Blood Groups of Apes and Monkeys
IV. The Rh-Hr Blood Types of Anthropoid Apes

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UP TO THE PRESENT TIME, only a few studies have been carried out on the Rh-Hr types[3] of anthropoid apes, all limited to chimpanzees (Wiener, 1952; Wiener, Gavan, and Gordon, 1953; Wiener and Gordon, 1961; Wiener, Baldwin, and Gordon, 1963). These investigations on a total of 37 chimpanzees showed the red cells of every chimpanzee to have the blood factors **Rh$_0$** and **hr′**, and to lack the factors **rh′**, **rh″**, and **hr″**. Thus, all chimpanzees tested were of the same Rh-Hr type, to which was assigned the symbol $(\bar{R}h_0)^{Ch}$. In the course of our recent investigations in the blood groups of primates, the opportunity presented itself to extend the studies on the Rh-Hr types to a larger series of chimpanzees as well as a series of gibbons and orangutans and one gorilla maintained at Yerkes Regional Primate Research Center, Orange Park, Florida. A preliminary report of the findings has been prepared (Wiener and Moor-Jankowski, 1963). The purpose of this report is to present the results of these studies in detail.

MATERIALS AND METHODS

For information regarding the immunogenetics of the Rh-Hr blood types and their nomenclature, one should consult Wiener and Wexler (1958, 1963). The techniques used for testing for the various Rh-Hr blood factors were described by Wiener and Gordon (1961). The method of collecting and preserving the blood samples of nonhuman primates has been described in detail in previous papers of this series (Moor-Jankowski, Wiener, and Gordon, 1963a; Wiener, Moor-Jankowski, and Gordon, 1963). The present study includes a series of 44 chimpanzees, nine gibbons, ten orangutans, and one gorilla. The ABO groups, secretor status, Lewis types, and MN factors of these animals were described in previous papers of these series (Wiener, Moor-Jankowski, and Gordon, 1963; Moor-Jankowski, Wiener, and Gordon, 1963a, b).

Received October 10, 1963.

[3]To avoid ambiguity, symbols for blood factors and their corresponding antibodies are printed in **boldface** type, symbols for genes and genotypes are printed in *italics*, while symbols for agglutinogens, phenotypes, and blood group systems are printed in regular type.

RESULTS

In Table 1 are shown the reactions of red cells of apes with various Rh-Hr reagents in comparison with the reactions of human red cells of known Rh-Hr blood types. The red cells of all 44 chimpanzees gave indistinguishable reactions with these reagents, so that only four are shown as typical in Table 1. As in previous studies, the chimpanzees proved to have the blood factors **Rh$_0$** and **hr′** and to lack the blood factors **rh′**, **rh″**, and **hr″**. Thus, every one of these 44 chimpanzees belongs to type $(\overline{\text{Rh}}_0)^{\text{Ch}}$. When these findings are combined with our previous observations, a total of 81 chimpanzees have been tested by us to date, all of the same type, $(\overline{\text{Rh}}_0)^{\text{Ch}}$.

In contrast, the red blood cells of all nine gibbons failed to react with the anti-**Rh$_0$** reagents. They did react with anti-**hr′** sera but not, or only feebly, with anti-**rh′**, anti-**rh″**, or anti-**hr″** sera. Thus, gibbon red cells apparently have only blood factor **hr′** and therefore may be assigned the symbol $(\bar{\text{r}}\text{h})^{\text{Gi}}$.

The blood cells of the ten orangutans showed definite clumping only with the anti-**Rh$_0$** and anti-**hr′** sera, although the intensity of the reactions was not as great as that of the human red cells used as standards. The blood cells of the gorilla also gave distinct agglutination only with anti-**Rh$_0$** and anti-**hr′**. On the other hand, red cells from a Java monkey failed to clump in any of the Rh-Hr sera tried.

In order to verify the specificity of the reactions observed, the tests were repeated by the titration method (cf. Table 2). In the gibbons, no distinct clumping was observed with anti-**Rh$_0$** reagents having titers as high as 500 units for human Rh+ red cells. In contrast, anti-**hr′** reagents reacted to almost the same titer with gibbon red cells as with human red cells having the **hr′** factor. Rh-Hr antisera of other specificities did not clump gibbon red cells. These results unequivocally confirm the classification of the blood of these gibbons as type $(\bar{\text{r}}\text{h})^{\text{Gi}}$.

In the orangutans, the situation is not as clear (cf. Table 3). First, some blood specimens reacted weakly with the anti-**rh′** and anti-**hr″** reagents, but these irregular weak reactions probably can be discounted. (See Moor-Jankowski, Wiener, and Gordon, 1963a.) The fact that an antiserum bears the label anti-**rh′**, for example, does not mean that every weak clumping produced by the reagent is due to its anti-**rh′** antibody, since other antibodies generally are also present. The positive reactions of anti-**hr′** and anti-**Rh$_0$** with orangutan blood appear to be significant, however. The titers for orangutan red blood cells are considerably lower than those for human red cells, but this can mean that the **Rh$_0$** and **hr′** factors of orangutan blood do not resemble the corresponding factors of human blood as closely as do those of chimpanzee red cells. Findings in the single gorilla tested indicate the presence of blood factors **Rh$_0$** and **hr′** in the red cells but not factors **rh′**, **rh″**, or **hr″** (cf. Tables 1 and 3). The titers of the gorilla are intermediate between those of chimpanzee and gibbons and those of orangutans.

The specificity of the reactions of the anti-**Rh$_0$** and anti-**hr′** sera with chimpanzee red cells was examined further by means of absorption experi-

TABLE 1. RESULTS OF TESTS WITH RH-HR ANTISERA ON RED BLOOD CELLS FROM CHIMPANZEES, GIBBONS, ORANGUTANS, A GORILLA, AND A JAVA MONKEY

The strength of the reactions is indicated by the number of plus signs, +++ being the strongest reaction possible, one large clump of cells.

	Reactions with Rh antisera†					Reactions with Hr antisera	
	Anti-rh′		Anti-rh″		Anti-Rh_0	Anti-hr′	Anti-hr″
	Serum No. 1 saline‡	Serum No. 2 ficin‡	Serum No. 3 saline‡	Serum No. 4 ficin	Serum No. 5 ficin‡	Serum No. 6 ficin	Serum No. 7 ficin‡
CHIMPANZEES*							
Pan satyrus							
Wendy Ch 4	—	—	—	—	++±	++±	—
Alpha Ch 28	tr.	—	—	—	++±	++±	—
Soda Ch 12	—	—	tr.	—	++±	++±	—
Alf Ch 59	—	—	tr.	—	++±	++±	—
GIBBONS							
Hylobates lar							
Burma	+	—	—	—	—	++	—
Charlie	+	—	—	—	—	++±	—
Viet	+	—	—	—	—	++±	—
Suma	+	—	—	—	—	++	—
Thai	+	—	—	—	—	++	—
Becky	+	tr.	—	—	—	++±	—
But	+	+	—	—	—	++±	—
Kerry	—	tr.	—	—	±	++±	—
Hylobates pileatus							
Indo	±	tr.	—	—	±	++±	—
ORANGUTANS							
Pongo pygmaeus							
Lipis OR 1	tr.	+	—	—	++	+±	±
Kuala OR 2	—	tr.	—	—	++	++±	±
Sampit OR 3	—	±	—	—	+±	+±	tr.
Kitchie OR 4	—	±	—	—	+±	++	±
Lambak OR 5	—	tr.	—	—	++	+±	—
Sya OR 6	+	±	tr.	—	+±	+±	—
Bagan OR 7	tr.	±	—	—	+±	+±	—
Djambis OR 8	tr.	+	—	—	+±	+±	tr.
Sungei OR 10	+	tr.	—	—	++	++	—
Sibu OR 12	tr.	+	—	—	++	++	—
GORILLA							
G. gorilla gorilla							
Mary Lou	tr.	—	—	—	++	++	—
JAVA MONKEY	—	—	—	—	—	—	—
MAN (controls)							
Homo sapiens							
Rh_1rh	++±	++±	—	—	++±	++±	++±
Rh_1Rh_1	++±	++±	—	—	++±	—	++±
Rh_2rh	—	—	++±	++±	++±	+++	++±
Rh_2Rh_2	—	—	++±	++±	++±	+++	—
rh	—	—	—	—	—	+++	++±

*A total of 44 chimpanzees were tested, all of which gave the same reactions. Of these 44, only four are shown in the table for purposes of illustration.

†Serum No. 1 is a blocked anti-Rh_0′ serum, and serum No. 3 is a blocked anti-Rh_0″ serum. Serum No. 2 is a pure anti-rh′ serum, and Serum No. 4 is a pure anti-rh″ serum.

‡The weak reactions (tr., ±, +) in these columns are not consistently reproducible and are, therefore, discounted as due to presence in the reagents of weak, nonspecific heteroagglutinins for non-human primate red cells.

TABLE 2. RESULTS OF TESTS BY THE TITRATION METHOD FOR THE RH-HR FACTORS ON THE RED CELLS OF GIBBONS

	Direct reactions by ficin method with				Titers* by ficin method with			
	Anti-rh′ Serum No. 2	Anti-rh″ Serum No. 4	Anti-rh′ + rh″ Serum No. 8	Anti-hr″ Serum No. 7	Anti-Rh_0 Serum No. 5†	Anti-Rh_0 Serum No. 9†	Anti-hr′ Serum No. 6	Anti-hr′ Serum No. 10
GIBBONS								
Hylobates lar								
Burma	—	—	—	—	½	0	44	88
Charlie	—	—	—	—	1	0	96	192
Viet	—	—	—	—	0	0	88	96
Suma	—	—	—	—	½	0	54	88
Thai	—	—	—	—	0	0	80	48
Becky	—	—	—	—	1	0	60	96
Britt	—	—	—	—	½	1	96	128
Kerry	—	—	—	—	0	0	88	80
Hylobates pileatus								
Indo	—	—	—	—	1	–	176	128
MAN (controls)								
Homo sapiens								
Type Rh_2Rh_2	—	++±	++	—	500	350	214	214
Type Rh_1Rh_1	++±	—	++±	++±	320	500	0	0
Type rh	—	—	—	+++	0	0	214	256

*The titer (in units) is the reciprocal of the highest dilution giving a + reaction. Where no tube in a titration showed a + reaction, the end point was estimated by interpolation. Differences in titer up to two serial dilutions are generally not reproducible, so that variations in titer which are fourfold or less are not considered significant.

†The weak reactions in these columns may be discounted as due to weak, nonspecific heteroagglutinins in the reagents (cf. Table 1).

ments. (When additional material becomes available, it is planned to extend these absorption experiments to the red cells of the other anthropoid apes). As shown in Table 4, when the anti-$\mathbf{Rh_0}$ and anti-**hr′** sera were absorbed with ficinated human red cells having the corresponding blood factors, there was a reduction or elimination of the reactivity of the antisera not only for human red cells but also for chimpanzee red cells. This is further evidence that the reactions of these antisera with chimpanzee red cells are due to their $\mathbf{Rh_0}$ and **hr′** antibodies rather than to any species specific heteroagglutinins for chimpanzee red cells which might be present in these human sera. When the anti-**hr′** sera were absorbed with ficinated chimpanzee red cells there was a reduction in titer for human as well as chimpanzee red cells, and the results with the two reagents tried (7 Gav. and 8 Rin.) suggest that chimpanzee and human red cells were almost equally efficient in absorbing the antibody. In the experiments with anti-$\mathbf{Rh_0}$ sera, absorption with chimpanzee red cells removed the reactivity for chimpanzee red cells with only little apparent effect on the reactivity of the reagents for human $\mathbf{Rh_0}$-positive red cells. Thus, all six human anti-$\mathbf{Rh_0}$ sera tested behaved as if they contained at least two kinds of $\mathbf{Rh_0}$ antibodies, one reactive for chimpanzee as well as human red cells and the other reactive for human red cells alone. This proves that the $\mathbf{Rh_0}$ factor, or factors, of chimpanzee red cells is different from the $\mathbf{Rh_0}$ factors of human red cells.

TABLE 3. RESULTS OF TESTS BY THE TITRATION METHOD FOR THE RH-HR FACTORS ON THE RED CELLS OF ORANGUTANS AND A GORILLA

	Titers by ficin method with					
	Anti-rh' Serum No. 2*	Anti-rh'' Serum No. 4*	Anti-hr' Serum No. 6	Anti-hr' Serum No. 10	Anti-Rh_0 Serum No. 5	Anti-Rh_0 Serum No. 9
ORANGUTANS						
Pongo pygmaeus						
Lipis OR 1	3	2	6	12	14	5
Kuala OR 2	2	0	7	4	22	6
Sampit OR 3	3	3	6	12	24	5
Kitchie OR 4	1	0	6	10	11	4
Lemback OR 5	0	0	2	2	5	2
Sya OR 6	½	0	6	8	6	3
Djambi OR 8	½	0	3	3	6	3
GORILLA						
G. gorilla gorilla						
Mary Lou		0	56	48	22	12
Controls						
CHIMPANZEES						
Pan satyrus						
Jenda Ch 188	0	0	48	44	96	96
Boka Ch 200	0	0	28	40	96	160
GIBBON						
Hylobates lar						
Becky	½	0	96	44	1	0
MAN						
Rh_1rh	16	0	56	96	214	214
Rh_2rh	0	64				
rh	0	0			0	0
Rh_1Rh_1			0	0		

*The weaker reactions in these columns are not consistently reproducible, and are discounted as due to weak nonspecific heteroagglutinins in the reagents.

DISCUSSION

At the time of our first studies on the Rh-Hr types of chimpanzees (Wiener and Wade, 1945), the conglutination, anti-globulin, and proteolytic enzyme techniques had not yet been perfected, and only reagents active by the saline agglutination method could be used. With the aid of an exceptionally potent anti-**hr'** agglutinating serum, it was shown that each of ten chimpanzees was **hr'** positive but the red cells failed to clump with the anti-$\mathbf{Rh_0}$ agglutinating serum available at that time. Chimpanzee cells also failed to react with anti-**rh'** and anti-**rh''** sera, and these results were interpreted to mean that all ten chimpanzees were type rh, especially since chimpanzee red cells absorbed the anti-**hr'** agglutinins but not the anti-$\mathbf{Rh_0}$ agglutinins. Mourant and Race (1946) repeated the experiment and also found that chimpanzee red cells absorbed anti-**hr'** but not anti-$\mathbf{Rh_0}$, anti-**rh'**, or anti-**rh''** agglutinins. In subsequent investigations, however, it was found (Wiener,

TABLE 4. RESULTS OF ABSORPTION TESTS WITH CHIMPANZEE AND HUMAN RED CELLS OF ANTISERA OF SPECIFICITIES ANTI-Rh_0 AND ANTI-hr′

Lot No.	Specificity of antiserum	Titers of unabsorbed sera for		Titers* of sera absorbed with chimpanzee cells and tested against		Titers of sera absorbed with human cells and tested against	
		Human red cells	Chimpanzee red cells	Human red cells	Chimpanzee red cells	Human red cells	Chimpanzee red cells
1. And.	Anti-Rh_0	256	52	80	2	3	0
2. Roth	Anti-Rh_0	300	80	235	6	92	23
3. Swiat.	Anti-Rh_0	112	37	128	7	8	7
4. Schw.	Anti-Rh_0	40	16	40	0	0	0
5. Lough	Anti-Rh_0	28	14	40	1	2	0
6. Bud	Anti-Rh_0	112	31	64	1	15	2
7. Gav.	Anti-hr′	64	26	7	1	2	0
8. Rin.	Anti-hr′	88	128	48	28	18	17

*Each serum was absorbed with an equal volume of ficinated red cells. Titrations are against ficinated red cell suspensions. The titer values given are the average in most cases of two titrations for human red cells and three titrations for chimpanzee red cells.

Gavan, and Gordon, 1953) that ficinated chimpanzee red cells are strongly clumped by all anti-Rh_0 as well as anti-hr′ antisera but not by anti-rh′, anti-rh″, or anti-hr″ sera. Moreover, as shown by the quantitative antiglobulin technique, chimpanzee red cells can be coated with Rh_0 and hr′ antibodies in saline media as heavily as human red cells having the corresponding blood factors. These observations were confirmed by Butts (1953), Wiener and Gordon (1961), and Wiener, Baldwin, and Gordon (1963) and have been extended still further by the present study on 44 chimpanzees. To date, more than 80 chimpanzees have been tested by us (not counting the ten of the original study of Wiener and Wade, 1945), and all have been found to have blood factors Rh_0 and hr′ but to lack rh′, rh″, hr″. Thus, the recent report by Eyquem, Podliachouk, and Millot (1962)—that in one series of 10 chimpanzees only one had the D(Rh_0) antigen while in another series D(Rh_0) was found in only 8 of 13 chimpanzees—does not conform to our extensive experience.

The Rh_0 factors of chimpanzee blood are different from the Rh_0 factors of human blood, as proved by the absorption experiments described in the present paper, as well as observations of Wiener and Gordon (1961) using anti-rhesus guinea pig sera. To date, individual differences with respect to the Rh-Hr types have not been found among more than 80 chimpanzees tested. The symbol $\bar{R}h_0^{Ch}$ was suggested by Wiener and Gordon (1961) to represent the Rh-Hr type characteristic of chimpanzees. The type $(\bar{R}h_0)^{Ch}$ has its counterpart in man, but in man the type $\bar{R}h_0$ is extremely rare and has been found so far only among Negroids (Wiener, Gordon, and Cohen, 1952). In the symbol $\bar{R}h_0^{Ch}$ the bar above the R represents the absence of the pair of contrasting factors rh″ and hr″, and one must also bear in mind that the Rh_0 factors of chimpanzee blood are not identical with the Rh_0 factors of human blood. Moreover, although in tests up to the present time

the **hr′** factors of chimpanzee and human blood have given similar or identical reactions, the possibility is not excluded that anti-**hr′** reagents may be found which can show them to be different.

If the Rh-Hr agglutinogens of chimpanzees are determined by genes homologous to those which determine the Rh-Hr agglutinogens in man, then, in conformity with Wiener's (1943) theory of multiple allelic genes, it can be postulated that all chimpanzees are homozygous for a gene $\overline{R}^{oCh}$ which determines the corresponding agglutinogen $\overline{\text{Rh}}_o^{Ch}$ having the serological specifities $\mathbf{Rh}_o$ (similar to, but not identical with, $\mathbf{Rh}_o$ of man) and **hr′**, but lacking **rh′**, **rh″**, and **hr″**. Thus all chimpanzees may be assumed to be genotype $R^{oCh}R^{oCh}$.

It is of interest that the Rh-Hr blood factors, which determine such a variety of phenotypes in man, determine but a single phenotype among the many chimpanzees we have tested. Whatever may be the reason for this lack of polymorphism, it would appear that erythroblastosis fetalis caused by isosensitization to the Rh-Hr blood factors is a problem with which chimpanzees do not have to contend.

In contrast to the findings in chimpanzees, all nine gibbons tested in the present investigation belong to the single phenotype $(\bar{\text{rh}})^{Gi}$, that is, their red cells have the blood factor **hr′** but lack $\mathbf{Rh}_o$, **rh′**, **rh″**, and **hr″**. Due to limitations of material, the results of the **hr′** tests have not yet been confirmed by absorption experiments, but the similarity in titer of anti-**hr′** reagents for gibbon and human red cells leave little doubt that gibbon cells really have a factor related to the human **hr′** factor.

The red cells of the ten orangutans tested, like the red cells of chimpanzees, appear to have the two factors $\mathbf{Rh}_o$ and **hr′**, but the relatively low titers obtained with the antisera indicate that the blood factors must be quite different from the corresponding factors of chimpanzee and man.

The red cells of the single gorilla tested also had both $\mathbf{Rh}_o$ and **hr′** factors, with titers intermediate between those of chimpanzees and orangutans. Therefore, according to the degree of resemblance of the Rh-Hr reactions to those of man, the apes could be arranged in the order: chimpanzee, gibbon, gorilla, and orangutan. As pointed out in the previous papers of this series, the order in which the apes could be arranged varies depending on the characteristic used as the basis for comparison; but, in all tests, chimpanzees consistently take the position closest to man.

SUMMARY

A total of 44 chimpanzees, ten gibbons, nine orangutans and one gorilla have been tested for the Rh-Hr factors, $\mathbf{Rh}_o$, **rh′**, **rh″**, **hr′**, and **hr″**. The present findings combined with our previous results now comprise a total of 81 chimpanzees tested and show all to be of the identical type $(\overline{\text{Rh}}_o)^{Ch}$, *viz.* with red cells having factors $\mathbf{Rh}_o$ and **hr′** but lacking **rh′**, **rh″**, and **hr″**.

In gibbons, in contrast, the single type $(\bar{\text{rh}})^{Gi}$ exists, namely, the red cells have only factor **hr′** and lack the other four Rh-Hr factors. The red blood cells of orangutans and of the gorilla tested appear to have the two factors

Rh_0 and **hr'**, but the reactions are of lower intensity. The significance of these findings is discussed.

ACKNOWLEDGMENTS

The tests carried out in the Serological Laboratories of the Chief Medical Examiner of New York City were aided in whole by U. S. Public Health Service grant GM-09237-02 from the National Institutes of Health. The authors are greatly indebted to Dr. Willard H. Eyestone, Chief, Animal Resources Branch, National Institutes of Health, for having facilitated the comparative study of blood groups in primates maintained at the Regional Primate Research Centers. They wish gratefully to acknowledge the help of Dr. Geoffrey H. Bourne, Director, Yerkes Regional Primate Research Center, Emory University, who arranged for the sampling on the anthropoid apes reported in this paper, and of Dr. Charles M. Rogers who helped in collecting blood and saliva from these animals. Mr. Charles B. Guthrie, Jr., National Institute of Dental Research, and Misses Pat Ryan, Dina Santana, and Sybil Gordon, Office of the Chief Medical Examiner of New York City, assisted in the performance of the tests. Parke, Davis and Company kindly supplied "Sernylan," making possible the handling of large numbers of animals.

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