The Geographic Apportionment of Mitochondrial Genetic Diversity in East African Chimpanzees, Pan troglodytes schweinfurthii

Tony L. Goldberg1 and Maryellen Ruvolo
Harvard University, Department of Anthropology

This study is a geographically systematic genetic survey of the easternmost subspecies of chimpanzee, Pan troglodytes schweinfurthii. DNA was noninvasively collected in the form of shed hair from chimpanzees of known origin in Uganda, Rwanda, Tanzania, and Zaire. Two hundred sixty-two DNA sequences from hypervariable region 1 of the mitochondrial control region were generated. Eastern chimpanzees display levels of mitochondrial genetic variation which are low and which are similar to levels observed in humans (Homo sapiens). Also like humans, between 80% and 90% of the genetic variability within the eastern chimpanzees is apportioned within populations. Spatial autocorrelation analysis shows that genetic similarity between eastern chimpanzees decreases clinally with distance, in a pattern remarkably similar to one seen for humans separated by equivalent geographic distances. Eastern chimpanzee mismatch distributions (frequency distributions of pairwise genetic differences between individuals) are similar in shape to those for humans, implying similar population histories of recent demographic expansion. The overall pattern of genetic variability in eastern chimpanzees is consistent with the hypothesis that the subspecies has responded demographically to paleoclimatically driven changes in the distribution of eastern African forests during the recent Pleistocene.

Introduction

Humans are generally considered unusual in the extent and apportionment of their genetic diversity. Lewoitin (1972) first documented the surprisingly low degree of genetic differentiation among human subpopulations (races). Subsequent studies have replicated these results using mitochondrial DNA (e.g., Merriwether et al. 1991; Excoffier, Smouse, and Quattro 1992; Ruvolo et al. 1993). Phylogenetic analyses have led to the hypothesis, now widely accepted, that human genetic diversity is low because humans share a recent common origin (Cann, Stoneking, and Wilson 1987; Vigilant et al. 1991). A Late Pleistocene population bottleneck has been specifically implicated as the key event marking the genetic origin of modern human populations (Harpending et al. 1993; Rogers 1995).

Despite rapid advances in our understanding of human mitochondrial genetic evolution, comparative data from related taxa have been slow in coming. Direct comparisons of humans with great apes have indicated that humans may represent the low end of the diversity spectrum within the hominoids (Ferris et al. 1981; Ruvolo et al. 1994). However, great ape species are fundamentally different from humans in that they consist of reproductively isolated subpopulations corresponding to recognized subspecies. Chimpanzee (Pan troglodytes), gorilla (Gorilla gorilla), and orang-utan (Pongo pygmaeus) subspecies have largely nonoverlapping geographic distributions (Schwartz 1934; Groves 1971; von Koenigswald 1982) and have evolved distinguishing morphological differences (Groves 1970; Jacobshagen 1974; Shea and Coolidge 1988; Uchida 1992).

Intersubspecific genetic differences could account for the observed large genetic diversity within ape species. This is especially likely since the geographic origins of apes used in early comparative studies were unknown. Indeed, genetic distances among subspecies are now known to be large in chimpanzees, gorillas, and orang-utans (Ruvolo et al. 1994). The most detailed analysis is that of Morin et al. (1994), who found, using mitochondrial DNA from chimpanzees of known subspecies, that west African chimpanzees (P. t. verus) diverged from central (P. t. troglodytes) and eastern (P. t. schweinfurthii) chimpanzees approximately 1.6 MYA. This amount of genetic divergence is between four and eight times that observed between the most divergent individuals within any one chimpanzee subspecies. Furthermore, chimpanzee subspecies correspond to clades on the Morin et al. (1994) phylogenetic tree, suggesting that they do, in fact, represent reproductively isolated subpopulations. Unfortunately, the precise geographic origins of many of these chimpanzees are unknown, and sample sizes within subspecies are still small.

In this study, we provide the first geographically systematic genetic survey of an ape subspecies, the eastern subspecies of chimpanzee, P. t. schweinfurthii. We analyze a large data set of 262 mitochondrial DNA sequences from eastern chimpanzees of known geographic origin to explore levels and the apportionment of genetic diversity within the subspecies. We predict that genetic diversity within eastern chimpanzees should be more similarly apportioned to that in humans than to that within chimpanzees as a species. Aside from indications by previous studies that this may be the case, there are independent reasons to expect genetic diversity within P. t. schweinfurthii to follow this pattern.

Pan troglodytes is a forest taxon in the sense that its current (and historical) distribution does not extend far beyond the limits of African forest (Kortlandt 1983; Teleki 1989). Chimpanzees can and do live in areas of...
high aridity (McGrew, Baldwin, and Tutin 1981; Moore 1992). However, they cannot survive in the complete absence of forest habitat, probably due to dependence on forest foods and standing water (Kortlandt 1983).

To the extent that eastern chimpanzees have been restricted to forest habitats, their historical distribution should have tracked cyclic changes in the distribution of forest cover which occurred during the Pleistocene. In eastern Africa, forest cover was severely reduced during periods of maximal global aridity and minimal global temperature (Hamilton 1981). During these periods, African forests and forest animals were restricted to small “refugia,” where local conditions allowed their persistence despite general climatic aridity (Grubb 1982). Forests reexpanded rapidly during postglacial global warming (most recently at 12,000 and 130,000 years ago, but cyclically throughout the Pleistocene).

As a result of these events, eastern chimpanzees should have experienced one or several recent population bottlenecks corresponding to periods when forests were restricted to Pleistocene refugia. Postglacial climatic amelioration should have led to rapid population expansion as forests spread. Eastern chimpanzees should therefore harbor low genetic diversity and should show evidence of recent population expansion. A second goal of this study is to test the hypothesis that the genetic structure of P. t. schweinfurthii does indeed reflect these paleoclimatic events.

Materials and Methods

Our sampling area lies entirely within the range of P. t. schweinfurthii, between 26° and 32° longitude, and between 3° and −5° latitude (fig. 1). We collected genetic material noninvasively in the form of shed hair from eastern chimpanzees in 19 geographically defined sampling locations within this geographic range, and from one captive population known to be P. t. schweinfurthii (Goldberg 1997). Natural sampling locations correspond to forested areas of approximately 25 km², in which chimpanzee nests were located and searched during ground surveys. These sampling locations represent nine “insular” forests on the eastern extreme of the subspecies range and five locations within the expansive lowland rain forest block of eastern Zaire.

After extracting and PCR-amplifying DNA from hair follicles found in each nest, we sequenced a 368-bp segment of the mitochondrial control region corresponding to Anderson reference coordinates 16041--16413 (Anderson et al. 1981). This is the most quickly evolving region in the mitochondrial genome (Kocher and Wilson 1991). We chose it specifically because of its rapid evolutionary rate and because it has been well characterized for humans and chimpanzees (Vigilant et al. 1991; Morin et al. 1994). We sequenced both DNA strands at least twice on an automated DNA sequencer and checked all reads manually. Details of PCR amplification and DNA sequencing are presented elsewhere (Goldberg 1996). We also incorporated 19 published Tanzanian sequences from Morin et al. (1994) into the study.

Results

We generated 262 DNA sequences, yielding, along with the 19 Morin et al. (1994) sequences, 123 unique haplotypes and 90 variable nucleotide positions. Sample sizes for individual sampling locations ranged between 10 and 23. The DNA sequences are available through GenBank (accession numbers U77181–U77293).

Overall Genetic Diversity

To compare eastern chimpanzee genetic diversity directly to human diversity, we aligned the chimpanzee sequences to Vigilant et al.’s (1991) world sample of 135 human control region sequences. We edited the human sequences to exclude all but the homologous 368-bp region sequenced in the present study. The resulting human sample contained 110 unique haplotypes and 115 variable nucleotide positions.

Mean pairwise sequence difference in eastern chimpanzees was 2.08%. The corresponding human estimate was slightly higher (2.60%). Collapsing all identical haplotypes within the human sample (resulting sample size = 110 sequences) did not change the human estimate. When we collapsed all identical haplotypes within the eastern chimpanzee sample (resulting sample size = 123 sequences), mean pairwise sequence difference in eastern chimpanzees increased only to 2.12%. Modal pairwise sequence difference within eastern chimpanzees (1.90%) was similarly lower than the corresponding human estimate (2.70%). Finally, maximum pairwise sequence difference was also lower in eastern chimpanzees (5.43%) than in humans (5.93%).

For individual sampling locations, mean pairwise sequence difference ranged from 0.85% to 2.97%, modal pairwise sequence difference ranged from 0% to 3.24%, and maximum pairwise sequence difference ranged from 1.75% to 5.30%. Detailed analyses of individual sampling locations are presented elsewhere (Goldberg and Ruvolo 1997). However, it is worth noting that two sampling locations contained the highest genetic diversities by all measures and contained the most divergent alleles within the eastern chimpanzee sample. These populations were located in Rwenzori Forest, Uganda and in Ituri Forest, Zaire, and are indicated by closed circles in figure 1.

The Apportionment of Eastern Chimpanzee Diversity

Analysis of molecular variance (AMOVA) is a generalized technique invented by Excoffier, Smouse, and Quattro (1992) which apportions genetic diversity into hierarchical components (e.g., populations, regions, species). It differs from previous similar approaches in that it is adaptable to a range of genetic systems and can incorporate information about molecular distances among haplotypes.

We applied this approach to the eastern chimpanzee data. We defined populations as forests, in which we combined sampling locations within forest blocks. We defined regions as “Zaïrian forests” and “eastern forests.” These definitions are not geographically equivalent to those typically used for humans. Typically defined human populations (countries, tribes, ethnic
groups) and regions (continents) are larger by an order of magnitude than those defined here for eastern chimpanzees. However, eastern chimpanzees are not, like humans, globally distributed. The populations and regions defined for eastern chimpanzees parallel those for humans not in absolute scale, but in the proportion of the taxon's total geographic range which they represent.

We analyzed two matrices of interallelic distance. The first, "multiallelic," matrix treats all haplotypes as genetically equidistant. The second, "haplotypic," matrix incorporates euclidean distances among haplotypes, inferred from the numbers of nucleotide differences between pairs of sequences without regard to the nature of these differences (transitions or transversions).

Table 1 presents the eastern chimpanzee results, along with results from Excoffier, Smouse and Quattro's (1992) analysis of a world sample of 672 human mitochondrial RFLPs. The human data (whole mitochondrial restriction digests) are not homologous to the eastern chimpanzee data (368-bp mitochondrial gene sequences). We nevertheless chose this human data set for comparison because of its equal and thorough sampling of individuals within and between human populations and regions (continents). We suspect that results obtained from a comparable data set of human mitochondrial control region sequences would not differ appreciably; mitochondrial restriction data and sequence data have yielded strikingly similar results in the past (e.g. Cann, Stoneking, and Wilson 1987; Vigilant et al. 1991).

Humans and eastern chimpanzees display similar proportions of within-population variance (between 80% and 90%). Genetic differences between populations of
both eastern chimpanzees and humans are comparatively much smaller. In both taxa, the among-population/within-region variance component (\(\sigma_v^2\); 12%-18% in chimpanzees, 3.5%–3.6% in humans) is markedly lower than the within-population component. Interregional variation in eastern chimpanzees is very low, accounting for a maximum of only 2% of the variation within the subspecies. Unlike the other diversity components measured, the inter-regional variance component is not statistically distinguishable from chance, either in the multiallelic or haplotypic case (see table 1). This contrasts markedly with the human data, in which interregional variance accounts for between 15% and 22% of the variation within the species and is significantly different from chance.

The results described above for eastern chimpanzees did not differ when we used alternate definitions of populations and regions. When we defined populations as individual sampling locations, the proportions of among-region, among-population/within-region, and within-region variance were, respectively, 0.11%, 12.80%, and 87.09% (multiallelic) and 2.01%, 18.01%, and 79.98% (haplotypic). The proportion of variance among regions ranged between approximately 0% and 2% when we explored alternate definitions of regions.

The multiallelic value of \(\Phi_{ST} = 0.129\) for eastern chimpanzees is equivalent to Wright’s (1969) \(F_{ST}\) and is low in comparison to taxa which show strong population substructure (Allendorf 1983). A high degree of migration may account for this low value. \(F_{ST}\) bears a direct relationship to \(Nm\), the product of a population’s effective size and its average per generation migration rate (Wright 1969). \(Nm\) thus estimates the absolute number of individuals which on average migrate among populations per generation. The relationship \(F_{ST} = 1/(2Nm + 1)\), which is specific for extranuclear genetic data (Takahata and Palumbi 1985), yields an estimate of 3.38 female migrants exchanged, on average, between sampling locations per generation in eastern chimpanzees. Migration is indeed high among eastern chimpanzee populations; a value of \(Nm\) of approximately 1 is theoretically sufficient to prevent population differentiation due to drift alone (Wright 1969).

This degree of female migration represents an average value for the entire subspecies and does not reflect the fact that gene flow among adjacent populations may be even higher. Figure 2 depicts the extent of haplotype sharing among sampling locations on a map. Linkages (straight lines) are proportional in width to the numbers of haplotypes shared between locations. Haplotype sharing appears greatest among populations separated by small distances. The maximal distance over which any haplotype is shared is 583 km. This distance is, however, less than the maximum geographic distance among populations (772 km).

We used spatial autocorrelational analysis to quantify the relationship between distance and genetic similarity in eastern chimpanzees. Spatial autocorrelational analysis measures the strength of association between a variable and itself as a function of spatial distance (Sokal and Oden 1978). We calculated Barbujani et al.’s (1995) AIDA (autocorrelation index for DNA analysis, designed specifically for DNA sequence data) for nine distance classes (including zero) of even width (100 km) using great-circle geographic distances. To account for the possibility that individuals within sampling locations were inadvertently sampled twice, we analyzed a reduced data set in which all identical haplotypes within sampling locations were collapsed (resulting sample size = 164). Results were similar for the full data set (not shown).

The autocorrelogram (fig. 3) shows significant positive spatial autocorrelation for the zero distance class, and generally negative and decreasing autocorrelation for larger distance classes. This pattern conforms best to one of long-distance differentiation (Sokal and Oden 1978). Gene flow in eastern chimpanzees is, in other words, clinally limited by distance. The autocorrelogram

---

### Table 1
Hierarchical Analysis of Molecular Variance for Humans and Eastern Chimpanzees

<table>
<thead>
<tr>
<th>Variance Component</th>
<th>Multiallelic Variance</th>
<th>Haplotypic Variance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Observed Partition</td>
<td>Haplotypic Statistics</td>
</tr>
<tr>
<td></td>
<td>Variance % Total P*</td>
<td>(\Phi) Statistics</td>
</tr>
<tr>
<td>Among regions</td>
<td>(\sigma_v^2)</td>
<td>(\Phi_{CT} = 0.157)</td>
</tr>
<tr>
<td>Among populations/regions</td>
<td>(\sigma_v^2)</td>
<td>(&lt;0.0001)</td>
</tr>
<tr>
<td>Within populations</td>
<td>(\sigma_v^2)</td>
<td>(\Phi_{ST} = 0.193)</td>
</tr>
</tbody>
</table>

* Multiallelic variances were calculated assuming all haplotypes were equidistant.

* Haplotypic variances were calculated using a matrix of uncorrected genetic distances between haplotypes.

* Probability of having a more extreme variance component and \(\Phi\) statistic than the observed value by chance alone. Probabilities were calculated by a random permutation procedure (see Excoffier, Smouse, and Quattro 1992).

* World sample of 672 Human mtDNAs (restriction digest). Data were taken from Excoffier, Smouse, and Quattro (1992).

* Two hundred fifty-five eastern chimpanzee mitochondrial control region sequences from 19 forest locations. Populations were defined as forests (sampling locations within eastern insular forests were combined). Two regions were defined: eastern forests and Zairian forests (see fig. 1).
sequences in either analysis, because they contained large amounts of missing data. We constructed the human distribution from the Vigilant et al. (1991) data described above.

The chimpanzee distributions are similar to one another, indicating that double-sampling was not a significant problem. Like the human distribution, both chimpanzee distributions are wavelike in form, implying sudden population expansion. The estimated values of $\tau$ (proportional to the age of the population expansion event) for the chimpanzee distributions (5.37 and 5.73) are, however, lower than that for the human distribution (8.34). The full-data-set chimpanzee distribution also differs from the human distribution in showing some evidence of bimodality.

Confidence regions have been placed around the estimated parameters of human mismatch distributions to exclude scenarios of low (or zero) population growth subsequent to the inferred bottleneck (Rogers 1995; Rogers and Jorde 1995). In practice, confidence regions are calculated by comparing empirically derived mismatch estimators with distributions of estimators obtained from large numbers of data sets of equal size simulated under specified population histories. Human genetic data are generally consistent with degrees of 100-fold population expansion or greater (Rogers 1995; Rogers and Jorde 1995).

We constructed confidence regions for the chimpanzee mismatch distributions following the method of Rogers (1995). We simulated a broad range of plausible population histories, including multiple bottlenecks, varying numbers of subpopulations, and varying degrees of migration. Surprisingly, confidence region analysis did not exclude scenarios of zero population growth in eastern chimpanzees under any population history tested, despite the prominent wavelike shape of the chimpanzee mismatch distributions in figure 4. Statistically, the eastern chimpanzee population may have expanded, or it may have been demographically stable for a long period of time. The reason for the inability of the confidence region technique to distinguish between these possibilities is not clear at present, but this inability may reflect a lack of power of the Rogers method.

Assuming that an eastern chimpanzee population expansion event did occur between 5.37 and 5.73 mutational units of time ago, as the wavelike shape of the chimpanzee mismatch distribution implies, its date can be estimated. Published estimates of nucleotide divergence rates for the mitochondrial control region range from 11.5% per Myr (Vigilant et al. 1991) to 33% per Myr (Ward et al. 1991). The method of Rogers and Jorde (1995), used with a median nucleotide divergence rate of 22.5% and both $\tau$ estimates, yields an expansion date of between 31,500 and 33,600 years ago. An acceptable range of dates for the expansion (using high and low-end published estimates of nucleotide substitution rates) would be between approximately 20,000 and 61,000 years ago.

Similarly, the magnitude of expansion can be estimated from the estimator $\theta_0$, which is directly proportional to the size of the preexpansion population. Confidence region analysis in this case indicated an upper

![Figure 2](image-url)

**Figure 2**—Geographic linkages between sampling locations based on shared haplotypes. Individual sampling locations ($n = 19$) are represented by closed circles. Shared haplotypes are indicated by straight lines. Line widths are proportional to numbers of haplotypes shared.
FIG. 3.—Spatial autocorrelogram constructed according to the method of Barbujani et al. (1995). Values of the AIDA (autocorrelation index for DNA analysis, abbreviated II) were calculated for nine distance classes of 100 km width. The autocorrelogram is based on a reduced data set of 164 sequences created by collapsing identical haplotypes within sampling locations. Asterisks indicate the level of statistical significance for each distance class, determined by comparing observed AIDA’s to values obtained from 1000 random permutations of the data. * P < 0.05; ** p < 0.01; *** P < 0.005.

Discussion

A striking feature of the analyses presented above is the general similarity of eastern chimpanzees to humans. Overall levels of mitochondrial control region variability in eastern chimpanzees are comparable to those in a world sample of humans. The proportion of eastern chimpanzee genetic diversity contained in individual populations (80%–90%) is similar to the proportion of human diversity contained in human populations. The autocorrelational decline of genetic similarity with distance follows a similar pattern in eastern chimpanzees as in humans separated by similar distances. Eastern chimpanzee and human mismatch distributions are both wavelike in shape, implying recent population expansion. Apparently, the widely held view that human genetic diversity is fundamentally different from that in apes must now be qualified. Humans are clearly genetically similar to at least one ape subspecies.

Eastern chimpanzees are not, however, the genetic equivalents of humans. Mean, modal and maximum lev-
els of nucleotide difference are actually slightly lower in eastern chimpanzees than in humans. The last common maternal ancestor of eastern chimpanzees may therefore be even younger than the last common maternal ancestor of all humans. However, this observation could be an artifact of incomplete geographic sampling. Increasingly divergent eastern chimpanzee haplotypes would probably surface with additional sampling. Maximally divergent human haplotypes, however, have probably already been discovered (Ruvolo et al. 1994). Whether eastern chimpanzee diversity estimates will someday exceed human ones remains to be seen.

The apportionment of eastern chimpanzee genetic diversity within and among populations follows a pattern similar to that for humans. However, interpretation of these results is complicated by the different geographic scales over which the taxa were analyzed. In the AMOVA analysis described above, human populations (corresponding to countries or ethnic groupings) inhabit regions of several thousand square kilometers but were considered equivalent to chimpanzee populations (corresponding to forests) inhabiting regions of only several hundred square kilometers. That the proportion of diversity contained within human and chimpanzee populations should nevertheless be similar is remarkable. Human populations appear, for all intents and purposes, to be dramatically geographically expanded genetic versions of eastern chimpanzee populations. This result underscores the exceptional ability of humans to migrate and to maintain gene flow over large geographic distances. Chimpanzees, although extraordinarily vagile primates, apparently do not possess an equivalent capacity for maintaining long-distance relationships.

This same ability may paradoxically explain the high interregional variability component in humans and the lack of a significant interregional variability component in eastern chimpanzees. Eastern chimpanzees have not historically colonized regions equivalent to those which humans now occupy (continents). For chimpanzees, populations inhabiting geographically distinct biogeographic zones within Africa correspond to subspecies. Subspecific differences in eastern chimpanzees are, in turn, far greater than differences among human races; indeed, they are far greater than the maximum genetic difference within the entire human species (Morin et al. 1994; Ruvolo et al. 1994). This observation attests again to the great vagility of humans and their ensuing ability to maintain long-distance gene flow. In this light, it is interesting that AIDA analysis of eastern chimpanzees showed a clinal decrease of genetic similarity with distance which strongly resembled that for Italian humans over an equivalent geographic scale (800 km; Barbujani et al. 1995). Local restrictions to gene flow in populations of humans may be creating microgeographic genetic patterns which are similar to those observed across the entire range of eastern chimpanzees.

Human and eastern chimpanzee mismatch distributions also indicate the differences between the two taxa. The mode of the eastern chimpanzee distribution is lower than that for the human distribution, suggesting a more recent population expansion event for eastern chimpanzees. This would argue against a previous conclusion of Rogers and Jorde (1995) that eastern chimpanzees show evidence of population expansion which is coincident with that in humans. However, confidence regions around the mismatch estimators for humans and eastern chimpanzees overlap considerably. While Rogers and Jorde's claim that a single climatic event drove both expansion events (they suggest the Toba volcanic eruption at 73,500 years ago) cannot be rejected, it is also not strongly supported. Data from many sympatric eastern African taxa should eventually elucidate any broad climatic influences (Ruvolo 1996).

Both mismatch distribution analysis and the overall pattern of low genetic variability in eastern chimpanzees support the more general hypothesis that the subspecies has responded demographically to climatically induced changes in the distribution of forest cover in eastern Africa. Bottlenecks caused by the cyclic contraction and expansion of equatorial forests could indeed have created the pattern of low variability observed for eastern chimpanzees. Population expansion during subsequent global warming and reforestation could have created a wavelike mismatch distribution. The range of acceptable date estimates for such an expansion (20,000–61,000 years ago) is, however, wide, principally because of error associated with the mutation rate estimates used in calculating absolute dates. Attributing causality to any specific deglaciation/reforestation event would therefore be premature, except to say that such an event would likely have occurred on the order of tens, rather than hundreds, of thousands of years ago.

The observation that high genetic diversities and high proportions of divergent alleles are localized to populations in Rwenzori and Ituri forests (see fig. 1) provides independent evidence that these locations may have contained large preexpansion chimpanzee populations. Species distribution data suggest that these two areas differ from the other forests examined in this study in being the probable locations of Pleistocene forest refugia (Hamilton 1981; Grubb 1982; Colyn, Gautier-Hion, and Verheyen 1991). Rwenzori is noted for its unique montane vegetation, unusually high rainfall, and remarkably diverse mammalian community (Rodgers, Owen, and Homewood 1982; Howard 1991). Ituri Forest is renowned for its exceptional biotic richness, including many endemic species found nowhere else in Africa (Kingdon 1989; Pomeroy 1993).

A large Rwenzori-centered population of chimpanzees during glacial periods would explain the localization of divergent alleles to Rwenzori. Similarly, a large Ituri-centered population would explain the high genetic diversity of present-day Ituri chimpanzees. Such interpretations should, however, be made with caution. More detailed phylogeographic analyses of these chimpanzee populations suggest that refugia in the traditional sense have had minimal, if any, effects on the phylogenetic structure of the eastern chimpanzee subspecies (Goldberg and Ruvolo 1997).

Major climatic events should have had a significant impact on a wide variety of phylogenetically distinct tropical forest species, if these events were indeed cat-
astrophic in nature (Ruvolo 1996). Systematic geographic analyses of genetic variability within the remaining ape subspecies may someday indicate whether (and which) paleoclimatic events have played particularly important roles in hominoid genetic evolution. The broad comparative perspective which such studies would offer may someday indicate that human genetic variability is more typical in its extent and apportionment than previously thought, except for the unusually large geographic range over which it is distributed.

Acknowledgments

Richard Wrangham, David Pilbeam, and Mark Leighton made significant intellectual contributions to the planning of this project and, along with two anonymous reviewers, to the writing of the manuscript. Many thanks also go to Alan Rogers for providing invaluable technical advice. Colin and Lauren Chapman, John and Terese Hart, Tuhairwe Peter Arwooki, Katembo Mushgezni Vital, and the faculty and staff of Makerere University Biological Field Station (Kanyawara, Uganda) and the Centre de Formation et de Recherche en Conservation Forestiere (Epulu, Zaïre) helped immensely in the field. Phil Harrell, Elizabeth Williamson, Christine Manning, Ellen Jacobs, Onyach Onecimo, and Phil Moran helped collect or otherwise provide valuable samples.

Financial support for this project came from the Wenner-Gren Foundation for Anthropological Research, the L. S. B. Leakey Foundation, the Charles A. and Anne Morrow Lindbergh Foundation, the Mellon Foundation, and the Department of Anthropology at Harvard University. The Uganda National Council for Science and Technology and the government of Zaïre generously approved and supported fieldwork. Additional funding came from Harvard University, the U.S. Department of Education, and the Cora Du Bois Charitable Trust.

LITERATURE CITED


SIMON EASTEAL, reviewing editor

Accepted May 30, 1997