THE S SYSTEM OF BOVINE BLOOD GROUPS

CLYDE STORMONT, W. J. MILLER AND YOSHIKO SUZUKI

*The Serology Laboratory, Department of Microbiology,
University of California, Davis, California*

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THIS report is concerned with the bovine blood factors named S, U₁, U₂ and H' (FERGUSON, STORMONT and IRWIN 1942; STORMONT 1950) which came to be assigned to two separate genetic systems of cattle blood (see STORMONT 1954; IRWIN 1955, 1956; also see discussions by NEIMANN-SORENSEN 1958; RENDEL 1958). As will be shown in this report, those four blood factors actually belong to the same genetic system, a system referred to hereafter as the S system of bovine blood groups.

MATERIALS AND METHODS

The blood-typing reagents used in this study are designated S, U₁, U₂, S₂, H' and U'. The S, U₁ and U₂ reagents were known replicas of S, U₁ and U₂ reagents used by STORMONT (1950) in the first analysis of serological relationships involving blood factors S, U₁ and U₂. In that report, a blood-typing reagent was described which reacted with the bloods of all cattle of phenotypes S, U₂, SU₁ and SU₂ but not with bloods of cattle of phenotypes U₁ and — (i.e., SU-negative bloods) thereby establishing a close serological relationship between blood factors S and U. Because of the perfect correlation of the reactions of that reagent with the presence of either or both blood factors S and U₂, STORMONT named it (SU₂), in which symbolism the parentheses were intended to indicate that the antibodies were not fractionable by absorption. In this report the (SU₂) reagent and its equivalent blood factor are designated by means of the much simpler symbol S₂.

The S₂ reagent used in the present study was prepared from an aliquot of the 26Z (6g) isoimmune serum (see STORMONT 1950), which was the original source-antiserum for (SU₂) reagent. Because of the small supply of 26Z (6g) antiserum, the S₂ reagent was used very sparingly in the present study. When U' reagents (STONE and MILLER 1961) were reproduced in this laboratory, the use of S₂ reagent was discontinued since U', as demonstrated elsewhere in this report, serves as an effective substitute for S₂ reagent in distinguishing phenotypes in the S system.

The H' reagents of this study were known replicas of the first H' reagent obtained from bovine isoimmune serum (STORMONT 1947). Actually, all H' reagents now in use in the various cattle blood-typing laboratories are replicas of that H' reagent. We emphasize this point of reference since it is now known, as discussed elsewhere in this report, that contemporary H' reagents are not of the same specificity as the original H' reagent described by FERGUSON *et al.* (1942).

One of the H' reagents used in the present study, namely, an H' reagent obtained from a rabbit antiserum coded RC35, served effectively as a dosage reagent.

The blood samples used in the family studies were essentially the same as those used in the report on the A system of bovine blood groups (STORMONT 1961) except that those samples were supplemented by addition of samples from the families of eight Holstein-Friesian bulls of phenotype SU₁H' (see Table 2) owned by various artificial breeding organizations in United States. In all, there were 95 sire-families with a total of 2,723 offspring for an average of approximately 28.7 offspring per family.

Lytic tests, in which pooled, fresh-frozen serum from selected rabbits was used as complement, were performed as described in a number of the reports already cited.

RESULTS

The nine phenotypes defined to date in tests of representatives of various breeds of *Bos taurus* with the reagents S, U₁, U₂, S₂, H' and U' are shown in Table 1.

Attention is called first to the fact that the phenotype designations U₂, SH', U₁H', U₂H', SU₁H', SU₂H' and U₁U₂H' are actually shorthand designations for the phenotypes U₂S₂U', SS₂H', U₁U₂H', U₂S₂H'U', SU₁U₂S₂H', SU₂S₂H'U' and U₁U₂S₂H'U'. As may be noted by inspecting the reactions shown in Table 1, the main utility of reagents S₂ and U' is that of distinguishing phenotype U₁H' from U₁U₂H' (cf. discussion in reports by STORMONT 1950; STONE and MILLER 1961). In that capacity, the two reagents are equally effective. Consequently, once U' reagents were developed in this laboratory we were able to discontinue use of the S₂ reagent.

TABLE 1

Nine phenotypes in the S system of Bos taurus showing the serological reactions which define them

Phenotypes	S	Reactions with the reagents*					Diploid combinations of the five postulated phenogroups†
		U ₁	U ₂	S ₂	H'	U'	
—	0	0	0	0	0	0	—/—
U ₂	0	0	+	+	0	+	U ₂ /—, U ₂ /U ₂
H'	0	0	0	0	+	0	H'/—, H'/H'
SH'	+	0	0	+	+	0	SH'/—, SH'/H', SH'/SH'
U ₁ H'	0	+	+	0	+	0	U ₁ H'/—, U ₁ H'/H', U ₁ H'/U ₁ H'
U ₂ H'	0	0	+	+	+	+	U ₂ /H'
SU ₁ H'	+	+	+	+	+	0	SH'/U ₁ H'
SU ₂ H'	+	0	+	+	+	+	SH'/U ₂
U ₁ U ₂ H'	0	+	+	+	+	+	U ₁ H'/U ₂

* Reagents of specificity U₂ were originally designated as U reagents (FERGUSON *et al.* 1942; STORMONT 1950). The S₂ reagent of this study was formerly designated as the (SU₂) reagent (STORMONT 1950).

† See discussion in text.

TABLE 2

Summary of the results of progeny testing 95 bulls with respect to their genotypes at the S locus

Phenotypes	Genotypes	Number of bulls by breeds* showing number of offspring within parentheses				
		AA	G	H	HF	J
1. —	ss	6 (302)		3 (54)	8 (290)	5 (138)
2. H'	sH's	4 (192)		4 (129)	12 (293)	3 (17)
3. H'	sH'sH'	1 (5)		1 (7)	4 (208)	5 (180)
4. SH'	sSH's	1 (29)	5 (186)		4 (51)	4 (122)
5. SH'	sSH'sH'		2 (25)		2 (25)	3 (50)
6. SH'	sSH'sSH'		1 (154)			5 (115)
7. U ₁ H'	sU ₁ H's				1 (11)	
8. U ₁ H'	sU ₁ H'sH'				2 (92)	
9. U ₂ H'	sU ₂ H'				1 (16)	
10. SU ₁ H'	sSH'sU ₁ H'				8 (32)	

* AA (Aberdeen-Angus), G (Guernsey), H (Hereford), HF (Holstein-Friesian), J (Jersey).

Subtyping relationships of blood factors S, U₁, U₂, S₂, H' and U': Asymmetries in the occurrence of combinations of reactions with blood-typing reagents are spoken of as subtyping relationships. A number of subtyping relationships involving both linear and nonlinear patterns of cross reactions have already been described in the cattle studies (STORMONT 1950, 1955) and many more are yet to be described (MILLER, SUZUKI and STORMONT 1961).

Those subtyping relationships involving linear patterns of cross reactions are generally, although not invariably, indicated by special symbolic designations, as C₁ and C₂, O₁, O₂ and O₃, T₁ and T₂, U₁ and U₂, . . . etc. For example, the bovine blood factors named C and E by FERGUSON (1941) were observed in only three of four possible phenotypic combinations. The observed combinations were C and E together, C alone and no-CE. In keeping with subtyping designations, it was suggested (STORMONT 1950) that the combination C and E together be indicated by the symbol C₁ and C alone by the symbol C₂. Likewise, the bovine blood factors B and K were observed in only three of four phenotypic combinations, namely, BK, B alone and no-BK, and the same was true of G and K but B and G were observed in all four possible combinations, as evidenced by examining the five recognized phenotypic combinations of blood factors B, G and K, namely, BGK, BG, B, G and no-BGK (STORMONT 1950). Consequently in that and similar situations in which both linear and nonlinear patterns of cross reactions were involved, subtyping symbolism was avoided. Much discussion has been made about the immunogenetic implications of the BGK relationship but that relationship is by no means unique as evidenced by the relationships now described.

Attention is called first to the reactions of reagents S, S₂ and H' in Table 1. The observed phenotypic combinations of those reactions are SS₂H', S₂H', S₂, H' and no-SS₂H'. It is apparent that this pattern of reactions is a repetition of the subtyping relationships exhibited by blood factors B, G and K, with blood factor S playing the role of K. The present significance of the observed relationships exhibited by blood factors S, S₂ and H' was that they provided the first line of

evidence that blood factor H' must belong to the same blood-group system as blood factors S and S₂.

Likewise, we note from the data presented in Table 1 that the phenotypic combinations of blood factors U₁, U₂ and H' provide another BGK-like relationship in which blood factor U₁ plays the role of K. The present significance of the observed subtyping relationships involving U₁, U₂ and H' was that those relationships provided another independent line of evidence relating blood factor H' to the S system.

Finally, attention is called to still a third BGK-like relationship involving the blood factors S₂, U₂ and U', in which U' plays the role of K.

The subtyping interrelationships of blood factors S, U₁, U₂, S₂, H' and U' provide the strongest kind of evidence that those blood factors all belong to the same system of blood groups.

Phenogroups in the S system: The inability to resolve subtyping relationships on the basis of the concept of unit antigens alleged to be controlled by single genes (see STORMONT 1950; STORMONT, OWEN and IRWIN 1951) led to the use of the term "blood factor" or "serological factor" (LANDSTEINER 1945) as a replacement for such terms as "unit antigen", "antigenic substance", "antigenic character" and so on. It also led to the concept "phenogroup" although the term itself was not introduced until over a decade later (STORMONT 1955). The concept phenogroup, which is equivalent in all respects to the concept "agglutininogen" (WIENER and WEXLER 1952), holds that subtyping relationships are merely the reflections of reciprocal and nonreciprocal cross reactions of a series of immunochemically related structures on the surfaces of red cells. These hypothetical structures are referred to as phenogroups in the cattle and sheep studies (RASMUSEN 1960).

The question arises, "What is the minimum number of phenogroups that need be postulated to account for the patterns of reactions shown in Table 1?" The answer is five, as now demonstrated.

The five phenogroups postulated to account for the cross reactions with S, U₁, U₂, S₂, H' and U' antibodies are designated —, U₂, H', SH' and U₁H'.

The postulated phenogroup "—" is characterized by its inability to react with any of the antibodies in the reagents S, U₁, U₂, S₂, H' and U'. In the diploid combination —/—, that phenogroup would account for phenotype "—" in Table 1.

The postulated phenogroup U₂ is characterized by reactions with U₂, S₂ and U' antibodies. In the diploid combinations U₂/— and U₂/U₂, phenogroup U₂ would account for the phenotype U₂ in Table 1.

The postulated phenogroup H' is characterized by its reactions with H' antibodies. In the diploid combinations H'/— and H'/H', it would account for phenotype H' in Table 1.

The postulated phenogroup SH' is characterized by reactions with S, S₂ and H' antibodies. In the diploid combinations SH'/—, SH'/H' and SH'/SH', it would account for phenotype SH' in Table 1.

The postulated phenogroup U₁H' is characterized by reactions with U₁, U₂ and

H' antibodies. In the diploid combinations $U_1H'/-$, U_1H'/H' and U_1H'/U_1H' , it would account for phenotype U_1H' in Table 1.

Finally, the four remaining diploid combinations U_2/H' , SH'/U_1H' , SH'/U_2 and U_1H'/U_2 would account for, respectively, the phenotypes U_2H' , SU_1H' , SU_2H' and U_1U_2H' in Table 1.

It is implied, although it is not a necessary part of the concept phenogroup, that the immunochemically related structures postulated to account for the cross reactions of such antibodies as S, U_1 , U_2 , S_2 , H' and U' are controlled by genes that are closely related in evolutionary descent. Such genes are generally referred to in genetics as alleles. It is now shown that the phenogroups $-$, U_2 , H', SH' and U_1H' do segregate in inheritance as if controlled by allelic genes.

Progeny tests: Six of the nine phenotypes shown in Table 1 were represented in the 95 bulls which headed the sire-families of this study. Those were the phenotypes $-$, H', SH', U_1H' , U_2H' and SU_1H' . Corresponding to those six phenotypes, ten genotypes were proved in the progeny tests of the bulls as summarized in Table 2. Represented in the ten genotypes were the five alleles s , s^{U_1} , $s^{H'}$, $s^{SH'}$ and $s^{U_1H'}$ corresponding, respectively, to the five postulated phenogroups $-$, U_2 , H', SH' and U_1H' .

Details of the evidence, excepting the progeny tests involving the six bulls (line 6 of Table 2) which proved to be of genotype $s^{SH'}s^{SH'}$, are presented in Tables 3-11. All except one of the 269 offspring of the six bulls of genotype $s^{SH'}s^{SH'}$ were of phenotype SH'. The one was of phenotype SU_1H' (presumably genotype $s^{SH'}s^{U_1H'}$), and she resulted from a mating to a dam of that same phenotype.

Table 3 is a summary of the matings of the 22 bulls of phenogroup-formula $-/-$. The results in that table are consistent with the proposal that all animals of phenotype " $-$ " are of genotype ss .

Table 4 is a summary of the matings of the 23 bulls (line 2 of Table 2) which bred as if of genotype $s^{H'}s$. The observed ratio of 138:122 in matings to "negative" dams is consistent with the proposal that those bulls were of genotype $s^{H'}s$. Furthermore, their red cells exhibited the "weak" type of reactions in tests with dosage H' reagent.

TABLE 3

Summary of the matings of 22 bulls of phenogroup-formula $-/-$ and genotype ss (see line 1 of Table 2)

Matings Males $\times$ Females	—	Number of offspring of phenotypes			
		U_2	H'	SH'	U_1H'
$- \times -$	202	0	0	0	0
U_2	5	3	0	0	0
H'	160	0	303	0	0
SH'	21	0	22	54	0
U_1H'	1	0	1	0	6
U_2H'	0	5	1	0	0

TABLE 4

Segregation of phenogroups H' and — as alternatives in 631 progeny of 23 bulls of phenogroup-formula H'/— and genotype s^H's (see line 2 of Table 2)

Matings Males × Females	—	U ₂	Number of offspring of phenotypes H' SH'		U ₁ H'	U ₂ H'
H' × —	138	0	122	0	0	0
U ₂	0	3	5	0	0	2
H'	73	0	240	0	0	0
SH'	6	0	9	26	0	0
U ₁ H'	0	0	1	0	2	0
U ₂ H'	0	0	2	0	0	2

TABLE 5

Summary of the matings of 11 bulls of phenotype-formula H'/H' and genotype s^H's^H' (see line 3 of Table 2)

Matings Males × Females	H'	Number of offspring of phenotypes SH' U ₁ H'		U ₂ H'
H' × —	92	0	0	0
U ₂	0	0	0	2
H'	189	0	0	0
SH'	51	62	0	0
U ₁ H'	1	0	3	0

Table 5 is a summary of the matings of the 11 bulls (line 3 of Table 2) which bred as if of genotype s^H's^H'. Their red cells exhibited the "strong" type of reactions with dosage H' reagents.

Table 6 shows the segregation of phenogroups SH' and — in the progeny of 14 bulls (line 4 of Table 2) which bred as if of genotype s^{SH}'s, and whose red cells exhibited the weak reaction with dosage H' reagent. In matings to negative dams the expected ratio of SH' to — was 1:1 and the observed ratio was 28:23.

Table 7 shows the segregation of phenogroups SH' and H' as alternatives in the progeny of the seven bulls (line 5 of Table 2) which bred as if of genotype s^{SH}'s^H' and whose red cells exhibited the strong reaction with dosage H' reagent.

TABLE 6

Segregation of phenogroups SH' and — as alternatives in 388 progeny of 14 bulls of phenogroup-formula SH'/— and genotype s^{SH}'s (see line 4 of Table 2)

Matings Males × Females	—	Number of offspring of phenotypes H' SH'		U ₁ H'	SU ₂ H'
SH' × —	28	0	23	0	0
U ₂	2	0	0	0	2
H'	9	50	52	0	0
SH'	15	17	185	0	0
SU ₁ H'	0	0	4	1	0

The test matings to negative dams and dams of phenotype H' were expected to produce a 1:1 ratio of H' to SH'. The observed ratio was 6+18:5+27.

Table 8 shows the segregation of phenogroups U_1H' and — as alternatives in the 11 progeny of the one bull (line 7 of Table 2) which bred as if of genotype $s^{U_1H'}s$ and whose red cells exhibited the weak reaction with dosage H' reagent.

Table 9 shows the segregation of phenogroups U_1H' and H' as alternatives in the offspring of the two bulls (line 8 of Table 2) which bred as if of genotype $s^{U_1H'}s^{H'}$ and whose red cells exhibited the strong reaction with dosage H' reagent. A 1:1 ratio was expected in matings of those bulls to negative cows and cows of phenotype H'. The observed ratio was 16+29:12+32.

Table 10 shows the segregation of phenogroups U_2 and H' as alternatives in the 16 progeny of the one bull (line 9 of Table 2) which bred as if of genotype $s^{U_2}s^{H'}$ and whose red cells showed weak reaction with dosage H' reagent. In

TABLE 7

Segregation of phenogroups SH' and H' as alternatives in 100 offspring of seven bulls of phenogroup-formula SH'/H' and of genotype $s^{SH'}s^{H'}$ (see line 5 of Table 2)

Matings Males × Females	Number of offspring of phenotypes	
	H'	SH'
SH' × —	6	5
H'	18	27
SH'	6	37
U_1H'	0	1

TABLE 8

Segregation of the phenogroups U_1H' and — as alternatives in 11 offspring of a bull of phenogroup-formula $U_1H'/—$ and of genotype $s^{U_1H'}s$ (see line 7 of Table 2)

Matings Males × Females	Number of offspring of phenotypes		
	—	H'	U_1H'
$U_1H' \times —$	2	0	1
H'	0	2	5
U_1H'	1	0	0

TABLE 9

Segregation of phenogroups U_1H' and H' as alternatives in 92 progeny of two bulls of phenogroup-formula U_1H'/H' and genotype $s^{U_1H'}s^{H'}$ (see line 8 of Table 2)

Matings Males × Females	H'	Number of offspring of phenotypes		
		SH'	U_1H'	SU_1H'
$U_1H' \times —$	16	0	12	0
H'	29	0	32	0
SH'	0	1	0	1
U_1H'	0	0	1	0

$U_2H' \times -$ matings we should expect a 1:1 ratio of U_2 to H' . By combining the results in line 1 of Table 10 with those in the last line of Table 3, the observed ratio was 1+5:2+1.

Table 11 shows the segregation of phenogroups SH' and U_1H' as alternatives in the progeny of the eight bulls (line 10 of Table 2) which bred as if of genotype $s^{SH'}s^{U_1H'}$. A 1:1 ratio of SH' to U_1H' is expected in $SU_1H' \times -$ matings and also in $SU_1H' \times H'$ matings. The observed ratio was 1+10:1+8.

Attention is called to the fact that there were no matings involving the rare phenotypes SU_2H' and U_1U_2H' . There were, however, four offspring of phenotype SU_2H' (Tables 6 and 10) and one of phenotype U_1U_2H' (Table 10).

Estimates of the frequencies of the alleles which control the phenogroups $-$, U_2 , H' , SH' and U_1H' in Guernsey, Holstein-Friesian and Jersey cattle in United States are given in another report (STORMONT 1958). Those estimates were based on very small samples. It is our intention to submit elsewhere gene-frequency data based upon considerably larger samples of various populations of *Bos taurus*.

TABLE 10

Segregation of phenogroups U_2 and H' as alternatives in 16 offspring of a bull of phenogroup-formula U_2/H' and genotype $s^{U_2}H'$ (see line 9 of Table 2)

Matings Males $\times$ Females	U_2	H'	Number of offspring of phenotypes			
			SH'	U_2H'	SU_2H'	U_1U_2H'
$U_2H' \times -$	1	2	0	0	0	0
H'	1	4	0	2	0	0
SH'	1	0	2	0	2	0
U_1H'	0	0	0	0	0	1

TABLE 11

Segregation of phenogroups SH' and U_1H' as alternatives in 32 offspring of eight bulls of phenogroup-formula SH'/U_1H' and genotype $s^{SH'}s^{U_1H'}$ (see line 10 of Table 2)

Matings Males $\times$ Females	SH'	Number of offspring of phenotypes	
		U_1H'	SU_1H'
$SU_1H' \times -$	1	1	0
H'	10	8	0
SH'	7	2	1
U_1H'	1	0	1

DISCUSSION

The foregoing analysis of the S system of bovine blood groups was presented in a series of four steps. First we considered the nine S-system phenotypes in *Bos taurus* and the reactions which defined those phenotypes. The second step was concerned with a description of the subtyping relationships exhibited by the blood factors S, U_1 , U_2 , S_2 , H' and U' . The third step was concerned with an

analysis of the number of phenogroups in *Bos taurus* that need be postulated to account for the observed phenotypes. The fourth and final step was an analysis of family data which, in retrospect, simply provided genetic proof for the existence of the five postulated phenogroups. Thus, serological relationships alone can serve in lieu of genetic tests in the analysis of blood-group systems. Such an approach may have application in marine population research where genetic tests are not possible. The postulated phenogroups can then be tested by gene-frequency analysis.

The results of this analysis of S-system phenogroups may be contrasted with recent studies (STORMONT, MILLER and SUZUKI 1961) of S-system phenogroups in American buffalo (*Bison bison* or *Bos americanus*). Only two S-system phenogroups were distinguished in the bison studies. One of those two phenogroups was equivalent to the "—" phenogroup of *Bos taurus*. The other, designated S_b , was characterized by reactions with S reagent and by weak, partial cross reactions with one of two U_1+H' reagents. (S_2 reagent was not used in those studies.) We were able to show that S-positive bison bloods will readily absorb S antibodies in $S+H'$ reagents without affecting the H' antibodies. Whether a phenogroup equivalent in specificity to S_b exists in *Bos taurus* is an open question. In view of the fact that most bison phenogroups have homologues or near-homologues in *taurus*, it is suggestive that such a phenogroup may one day be found in *taurus*.

It was stated elsewhere in this report that contemporary H' reagents cannot be of the same specificity as the original H' described by FERGUSON *et al.* (1942). Some of the evidence for that statement was obtained in examining the S and H' reactions shown in Table 1 of the report by FERGUSON *et al.* (1942) in which table it is seen that blood factor S occurred with and without H' , which is not in keeping with the results reported here. The original source-antiserum for H' antibodies was exhausted very early in those studies and, as may be seen in the report by STORMONT *et al.* (1951), H' was not among the 38 blood factors examined in the analyses of the blood group systems B, C, F-V and Z. Actually, those studies were conducted largely over the years 1941 to 1944. We cannot, therefore, be certain just when the transition in H' reagents took place. But the important point, it seems, is to note here that the blood factor now called H' bears no known relationship to the original H' of FERGUSON *et al.* (1942).

In the studies of the B, C, F-V and Z systems of cattle (STORMONT, OWEN and IRWIN 1951; STORMONT 1952) the blood factors left unassigned were A, H, J, S, U_1 , U_2 and Z' . J, of course, represented a special case of a blood factor which is only a secondary attribute of the red cells (STORMONT 1949). Studies of the genetics of the J property were reported by STONE and IRWIN (1954) and by SPRAGUE (1958). The basis for the assignment of A, H and Z' to the A system, along with the more recently described blood factor D, is given in another report (STORMONT 1961). S, U_1 and U_2 , along with contemporary H' , were shown in this report to be members of the S system, thereby completing the analysis of the genetic positions of the 38 bovine blood factors examined by STORMONT *et al.* (1951).

Tests for independence of the seven loci (A, B, C, F-V, J, S and Z) implicated in the control of those 38 blood factors along with evidence for two additional systems are to be presented in a following report.

SUMMARY

On the basis of an analysis of the cross reactions of the bovine blood-typing reagents named S, S₂ (formerly designated as (SU₂) reagent), U₁, U₂, H' and U', five phenogroups designated "—", U₂, H', SH' and U₁H' are postulated to account for the equivalent blood factors. Genetic evidence is then offered in proof of the existence of the five phenogroups which segregate as if controlled by allelic genes. The alleles are designated, respectively, as *s*, *s^{U₂}*, *s^{H'}*, *s^{SH'}* and *s^{U₁H'}* in which symbolism the phenogroups are written as superscripts.

Two subtyping relationships, one involving the trio of blood factors SS₂H' and the other involving the trio U₁U₂H' provided the first lines of evidence that blood factor H', contrary to previous opinion, is a member of the S system. It is pointed out that those subtyping relationships parallel the often discussed BGK relationship.

In the course of study it became evident that contemporary H' reagents bear no known relationship to the original H' reagent described in 1942.

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