

Phylogenetic Relationships and Rates of Evolution in Primates: Allozymic Data from Catarrhine and Platyrrhine Species

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ABSTRACT. The genetic electrophoretic variation at up to 43 protein loci was studied in four hominoid, three cercopithecoid, and three ceboid species. Phylogenetic reconstructions based on genetic distances show that the two chimpanzee species are closest to humans, while the gorilla diverged earlier than the split between humans and the chimpanzee. Within the cercopithecoids the green monkey apparently diverged earlier than the macaques, and within the ceboids, the owl monkey is only distantly related to the capuchin and squirrel monkeys. The hypothesis that rates of evolution at the level of protein electrophoretic variation are equal both among the groups, as well as within each group, could not be rejected.

Key Words: Cercopithecoids; Ceboids; Hominoids; Phylogeny; Rate of molecular evolution; Electrophoretic variation.

INTRODUCTION

Several molecular methods have been used in the past to investigate phylogenetic relationships and rates of evolution in primates. These included immunological assays, amino acid sequencing, electrophoretic tests of enzymes and other proteins, DNA-DNA hybridization analyses, restriction-enzyme analyses of mitochondrial DNA, and more recently, nucleotide sequencing of genes and pseudogenes (for a review of the literature, see AYALA, 1980; ANDREWS, 1986; HAYASAKA et al., 1988). In respect to the rate of evolution, there are two opposing views in the literature, one claiming that the rate of evolution in hominoids, and in particular in humans, has slowed down considerably in comparison to other primate lineages (e.g., LI & TANIMURA, 1987), and the other suggesting that the rate in all lineages has remained roughly constant throughout primate evolution (e.g., SARICH & CRONIN, 1976).

In regard to phylogenetic relationships, the following features have emerged: (1) Each of the two groups, catarrhine primates and platyrrhine primates, constitutes a natural clade. (2) The hominoids branched off the cercopithecoid lineage after the split between the catarrhine and platyrrhine primates, such that the hominoids and the cercopithecoids constitute a natural clade, the Catarrhini. It is not known whether the divergence of the apes occurred a long time after the platyrrhine-catarrhine split, or whether the apes diverged in immediate temporal proximity to this event. (3) The orangutan (*Pongo*) diverged considerably earlier than the human-chimpanzee-gorilla lineage. The human-chimpanzee-gorilla trichotomy, however, is unresolved at the present time, although the accumulating empirical evidence

strongly favors a clustering of *Homo* and *Pan*, with *Gorilla* branching off a little earlier in time.

Data collected at the Institut für Anthropologie und Humangenetik, Universität Tübingen, in the last ten years afford us to tackle some of these questions at the level of electrophoretic mobility of proteins. Moreover, simultaneous comparisons between and within the catarrhines (cercopithecoids and hominoids) and platyrrhines (ceboids) are now possible for the first time. Thus, for instance, by comparing the genetic distances between a reasonably close outgroup species and a well-established phylogenetic clade comprised of several genera or species, we can test whether the different members within that clade evolved at equal rates or not.

MATERIALS AND METHODS

Up to 43 protein systems were studied in four hominoid species (humans, *Homo sapiens*; common chimpanzees, *Pan troglodytes*; pygmy chimpanzees, *Pan paniscus*, and lowland gorillas, *Gorilla gorilla gorilla*), in three ceboid species (squirrel monkeys, *Saimiri sciureus*; black-capped capuchins, *Cebus apella*; and owl monkeys, *Aotus trivirgatus*), and in three cercopithecoid species (rhesus macaques, *Macaca mulatta*; crab-eating macaques, *Macaca fascicularis*; and green monkeys, *Cercopithecus aethiops*). Individual comparisons, such as between *Macaca fascicularis*, *Homo sapiens*, and *Cercopithecus aethiops*, could be made for up to 61 protein loci. The origin of animals from which the electrophoretic samples were taken are listed in Table 1.

Description of the electrophoretic methods and staining procedures that were used in the present study are similar to those given in HARRIS and HOPKINSON (1976). The list of enzymes studied in each of the ten primate species is given in Table 2. Allele frequencies at each of the 43 loci for the ten species in this study are listed in Table 3.

Nei's modified genetic identity values (I) and genetic distances (D), as well as the standard errors associated with both these variables were calculated according to HILLIS (1984) and TOMIUK and GRAUR (1986). We note, however, that the difference between these values and Nei's original measures (NEI, 1972) are small and do not in any way affect the conclusions.

Table 1. Origin of animals from which the samples were obtained.

| Species | Source |
|-------------------------------|---|
| <i>Homo sapiens</i> | Random sample of patients of the University Hospital in Tübingen. No sample size is given in subsequent tables because only the most common allele is considered. |
| <i>Pan troglodytes</i> | Individuals from different breeding groups in Germany. Origins unknown. |
| <i>Pan paniscus</i> | Individuals from different breeding groups in Germany. Origins unknown. |
| <i>Gorilla gorilla</i> | Adults from a breeding group in the "Wilhelma" Zoological Garden in Stuttgart, and from different breeding groups in Germany. Origins unknown. |
| <i>Macaca fascicularis</i> | Individuals from breeding groups in Germany, received from exporters in Kuala Lumpur. |
| <i>Macaca mulatta</i> | Individuals from two breeding groups in Germany, one which originated in Cayo, Puerto Rico, the other population received from exporters in India. |
| <i>Cercopithecus aethiops</i> | Individuals from breeding groups in Germany, originally received through exporters in Africa. |
| <i>Saimiri sciureus</i> | Individuals sampled from breeding groups in Germany. Origin unknown. |
| <i>Cebus apella</i> | Individuals sampled from breeding groups in Germany. Origin unknown. |
| <i>Aotus trivirgatus</i> | Individuals sampled from breeding groups in Germany. Origin unknown. |

Table 2. List of protein system studied in at least three primate species.

| Protein | Locus | Hominoids ¹⁾ | | | | Cercopithecoids ²⁾ | | | Ceboids ³⁾ | | |
|-------------------------------------|-------------|-------------------------|----|----|----|-------------------------------|----|-----|-----------------------|----|----|
| | | Hs | Pt | Pp | Gg | Mf | Mm | Cae | Ss | Ca | At |
| Glycerol-3-phosphate dehydrogenase | GPD | + | + | + | + | + | - | - | - | - | - |
| Sorbitol dehydrogenase | SDH | + | - | - | - | + | + | + | - | - | - |
| Lactate dehydrogenase | LDHA | + | + | + | + | + | + | + | + | + | + |
| | LDHB | + | + | + | + | + | + | + | + | + | + |
| Malate dehydrogenase | MDH1 | + | + | + | + | + | + | + | + | + | + |
| | MDH2 | + | + | + | + | + | + | + | - | - | - |
| Malic enzyme | MOD1 | + | + | + | + | + | + | + | - | - | - |
| | MOD2 | + | - | - | - | + | + | + | - | - | - |
| Isocitrate dehydrogenase | ICD1 | + | + | + | + | + | + | + | + | + | + |
| | ICD2 | + | + | + | + | + | + | + | + | + | + |
| Phosphogluconate dehydrogenase | PGD | + | + | + | + | + | + | + | + | + | + |
| Glucose-6-phosphate dehydrogenase | G6PD | + | + | + | + | + | + | + | - | - | - |
| α -Keto acid reductase | KAR | + | - | - | - | + | - | - | - | + | + |
| Diaphorase | DIA1 | + | + | + | + | + | + | + | + | + | + |
| | DIA2 | + | + | + | + | + | + | + | + | + | + |
| Catalase | CAT | + | - | - | - | + | + | + | - | - | - |
| Superoxide dismutase | SOD1 | + | + | + | + | + | + | + | + | + | + |
| | SOD2 | + | + | + | + | + | + | + | - | - | - |
| Glutamate oxaloacetate transaminase | GOT1 | + | + | + | + | + | + | + | + | + | + |
| | GOT2 | + | + | + | + | + | + | + | + | + | + |
| Glutamate pyruvate transaminase | GPT | + | - | - | - | + | + | + | + | + | + |
| Adenylate kinase | AK1 | + | - | - | - | + | - | - | + | + | + |
| Phosphoglucomutase | PGM1 | + | + | + | + | + | + | + | + | + | + |
| | PGM2 | + | + | + | + | + | + | + | + | + | + |
| | PGM3 | + | + | + | + | + | - | - | - | - | - |
| Galactose-1-p-uridyl transferase | GALT | + | + | + | + | + | + | + | + | + | + |
| Carboxylic ester hydrolase | ESD | + | + | + | + | + | + | + | + | + | + |
| Glyoxalase II | GLO2 | + | + | + | + | + | - | - | - | - | - |
| Alkaline phosphatase | ALP | + | - | - | - | + | + | + | - | - | - |
| Acid phosphatase | ACP1 | + | + | + | + | + | + | + | + | + | + |
| | ACP2 | + | + | + | + | + | - | - | - | - | - |
| Fructose-1, 6-diphosphatase | FDP | + | + | + | + | + | - | - | - | - | - |
| β -Glucosidase | β GLU | - | - | - | - | + | + | + | - | - | - |
| Arginase | ARG | - | - | - | - | + | + | + | - | - | - |
| Adenosine deaminase | ADA | + | - | - | - | + | + | + | - | - | - |
| Aldolase | ALD | + | - | - | - | + | + | + | + | + | + |
| Carbonic anhydrase | CA1 | + | + | + | + | + | + | + | - | - | - |
| | CA2 | + | + | + | + | + | + | + | + | + | + |
| Aconitate hydratase | ACO1 | + | + | + | + | + | - | - | - | - | - |
| | ACO2 | + | + | + | + | + | - | - | - | - | - |
| Ribulose-5-phosphate-3-epimerase | RPI | + | - | - | - | + | - | - | - | + | + |
| Ribose phosphate isomerase | RPE | + | - | - | - | + | - | - | - | + | + |
| Mannose phosphate isomerase | MPI | + | + | + | + | + | - | - | + | + | + |
| Glucose phosphate isomerase | GPI | + | + | + | + | + | + | + | + | + | + |
| Haptoglobin | HP | + | - | - | - | + | + | + | - | - | - |
| Hemoglobin | HB | + | - | - | - | - | - | - | + | + | + |
| Protease inhibitor | PI | + | + | + | + | + | - | - | - | - | - |
| Serum albumin | ALB | + | + | + | + | + | + | + | + | + | + |
| Transferrin | TF | + | + | + | + | + | + | + | - | + | + |

1) Hs: *Homo sapiens*; Pt: *Pan troglodytes*; Pp: *Pan paniscus*; Gg: *Gorilla gorilla*; 2) Mf: *Macaca fascicularis*; Mm: *Macaca mulatta*; Cae: *Cercopithecus aethiops*; 3) Ss: *Saimiri sciureus*; Ca: *Cebus apella*; At: *Aotus tri-virgatus*.

Table 3. Allele frequencies at 43 protein loci in primates. (For abbreviations see the end of the table.)

| Enzyme | Hs | Pt | Pp | Gg | Mf | Mm | Cae | Ss | Ca | At |
|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| GPD | — | 2 | 4 | 2 | 172 | | | | | |
| | 1.000 | 1.000 | 1.000 | — | 0.012 | | | | | |
| | — | — | — | — | 0.988 | | | | | |
| SDH | — | | | 1.000 | — | | | | | |
| | 1.000 | | | | 442 | 81 | 32 | | | |
| | — | | | | 0.025 | — | 0.016 | | | |
| LDH-A | — | | | | 0.948 | 1.000 | 0.984 | | | |
| | 1.000 | 7 | 6 | 8 | 0.027 | — | — | | | |
| | — | — | — | — | 283 | 108 | 98 | 10 | 4 | 11 |
| LDH-B | — | | | | — | | | 1.000 | | |
| | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | — | — | — |
| | — | — | — | — | — | — | — | — | 1.000 | — |
| MDH-1 | — | | | | — | | | | | 1.000 |
| | 1.000 | 7 | 6 | 8 | 283 | 108 | 98 | 10 | 4 | 11 |
| | — | 1.000 | 1.000 | 1.000 | 0.998 | 0.995 | 1.000 | 1.000 | 1.000 | 1.000 |
| MDH-2 | — | | | | 0.002 | | | | | |
| | 1.000 | 9 | 3 | 9 | 472 | 152 | 107 | 23 | 7 | 7 |
| | — | — | — | — | 0.001 | — | — | — | — | — |
| MOD-1 | — | | | | 0.999 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| | 1.000 | 1.000 | 1.000 | 1.000 | 472 | 152 | 107 | | | |
| | — | — | — | — | — | — | — | | | |
| MOD-2 | — | | | | 1.000 | 1.000 | 1.000 | | | |
| | 1.000 | 2 | 2 | 7 | 472 | 54 | 61 | | | |
| | — | — | — | — | — | — | — | | | |
| ICD-1 | — | | | | 0.999 | 1.000 | 1.000 | | | |
| | 1.000 | 1.000 | 1.000 | 1.000 | 0.001 | — | — | | | |
| | — | — | — | — | 472 | 54 | 61 | | | |
| ICD-2 | — | | | | 0.999 | 1.000 | 1.000 | | | |
| | 1.000 | 10 | 10 | 14 | 0.001 | — | — | | | |
| | — | — | — | — | 1037 | 116 | 175 | 11 | 25 | 15 |
| PGD | — | | | | 0.750 | | | | | |
| | 1.000 | 1.000 | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | — | 0.250 | | | | | |
| G-6-PD | — | | | | — | | | | | |
| | 1.000 | 1.000 | 1.000 | — | 0.797 | 1.000 | — | 1.000 | 0.960 | 1.000 |
| | — | — | — | — | — | — | 0.983 | — | — | — |
| G-6-PD | — | | | | — | | | | | |
| | 1.000 | 1.000 | 1.000 | 1.000 | 0.195 | — | — | — | 0.040 | — |
| | — | — | — | — | 0.005 | — | — | — | — | — |
| G-6-PD | — | | | | 0.002 | — | — | — | — | — |
| | 1.000 | 10 | 10 | 14 | 0.001 | — | — | — | — | — |
| | — | — | — | — | 1037 | 116 | 175 | 11 | 25 | 15 |
| G-6-PD | — | | | | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| | 1.000 | 1.000 | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | — | — | — | — | — | — | — |
| G-6-PD | — | | | | — | | | | | |
| | 1.000 | 10 | 10 | 14 | 862 | 116 | 127 | 21 | 8 | 15 |
| | — | — | — | — | 0.679 | — | — | — | — | — |
| G-6-PD | — | | | | — | | | | | |
| | 1.000 | 1.000 | 1.000 | — | 0.650 | — | — | — | — | — |
| | — | — | — | — | 0.350 | — | — | — | — | — |
| G-6-PD | — | | | | — | | | | | |
| | 1.000 | 1.000 | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | — | 0.898 | 0.909 | 1.000 | 1.000 | — | 1.000 |
| G-6-PD | — | | | | 0.093 | 0.091 | — | — | — | — |
| | 1.000 | 2 | 4 | 2 | 0.007 | — | — | — | — | — |
| | — | — | — | — | 0.002 | — | — | — | — | — |
| G-6-PD | — | | | | — | | | | | |
| | 1.000 | 2 | 4 | 2 | 21 | 60 | 249 | — | 1.000 | — |
| | — | 1.000 | — | 1.000 | 0.024 | — | — | — | — | — |
| G-6-PD | — | | | | 0.976 | 1.000 | 1.000 | | | |
| | 1.000 | — | — | — | — | — | — | | | |
| | — | 1.000 | — | 1.000 | — | — | — | | | |

(continued)

Table 3. (continued)

| Enzyme | Hs | Pt | Pp | Gg | Mf | Mm | Cae | Ss | Ca | At |
|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| DIA-1 | — | 6 | 8 | 7 | 470 | 116 | 129 | 28 | 44 | 24 |
| | 1.000 | — | — | — | 0.026 | — | — | — | — | — |
| | — | 0.833 | 1.000 | — | 0.926 | 0.660 | 0.016 | — | 0.011 | 1.000 |
| | — | 0.167 | — | — | 0.048 | 0.340 | 0.984 | — | — | — |
| | — | — | — | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | — | — | — | 0.893 | 0.989 | — |
| DIA-2 | — | 6 | 8 | 7 | 310 | 116 | 72 | 28 | 34 | 10 |
| | 1.000 | — | — | — | — | — | — | — | — | — |
| | — | 1.000 | — | — | 0.102 | 0.272 | — | — | — | — |
| | — | — | — | — | 0.898 | 0.728 | — | — | — | — |
| | — | — | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | 1.000 | — | — | — | — | — | — |
| CAT | — | — | — | — | — | — | 1.000 | — | — | — |
| | — | — | — | — | — | — | — | 1.000 | 1.000 | — |
| | — | — | — | — | — | — | — | — | — | 1.000 |
| | — | — | — | — | 85 | 260 | 60 | — | — | — |
| | 1.000 | — | — | — | — | — | — | — | — | — |
| | — | — | — | — | 1.000 | 1.000 | 0.992 | — | — | — |
| SOD-1 | — | 4 | 5 | 8 | 110 | 60 | 65 | 21 | 7 | 11 |
| | 1.000 | 1.000 | 1.000 | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 1.000 | 1.000 | — | — | 1.000 | — |
| SOD-2 | — | 4 | 5 | 8 | 110 | 60 | 65 | — | — | — |
| | 1.000 | 1.000 | 1.000 | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 1.000 | 1.000 | — | — | — | 1.000 |
| GOT-1 | — | 2 | 2 | 6 | 258 | 141 | 24 | 15 | 6 | 15 |
| | 1.000 | 1.000 | 1.000 | 1.000 | — | — | 0.042 | — | — | — |
| | — | — | — | — | 0.994 | 1.000 | 0.958 | 1.000 | 1.000 | 0.500 |
| GOT-2 | — | 2 | 2 | 6 | 258 | 141 | 24 | 15 | 6 | 15 |
| | 1.000 | 1.000 | — | 1.000 | 0.002 | — | — | — | — | — |
| | — | — | 1.000 | — | 0.998 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| GPT | — | — | — | — | 597 | 54 | 28 | 11 | 12 | 15 |
| | 1.000 | — | — | — | — | — | — | — | — | — |
| | — | — | — | — | 0.792 | — | — | — | — | — |
| | — | — | — | — | 0.152 | 0.889 | 0.982 | — | — | — |
| | — | — | — | — | 0.032 | — | — | — | — | — |
| | — | — | — | — | 0.013 | — | — | — | — | — |
| | — | — | — | — | 0.009 | — | — | — | — | — |
| | — | — | — | — | — | — | 0.018 | — | — | — |
| | — | — | — | — | — | 0.083 | — | — | — | — |
| | — | — | — | — | — | 0.028 | — | — | — | — |
| AK-1 | — | — | — | — | — | — | — | 1.000 | 0.958 | 0.967 |
| | — | — | — | — | — | — | — | — | 0.042 | — |
| | — | — | — | — | — | — | — | — | — | 0.033 |
| | — | — | — | — | 144 | — | — | 13 | 5 | 10 |
| | 1.000 | — | — | — | 0.007 | — | — | 1.000 | — | — |
| PGM-1 | — | 4 | 10 | 12 | 597 | 178 | 225 | 6 | 5 | 15 |
| | 1.000 | 1.000 | 1.000 | 0.917 | 0.932 | 1.000 | 1.000 | — | 1.000 | — |
| | — | — | — | 0.083 | — | — | — | — | — | — |
| | — | — | — | — | — | — | — | — | — | — |
| | — | — | — | — | — | — | — | — | — | — |

(continued)

Table 3. (continued)

| Enzyme | Hs | Pt | Pp | Gg | Mf | Mm | Cae | Ss | Ca | At |
|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| | — | — | — | — | 0.049 | — | — | — | — | — |
| | — | — | — | — | 0.019 | — | — | — | — | — |
| | — | — | — | — | — | — | — | 1.000 | — | — |
| | — | — | — | — | — | — | — | — | — | 1.000 |
| PGM-2 | — | 4 | 10 | 12 | 597 | 178 | 225 | 6 | 5 | 10 |
| | 1.000 | 1.000 | 1.000 | 0.083 | — | — | — | — | — | — |
| | — | — | — | 0.917 | — | — | — | — | — | — |
| | — | — | — | — | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.050 |
| | — | — | — | — | — | — | — | — | — | 0.950 |
| PGM-3 | — | 4 | 2 | 8 | 597 | — | — | — | — | — |
| | 1.000 | 1.000 | 1.000 | — | 0.030 | — | — | — | — | — |
| | — | — | — | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 0.022 | — | — | — | — | — |
| | — | — | — | — | 0.948 | — | — | — | — | — |
| GALT | — | 4 | 4 | 4 | 597 | 138 | 113 | 18 | 5 | 12 |
| | 1.000 | 1.000 | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 0.723 | 0.993 | 0.894 | — | — | — |
| | — | — | — | — | 0.229 | — | — | — | — | — |
| | — | — | — | — | 0.048 | 0.007 | — | — | — | — |
| | — | — | — | — | — | — | 0.093 | — | — | — |
| | — | — | — | — | — | — | 0.013 | — | — | — |
| | — | — | — | — | — | — | — | 1.000 | 1.000 | — |
| | — | — | — | — | — | — | — | — | — | 0.958 |
| | — | — | — | — | — | — | — | — | — | 0.042 |
| ESD | — | 6 | 11 | 6 | 93 | 223 | 144 | 21 | 57 | 23 |
| | 1.000 | 1.000 | 1.000 | 1.000 | — | — | — | 0.095 | 0.500 | — |
| | — | — | — | — | — | — | 0.014 | 0.905 | 0.500 | 1.000 |
| | — | — | — | — | — | — | 0.986 | — | — | — |
| | — | — | — | — | 0.516 | 0.998 | — | — | — | — |
| | — | — | — | — | 0.274 | 0.002 | — | — | — | — |
| | — | — | — | — | 0.102 | — | — | — | — | — |
| | — | — | — | — | 0.065 | — | — | — | — | — |
| | — | — | — | — | 0.043 | — | — | — | — | — |
| GLO-II | — | 2 | 4 | 2 | 4 | — | — | — | — | — |
| | 1.000 | 1.000 | 0.125 | — | — | — | — | — | — | — |
| | — | — | 0.875 | — | — | — | — | — | — | — |
| | — | — | — | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 1.000 | — | — | — | — | — |
| ALP | — | — | — | — | 32 | 8 | 249 | — | — | — |
| | 1.000 | — | — | — | 1.000 | 1.000 | 0.944 | — | — | — |
| | — | — | — | — | — | — | 0.052 | — | — | — |
| | — | — | — | — | — | — | 0.004 | — | — | — |
| ACP-1 | — | 8 | 5 | 11 | 337 | 169 | 117 | 17 | 19 | 15 |
| | 1.000 | — | — | 1.000 | — | — | — | — | — | — |
| | — | 1.000 | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | — | 0.988 | 0.997 | 0.923 | — | — | — |
| | — | — | — | — | 0.010 | 0.003 | — | — | — | — |
| | — | — | — | — | 0.002 | — | 0.073 | — | — | — |
| | — | — | — | — | — | — | 0.004 | — | — | — |
| | — | — | — | — | — | — | — | 1.000 | 1.000 | 0.200 |
| | — | — | — | — | — | — | — | — | — | 0.800 |
| ACP-2 | — | 8 | 5 | 11 | 337 | — | — | — | — | — |
| | 1.000 | 1.000 | 1.000 | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 1.000 | — | — | — | — | — |
| FDP | — | 2 | 2 | 2 | 22 | — | — | — | — | — |
| | 1.000 | 1.000 | 1.000 | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 1.000 | — | — | — | — | — |

(continued)

Table 3. (continued)

| Enzyme | Hs | Pt | Pp | Gg | Mf | Mm | Cae | Ss | Ca | At |
|--------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| ADA | — | | | | 122 | 12 | 170 | | | |
| | 1.000 | | | | — | — | — | | | |
| | — | | | | 0.992 | 1.000 | — | | | |
| | — | | | | 0.008 | — | — | | | |
| | — | | | | — | — | 0.991 | | | |
| | — | | | | — | — | 0.009 | | | |
| ALD | — | | | | 147 | 54 | 43 | 4 | 6 | 6 |
| | 1.000 | | | | — | — | — | — | — | — |
| | — | | | | 1.000 | 1.000 | — | 1.000 | 1.000 | 1.000 |
| | — | | | | — | — | 1.000 | — | — | — |
| CA-1 | — | 2 | 2 | 4 | 40 | 28 | 90 | | | |
| | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | | | |
| CA-2 | — | 2 | 2 | 4 | 149 | 116 | 90 | 8 | 10 | 6 |
| | 1.000 | — | — | 1.000 | — | — | — | — | — | — |
| | — | 1.000 | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | — | 0.634 | 0.840 | — | — | — | — |
| | — | — | — | — | 0.366 | 0.160 | — | — | 0.750 | — |
| | — | — | — | — | — | — | 1.000 | — | 0.250 | — |
| | — | — | — | — | — | — | — | 1.000 | — | — |
| | — | — | — | — | — | — | — | — | — | 1.000 |
| ACO-1 | — | 2 | 4 | 5 | 1037 | | | | | |
| | 1.000 | 1.000 | 1.000 | — | 0.002 | | | | | |
| | — | — | — | 1.000 | 0.004 | | | | | |
| | — | — | — | — | 0.005 | | | | | |
| | — | — | — | — | 0.012 | | | | | |
| | — | — | — | — | 0.977 | | | | | |
| ACO-2 | — | 2 | 4 | 5 | 1037 | | | | | |
| | 1.000 | 1.000 | 1.000 | 1.000 | — | | | | | |
| | — | — | — | — | 1.000 | | | | | |
| MPI | — | 2 | 5 | 4 | 747 | | | 11 | 2 | 1 |
| | 1.000 | — | — | — | — | | | — | — | — |
| | — | 1.000 | 1.000 | — | — | | | — | — | 1.000 |
| | — | — | — | 1.000 | — | | | — | — | — |
| | — | — | — | — | — | | | 1.000 | 1.000 | — |
| | — | — | — | — | 0.978 | | | — | — | — |
| | — | — | — | — | 0.017 | | | — | — | — |
| | — | — | — | — | 0.005 | | | — | — | — |
| GPI | — | 12 | 6 | 11 | 982 | 116 | 105 | 18 | 53 | 24 |
| | 1.000 | — | — | — | — | — | — | — | — | — |
| | — | 1.000 | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 0.981 | 0.983 | 0.981 | — | — | — |
| | — | — | — | — | 0.013 | — | 0.019 | — | — | — |
| | — | — | — | — | 0.006 | 0.017 | — | — | — | — |
| | — | — | — | — | — | — | — | — | 0.991 | — |
| | — | — | — | — | — | — | — | 0.944 | 0.009 | 0.896 |
| | — | — | — | — | — | — | — | 0.056 | — | 0.083 |
| | — | — | — | — | — | — | — | — | — | 0.021 |
| ALB | — | 2 | 10 | 9 | 132 | 116 | 42 | 16 | 4 | 7 |
| | 1.000 | — | — | — | 0.125 | — | — | — | — | — |
| | — | 1.000 | 1.000 | — | — | — | — | — | — | — |
| | — | — | — | 1.000 | — | — | — | — | — | — |
| | — | — | — | — | 0.867 | 0.328 | 1.000 | — | — | 1.000 |
| | — | — | — | — | 0.008 | 0.672 | — | — | — | — |
| | — | — | — | — | — | — | — | 1.000 | 1.000 | — |
| Hb | — | | | | | | | 4 | 4 | 8 |
| | 1.000 | | | | | | | — | — | — |
| | — | | | | | | | 1.000 | — | — |
| | — | | | | | | | — | 1.000 | 1.000 |

(continued)

Table 3. (continued)

| Enzyme | Hs | Pt | Pp | Gg | Mf | Mm | Cae | Ss | Ca | At |
|--------|-------|-------|-------|-------|-------|-------|-------|----|-------|-------|
| PI | — | 2 | 8 | 6 | 228 | | | | | |
| | 1.000 | 1.000 | 1.000 | 0.333 | — | | | | | |
| | — | — | — | 0.667 | — | | | | | |
| | — | — | — | — | 0.634 | | | | | |
| | — | — | — | — | 0.366 | | | | | |
| TF | — | 4 | 9 | 14 | 228 | 76 | 55 | | 16 | 10 |
| | 1.000 | — | — | — | — | — | — | | — | — |
| | — | 1.000 | — | — | — | — | — | | — | — |
| | — | — | 1.000 | — | — | — | — | | — | — |
| | — | — | — | 1.000 | — | — | — | | — | — |
| | — | — | — | — | 0.733 | 0.270 | — | | — | — |
| | — | — | — | — | 0.134 | 0.513 | — | | — | — |
| | — | — | — | — | 0.042 | 0.178 | — | | — | — |
| | — | — | — | — | 0.033 | — | — | | — | — |
| | — | — | — | — | 0.024 | — | — | | — | — |
| | — | — | — | — | 0.009 | 0.020 | — | | — | — |
| | — | — | — | — | 0.024 | 0.019 | — | | — | — |
| | — | — | — | — | — | — | 1.000 | | — | — |
| | — | — | — | — | — | — | — | | 1.000 | 1.000 |

Hs: *Homo sapiens*; Pt: *Pan troglodytes*; Pp: *Pan paniscus*; Gg: *Gorilla gorilla*; Mf: *Macaca fascicularis*; Mm: *Macaca mulatta*; Cae: *Cercopithecus aethiops*; Ss: *Saimiri sciureus*; Ca: *Cebus apella*; At: *Aotus trivirgatus*.

Phylogenetic reconstructions were carried out according to the UPGMA method (SNEATH & SOKAL, 1973).

RESULTS

HOMINOIDS

Genetic identity values and Nei's modified distances among the hominoids and between the hominoids and the crab-eating macaques, *Macaca fascicularis*, were calculated on the basis of 34 protein systems. These are shown in Table 4.

The phylogenetic relationships among the hominoids are shown in Figure 1. As expected, the two chimpanzee species, *Pan troglodytes* and *P. paniscus* are the closest species within this clade. Moreover, by using genetic identity values we are able to resolve the human-chimpanzee-gorilla trichotomy. The results show that *Homo* clusters with *Pan*, while *Gorilla*

Table 4. Genetic identities (above diagonal) and distances (below diagonal) and their respective standard errors among hominoid species and *Macaca fascicularis*.

| | <i>Homo sapiens</i> | <i>Pan troglodytes</i> | <i>Pan paniscus</i> | <i>Gorilla gorilla</i> | <i>Macaca fascicularis</i> |
|----------------------------|---------------------|------------------------|---------------------|------------------------|----------------------------|
| <i>Homo sapiens</i> | — | 0.618 | 0.622 | 0.511 | 0.125 |
| | — | ±0.085 | ±0.084 | ±0.085 | ±0.056 |
| <i>Pan troglodytes</i> | 0.481 | — | 0.798 | 0.486 | 0.239 |
| | ±0.137 | — | ±0.069 | ±0.085 | ±0.073 |
| <i>Pan paniscus</i> | 0.475 | 0.226 | — | 0.409 | 0.208 |
| | ±0.135 | ±0.087 | — | ±0.083 | ±0.070 |
| <i>Gorilla gorilla</i> | 0.671 | 0.721 | 0.893 | — | 0.176 |
| | ±0.165 | ±0.175 | ±0.202 | — | ±0.066 |
| <i>Macaca fascicularis</i> | 2.081 | 1.430 | 1.571 | 1.735 | — |
| | ±0.447 | ±0.306 | ±0.338 | ±0.376 | — |

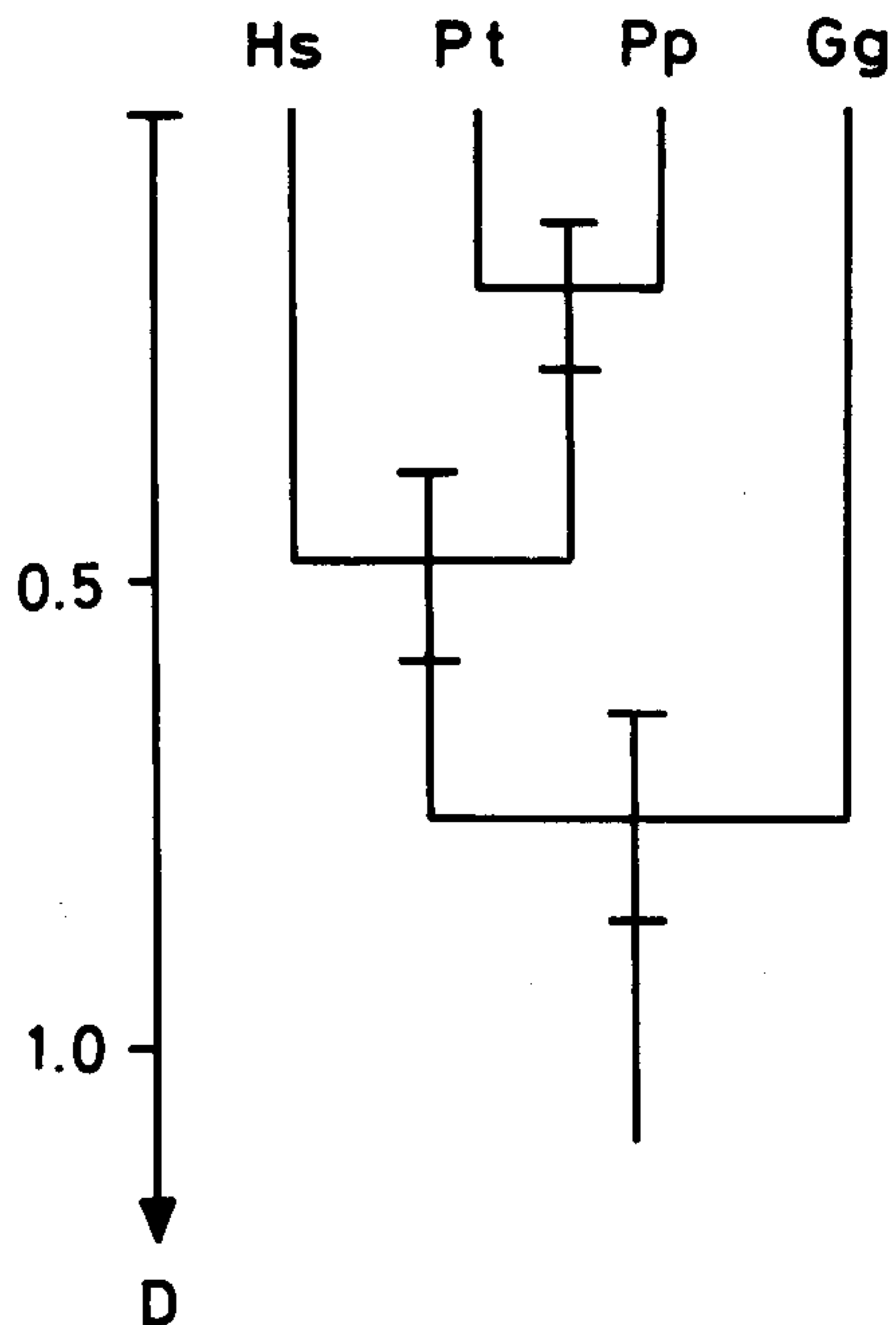


Fig. 1. Phylogenetic relationships among hominoid species reconstructed on the basis of 34 protein loci.

diverged sometime earlier. The mean genetic identity between humans and the two chimpanzee species was larger than either that between the two chimpanzee species and gorilla, or that between human and gorilla. The differences become statistically significant when the human-chimpanzee cluster is pooled. Our phylogeny of the three hominoid genera, i.e., the clustering of *Homo* and *Pan* subsequent to the divergence of *Gorilla*, agrees with the topology in many other reports (e.g., SIBLEY & AHLQUIST, 1984, 1987; KOOP et al., 1986; MIYAMOTO et al., 1988). Our findings do not support the chimpanzee-gorilla clade proposed, for instance, by BIANCHI et al. (1985).

Based on 34 proteins systems which could be compared between the common chimpanzee and the pygmy chimpanzee, we calculated the genetic distance between these two species to be 0.226. This value is almost twice that calculated by BRUCE and AYALA (1979) on the basis of 22 enzyme systems. However, the genetic distance is well within the range of other primate species. For instance, the genetic distance between *Macaca fascicularis* and *M. mulatta* is only 0.070 [with 46 loci the distance value decreases to 0.064 (SCHMITT & TOMIUK, unpub.)]. Assuming the divergence dates of SIBLEY and AHLQUIST (1984, 1987) for the gorilla (8–10 million years ago) and for the chimpanzee (6.3–7.7 million years ago), we can calculate that *Pan troglodytes* and *P. paniscus* diverged from each other 2.7–3.7 million years ago. Alternatively, by using HASEGAWA et al.'s (1987) more recent divergence times, we can calculate that the two chimpanzee species have separated from each other 2.2–3.0 million years ago.

A comparison of genetic distances between an outgroup species, *Macaca fascicularis*, and each of the four hominoid species shows that no slowdown occurred in the rate of evolution in the human lineage in comparison with that for the other apes. The genetic distances between the macaque species, on the one hand, and human, common chimpanzee, pygmy chimpanzee, and gorilla, on the other, were 2.081 ± 0.447 , 1.430 ± 0.306 , 1.571 ± 0.338 , 1.735

± 0.376 , respectively. While the genetic distance between *Homo* and *Macaca* seems to be larger than the other values, because of the standard errors associated with this measure no statistically significant difference could be demonstrated.

CERCOPITHECOIDS

Genetic identity and distance values among the cercopithecoids and between them and humans were calculated on the basis of 32 protein systems. These are shown in Table 5. In our study, the genetic distance between *Cercopithecus* and *Macaca* is approximately twice that reported by TETUSHKIN (1981).

Comparing the genetic distances between an outgroup species, *Homo sapiens*, and the three cercopithecoid species, we can conclude that all the three species evolved at equal rates in terms of their electrophoretic divergence.

The phylogenetic relationships among the cercopithecoids are shown in Figure 2. As expected the two *Macaca* species cluster well before the *Cercopithecus* divergence.

Table 5. Genetic identities (above diagonal) and distances (below diagonal) and their respective standard errors among cercopithecoid species and *Homo sapiens*.

| | <i>Macaca fascicularis</i> | <i>Macaca mulatta</i> | <i>Cercopithecus aethiops</i> | <i>Homo sapiens</i> |
|-------------------------------|----------------------------|-----------------------|-------------------------------|---------------------|
| <i>Macaca fascicularis</i> | — | 0.932 | 0.662 | 0.163 |
| | — | ± 0.032 | ± 0.083 | ± 0.065 |
| <i>Macaca mulatta</i> | 0.070 | — | 0.684 | 0.156 |
| | ± 0.034 | — | ± 0.080 | ± 0.065 |
| <i>Cercopithecus aethiops</i> | 0.413 | 0.380 | — | 0.158 |
| | ± 0.126 | ± 0.117 | — | ± 0.065 |
| <i>Homo sapiens</i> | 1.813 | 1.856 | 1.844 | — |
| | ± 0.386 | ± 0.418 | ± 0.412 | — |

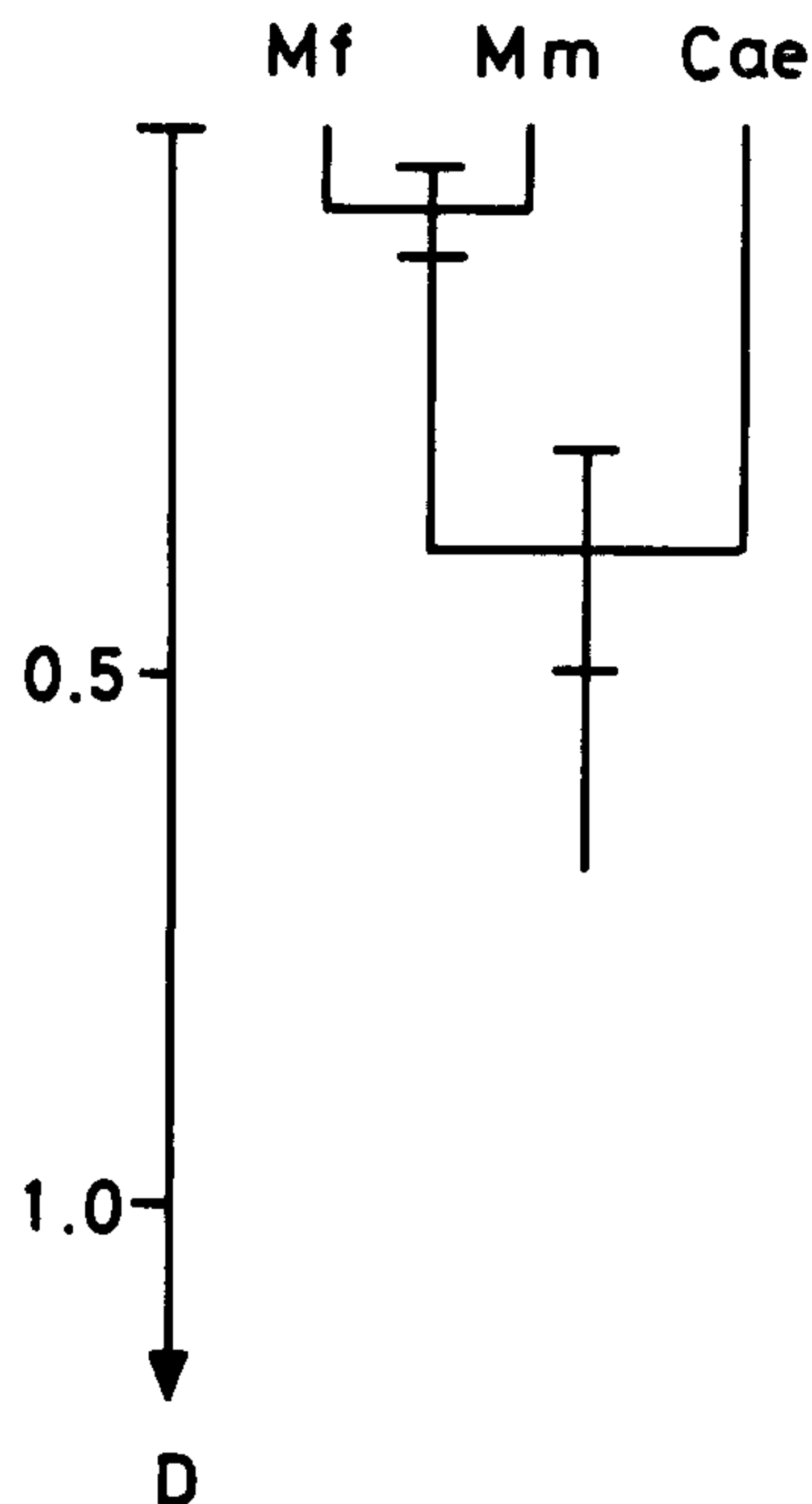
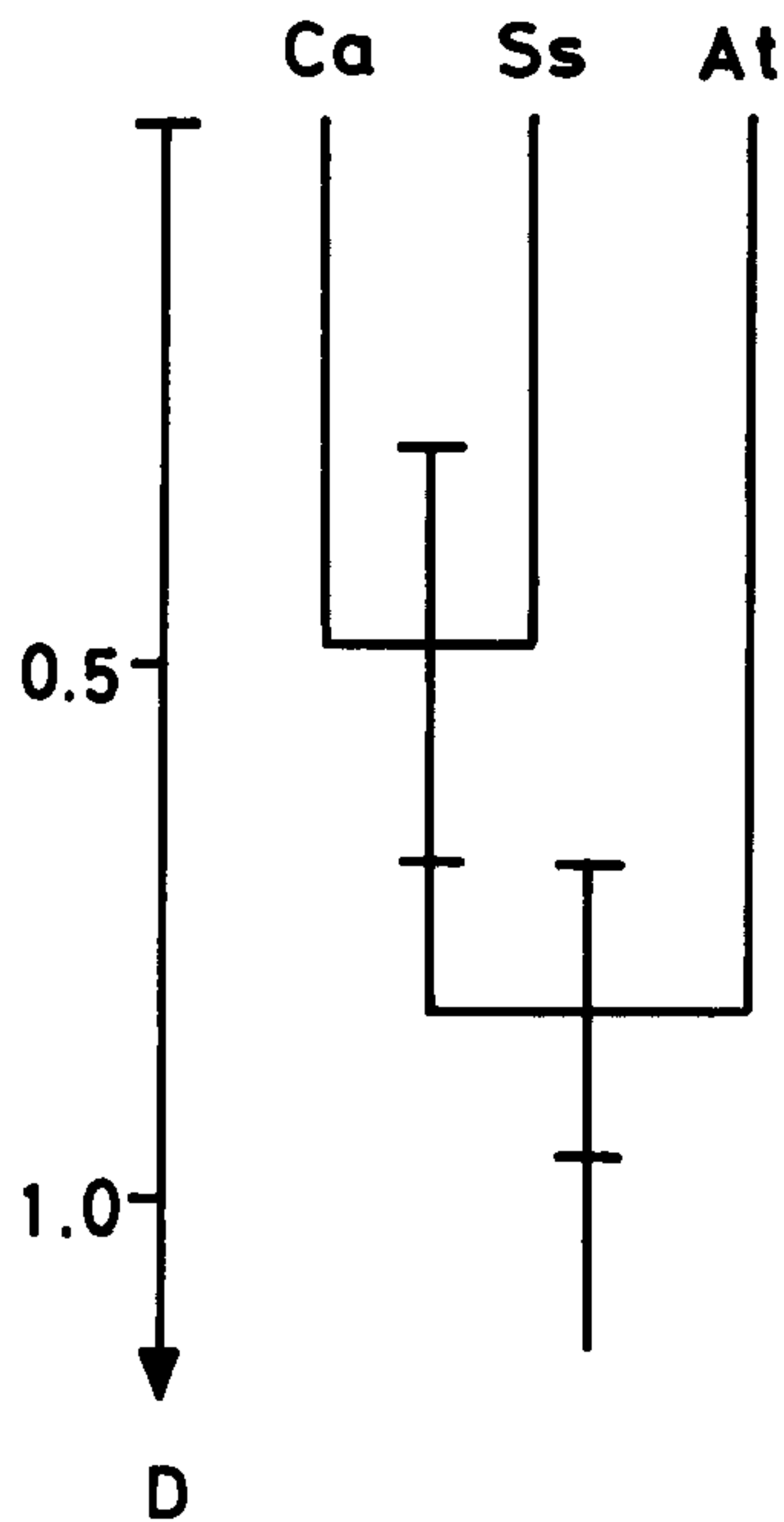


Fig. 2. Phylogenetic relationships among cercopithecoid species reconstructed on the basis of 35 protein loci.

Table 6. Genetic identities (above diagonal) and distances (below diagonal) and their respective standard errors among ceboid species and *Homo sapiens*.

| | <i>Saimiri sciureus</i> | <i>Cebus apella</i> | <i>Aotus trivirgatus</i> | <i>Homo sapiens</i> |
|--------------------------|-------------------------|---------------------|--------------------------|---------------------|
| <i>Saimiri sciureus</i> | — | 0.658 | 0.458 | 0.129 |
| <i>Cebus apella</i> | — | ±0.097 | ±0.100 | ±0.069 |
| <i>Aotus trivirgatus</i> | 0.419 | — | 0.472 | 0.155 |
| <i>Homo sapiens</i> | ±0.148 | — | ±0.096 | ±0.073 |
| | 0.781 | 0.752 | — | 0.083 |
| | ±0.218 | ±0.204 | — | ±0.058 |
| | 2.045 | 1.868 | 2.485 | — |
| | ±0.531 | ±0.471 | ±0.692 | — |

**Fig. 3.** Phylogenetic relationships among ceboid species reconstructed on the basis of 24 protein loci.

CEBOIDS

Genetic identities and distances among the ceboids, and between them and humans were calculated on the basis of 24 protein loci. These are shown in Table 6. In comparison with the outgroup species, *Homo sapiens*, we find that all the three genera of New World monkeys evolved at comparable rates.

The phylogenetic relationships among the platyrrhines are shown in Figure 3.

DISCUSSION

The reliability of our electrophoretic results could only be confirmed for the two *Macaca* species, for which we have data on numerous loci. Our *I* values are close to those reported by NOZAWA et al. (1977). In their study, *I* varies between 0.904 and 0.954 for the comparisons between populations of *Macaca fascicularis* and *M. mulatta* populations. Our value is 0.932.

On the basis of electrophoretical data, we can schematically summarize the phylogenetical

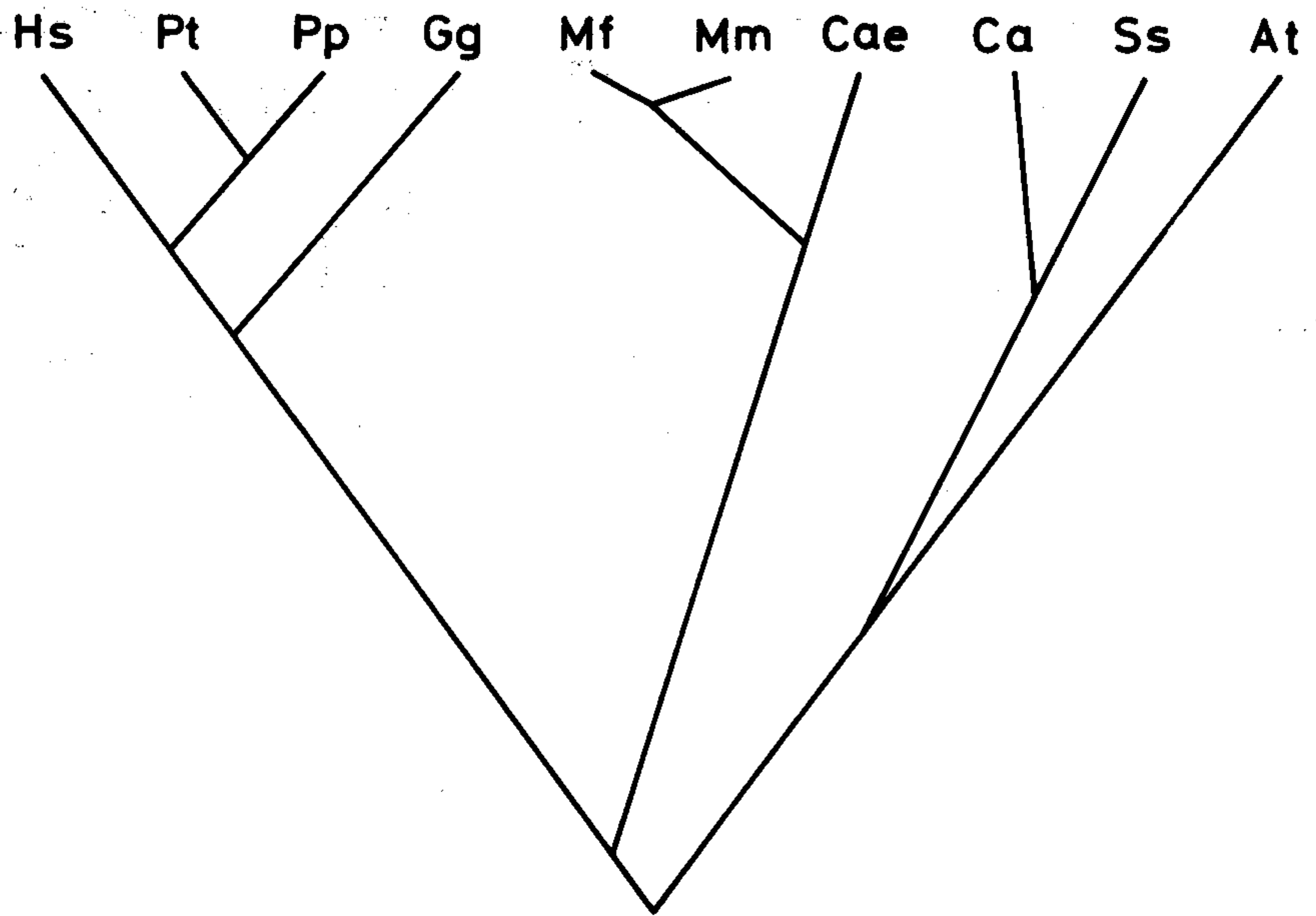


Fig. 4. Schematic representation of the phylogenetic relationships between and within ceboids, cercopithecoids, and hominoids.

relationships between the primate species in our study as in Figure 4. Our phylogenetic tree generally agrees with other phylogenetic reconstructions in the literature. The only outstanding feature is that the ceboid-cercopithecoid-hominoid trichotomy could not be resolved. There are two possible explanations for this failure. It is possible, for instance, that electrophoretic distances rapidly lose their discriminating power with increased divergence time (NEI & ROYCHOUDHURY, 1974). Alternatively, we may conclude that the hominoid lineage diverged from the cercopithecoid line in immediate temporal proximity to the catarrhine-platyrrhine split.

LI and TANIMURA (1987) showed that humans evolve slower than apes and monkeys in terms of nucleic acid substitutions accumulated since their evolutionary divergence. The same has been shown for amino acid substitution rates (e.g., GOODMAN et al., 1983), although the generality of this rule at the protein level has not been established unambiguously. A retardation of rates of evolution has also been proposed for protein electrophoretic changes (TETUSHKIN, 1981). LI and TANIMURA (1987) also reported that the rate of molecular evolution in apes is retarded in comparison to monkeys. We find, however, no evidence that these phenomena extend to the level of protein electrophoretic variation. Notwithstanding, there are cases reported in the literature in which simian primates, i.e., monkeys and apes, even at the DNA level have accumulated more substitutions than prosimian primates, i.e., lemurs and lorises (DE JUNG & GOODMAN, 1988).

The findings at the molecular level stand in marked contrast with the morphological and paleontological evidence. Despite the fact that no satisfactory method for scoring the extent of morphological divergence exists (GOODMAN & LASKER, 1975), it is generally agreed without much objections that the rate of morphological evolution in the human lineage is extremely rapid (CHIARELLI, 1973; OXNARD, 1981).

The picture emerging from our study and from many reports in the literature seems to be that in terms of nucleic acid and amino acid substitutions humans evolve faster than apes,

which in turn, evolve faster than monkeys. The rates of evolution, however, become equal among humans, apes, and monkeys at the level of electrophoretic and immunological variation (SARICH & CRONIN, 1976). In other words, it seems that the rate of change in either antigenic sites of proteins or electrical charge is more or less equal in all simian primate lineages. In fact, by comparing genetic distances based on 21 common loci between *Aotus trivirgatus*, the outgroup species, and *Homo* (2.351), *Gorilla* (2.351), *Macaca* (0.880), and *Cebus* (1.000), we see just the opposite trend. (The standard errors associated with these distances are too large, however, to render this trend statistically significant.) In addition, at the phenotypic level, the rates of evolution assume an inverse quantitative relationship among the primates. To put it another way, in terms of morphometry and anatomy, humans seem to evolve much faster than apes, and these in turn evolve faster than the monkeys (TUTTLE, 1975).

KING and WILSON (1975) advanced the idea that the evolution in primates proceeds independently at the molecular and morphological levels. On the one hand, evolution occurs at a very conservative pace as far as macromolecules are concerned, while organismic differentiation occurs at an amazingly rapid rate. Extending KING and WILSON's (1975) metaphor, it seems that as far as primates are concerned, we are dealing not with two, but with three levels of evolution.

To explain the discrepancies in rates of evolution at the different levels of genetic expression we advance the following hypothesis: Rates of nucleic acid and amino acid substitution are different in humans, apes, and monkeys. These substitutions are mostly neutral and are, thus, affected mainly by the mutation rate, which in turn may bear a positive relationship with the generation time (LI & TANIMURA, 1987). Only a very minute fraction of the changes at the molecular level are expressed as changes in either antigenic specificity or electrical charge of proteins (GRAUR, 1986). The fraction of substitutions that brings about such changes out of the entire body of substitutions is so small that despite the fact that these substitutions are also neutral in terms of their effect on fitness, the differences in rates of evolution between the primate groups are obliterated. Furthermore, the proportion of molecular changes that are detectable at the phenotypic level is even smaller than the proportion detected by either immunological or electrophoretic methods. In addition, the mutational changes which affect the phenotype are fixed in populations due to positive selection, as opposed to random genetic drift which is the major factor affecting the fate of all other mutations. Thus, the rate of evolution can change in either direction. For reasons unknown, the positive selection operating on human populations is of a larger magnitude than that operating in other primates.

Acknowledgements. This study was supported in part by the Deutsche Forschungsgemeinschaft and a grant from the Alexander von Humboldt Stiftung to DAN GRAUR. He wishes to thank Prof. Dr. KLAUS WOHRMANN for his unequalled hospitality.

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—Received March 8, 1989; Accepted May 19, 1989

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