGal→4βGlcNAc→6Man > αMan→4βMan→(GlcNAc)$_2$ > βGlcNAc→4Glc.
More information is available in ref. 85.

ECL, *Erythrina cristagalli* lectin (coral tree)[38].
Tetra- and tri-antennary oligosaccharides containing β-Gal→4GlcNAc-linked units at nonreducing end > βGal→4βGlcNAc→6Gal (blood group I Ma specific) > βGal→4GlcNAc > βGal→3GlcNAc > > lactose > > > βGal→6Gal and αGal→3Gal > raffinose.

GCL, *Geodia cydonium* lectin[39].
βGal→4GlcNAc, βGal→3GlcNAc, and lactose > GalNAc.

TABLE X (continued)

LEL, *Lycopersicon esculentum* lectin (tomato)[85a,b].
In addition to (βGlcNAc→4)$_{2-4}$, βGal→4βGlcNAc→3Gal→4βGlcNAc→6Gal-ol sequence is also one of active oligosaccarides.

EVL, *Erythyina variegata* lectin[85c].
βGal→4βGlcNAc→3 [βGal→4βGlcNAc→6] Gal sugar sequence is the active one.

Other *Erythrina* lectins[88].
E. caffra$^+$ (ECaf, L), *E. corallodendron* (ECor, L), *E. flabelliformis* (EFL), *E. humeana* (EHL), *E. latissima* (ELat, L), *E. lysistemon* (Elys, L), *E. perrierie*$^+$ (EPL), *E. stricta* (ESL), and *E. zeyheri* (EZL).
Tri- or bi-antennary oligosaccharides containing βGal→4GlcNAc at nonreducing end > *N*-acetyllactosamine > lactose ⩾ GalNAc > Gal (GalNAc ⩾ lactose ⩾ Gal).

PHA-E, *Phaseolus vulgaris* (isolectin E_4) erythroagglutinin (red kidney bean)[89–91].
Structure **3**, in which R^1 and R^2 represent either hydrogen atoms or sugars, and R^3 represents either GlcNAc or αFuc→6)-GlcNAc, is the minimum structural unit.

PAL, *Phytolacca americana* lectin (pokeweed mitogen).
Three different carbohydrate specificities have been reported; their relationship has not been established. βGal→4βGlcNAc→6 linked[85a]. Branched poly(βGal→4GlcNAc) complex[92], (βGlcNAc→4)$_{n>5}$ units[93], or αMan→2αMan→2αMan→3βMan→4βGlcNAc→4GlcNAc-Asn[94].

PHA-L, *Phaseolus vulgaris* (isolectin L_4) leukoagglutinin[89,95].
Tri- and tetra-atennary oligosaccharides containing βGal→4GlcNAc-linked units at nonreducing end > > Penta-2,6 (1) > Tri-2,6 (4) > **5** > βGal→4βGlcNAc→2Man > βGlcNAc→2Man.

EHL, *Eranthis hyemalis* agglutinin (from winter-aconite root tubers)[96].
βGal→4GlcNAc > βGal→4Glc > Gal, melibiose > raffinose.

PNL, *Arachis hypogaea* lectin (see βGal→3GalNAc-specific lectins, Table IX, II-1).

BPL, *Bauhinia purpurea alba* lectin (see βGal→3GalNAc-specific lectin, Table IX, II-1).
Ricin (see Galβ1→3GalNAc specific lectins, Table IX, II-1).

UDL, *Urtica dioica* lectin (stinging nettle)[97].
(βGlcNAc→4)$_4$ > (βGlcNAc→4)$_3$ > > βGlcNAc→4GlcNAc and βGal→4βGlcNAc→6Man ⩾ αMan→3βMan→4GlcNAc > βGal→4GlcNAc (*N*-acetyllactosamine) > > GlcNAc > > GalNAc.

SNL, *Sambucus nigra* lectin[98,99].
Bovine fetuin triantennary carbohydrate chains or porcine thyroglobulin biantennary carbohydrate chains > αNeu5Ac→6βGal→4βGlcNAc→3βGal→4Glc > αNeu5Ac→6βGal→4Glc > αNeu5Ac→6βGal→4Glcol > > αNeu5Ac→3βGal→4Glc > αNeu5Ac→3βGal→3βGlcNAc→3βGal →4Glc > βGal→4GlcNAc and βGalNAc→6Gal > βGal→4Glc and αGalNAc→6Gal > GalNAc and αGalNAc→3Gal ⩾ Gal > melibiose, raffinose, and stachyose.

WGA, *Triticum vulgaris* agglutinin (wheat germ)[47,85a,85d–h].
βGal→4βGlcNAc→6Gal, (βGal→4) βGlcNAc→6GalNAc and (βGlcNAc→4)$_{2or3}$ > βGal→4βGlcNAc→3Gal > > > βGal→4GlcNAc (*N*-acetyllactosamine) > βGal→3GalNAc (inactive).
In addition to βGlcNAc→4GlcNAc, the βGlcNAc→6 sequence is the most important structure for binding. βGlcNAc→4GlcNAc sequence, the lectin C determinant, can be found in mammalian *N*-linked carbohydrate chains as part of core trisaccharide and βGal→4βGlcNAc→6Gal frequently found in mammalian *O*- and *N*-linked glycoproteins.

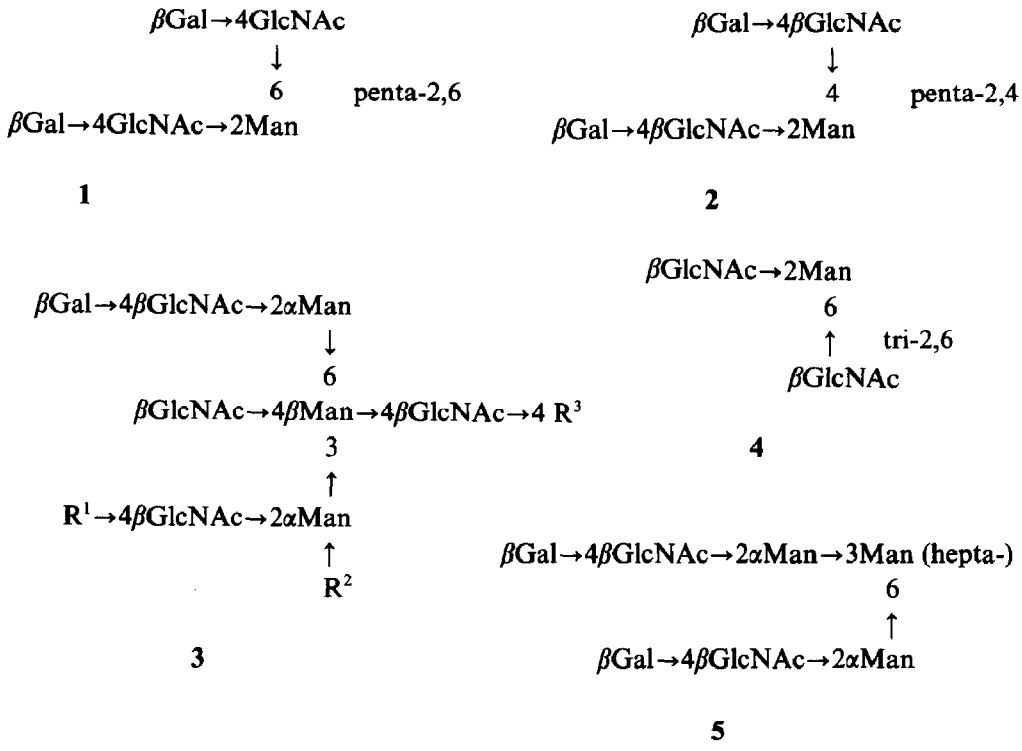


TABLE XI

II-3. αGal→3Gal (B)-specific lectin

GSL-B_4, *Griffonia (Bandeiraea) simplicifolia* I-B_4 lectin[27].
αGal→3Gal > melibiose > raffinose > Gal > > > GalNAc (inactive).

TABLE XII

II-4. Other Gal-specific lectins and those requiring more information for classification

AXP-I and II, *Axinella polypoides* I and II lectins[100].
βGal→6R > βGal→4R > melibiose and raffinose > Gal.
MXL, *Myxococcus xanthus* lectin[101].
NeuNAc-βGal→3GalNAc-3Ser(Thr) (possibly).
APL, *Abrus precatorius* lectin (jequirity bean)[102,103].
Lactose and Gal > melibiose > Fuc.
Abrin[102,103].
Gal > lactose > melibiose > Fuc and Ara > Glc.
ADL, *Aplysia depilans* lectin[104].
Galacturonic acid > Gal.
AML, *Ascidia malaca* lectin[105].
Melibiose > raffinose > Gal > lactose > Ara.
ABL, *Abramis brama* lectin[106].
Rhamnose > Gal.

TABLE XII (continued)

BCL, *Bauhinia carronii* lectin[107].
Gal and lactose.
BFL, *Butea frondosa* lectin[63].
Lactose > D-Fuc > Gal > GalNAc > Ara.
CJL, *Crotalaria juncea* lectin (Sunn hemp)[108].
Lactose > melibiose > raffinose > GalNAc > Gal.
CML-I, *Cytisus multiflorus*-I lectin[109].
Gal, lactose, and melibiose > stachyose > raffinose.
CSL, *Cytisus scoparius* lectin[110].
Gal and GalNAc.
DCL, *Didemnum candidum* lectin[111].
Lactose > Gal > melibiose > stachyose > GalNAc.
DDL-II, *Dictyostelium discoideum*-II lectin (discoidin II)[57].
Lactose and D-Fuc > Gal > melibiose > GalNAc > Fuc.
EAL, *Erythrina arborescens* lectin[112].
Lactose and GalNAc > melibiose and Gal > D-Fuc.
EIL, *Erythrina indica* lectin[63,112].
Lactose > GalNAc and melibiose > Gal and raffinose > D-Fuc.
ELL, *Erythrina lithosperma* lectin[112].
Lactose and melibiose > GalNAc and raffinose > Gal > D-Fuc.
ESL, *Erythrina suberosa* lectin[112].
Lactose > GalNAc > melibiose and Gal > raffinose > D-Fuc.
ECL, *Euphorbia characias* L. lectin (Mediterranean spurge)[113].
Lactose > melibiose > Gal > D-Fuc > Ara.
HRL, *Halocynthia roretzi* lectin[114].
Melibiose > lactose, Gal and D-Fuc > Fuc and stachyose.
HaCL, *Hardenbergia comptoniana* lectin[107].
Raffinose.
HuCL, *Hura crepitans* latex lectin (sand-box tree)[113].
Lactose > Gal and melibiose > Ara.
LAL, *Laccaria amethystina* lectin (LAL) (mushroom)[115].
Lactose > GalNAc.
OVL, *Octopus vulgaris* lectin[116].
Lactose and *N*-acetyllactosamine.
PAL, *Phaseolus aureas* or *Vigna radiata* lectin (mung bean)[117].
Gal > Xyl > inositol.
PPL, *Polysphondylium pallidum* lectin (pallidin)[56,118].
Lactose > Gal > GalNAc and D-Fuc > Fuc.
RRL, *Rutilus rutilus* lectin[106].
Rha > Gal and Ara > lactose.
SaSL, *Sarothamnus scoparius* lectin[55].
Raffinose > GalNAc > Gal > lactose.
SEL, *Scardinus erythrophtalmus* lectin[106].
Rha > Ara > Gal.
ViVL, *Vimba vimba* lectin[106].
Rha > raffinose > Gal and Ara > lactose.
TKL, *Trichosanthes kirilowii* lectin[119].
Lactose > Gal > melibiose > raffinose.
VAL-I, *Viscum album* I lectin (mistletoe)[71,120].
Lactose > melibiose, raffinose and Gal.
VUL, *Vigna unguiculate* lectin (cow-pea)[121].
Gal.

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