Primatology today
Akiyoshi Ehara et al., editors


# PHYLOGENY OF EXTANT HOMINOIDS RECONSTRUCTED FROM MOLECULAR DATA

NARUYA SAITOU
Department of Anthropology, Faculty of Science, University of Tokyo
Hongo, Bunkyo-ku, Tokyo 113 (Japan)

## INTRODUCTION

The phylogeny of extant hominoids has been studied extensively by a variety of molecular techniques. Now it seems to be established that Asian apes (orangutan and gibbon) are more distantly related to human than African apes (chimpanzee and gorilla) are. Despite the large data set that has been accumulated, however, there is no consensus on the problem of the branching order of human, chimpanzee, and gorilla.

A point that complicates the determination of branching patterns in a phylogenetic tree is that different methods for tree construction can produce different trees even if the same data set is used. Saitou and Nei (1) proposed the neighbor-joining (NJ) method for phylogenetic tree construction from evolutionary distance matrices. The NJ method does not depend on the assumption of a molecular clock, and has been shown to find the correct unrooted tree efficiently from nucleotide sequence data (1-3). Recently, Saitou (4) applied the NJ method to various nucleotide sequence data of hominoids, and showed that human and chimpanzee are clustered in most of the trees obtained. In this paper, we applied the NJ method to other kinds of molecular data for hominoids and phylogenetic trees thus obtained are compared with those based on the nucleotide sequence data.

## RESULTS AND DISCUSSION

Genetic distance matrices based on one-dimensional protein electrophoresis data (5), two-dimensional protein electrophoresis data (6), restriction-site data of mitochondrial DNA (7), and DNA-DNA hybridization data (8,9) are used, and the trees obtained by applying the NJ method are shown in Figs. 1-5. For restriction-site data, a distance matrix computed by Nei *et al.* (10) was used. In all figures, horizontal lines are proportional to genetic differences.

Fig. 1 is a tree based on one-dimensional (1D) protein electrophoresis. Because the NJ method produces an unrooted tree, gibbon is assumed to be the outgroup to locate the root. Although two chimpanzee species and two subspecies of orangutan are clustered as expected, African apes and human do not form a cluster. Instead,

chimpanzees and orangutan are clustered. The branching pattern of Fig. 1 is the same as that presented by Bruce and Ayala (5).

Fig. 2 is a tree for two-dimensional (2D) protein electrophoresis. Crab-eating macaque is assumed to be the outgroup to locate the root. Here too, human, chimpanzee, and gorilla do not form a monophyletic group. This clustering pattern is different from that of Goldman *et al.* (6), in which gorilla is barely clustered to the human-chimpanzee cluster.

Fig. 3 is a tree for restriction site data of mitochondorial DNA. Gibbon is assumed to be the outgroup. Chimpanzee and gorilla are clustered as well as human and orangutan in this tree. This branching pattern is different from that made by using UPGMA (10), in which human is clustered to the African ape cluster.

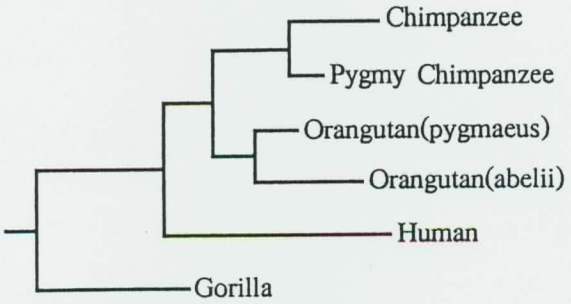


Fig. 1. Tree for 1D electrophoresis data. Data from Bruce and Ayala (5) .

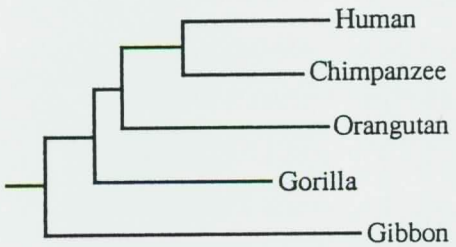


Fig. 2. Tree for 2D electrophoresis data. Data from Goldman *et al.* (6).

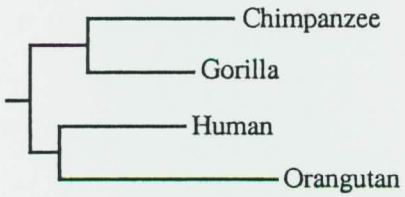


Fig. 3. Tree for restriction site data of mitochondrial DNA. Data from Ferris *et al.* (7).

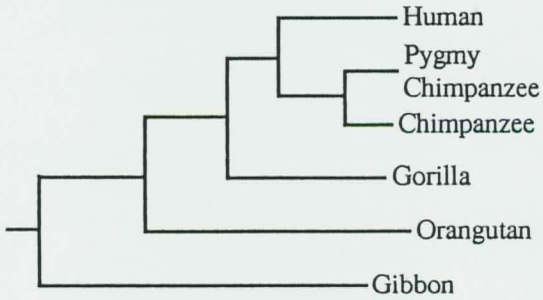


Fig. 4. Tree for DNA-DNA hybridization data. Data from Sibley and Ahlquist (8).

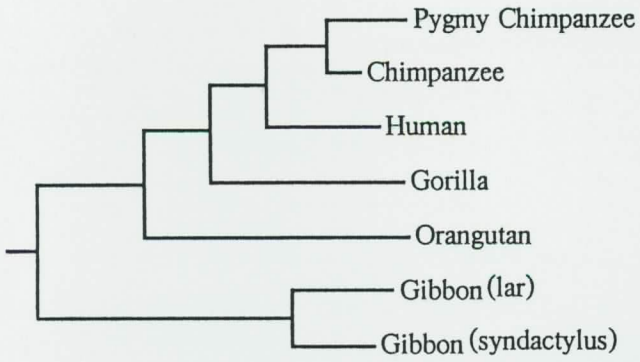


Fig. 5. Tree for DNA-DNA hybridization data.
Data from Caccone and Powel (9).

Figs. 4 and 5 are molecular phylogenies for DNA-DNA hybridization data. If we neglect the clustering of two gibbon species in Fig. 5, the branching pattern of the both trees are identical, and now human and African apes are monophyletic, as in the case of nucleotide sequence data (4). It should also be noted that the amount of divergence from the common ancestor is more or less the same for all hominoid lineages for Figs. 4 and 5.

Because parallel charge changes are expected to occur in protein electrophoresis, genetic distances estimated by both 1D and 2D protein electrophoresis may result in inconsistent results. For example, the genetic distance (0.115) between pygmy chimpanzee and a subspecies *pygmaeus* of orangutan is much smaller than that (0.385) between pygmy chimpanzee and gorilla for 1D electrophoresis (5), and the genetic distance (0.103) between chimpanzee and orangutan is smaller than that (0.107) between chimpanzee and gorilla for 2D electrophoresis (6). These anomalies in genetic distance matrices probably affected the determination of the branching pattern in the NJ method.

As for the restriction site data of mitochondrial DNA (7), the number of nucleotides covered by this data set was estimated to be 280 (10), which is rather small compared to nucleotide sequence data. This small sample size is probably responsible for producing a tree in which human and orangutan are clustered (see Fig. 3).

In contrast to the above three kinds of molecular data, DNA-DNA hybridization data (8,9) both gave the same branching pattern as those for nucleotide sequence

data (4). Although there exist controversies over the validity of DNA-DNA hybridization method (*e.g.*, 11), it seems that DNA-DNA hybridization data may be more reliable than the other molecular data, aside from nucleotide sequence data.

REFERENCES

1. Saitou N, Nei M (1987) Mol Biol Evol 4:406-425
2. Sourdis J, Nei M (1988) Mol Biol Evol 5:298-311
3. Saitou N, Imanishi T (1989) Mol Biol Evol 6:514-525
4. Saitou N (1990) Amer J Phys Anthropol (in press)
5. Bruce EJ, Ayala FJ (1979) Evolution 33:1040-1056
6. Goldman D, Giri PR, O'Brien SJ (1987) Proc Natl Acad Sci USA 84: 3307- 3311
7. Ferris SD, Wilson AC, Brown WM (1981) Proc Natl Acad Sci USA 78: 2432-2436
8. Sibley CG, Ahlquist JE (1987) J Mol Evol 26:99-121
9. Caccone A, Powell JR (1989) Evolution 43:925-942
10. Nei M, Stephens JC, Saitou N (1985) Mol Biol Evol 2:66-85
11. Marks J, Schmid CW, Sarich VM (1988) J Hum Evol 17:769-786