Macaque "Semispecies"

A recent report by Goodman *et al.* (*1*) presents interesting data on individual variation of serum transferrins in macaques. In this article statements previously published by me (*2*) have been misconstrued to support a taxonomically revolutionary hypothesis to which I do not subscribe. On the basis primarily of their findings for crab-eating macaques, "*M. irus*," and stump-tailed macaques, "*M. speciosa*," the authors suggest that taxonomic subdivisions of the genus *Macaca* should be regarded as "semispecies rather than complete species." The crab-eating macaques and stump-tailed macaques discussed by the authors occur together with pig-tailed macaques in large areas of southeast Asia without showing the slightest evidence of intergradation or interbreeding. There is no basis for regarding these three sympatric kinds of macaques as representatives of anything but three distinct species. The term "semispecies" proposed by Mayr (*3*) is explicitly defined to apply only to allopatric forms, not to sympatric forms. My remarks (*2*, p. 364) on known and probable intergradation of allopatric forms of macaques also have been misapplied to sympatric forms; this distortion results from the authors' paraphrased citation of my words "another enlarged species" as "an enlarged species" (*1*, p. 886). Transferrin phenotypes discussed by the authors appear to vary individually within and between species; such individual variables are irrelevant in species determination.

Information presented by the authors on the geographic source of their specimens also appears to require correction. In their map (*1*, Fig. 2), sources of two of seven groups of specimens are indicated outside the known range of the race or species to which the specimens belong; crab-eating macaques are not known from northeastern Burma (circle no. 5), and stump-tailed macaques are not known from west of the Bay of Bengal (circle no. 6).

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2. J. Fooden, *ibid.* **143**, 363 (1964).
3. E. Mayr, *Animal Species and Evolution* (Belknap, Cambridge, Mass., 1963), p. 501.

1 March 1965

Because of the smallness of the map in our Fig. 2, only an approximation of geographic locations was attempted. Group 5 is not meant to be from northeastern Burma any more than groups 4 and 3 are meant to be from the ocean. The legend to Fig. 2 and the information on geographic sources in Table 1 make it clear that group 5 (*M. irus*, Mainland) was from Thailand, Viet Nam, and Malaya. The only information we have about group 6 (*M. speciosa*, India) is that the monkeys in this particular group were always imported from India.

In support of our suggestion that it may be helpful to look upon the genus *Macaca* as a monophyletic assemblage of "semispecies," we wish to emphasize the possibility that the sympatry of several of the distinct species of macaques is a secondary sympatry of former geographic races—in other words, that the degree of speciation had progressed far enough in these former geographic races so that on secondary contact with each other they could interbreed only to a limited extent, even after extensive geographic overlap, rather than freely as would be the case with conspecific populations or races of a single species. We believe (perhaps erroneously) that the term "semispecies" as recently described by Mayr (pp. 118, 455, 501) appropriately designates the species groups in such a situation. Since the term "semispecies" is not a designation of formal taxonomic rank, the suggestion that the species groups of macaques are an assemblage of semispecies does not in itself call for any revision of the current taxonomic classification of macaques.

We doubt that Fooden has the evidence to rule out the view that a limited degree of gene exchange or introgression is possible between sympatric macaque groups such as *M. irus* and *M. speciosa*, or *M. irus* and *M. nemestrina*, in their zones of geographic overlap. If we now have a correct understanding of the concluding remarks in his report, he believes his preliminary studies indicate that *M. nemestrina* and *M. assamensis* (and perhaps some other macaque groups?) may intergrade to constitute an enlarged species which is distinct from the enlarged species group he would create consisting of *M. mulatta, M. fascicularis* (*irus*), and perhaps some other currently recognized macaque species. However, a not uncommon view among students of the primates is that *M. assamensis* (along with *M. cyclopis*) is closely allied to *M. mulatta*. There are probably other conflicting opinions on the phyletic relationships of different macaques. It is our position that biochemical and serological data on the polymorphic forms of macromolecules can help determine the actual genetic affinities which exist among the various populations within the genus *Macaca*. Admittedly, many genic alleles which are common to more than one lineage of macaques have resulted from either parallel mutations or from the retention in these lineages of alleles which were present in the common ancestral population. Nevertheless, a well-designed survey of the distribution of genic alleles in natural macaque populations throughout their geographic ranges would certainly shed some light on whether or not gene exchange has occurred among different macaque groups. We hope our article has indicated that it would be important to study geographic variations in the polymorphism of transferrin in such a survey.

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Primate Blood Groups and Evolution

In "Organisms and molecules in evolution" (*1*), G. G. Simpson discusses some reservations concerning the validity of comparing molecular and organismal data in order to elucidate phylogenetic relationships. In studies of primates, the basis of such a comparison could be broadened by making use of data on blood groups of man, apes, and monkeys. The considerable amount of information along these lines available since the work of Landsteiner and Miller (*2*) and, later on, of Wiener (*3*) has recently been greatly augmented by the introduction of new techniques of blood grouping and as a result of the greater accessibility of apes and monkeys in the newly created Regional Primate Research Centers. The present data on primate blood groups permit comparative studies in an area which, because of its early development and clinical importance, has the additional advantage of having been thoroughly investigated in man. The techniques applied are those of hemagglutination, known to be more sensitive than precipitation methods and more

selective than techniques based on electrophoretic mobility.

The "human-type" blood groups of apes and monkeys are determined by using suitably absorbed reagents originally produced for tests in man. The results of a recent series of tests (*4*) on numerous apes and monkeys confirm in many respects the old established hypothesis of phylogenetic relationship of primates based on nonmolecular data. Blood groups of apes have, in general, more characteristics similar to those of man than do the blood groups of *Catarrhini* (Old World monkeys); while blood groups of *Platyrrhini* (New World monkeys) are even more dissimilar to those of man and of apes. Moreover, the resemblance to man in this respect varies from one ape species to another, independently for each blood group. Thus, for blood groups the situation is similar to that for morphological features: With respect to certain characteristics one ape species may resemble man more closely than other species, while with respect to another characteristic a different ape species may appear closer to man. The same applies to monkeys if their overall greater dissimilarity to man is taken into account.

To quote some examples, all apes and monkeys tested to date secrete H and A or B or both blood group substances, with the exception of orangutans, which like man are polymorphic for their ABH secretor status. In the A-B-O blood groups, among the apes, chimpanzees are the most similar to, and gorillas the most different from man. Gorillas are more similar to *Catarrhini*. The red cells of *Catarrhini* give no A-B-O specific reactions, yet their A-B-O status is inferred from inhibition tests on blood group substances secreted in their body fluids and from the presence of reciprocal agglutinins in their serums. The distribution of A-B-O blood types in *Catarrhini* varies from species to species. For instance, blood types A, B, AB, and rarely also O are present in baboons, but only type B has been found in rhesus monkeys tested to date. In *Platyrrhini*, the serological characteristics of human-type blood factors are very different; for instance, the B agglutinogen on the red cell is not type-specific but heterophile, that is, it has been found in all the *Platyrrhini* species tested. Yet the A-B-O status of *Platyrrhini* can still be inferred from inhibition reactions by blood group substances secreted in body fluids. The serology of the A-B-O reactions in chimpanzees, orangutans, and gibbons is more similar to that in man than is the serology of their M-N types, although a varying degree of M-N polymorphism has been observed in these three ape species. As for the Rh-Hr system, the order of the degree of resemblance to man is as follows: chimpanzee, gibbon, gorilla, and orangutan. Tests for Lewis substance in saliva have revealed polymorphism of Lewis secretor status in some ape and *Catarrhini* species; in other species only secretors or only nonsecretors have been demonstrated. On the other hand, no *Platyrrhini* tested were Lewis secretors. Most interesting is the recent finding from Race and Sanger's laboratory on the Xg^a blood group antigen in gibbons (*5*), in a distribution suggestive of sex linkage. The Xg^a is sex-linked in man. It has not been found at all in chimpanzees, orangutans, baboons, drills, and rhesus monkeys tested to date. Thus, in respect to Xg^a, gibbons are more similar to man than other primates.

Our conclusions on the phylogenetic relationship of A-B-O blood group specificities in man, apes, and monkeys have been supported by the differential results of recent heterotransplantations of chimpanzee and baboon kidney to man (*6*). Here again, what yesterday was an esoteric concept becomes today an experimental tool and may become tomorrow a routine technique.

Further advances in comparative studies of blood group specificities in primates, including man, are expected to result from investigation of what has been designated "simian-type" blood factors, that is, blood group specificities detected with antiserums prepared against red cells of apes and monkeys. In fact, the Rh factor of Landsteiner and Wiener may now be called the first simian-type blood factor discovered, because the original reagents of 25 years ago were prepared by immunization of rabbits and guinea pigs with red cells of rhesus monkeys. The great advance of knowledge of genetic and selective mechanisms in man which resulted from this discovery is now part of biomedical history. Recently, with newly produced antiserums, simian-type blood factors have been determined in chimpanzees, gibbons, and Celebes black apes (*7*). One of the more important findings so far from the viewpoint of phylogenetic relationship is the identification of the V-A-B blood group system of chimpanzees, where $\mathbf{A}^c$ and $\mathbf{B}^c$ ("c" for chimpanzee) are simian type blood factors present in chimpanzees but not observed in man, but the **V** blood factor shares its specificity and serological characteristics with the human-type agglutinogen N of man. A second blood group system, designated the C-E-F system, and four additional blood factors have also been identified in chimpanzees.

More information along these lines is now forthcoming. Tests on human red cells with the newly developed simian-type specific antiserums are also expected to shed more light on phylogenetic relationships of primates. Moreover, it is more promising to see, in the work of Shulman (*8*), that an investigative approach that is similar, though by a complement fixation method, yields results on platelet and leucocyte antigen specificities of primates. Human antiserums stimulated by homologous transfusions identify isoantigenic differences in platelets and leucocytes of man, apes, and monkeys, while simian immune serums reveal isoantigenic differences in man. Thus, new markers on a molecular level are becoming available for further studies on phylogenetic relationship.

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