Chimpanzee Kinship

The article by Phillip A. Morin et al. "Kin selection, social structure, gene flow, and the evolution of chimpanzees" (26 Aug., p. 1193) exemplifies the valuable data that can be retrieved by use of the latest techniques of molecular genetics and the many creative uses to which such data can be put. Their use of genetic markers to test hypotheses about relatedness among chimpanzees of a population, and the sociobiological implications of its genetic structure, is innovative and exciting. However, we question some of their evolutionary and taxonomic conclusions. Morin et al. show that among "common" chimpanzees, a deep evolutionary divergence separates mitochondrial DNA (mtDNA) haplotypes carried by West African animals from those found in animals of Central and East African origin. They argue that this finding implies a population separation of about 1.6 million years. They also suggest that, if this result is confirmed, the western chimpanzee merits elevation from a subspecies of Pan to full species rank, as P. troglodytes. The latter suggestion has already gained some acceptance.

However, using genetic distances to differentiate species from subspecies is problematic, if for no other reason than that no consistent standard can be found. Genera of mammals differ by a factor of more than 5 in the degree of genetic differentiation among their constituent species. Among all vertebrates, there is a 200-fold range in the degree of genetic differentiation among congeneric species. From a "frog's point of view," the genetic distinctness of the western chimpanzee would appear trivial, while from a "bird's eye view," it would suggest separation at the family level.

Second, even if all the mtDNA haplotypes of chimpanzees from the extreme western end of their range are indeed very different from those found in other chimpanzees, this may be a result, not of ancient population isolation, but rather of recent extinction, or non-sampling, of geographically (and perhaps genetically) intermediate populations. The distribution map included by Morin et al. in their figure 1 shows a gap of about 1700 kilometers between chimpanzee populations in western Côte d'Ivoire and those on the Nigeria-Cameroon border. This significantly overstates the geographical isolation of western chimpanzees today, let alone 50 or 500,000 years ago. Reports dating from 1930 to 1965 suggest that chimpanzees survived into the middle decades of this century in much of southern Côte d'Ivoire, on the Ghana-Togo border, in western Nigeria, and in southern Benin. Recent surveys have confirmed the presence of chimpanzees in many areas of south-central and south-eastern Côte d'Ivoire as well as in Ghana, western Nigeria, and the Niger delta.

Thus, although West African chimpanzee populations are now undoubtedly highly fragmented and seriously threatened, their range within living memory appears to have been almost continuous from Senegal to Cameroon. This fact makes long-term genetic isolation of populations in the extreme west unlikely. Migration of female chimpanzees, and consequent interpopulation flow of mtDNA haplotypes, might have been impeded by the Dahomey Gap—a dry forest zone in southern Benin and southern Togo—or by major rivers, but this cannot be assumed. While we strongly agree that conservation efforts should take account of the genetic diversity of extant chimpanzee populations, we caution against drawing conclusions about their subspecific or specific status until a much broader sample has been surveyed.

Relict West African populations such as those in eastern Côte d'Ivoire, Ghana, and western Nigeria merit the highest priority for both conservation efforts and phylogenetic analysis. Morin et al. conclude from their mtDNA tree that "Pan paniscus is seen to lie closer..."
to the Pan-Homo split as postulated by Zihlman and others (9, p. 1199). This statement might be interpreted in several ways, but none of them seems to be supported by the tree. First, since all Pan haplotypes form a unified cluster, linked to the common human stem by a single line, no subspecies within the Pan grouping can be any closer cladistically to the common ancestor ("the split"). An alternative reading is that a special panitic relationship, with respect to mtDNA, links pygmy chimpanzees to the chimpanzee-human clade; that is, that P. paniticus sequences are consistently closer to the reconstructed ancestral sequence. But no such conservatism is implied by the mtDNA data in (1), or any other data we know. Alternatively, Morin et al. could mean that their results support the actual situation advanced by Zihlman et al. (9), namely, that all members of the chimpanzee-gorilla clade, pygmy chimpanzees most closely resemble the ancestral morphotype in some features of the skull, dentition, and postcervical vertebrae. As far as we can see, mtDNA data are not relevant to such a speculation, and can neither refute nor support it.

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References and Notes
2. J. C. Avise, Molecular Evolution, natural History and Evolution (Chapman and Hall, New York, 1984).
11. The concept has traditionally been assumed to exist on P. t. verus from P. t. tchiquensis (W. C. McGrew, J. Moore, in The Chimpanzee, Anatomy, Behavior, and Disease of Chimpanzees, G. H. Bourne, Ed. (Ranger Book, London, 1966).)

Response: Jolly et al. raise three points that are valid and well taken, but two were covered explicitly in our original article, and the third involves an ambiguous phrase, tangential to our thesis. They question "evolutionary and taxonomic conclusions" of our article, specifically discussing (i) the use of "generic distances" to differentiate species from subspecies, (ii) the appropriateness of our sample for measuring the distance between western and central chimpanzee subspecies, and (iii) the wording of a sentence that describes the affinities of Pan paniticus to the pygmy chimpanzee (Pan troglodytes).

In their first point, Jolly et al. use the term "generic distance" in a historical sense to include a large amount of research on allosyme variations and speciation. Our work was on DNA sequences (rather than proteins) and specifically on two loci, for which we calculate genetic distances individually. Our "distances" are not directly comparable to allonomic genetic distances, and we made that point in the article by comparing our data to those from other studies of the same loci only, and only those studies that reported the raw data so that we could use the same correction methods to calculate these distances. We further limited the comparison to other mammals only (our reference 35) because, as Jolly et al. correctly say, one cannot use all vertebrates as a standard. We carefully avoided any implication that genetic distance is an universal and simply interpretable metric. In a field where such data are still rare but accumulating quickly, it is up to informed readers to evaluate our data, which are placed within the literature, and to decide whether the data are significant, as stated in our article. Finally, we clearly stated that our data were (and still are) the only data available for this endangered species, and that more data (genetic and otherwise) are needed to confirm our result before further interpretation is justified.

Jolly et al.'s third point concerns our sentence "Pan paniticus is seen to lie closer to the Pan-Homo split as postulated by Zihlman and others" (on anatomical grounds). The issue here is that our choice of words created an ambiguity. Our sentence correctly describes what one sees when one looks at our figure. Jolly et al. correctly note that it could mean other things. Their description of a clades ic interpretation of our genetic data (including the putative ancestral sequence) is correct, but not what we meant to imply. Despite evidence reported since our publication that ape are more morphologically conserved (reference 1 in Jolly et al.'s letter), we did not mean to imply that there has been sequence conservatism in any one clade. Our study involved chimpanzee subspecies (P. troglodytes), not bonobos (P. paniticus), but because we included two bonobo sequences as outliers, we merely commented on their placement on the tree.

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