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Minireview

The Structure of Glycophorins of Animal Erythrocytes

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Glycophorins are red cell membrane sialoglycoproteins, which contain multiple *O*-linked oligosaccharide chains and carry most of the cell surface sialic acid. Due to this high content of sialic acid the glycophorins are strongly stained with periodic acid-Schiff (PAS) reagent after sodium dodecylsulfate-polyacrylamide gel electrophoresis (SDS-PAGE). The term "glycophorin" was proposed initially for human red cell sialoglycoproteins [1, 2] and now it is also used for sialoglycoproteins in animal red cell membranes. Furthermore, similar glycoproteins of non-erythrocyte origin have also been identified and given the same name [3], although the terms "leukosialin" and "sialophorin" were proposed for a major sialoglycoproteins of human leukocytes [4, 5]. In this article the term "glycophorin" will be used only for sialoglycoproteins existing in the erythrocyte membrane.

Glycophorins of human erythrocytes, carrying blood group MN, Ss and other determinants, have been thoroughly studied and their properties described in several review articles [3, 6, 7, 8]. The aim of this article is to summarize studies carried out on the structure of non-human glycophorins, although some data concerning human glycophorins are included for comparative purposes.

1. General Properties of Glycophorins

Glycophorins are integral membrane components and have three distinct structural domains (see Section 3) comprising an extracellular NH_2-terminal portion, which car-

Abbreviations: SDS-PAGE, sodium dodecylsulphate-polyacrylamide gel electrophoresis; PAS, periodic acid-Schiff; LIS, lithium diiodosalicylate.

Table 1. Some general properties of glycophorins identified in various species.

Origin of erythrocytes	M_r obtained from		Approximate carbohydrate content (w/w)	Presence of *N*-linked oligosaccharides	References
	SDS-PAGE	primary structure			
human A(α)	37 000	31 000 (131aa)[a]	60%	+	8,14-20
B(δ)	24 000			—	
C(β)	32 000	28 000 (128aa)	50%	+	
D(γ)	27 000				
monkey (*Macaca fuscata*)			49%	—	21
horse HA		20 000 (120aa)	30%	—	22-25
HB	22 000		20%	+	
bovine GPII	55 000 (dimer)		77%	+	10,26,27,28
GPI	34 000		27%	+	
pig	53 000 (dimer)	27 000 (133aa)	48%	+	29,30,31
sheep	27 000		56%		32,33
goat	25 000		50%	—	34
dog	23 000		37%	—	35
rabbit RA	120 000 (oligomer)		58%	+	36
rat	19 000 31 000		68%	—	37,38
mouse	31 000		68%	+	39-42
	46 000 (dimer)		49%	—	

[a] aa = amino acids

ries all oligosaccharide chains; an intramembranous hydrophobic domain, which spans the phospholipid bilayer; and the COOH-terminal cytoplasmic fragment.

Glycophorins are easily solubilized by dissolving the membranes and removing the membrane lipids. The most frequently used methods include biphasic hot phenol-water or butanol-water extraction, dissolving the membranes in lithium diiodosalicylate (LIS) followed by cold phenol extraction, solubilization with pyridine [9] or hot 75% ethanol extraction [10]. Due to their amphipathic properties, glycophorins strongly aggregate in water solution, giving aggregates of molecular weight up to 10^6 [11, 12]. The dissociation of aggregates in the presence of detergents is not complete; typical for many glycophorins is their existence in the form of dimers, even in SDS-containing solutions. Therefore, when red cell membranes are analyzed in SDS-PAGE, the number of PAS-positive bands does not reflect the number of different glycophorins, because some bands represent their homo- and heterodimers and also higher oligomers [6, 7]. The equilibrium between dimeric and monomeric forms of glycophorins is strongly dependent on their concentration in the solution [13].

Glycophorins show considerable heterogeneity in glycosylation, both in the diversity of the structure of oligosaccharide chains and in the incomplete glycosylation of some amino acid residues. Some interspecies similarities and some species-related differences between these sialoglycoproteins are described below.

2. Glycophorins Identified in Animal Erythrocytes

Some of the general features of the glycophorins are summarized in Table 1. The data on the apparent molecular weight of glycophorins were obtained from SDS-PAGE, but the position of the bands corresponding to monomers was not established in some cases. Besides human glycophorins A and C, the complete amino acid sequence has been determined for porcine and one of the horse glycophorins. The molecular weight of these glycophorins can be calculated on the basis of the amino acid sequence and carbohydrate composition and usually this value is lower than the apparent M_r determined in SDS-PAGE. The apparent M_r of most glycophorins is in the range of 20-30 000 and the glycophorins with known polypeptide sequences contain 120-133 amino acids.

The glycophorins are abundant glycoproteins of erythrocyte membranes, containing many *O*-glycosidic oligosaccharide chains and in some cases also one or two *N*-linked glycans. The carbohydrate content of glycophorins usually exceeds 40% by weight, of which about half is sialic acid. The exception is rabbit erythrocytes, which have a low content of sialic acid (slightly more than 10% of the amount found in the human erythrocyte membranes). As a consequence, the rabbit erythrocyte membranes do not show distinct glycophorin bands when analyzed in SDS-PAGE and stained with PAS reagent [36]. The rabbit erythrocyte membranes have another unusual property, in that they contain a large amount of a macroglycolipid [43] which may account for up to one-third of the crude, isolated "glycoprotein" fraction. The yield of the rabbit glycophorins is the lowest among animal erythrocytes (about 10 mg from 1 g of the dry red cell membranes), and it has been suggested that a large amount of the macroglycolipid may compensate for the small amount of glycophorin in the rabbit erythrocyte membranes [36]. One of two rabbit erythrocyte membrane glycophorins, designated RB, was shown to have a low content of sialic acid and to have no *O*-glycosidic chains at all. Thus it is doubtful whether this compound should be called a glycophorin, and it has not been included in Table 1. Preliminary data have also appeared on the monkey (*Macaca fuscata*) glycophorin [21]. Together with the total sugar content, the sequence of the first 28 amino acids from the *N*-terminus has been determined.

3. Structure of the Polypeptide Chains of Glycophorins

The amino acid sequence of three human and four animal glycophorins has been analyzed to date, but only four total sequences have been made (Fig. 1).

Human glycophorin A (MN glycoprotein) and glycophorin B (Ss glycoprotein) exhibit the same amino acid sequence for the first 26 residues. Furthermore, they have another region of homology starting from position 80 in glycophorin A and position 51 in glycophorin B. Glycophorin C is different and shows a low homology with glycophorins A and B. Pig and horse glycophorins show a significant homology with human glycophorins A and B in the amino acid sequence of the hydrophobic domains [22]. On

Figure 1. Total or partial amino acid sequence (one-letter code) and oligosaccharide attachment sites of human and some animal glycophorins.
*, *O*-glycosidic chains; +, *N*-glycosidic chains; <, blocked amino terminus; hydrophobic domains, inserted in the lipid bilayer, are shown within the boxes.

Table 2. The occurrence of different sialic acids in human and animal glycophorins.

Origin of red cell glycophorin	NeuAc	NeuGc	O-Ac-NeuAc	References
human	+	—	—	56-60
monkey *(Macaca fuscata)*	—	+	—	21
horse	—	+	—	61
bovine	—	+	—	62,63
pig	—	+	—	64
sheep	+	+	—	46
goat	—	+	—	46
dog	+	+	—	35,45,65
rabbit	—	+	—	65
rat	+	—	+	37,38
mouse	+	—	+	39,47

the other hand, the amino acid sequence of the amino-terminal domains of pig, horse and dog glycophorins is unique for each species and differs from those of human glycophorins. For monkey glycophorin it was observed, however, that the amino terminal sequence showed some similarity to the *N*-terminal region of human glycophorin A [21].

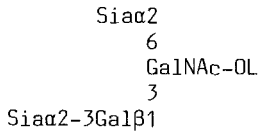
In conclusion, the data obtained so far indicate that interspecies differences are most pronounced in the amino-terminal, glycosylated portion of glycophorin molecules and that hydrophobic, intramembranous portions are most conserved. On the other hand, glycophorins of one species may also differ in amino acid sequence, as was shown for human glycophorin C, compared with glycophorins A and B.

4. Sialic Acids Present in Glycophorin Molecules

Three types of sialic acids have been identified in glycophorins: *N*-acetylneuraminic acid, *N*-glycolylneuraminic acid and *O*-acetyl-*N*-acetylneuraminic acids. The occurrence of these types of sialic acid in human and animal glycophorins is summarized in Table 2. In human glycophorins only *N*-acetylneuraminic acid is present, whereas most animal glycophorins contain *N*-glycolylneuraminic acid. Interesting results were obtained for dogs, since in individual dog breeds either *N*-acetylneuraminic acid or *N*-glycolylneuraminic acid occurred almost exclusively [45].

In sheep glycophorin *N*-acetylneuraminic acid and *N*-glycolylneuraminic acid were found in equimolar ratios [46]. In mouse glycophorins two kinds of sialic acid were found: *N*-acetylneuraminic acid and *O*-acetyl-*N*-acetylneuraminic acids [39]. One of the latter was identified in the Balb/c strain, using mass spectrometry, as 9-*O*-acetyl-*N*-acetylneuraminic acid [47]. According to the experimental data obtained during analysis of the *O*-linked oligosaccharides of tumor cell glycoproteins, the existence of both *N*-acetylneuraminic acid and *N*-glycolylneuraminic acid in glycoproteins is likely to arise from differences in the activity of *N*-acetylneuraminate mono-oxygenase [48].

1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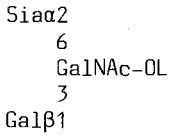
2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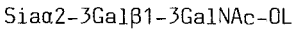
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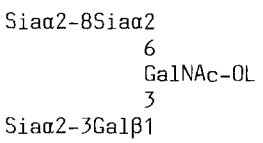
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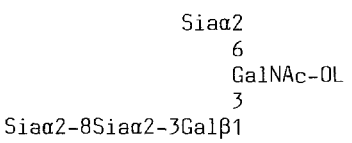
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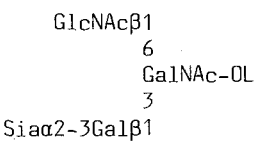
6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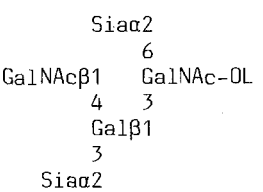
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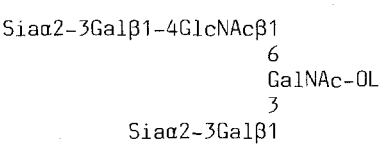
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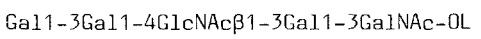
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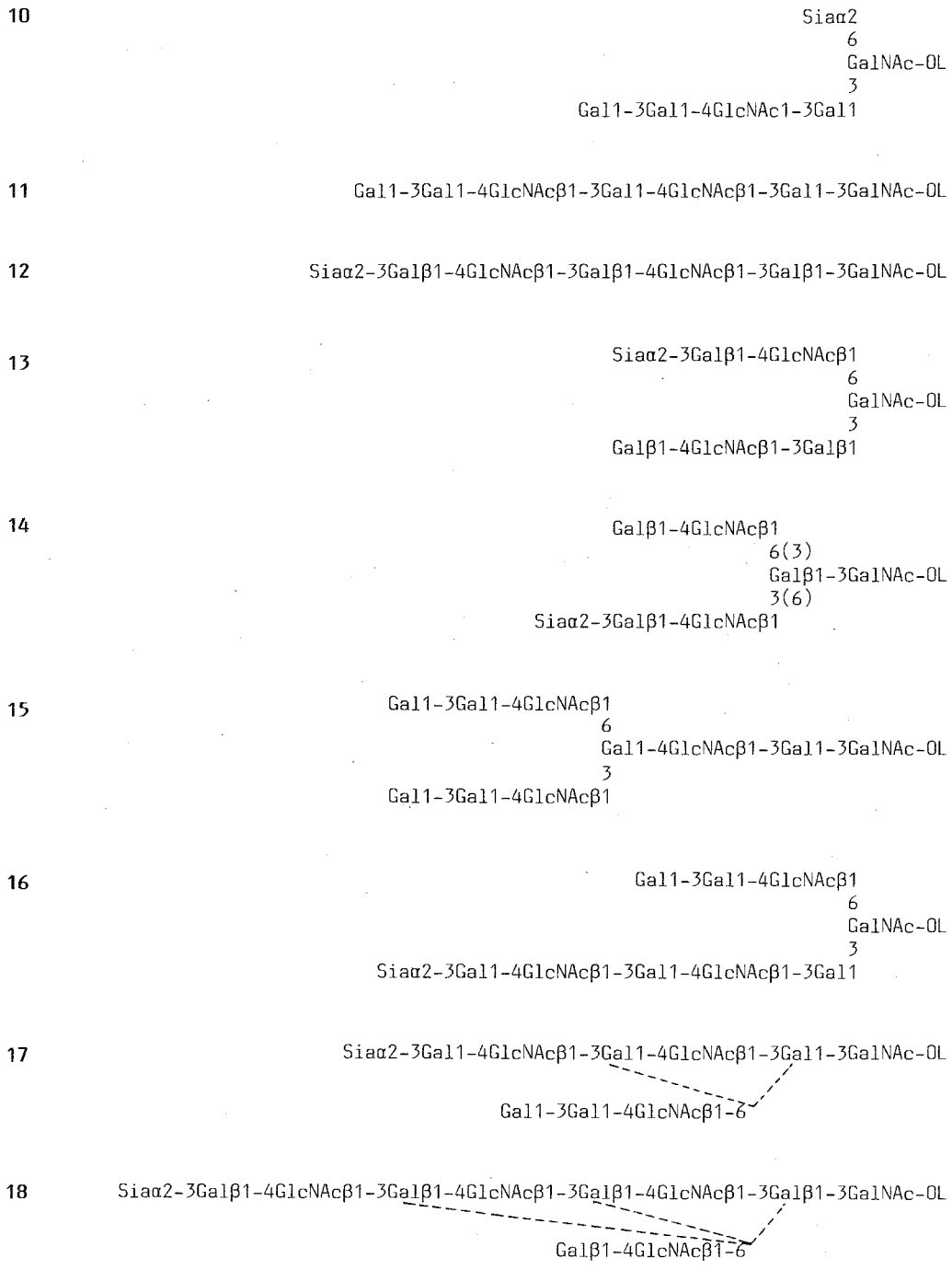


Figure 2. The structures of *O*-glycosidically linked oligosaccharides, found in the human and animal glycophorins. As a result of the isolation procedure these sugar chains were obtained in the reduced form. References to the structures are listed in Table 3; the dotted lines indicate the possible attachment sites. **6, 7** are oligosaccharides identified in rare human erythrocytes (MiIII and Cad) with variant glycophorin A [70, 73].

Table 3. Occurrence of *O*-glycosidic oligosaccharides in human and animal glycophorins.

Origin of glycophorin	Structures of *O*-glycosidic chains[a]	References
human	**1,2,3,4,5,6,7**	56,57,58,68,69,70,73
monkey	N.D.[b]	
horse	**1,2,3**	61
bovine	**9,11,12,13,14,15,16,17,18**	62,63,74
pig	**2,9,10**	64
sheep	**1**	75
goat	N.D.	
dog	**1,2,3**	45,65
rabbit	**1,2,3**	65
rat	**1,2,3,8**	38
mouse	**1,3,8**	76

[a] numbers refer to the structures shown in Fig. 2.
[b] N.D., not determined.

There are some experimental data indicating that the *O*-acetylated sialic acids have biological significance. For example, it was shown that 4-*O*-acetyl-*N*-acetylneuraminic acid was resistant to neuraminidase treatment [49] and that *O*-acetylated sialic acid residues may play a role in conferring the resistance of the oligosaccharides to serum neuraminidases [50]. Some viruses, containing agglutinins specific for sialic acid, reacted differently with glycophorins containing different forms of sialic acid [51, 52]. Other data indicated, that the difference in susceptibility of erythrocytes from different inbred mouse strains to lysis by the human alternate complement pathway was correlated with the degree of 9-*O*-acetylation of sialic acid residues [53]. Recently it was also shown that the influenza C virus has a highly specific requirement for the attachment to the cell surface, in that 9-*O*-acetyl-*N*-acetylneuraminic acid was the primary receptor determinant for this virus [54].

All the data mentioned above suggest that the chemical substitutions of neuraminic acids at different positions influence a number of physiological and pathological processes. The biological role of different forms of sialic acid has been reviewed recently [55].

5. Structure of the *O*-Glycosidic Oligosaccharide Chains of Glycophorins

Multiple *O*-glycosidic oligosaccharide chains, present in the glycophorins, are carbohydrate structures linked to the polypeptide chain through *N*-acetylgalactosamine-serine (or threonine) linkage [66]. These chains have been analyzed in glycophorins as reduced oligosaccharides after being released under mild alkaline/reducing conditions [67]. Several structures have been partially or completely characterized (Fig. 2). The occurrence of these structures in the glycophorins of different species is shown in Table 3.

The most common *O*-glycosidic oligosaccharide unit in the glycophorins is the tetrasaccharide **1**, containing two sialic acid residues. The trisaccharides **2** and **3**, lacking one of these sialic acids, have also been identified. The species differences in the

tetrasaccharide and trisaccharides include the different types of sialic acid residues (see Section 4). Most work has been done on the *O*-linked oligosaccharides of human glycophorin A and the tetrasaccharide **1** and linear trisaccharide **3** were found to be the most abundant structures. The branched trisaccharide **2**, found in small amounts, was considered to be an artifact formed by desialylation of the tetrasaccharide **1** during the isolation procedure [68]. Lately, two pentasaccharides **4** and **5**, each having three sialic acid residues, have also been identified in the human glycophorins [58].

Very unusual *O*-linked sugar chains were found in the bovine glycophorins, which possess a variety of *O*-glycosidically bound structures, up to deca- and undecasaccharides (**15-18**). Interesting and not found so far in *O*-glycosidic chains is the structure Gal1-3Gal1-., which was identified in some of the porcine and bovine oligosaccharides. In the rat and mouse glycophorins the hexasaccharide **8** was found, which contained *N*-acetylglucosamine linked (1-6) to the reducing *N*-acetylgalactosamine residue. *N*-Acetylglucosamine-containing *O*-glycosidically linked oligosaccharides of a similar size have also been found in the human variant MN erythrocytes [69, 70], and in mucins and other glycoproteins, such as those derived from tumor cells and platelets [38]. It should also be mentioned, that the blood-group ABH determinants are present on some of the *O*-glycosidically-linked oligosaccharides in human glycophorins [71, 72].

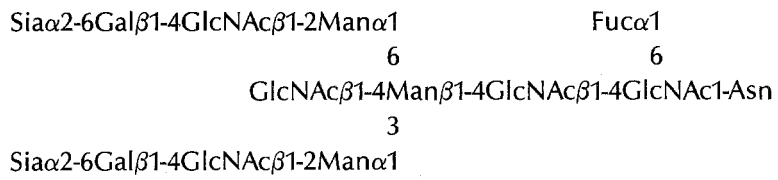
6. Structure of the *N*-Glycosidic Oligosaccharide Chains of Glycophorins

Most erythrocyte glycophorins contain one *N*-glycosidically bound oligosaccharide per molecule. However, in porcine glycophorin there are two *N*-glycosidic chains, and in some glycophorins there are no such glycans at all (Table 1, Fig. 1). To date, the structure of the *N*-linked oligosaccharide from human glycophorin A and one of two (or more) *N*-linked oligosaccharides from mouse glycophorins has been elucidated. These structures are shown in Fig. 3. The oligosaccharide of human glycophorin A is of the biantennary type with a bisecting *N*-acetylglucosamine residue and contains sialic acid (2-6)-linked to each galactose. Neutral and acidic *N*-linked oligosaccharides were also isolated from rat erythrocytes, using hydrazinolysis of the whole membranes [77, 78]. The authors claimed that these oligosaccharides originated from the plasma membrane glycoproteins, which can be assumed also to include glycophorins. Quite a variety of structures were determined, including high-mannose, bi-, tri- and tetra-antennary chains with branches having one or more *N*-acetyllactosamine units.

7. Final Remarks

Glycophorins were initially discovered in, and isolated from human erythrocyte membranes. Subsequently, the corresponding sialoglycoproteins from other cells such as lymphocytes, hepatoma cells and platelets were investigated [3-5]. During these studies it became clear that glycophorins from the defined cells often represent a family of glycoproteins, which are difficult to separate. From the human erythrocyte membranes three distinct glycophorins (A, B and C) have been isolated and studied extensively, and the existence of a fourth one has recently been described [8]. These human glycophorins differ structurally from each other in their orientation in the membrane, as well as in their antigenic properties and the number of molecules per erythrocyte.

human glycophorin A [59, 60]



mouse glycophorin [Krotkiewski H, Angel AS, Nilsson B; unpublished results]

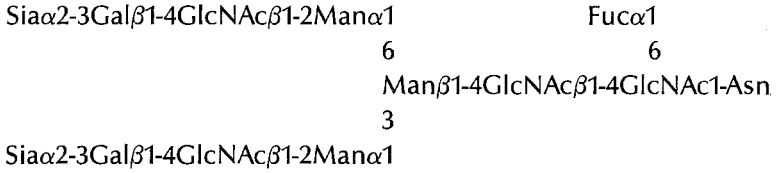


Figure 3. The *N*-glycosidic oligosaccharides found in glycophorins.

Despite the accumulating data on the sequence of the polypeptide chain and the structure of oligosaccharides in glycophorins, considerable uncertainty still remains regarding the biological role of this class of glycoprotein. This uncertainty was not alleviated when the erythrocytes of some individuals [En(a-)] were found to lack glycophorin A totally and this was not associated with any disease state [8].

Glycophorins, as transmembrane sialoglycoproteins, make a significant contribution to the negative charge on the surface of erythrocyte membranes, which may be a requirement preventing non-specific hemagglutination. The glycosylated domains of glycophorins are considered to carry blood-group antigens, virus and lectin receptors and markers of cell differentiation. It has also been suggested that the cytoplasmic domain of glycophorin A provides the attachment site for band 4.1, which is one of the membrane skeletal proteins [79]. The availability of glycophorin A, the major sialoglycoprotein of the human red cell membrane, could make it a suitable model for studies on the structure and assembly of mammalian integral proteins in the cell membranes.

The presence of glycophorin A in human erythroleukemic (K562) cells has helped the study of *in vitro* biogenesis and processing of this complex/glycosylated molecule [80, 81]. Recently, an interesting hypothesis on the biological role of some defined erythrocyte carbohydrate structures has been proposed in which a protective rather than an informative role has been suggested for the carbohydrates of erythrocyte membrane glycoproteins [82].

For comparative purposes the glycophorins from different animal species have also been studied, with the aim of elucidating their structure-function relationship. As long

ago as 1932 it was observed that the sera of patients with infectious mononucleosis contained antibodies which agglutinated sheep erythrocytes [83]. The glycophorin isolated from sheep erythrocytes was active in this interaction and showed much higher activity than the bovine, human and goat glycophorins. The sheep erythrocyte glycophorin also inhibited rosette formation between sheep erythrocytes and human peripheral blood lymphocytes [32]. Furthermore, the sialic acid present on rat erythrocyte membranes was found to act as a modulator of erythropoiesis [84] and of erythrocyte clearance from the circulation [85, 86].

Structural studies on the animal glycophorins are less advanced than those on the human ones, especially considering the sequence of the polypeptide chains. Blood still remains the most suitable source of biological material to study the glycophorins and our knowledge of the glycophorins from various animal species should grow. More information on the structure of both the peptide and carbohydrate portions of the glycophorins, as well as their antigenic properties, should lead to a better understanding of the behaviour of erythrocytes, both in health and in disease.

Note Added in Proof

Some additional data have appeared during the processing of this article. In human glycophorin B the total number of amino acids has been established to be 72 (alanine as the last residue) and two discrepancies have been noted: residue 50 - cysteine instead of phenylalanine, residue 65 - threonine instead of serine [Siebert PD, Fukuda M (1987) Proc Natl Acad Sci USA 84:6735-39]. In rabbit glycophorin the linear trisaccharide **3** has been found as the main *O*-glycosidic oligosaccharide, accompanied by tetrasaccharide **1** [Fukuda K, Honma K, Manabe H, Utsumi H, Hamada A (1987) Biochim Biophys Acta 926:132-38].

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