Some Hereditary Red-Cell Traits in Kalahari Bushmen and Bantu: Hemoglobins, Glucose-6-Phosphate Dehydrogenase Deficiency, and Blood Groups

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The sickle-cell trait has not been found in Kalahari Bushmen (Budtz Olsen, 1953; Griffiths, 1953), but no survey has been conducted to ascertain whether any other abnormal hemoglobins exist in these people or in their Bantu neighbors, the Kgalagadi. Charlton and Bothwell (1961) and Charlton (1962) tested small samples of Bushmen for glucose-6-phosphate dehydrogenase (G6PD) deficiency and found a very low incidence of the trait. The blood groups of the Bushmen have been previously studied by Pijper (1932) and more fully by Zoutendyk *et al.* (1953) and Weiner and Zoutendyk (1959). Two recent expeditions to Botswana (formerly the Bechuanaland Protectorate), organized as part of our departmental research program in human biology, under the direction of Professor P. V. Tobias, gave us the opportunity of collecting blood samples from both Bushmen and Kgalagadi and subjecting them to a number of field and laboratory investigations, the results of which we record here.

MATERIALS AND METHODS

The 227 subjects included representatives of the three major linguistic divisions of Bushmen—the Northern, Central, and Southern (Bleek, 1927). A further 62 subjects belonged to a group of so-called River Bushmen who live a settled existence on the Kwaai River, which runs along the northeastern edge of the Okovango Swamps. These latter had both Bush and Bantu physical features. Although they referred to themselves as Sarwa and spoke a Bush language, therefore fulfilling the major criteria for being classified as Bushmen (Tobias, 1957), we feel that, on the basis of the anthropometric and genetical features examined by us, they probably represent a Bush-Bantu hybrid population. We propose, therefore, to refer to them as Bush-Bantu hybrids.

The Kgalagadi are Bantu inhabitants of the Kalahari, and the group of 52 consisted of children attending Kang Government School in the Central Kalahari,

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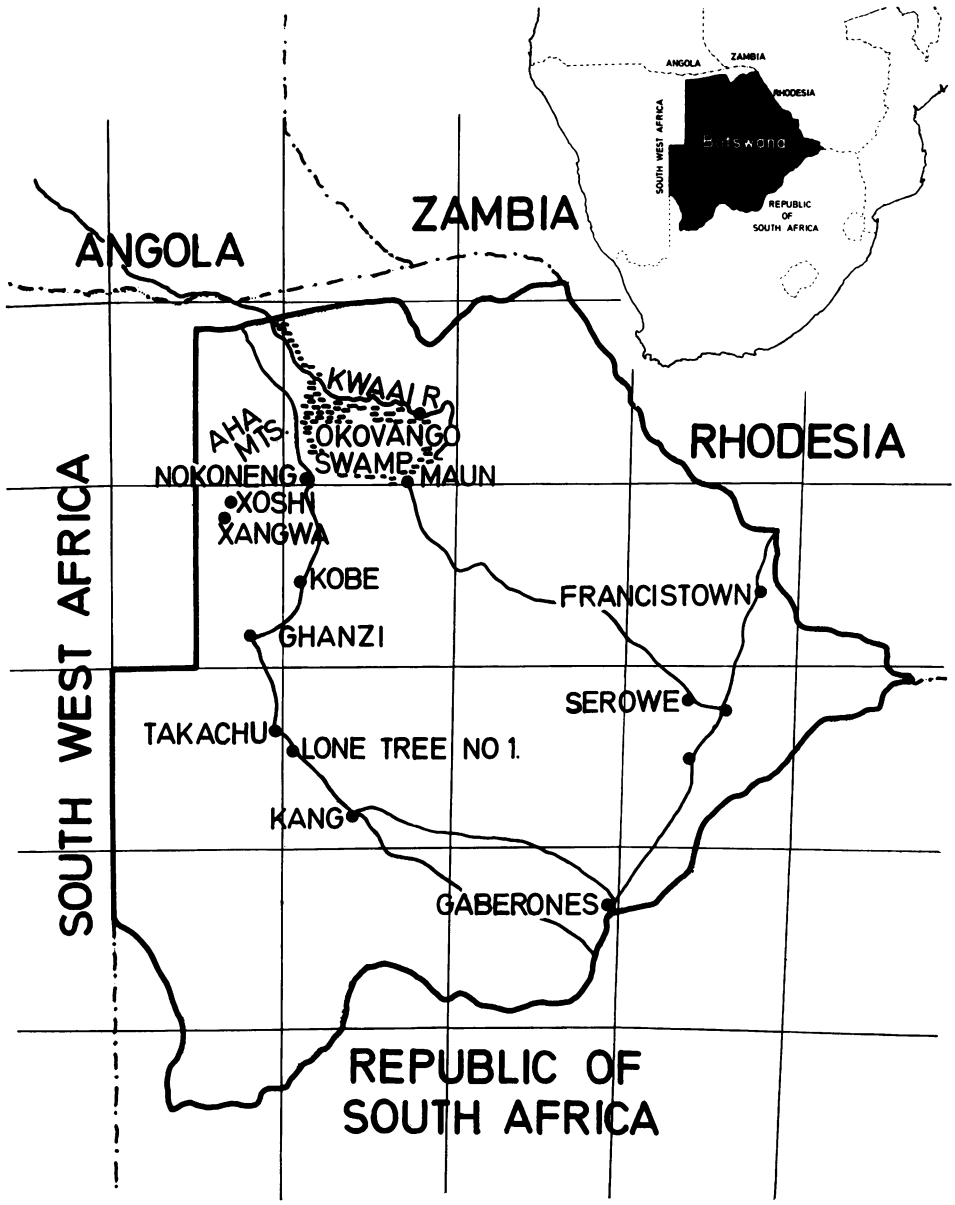

FIG. 1.—Map of Botswana showing places mentioned in text

about 180 miles southeast of Ghanzi. The relationship between the Kgalagadi and the Bushmen has been that of patron-client for several generations (Silberbauer, 1965). Intermarriage has taken place, and certain Bushman physical features are discernible in many of the Kgalagadi. Jenkins and Steinberg (1966) showed that, whereas all other Negroid populations were 100% Gm(5), no fewer than 38% of the Central and Southern Bushmen included in that study were Gm(−5). The fact that 4% (two of 48) of Kgalagadi were also Gm(−5) was taken to indicate a flow of Bushman genes into the Kgalagadi.

The Northern Bushmen belonged to the Kung "tribe" and were located at Xoshi and Xangwa about 80 miles southwest of Nokoneng, near the Aha Mountains, that is, between the Okovango Swamps and the South-West African border (see map, Fig. 1). The Southern and Central Bushmen belonged to two tribes: !Kõ (also known as Magon, which is the Bantu name for the tribe) and /Dukwe.* The majority of the subjects were living together as one large group of 70–80 persons during the winter of 1964, and there was evidence of intertribal marriage. Such tribal exogamy, prevously commented on by Tobias (1957), makes the division of these people into rigidly defined tribes meaningless to the physical anthropologist. During the week we spent studying the larger group, they remained at our camp at Lone Tree No. 1 Borehole (see map, Fig. 1). The remainder consisted of two separate groups who trekked to the borehole at Kang, where we were able to study them.

All the Bushmen included in this study were pursuing a hunting and food-gathering existence and had had little or no contact with European or Bantu farmers.

Venous blood was collected from all adults and large children and transferred by means of a large-bore autoclaved needle into two tubes—one plain and the other containing sodium oxalate as anticoagulant. In the case of small children, a capillary sample of blood was collected in an oxalate tube only. At the same time, thin and thick blood films were made, and sickling was tested for by means of the metabisulfite test—one drop of a 2% solution of sodium metabisulfite was added to, and mixed with, one drop of whole blood, and a cover slip was applied over the mixture and sealed with Vaseline. The slide was examined microscopically 2–4 hr later. Usually within 2 hr, and always within 6 hr of collection, a one-tube red-cell osmotic fragility test was performed on the oxalate sample of blood (from the Southern and also from the Central Bushmen and Kgalagadi groups only), using 0.38% buffered sodium chloride (Dacie, 1956). The degree of hemolysis was estimated photometrically by means of a portable EEL colorimeter. According to Barnicot *et al.* (1963), this is the most useful field test in discriminating between normal and thalassemic blood. On the same day, the Motulsky and Campbell-Kraut (1961) screening test for G6PD deficiency was carried out on the oxalate samples, and, in males, a decolorization time of 120 min or more was taken to indicate deficiency of the enzyme. Hemoglobin estimations were made on all samples giving a prolonged decolorization time, in order to exclude anemia as a possible cause, and the Dare Haemoglobinometer was used for this purpose.

Because there was no way of getting the blood samples of the Central and Southern

* The symbols ! and / indicate two of the click sounds which occur in the Khoisan group of languages.

Bushmen and Kgalagadi back to the laboratory in reasonable time, sera were separated from red cells in the field and stored at −15° C in a portable deep freeze. The red cells were grouped for ABO and Rh(D) in the field. The results of the plasma protein polymorphisms have been reported elsewhere (Jenkins and Steinberg, 1966). The other samples, which were transported back in good time, were subjected to ABO and Rh(CcDE) grouping by Dr. A. Zoutendyk of the South African Institute for Medical Research.

All red-cell antigen typing was carried out in 75 × 7 mm tubes, and group A_1 and A_2 cells were distinguished from each other by absorbed human anti-A serum. A specimen was called A_x if the cells were agglutinated by group O sera but not by nonimmune anti-A sera and if the serum could be shown to possess anti-A activity at room temperature. Brain (1966) has recently investigated this A_x antigen, renaming it A_{Bantu}.

The A_1, A_2, B, and O gene frequencies were determined, using the formulas of Wellisch and Thomsen (Race and Sanger, 1962, p. 25). Fisher's method was used to test for goodness of fit (Race and Sanger, 1962, p. 23), and his simple method (Race and Sanger, 1962, p. 143) was used for calculating the Rhesus gene frequencies.

After separation, the red cells were washed with normal saline and hemolyzed, and the hemoglobin was converted into cyanmethemoglobin and stored at 4° C in a portable refrigerator until arrival at the laboratory in Johannesburg, where the specimens were subjected to electrophoresis in starch gel at *p*H 8.4, using the discontinuous tris-borate buffer system of Poulik (1957), or on paper in veronal buffer at *p*H 8.6. The Singer *et al.* (1951) technique was employed for estimation of the percentage of fetal hemoglobin in most of the samples from the Central and Southern Bushmen and Kgalagadi groups. No attempt was made to measure the amount of Hb A_2 present other than by inspecting the stained starch-gel slices. The thin blood films were stained with Leishman's stain and examined microscopically for the presence of abnormal red cells. The thick films were stained with Giemsa's stain and examined for the presence of malaria and other parasites.

RESULTS

The results of the various investigations are presented in Tables 1–5.

The sickle-cell wet preparation of 341 samples failed to demonstrate any sickle cells, and electrophoresis of 302 hemolyzates revealed only one abnormal hemoglobin (Table 1). A nine-year-old Kgalagadi boy possessed Hb A and a slow-moving hemoglobin, which at *p*H 8.4 on starch-gel electrophoresis moved to a position identical with Hb S. The red-cell morphology was normal, and no elevation of Hb F was demonstrable using the Singer *et al.* (1951) technique. We have provisionally identified this slow hemoglobin as Hb D, and attempts are being made to obtain further samples of blood from the child and also from his relatives. No obvious case of raised or "split" Hb A_2 was encountered.

The one-tube osmotic fragility test carried out on 138 Bushmen and 30 Kgalagadi samples failed to reveal any altered fragility of the red cells. Thin blood films totaling 105 from the Central and Southern Bushmen and 50 from the Kgalagadi showed normal red-cell morphology in all cases, and a similar number of thick blood films

from the two populations did not show any parasites to be present. Unfortunately, the thin and thick blood films of the Northern Bushmen and Kwaai group were left too long before being stained and were consequently unsuitable for examination.

The Singer one minute alkali denaturation technique for Hb F estimation is notoriously unreliable if the Hb F is only slightly elevated, and so the very few hemolyzates that gave only slightly elevated levels have not been considered abnormal, particularly since the osmotic fragility and the red-cell morphology were normal in these cases.

TABLE 1

SICKLING AND HEMOGLOBIN ELECTROPHORESIS RESULTS ON BUSHMEN, BANTU, AND KWAAI RIVER HYBRIDS

POPULATION	SICKLE-CELL TRAIT		HEMOGLOBIN ELECTROPHORESIS	
	No. Tested	No. Positive	No.	Pattern
Bushmen:				
Southern and Central	144	0	113*	A only
Northern	83	0	80†	A only
Kwaai River hybrids	62	0	59†	A only
Kgalagadi	52	0	49* 1*	A only A+D

* Starch-gel electrophoresis at pH 8.4.
† Paper electrophoresis at pH 8.4.

TABLE 2

G6PD DEFICIENCY AMONG KALAHARI BUSHMEN, BANTU, AND KWAAI RIVER HYBRIDS

POPULATION	NO. TESTED (MALES ONLY)	DEFICIENT	
		No.	%
Bushmen:			
Southern and Central	73	1	1.5
Northern	44	2	4.5
Kwaai River hybrids	28	0	.....
Kgalagadi	49	0	.....

Sixty-three Southern and Central Bushmen samples were tested in the field with single anti-Rh(D) serum, and three gave a negative result; unfortunately, under these conditions it was not possible to test for the D^u antigen. Although true Rhesus-negatives have not previously been encountered in 792 Bushmen tested (see Zoutendyk *et al.*, 1953; Weiner and Zoutendyk, 1959), it is noteworthy that two were found among the 72 Kung Bushman samples of the present material tested by Dr. Zoutendyk in his laboratory (Table 4). One D^u specimen was found among the Kwaai hybrids, and this has been considered to be D for the purpose of calculating phenotype and gene frequencies.

TABLE 3

ABO BLOOD GROUPS OF BUSHMEN AND KWAAI RIVER HYBRIDS

POPULATION	No.	PHENOTYPES																		GENE FREQUENCIES				
		A_1		A_2		A_x		A		B		O		A_1B		A_2B		AB		p_1	p_2*	p	q	r
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%					
Southern and Central Bushmen	122	Not tested		Not tested		0	....	22	18	13	11	84	69	Not tested		Not tested		3	2	.....	.....	0.105	0.062	0.835
Kung Bushmen	72	22	31	13	18	4	6	39	54	4	6	27	38	1	1	1	1	2	3	0.176	0.169	0.345	0.044	0.613
Kwaai River hybrids	42	4	10	5	12	1	2	10	24	15	36	14	33	2	5	1	2	3	7	0.066	0.113	0.179	0.254	0.578
Central Kalahari Bushmen†	114	.....	26	.....	8	1	1	....	35	....	4	....	61	0	....	0	....	0	....	0.145	0.054	0.199	0.022	0.784
South-West African Bushmen‡	446	Not tested		Not tested		Not tested		151	34	38	9	250	56	Not tested		Not tested		7	2	.....	.....	0.197	0.052	0.751

* The A_x individuals have been included in the A_2 group for gene frequency calculations.

† Weiner and Zoutendyk (1959).

‡ Zoutendyk *et al.* (1953).

Because of the deviation from Hardy-Weinberg expectation revealed by the Rhesus system, the comparisons that are made between the various populations must be treated with considerable caution.

The highly significant difference between the ABO frequencies of the Kung and the Southern and Central Bushmen ($P < .001$) is most interesting, suggesting a possible difference between the Northern and other Bushmen. Tobias (1961) came to a similar conclusion using dermatoglyphics as the genetic parameter. It is very regrettable that we do not have Rhesus gene frequencies for the Southern and Central Bushmen. Despite the smallness of the range of phenotypes of Weiner and Zoutendyk's sample and the possible implications of this mentioned above, these results have been compared by means of a χ^2 test (Race and Sanger, 1962, p. 145) with our Kung sample. The smallness of some phenotype groups and the absence of others make it necessary to pool these, thus obscuring the differences with respect to presence or absence of a given phenotype. When this is done, no significant difference exists between the Central Kalahari Bushmen and the Kung Bushmen with respect to the Rhesus system ($\chi^2_{[2]} = 1.4$, $.5 > P > .3$).

The Bantu data with which we may compare the Bushman results are also not satisfactory, the series of Zoutendyk (1947) not consisting of a randomly mating population and Rhesus grouping having been carried out with only three antisera. When these Bantu are compared with the Kung Bushmen, however, no significant difference between the two is apparent ($.7 > P > .5$)! Another surprising discovery is the significant difference ($P < .005$) for the ABO system between the Southern-Central Bushmen of this study and the Central Kalahari Bushmen of Weiner and Zoutendyk (1959). Both these groups were encountered in a similar area of the Kalahari, near Ghanzi. All of the former were still following their hunting and gathering way of life, while about one-third of the latter were living on the farms in Ghanzi (see map, Fig. 1).

When the Kwaai hybrids are compared with the Kung Bushmen, an apparent discrepancy is evident. When the Rhesus system is used, the difference between them is insignificant ($.5 > P > .3$), but when the ABO system is employed, the difference is significant ($.01 > P > .001$). This might be taken as supportive evidence for the relatively greater stability of the Rhesus system when compared with the ABO blood-group system (see Mourant, 1961).

The Kung sample is noteworthy for the very high group A frequency, occurring at the expense of group O. The low B frequency (5.56%) closely approximates the findings of Pijper (1932) for three tribes of Northern Bushmen, including the Kung, and Zoutendyk *et al.* (1953) for Bushmen in South-West Africa (group not specified). The A_1 to A_2 ratio (approximately 2:1) is lower than that for the Central Bushmen (approximately 4:1) tested by Weiner and Zoutendyk (1959) and approaches the 1:1 ratio found in Southern Bantu (Zoutendyk, 1947). The Kung Rhesus data are also noteworthy for features suggesting a closer affinity with the Bantu than has been evident in previous studies on Bushmen: the occurrence in a sample of only 71 of two Rhesus-negatives (cde/cde), and a CcDe frequency of 28.16%.

The Kwaai people presented physical features which suggested Bush-Bantu hybridization, and the blood-group data would tend to confirm this impression, al-

DISCUSSION

Statistical tests for deviation from Hardy-Weinberg expectation were carried out on the three populations of the present study, as well as on the Bushman groups studied by Zoutendyk *et al.* (1953) and Weiner and Zoutendyk (1959). Using the Rhesus system, the Kwaai hybrids gave $.8 > P > .7$, indicating that the sample is in Hardy-Weinberg equilibrium and techniques were satisfactory. For the Kung Bushmen, $.02 > P > .01$, which is not quite satisfactory and might be explained by the fact the sample was drawn from two Bushman bands who, although living in geographical proximity, might not have interbred at random. The Central Kalahari Bushmen data of Weiner and Zoutendyk (1959) do not satisfy the test for internal

TABLE 4

RHESUS PHENOTYPES OF BUSHMEN AND KWAAI RIVER HYBRIDS

Population	No.	+++−*		−++−		−+++		−+−−		++++		++−−		+−+−	
		No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Kung Bushmen	71	20	28	44	62	0	....	2	3	0	....	0	....	5	7
Kwaai River hybrids	38	8	21	22	58	4	11	1	3	1	3	1	3	1	3

* Four sera were used, and the results (+ or −) with each of anti-C, anti-c, anti-D, and anti-E are shown in each column in that order.

TABLE 5

RHESUS GENE FREQUENCIES OF BUSHMEN AND KWAAI RIVER HYBRIDS

Population	r	R'	R^0	R^1	R^2	Reference
Kung Bushmen	0.168	0.000	0.637	0.265	0.000	Present study
Kwaai River hybrids	0.162	0.067	0.616	0.095	0.060	Present study
Central Kalahari Bushmen	0.000	0.000	0.822	0.000	0.178	Weiner and Zoutendyk (1959)
South-West African Bushmen	0.000	0.000	0.780	0.172	0.039	Zoutendyk *et al.* (1953)

consistency based on gene frequency calculations using Fisher's simple method (Race and Sanger, 1962, p. 143). This may be due to the narrow range of phenotypes observed by these authors. A larger range was observed by us in both the Kung and the Kwaai groups. It is not possible to determine from the small samples available whether these differences between Weiner and Zoutendyk's results and our own reflect differences of a biological nature between the groups studied or merely accidents of ascertainment. Considering the ABO blood-group system, the χ^2 test for goodness of fit gave satisfactory results for the three populations of the present study (Southern and Central Bushmen, $.5 > P > .3$; Kwaai hybrids, $.75 > P > .70$; Kung, $.98 > P > .95$), as well as for the South-West African Bushmen of Zoutendyk *et al.* (1953) ($.9 > P > .8$) and the Central Kalahari Bushmen studied by Weiner and Zoutendyk (1959) ($.5 > P > .3$).

though the very high B group frequency is the highest for any indigenous African people south of the equator. (Whether this is due to genetic drift or fairly recent intense selective pressures is not easy to decide.) In view of the claims by some workers that differences in the blood groups may be related to resistance to serious infectious diseases, such as plague and smallpox (for a recent review, see Muschel, 1966), caution must be exercised in interpreting the blood-group gene-frequency differences among various populations, especially if these populations are small and the data show certain internal inconsistencies. Generalizations are to be avoided at this stage because only inadequate samples of the various population groups of Southern Africa have been investigated.

Generally speaking the Bushmen enjoy fairly good health. The Bushmen who were the subjects of this study live a hunting and food-gathering existence and consequently move about in small bands, rarely more than 70–80 in number, and usually fewer. Because of their remoteness from other human beings, they are isolated from many infectious diseases, although virus antibody studies carried out on most of the sera of the Central and Southern Bushmen of this survey did show poliomyelitis antibodies to be present (J. H. S. Gear, 1965, personal communication).

In a recent publication, Silberbauer (1965) described how, during the summer of 1964, which had been drier than usual, an abnormally large number of Bushmen (about 300 men, women, and children) were concentrated in one place to share the water which workmen had obtained for themselves by sinking a borehole. Within two weeks of congregating, outbreaks of "colds, bronchitis, ear infections, and stomach trouble" and "a virtual epidemic of venereal disease amongst children" had occurred. He concludes: "In the years which had been spent with the people of that territory, I had not previously seen anything which compared with this."

The possible role played by infectious disease in the establishment and maintenance of genetic polymorphisms in man has been discussed by Motulsky (1960, 1964) for the sickle-cell, Hb C, Hb E, thalassemia, and G6PD-deficiency polymorphisms. The Bushman, by following his nomadic way of life, has not been subjected to the devastating effects of infectious disease which come from living a settled existence with the attendant evils of overcrowding. However, contact with Caucasoids and Bantu during recent times has led to epidemics of smallpox (the last major one was in 1957) and in 1962 to influenza (H. J. Heinz, 1965, personal communication). It even appears that many Bushmen may have deliberately denied themselves the luxury of living near a plentiful supply of water and, in so doing, have reduced the risk of possible exposure to infection with malaria and bilharzia.

All the groups studied, with the exception of the Kwaai River hybrids, lived more than 50 miles from swamps or rivers and would probably be exposed to malaria only during the rainy season. There is now conclusive evidence (see Motulsky, 1964) that in hyperendemic malaria areas the sickle-cell trait (and probably also G6PD deficiency), once occurring as a mutation or introduced by migration from another population, will increase in frequency until a balanced polymorphic state is reached. It is reasonable to assume that the Bushmen of the Kalahari were "settled" in their present habitat before the sickle-cell gene made its appearance in their Bantu neighbors to the north. Silberbauer (1965), because of the high degree of cultural adapta-

tion shown by the Bushmen and on the basis of certain linguistic evidence, rejects the traditional view that the Bushmen of Botswana are survivors who fled into the Kalahari as refugees following the clashes which took place in surrounding territories. The only Bantu with whom they have come in contact are the Kgalagadi and, to a lesser degree, the Tswana people, neither of whom have the sickle-cell trait or G6PD deficiency in any appreciable incidence (Griffiths, 1953; Charlton, 1962). It seems likely that the great southern migrations of the Bantu had taken place before the sickle-cell gene had been established—otherwise, it is extremely difficult to explain its virtual absence in the Bantu tribes living to the south of the Zambesi River. The gene for G6PD deficiency might have arisen in the Bushmen as the result of mutation, although its absence in the few Kgalagadi and Kwaai hybrids does not preclude the possibility of its introduction by other Bantu.

SUMMARY

The absence of the sickle-cell trait among Kalahari Bushmen has been confirmed, and a search for other abnormal hemoglobins has failed to reveal any. No sickling was found in a group of 50 Kgalagadi school children, but a slow-moving hemoglobin, presumed to be Hb D, was found in the blood of a nine-year-old schoolboy.

No evidence for the existence of β-thalassemia was found in the Bushmen or Kgalagadi. The low incidence of G6PD deficiency among Bushmen is confirmed, and its absence in the Kgalagadi and the Kwaai River Bush-Bantu hybrid group is reported.

ABO and Rhesus blood-group data are presented for the Bushmen and Kwaai hybrids and compared with existing data for Bushmen and Southern Bantu.

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