



## Combining Biogeographic and Phylogenetic Data to Examine Primate Speciation: An Example Using Cercopithecine Monkeys

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### ABSTRACT

We combined phylogenetic and biogeographic data to examine the mode of speciation in a group of African monkeys, the Cercopithecini. If allopatric speciation is the major force producing species, then there should be a positive relationship between the relative divergence time of taxa and their degree of geographic range overlap. Alternatively, an opposite relationship between divergence time and geographic range overlap is consistent with sympatric speciation as the main mechanism underlying the cercopithecine radiation. We collected biogeographic and phylogenetic data for 19 guenon species from the literature. We digitized geographic range maps and utilized three different phylogenetic hypotheses based on Y chromosome, X chromosome, and mitochondrial (mtDNA) data. We used regressions with Monte Carlo simulation to examine the relationship between the relative time since divergence of taxa and their degree of geographic range overlap. We found that there was a positive relationship between relative divergence time and the proportion of geographic range overlap between taxa using all three molecular data sets. Our findings provide evidence for allopatric speciation being the common mode of diversification in the cercopithecine clade. Because most of these primates are forest adapted mammals, the cyclical contraction and expansion of African forests from the late Miocene to the present has likely been an important factor driving allopatric speciation. In addition, geographic barriers such as the Congo and Sanaga rivers have probably played a complementary role in producing new species within the clade.

*Key words:* adaptive radiation; allopatric speciation; evolution; geographic range; hybridization; sympatric speciation.

WITH THE IMPORTANCE OF CONSERVATION BIOLOGY, studies investigating patterns and processes related to species diversity and the loss of this diversity are increasing rapidly. Much attention has been paid to questions related to the patterns of species diversity (Petchey & Gaston 2002, Grubb *et al.* 2003, Graham *et al.* 2005, Ricklefs 2006, Kamilar *In press*), and evidence for the mechanisms driving this diversity is growing (Chesser & Zink 1994, Coyne & Price 2000, Fitzpatrick & Turelli 2006). Although most researchers assume that allopatric speciation is the major force generating new vertebrate species, recent analyses have yielded mixed results (Fitzpatrick & Turelli 2006).

Speciation occurs when two or more groups of a population become reproductively isolated, resulting in the development of two or more species (Futuyma 1998). Since Darwin's (1859) *On the Origin of Species*, scientists have debated the theoretical and empirical evidence for the mode of speciation. Allopatric speciation is the evolution of genetic reproductive barriers between populations that are separated geographically by an extrinsic, physical barrier such as topography, water, land, or an unfavorable habitat (Futuyma 1998). Sympatric speciation is defined by Coyne and Orr (2004) as the origin of a reproductively isolating mechanism, such as the

evolution of a barrier to gene flow, among the members of an interbreeding population.

The recent development of macroevolutionary methods that combine geographic and phylogenetic data has attempted to provide an additional line of evidence supporting particular speciation mechanisms. Inferring the mode of speciation through this comparative biogeographic approach entails the correlation of species' time since divergence with their degree of sympatry (Barraclough *et al.* 1998). When a population becomes distinct from the parent species through allopatric speciation, a positive correlation is expected between the degree of sympatry and the time since divergence between taxa. This is because newly diverged species' ranges will not overlap, and thus their degree of sympatry, measured as a percentage of geographic range overlap, will equal zero. This theoretical framework assumes that as the time since divergence increases between taxa, their niche separation should increase, allowing their degree of sympatry to also increase. Conversely, in a sympatric speciation model, a negative correlation is expected. Newly diverged species once again reflect minimal time since divergence and should exhibit moderate-to-high degrees of range overlap. As time increases, the species home ranges should move randomly, eventually decreasing their degree of overlap (Barraclough & Vogler 2000).

The goal of this paper is to use comparative biogeographic methods to examine the possible mode of speciation in cercopithecine primates, also known as 'guenons'. This speciose group of

Received 25 April 2008; revision accepted 23 December 2008.

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African monkeys provides an ideal model for investigating such fundamental issues in evolutionary biology. First, this group includes subsets of taxa with overlapping ranges and other subsets that are geographically separated (Hamilton 1988, Kingdon 1997)—a mixture of biogeographic patterns that opens the possibility that recent divergence within the guenon radiation may include cases of both sympatric and allopatric speciation. Second, distribution maps are available for all guenon species (Lernould 1988, Kingdon 1997) and thus allow for estimations of range overlap. Finally, because the cercopithecins have been the subject of several recent molecular studies (Disotell & Raaum 2002; Tosi *et al.* 2004, 2005), a robust set of phylogenetic relationships has already been inferred and can serve as the foundation for the analyses performed here.

Several researchers have postulated that speciation has been predominantly allopatric among the Cercopithecini. The majority of these taxa are highly arboreal (Gautier-Hion *et al.* 1988) and their evolution is thought to be tied to Plio–Pleistocene fluctuations in the African forest block. Two general models have been proposed as underlying the allopatric divergence of these animals. A ‘refuge’ model holds that as the forest block fragmented during glacial maxima, inhabitant cercopithecine populations were likewise fragmented, resulting in unique species (Hamilton 1988, Kingdon 1989, Colyn *et al.* 1991). A ‘dispersal’ model emphasizes speciation during forest expansion, suggesting that in such times, the advancing front of cercopithecine stocks would meet a different set of environmental pressures compared with populations in the core range, thereby putting the ‘frontline’ individuals on a distinct evolutionary trajectory (Grubb 1978, 1982).

In contrast, cytogeneticists have proposed that sympatric speciation may form the foundation of the cercopithecine radiation (Dutrillaux *et al.* 1980, 1988). Different guenon species share various chromosomal rearrangements, but these rearrangements do not

follow a single dichotomous branching pattern. If the shared rearrangements represent identical evolutionary events, and not convergent mutations, their incongruent patterns may be explained by random descent from a karyotypically polymorphic ancestral population. Dutrillaux *et al.* (1980, 1988) hypothesize that particular combinations of more derived chromosomal elements would eventually yield offspring with increased levels of reproductive isolation, relative to their parental types. Offspring with similar karyotypes would interbreed and thereby found new lineages within the parental range (*i.e.*, sympatric speciation). By extension, species originating via hybridization would produce a pattern similar to sympatric speciation because new lineages would be created within the parental species range.

The present study builds on previous research to test whether sympatric or allopatric speciation is the most frequent mode of evolution underlying this primate radiation. The results of this study will provide a strong foundation on which to judge whether guenon divergence, in particular, was more likely driven by: (1) population expansion and fragmentation stemming from fluctuations of the African forest block; or (2) the assortative mating of individuals with highly derived karyotypes.

## METHODS

There are three recent molecular hypotheses for guenon phylogeny and these are derived from three different genetic systems: (1) X-chromosomal DNA (Tosi *et al.* 2005); (2) Y-chromosomal DNA (Tosi *et al.* 2004); and (3) mitochondrial DNA (mtDNA) (Disotell & Raaum 2002) (Fig. 1). The utility of these phylogenies is wholly dependent on their accuracy. If two deeply divergent taxa are mistakenly depicted as sister species, it will affect inferences of sympatric versus allopatric evolution, depending on whether the two taxa

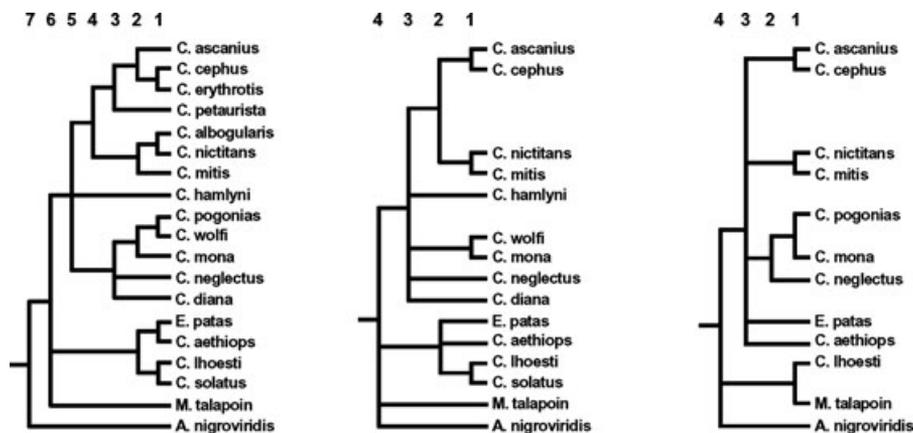


FIGURE 1. Phylogenetic hypotheses used in the analyses. Left: X chromosome (Tosi *et al.* 2005), center: Y chromosome (Tosi *et al.* 2004), and right: mtDNA (Disotell & Raaum 2002). Y-chromosomal, mitochondrial, and X-chromosomal topologies generally agree on the evolutionary relationships among the guenons. The only statistically significant exception is the phylogenetic position of *C. lhoesti*. The congruence of its placement in both nuclear trees argues that its mitochondrial position is not an accurate reflection of species-level relationships. Relative divergence time between taxa is indicated by the node level. Recently diverged taxa have low values, and more distantly related taxa display high values.

have overlapping or separate ranges. In the present case, the agreement of most relationships across Y-chromosomal, mitochondrial, and X-chromosomal topologies indicates that the three systems are probably all converging on the 'true' guenon phylogeny. Yet, because different portions of each phylogeny are polytomous—and polytomies open the possibility of incongruent patterns—all three molecular phylogenies will be examined in this study.

The present geographic ranges of guenon species were obtained from Lernoald (1988). The degree of sympatry was defined as the area of range overlap between two taxa as a percentage or fraction of the total range. To measure the area of overlap of the various clades in each phylogeny, Lernoald's (1988) maps were digitized and modified. Maps with each species' range were recorded using a SummaSketch III digitizing tablet (CalComp, Inc., Columbia, MD); values were recorded to the nearest 1.0 km<sup>2</sup>. Geographic range overlap was calculated between every possible sister taxon on the tree. It was measured as the area of overlap divided by the area of the taxon with the smaller area (Barraclough & Vogler 2000). When measuring overlap for clades at deeper nodes, the clades being compared include the geographic range of all the species in the clade.

In order to resolve the polytomies of the published trees without biasing the sample, each phylogeny was subjected to two different analyses. The first used the maximum area overlap between any of the groups at each polytomy in the phylogeny, and the second used the minimum area overlap. As suggested by T. Barraclough (pers. comm.), the maximum and minimum overlaps were determined by measuring all the possible overlaps at each polytomy. For example, if a polytomy includes species A, B, and C, there are three possible range overlap scenarios: AB, AC, and BC. Once the geographic range overlap has been measured, the highest percentage of overlap is used in the first analysis, and the lowest percentage of overlap is used in the second analysis.

Relative divergence time was calculated as the node level on the phylogeny, starting from the most recently diverged taxa (Barraclough & Vogler 2000). Sister taxa at the tips of the phylogeny were assigned a node level of 1, the node connecting this clade with their outgroup is node 2, and so on. Actual divergence times were not used because such information was not available for several nodes across all three trees; moreover, the wide error margins around these dates confound comparisons both within and across the topologies. Analyses using node levels, however, can be used in lieu of actual divergence times, as demonstrated in several examples by Barraclough and Vogler (2000).

Fitzpatrick and Turelli (2006) argue that if a significant correlation exists between divergence time and geographic range overlap, more recently diverged pairs of taxa should contain more information than comparisons at deeper nodes. This may be due to several reasons, including species geographic range shifts in the past and increasing measurement error by adding range estimates from multiple taxa. If allopatric speciation is the predominant mode of speciation within the clade, then we should find a positive relationship between the geographic range overlap and phylogenetic node age between species (Barraclough & Vogler 2000). Recently diverged species should display no or little geographic range overlap. Geographic range overlap should increase as divergence time

increases because of range shifts and/or expansions. In addition, the  $y$ -intercept should be  $< 0.5$  (Fitzpatrick & Turelli 2006). If sympatric speciation is the common mode of speciation, then there should be a negative relationship between range overlap and phylogenetic node age between species, with a  $y$ -intercept  $> 0.5$ . In this case, recently diverged taxa should exhibit high levels of range overlap. More distantly related taxa should display less overlap due to range shifts.

We tested these predictions by conducting regression analyses with Monte Carlo simulation using the EcoSim software (Gotelli & Entsminger 2001). Monte Carlo randomizations are advantageous because the geographic and phylogenetic data sets do not conform to the statistical assumptions of parametric statistics (Fitzpatrick & Turelli 2006). Two regressions were conducted for each phylogenetic hypothesis in order to include both minimum and maximum representations at the polytomies. We conducted 9999 randomizations for each regression.

## RESULTS

The results of the analyses performed here suggest that guenons diverged predominantly through allopatric speciation events. The regression analyses revealed a statistically significant positive slope and an intercept  $< 0.5$  for the relationship between geographic overlap and phylogenetic node level. These results were significant at the  $P < 0.004$  level for all phylogenetic hypotheses, with maximum overlap at each polytomy (Table 1). When we calculated the minimum amount of overlap at each polytomy, the relationships are weaker using the X chromosome and mtDNA data ( $P < 0.073$ ), yet the patterns are still in the direction expected, with a positive slope and an intercept  $< 0.50$ . The Y chromosome results are consistent using either method to account for polytomies (Fig. 2; Table 1).

Although the data suggest an overall allopatric mode of speciation for the guenons, an examination of the scatterplots show that some sister taxa exhibit relatively high degrees of range overlap relative to their node level (*i.e.*, divergence time). This is best illustrated by the data point representing *Erythrocebus patas* versus *Chlorocebus aethiops* using the X chromosome phylogeny. Based on this phylogenetic hypothesis, these species are each others' closest living relatives, yet have a relatively high degree of geographic range overlap. This 'outlier' may signal a case of sympatric speciation, yet it is more likely reflecting the good dispersal ability of the species, especially *C. aethiops*.

## DISCUSSION

GENERAL INFERENCES.—The results of the correlation and regression analyses are largely consistent across the molecular phylogenetic hypotheses, revealing robust support for allopatric speciation among the guenons. The inference of allopatric speciation, in turn, indirectly supports the idea that most guenon divergence events have been a function of population expansion and contraction stemming

TABLE 1. Monte Carlo regressions examining the relationship between relative divergence time and the proportion of geographic range overlap among taxa. P values were generated from 9999 randomizations of the data.

Phylogenetic hypothesis	Number of species	Number of nodes	Overlap at polytomy	$R^2$	Observed slope	Observed $y$ -intercept	P value
X chromosome	18	14	Max.	0.580	0.167	-0.078	0.001
X chromosome	18	14	Min.	0.189	0.074	0.035	0.072
Y chromosome	15	8	Max.	0.904	0.361	-0.339	0.003
Y chromosome	15	8	Min.	0.904	0.361	-0.339	0.002
mtDNA	12	7	Max.	0.924	0.342	-0.267	0.006
mtDNA	12	7	Min.	0.490	0.218	-0.163	0.070

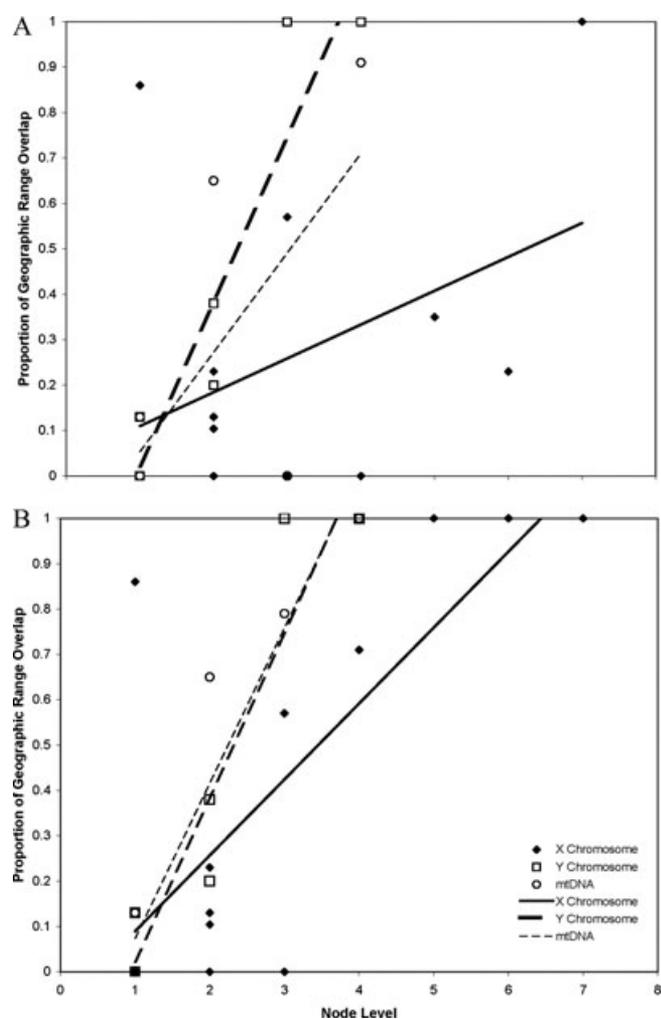


FIGURE 2. Plot of node level versus the proportion of geographic range overlap among guenon taxa. Three molecular data sets are included in each figure: X chromosome (filled diamonds), Y chromosome (open squares), and mitochondrial (open circles). Best-fit lines are generated from least squares methods. Panel (A) assumes minimum geographic range overlap at each polytomy, and panel (B) assumes maximum geographic range overlap at each polytomy.

from fluctuations in the African forest block (Grubb 1978, 1982; Hamilton 1988; Kingdon 1989; Colyn *et al.* 1991). In contrast, we can refute that assortative mating among derived karyotypes within an ancestral population, as described in the sympatric speciation model of Dutrillaux *et al.* (1980, 1988), is the most common mode of evolution. That being said, we cannot completely rule out limited cases of speciation due to hybridization. The method employed in our study tests for the most frequent form of speciation (allopatric in this case), but we cannot totally dismiss rare cases of alternative forms of evolution. Although the three molecular data sets we included in the study may also be differentially affected by hybridization, all of our analyses showed a positive relationship between divergence time and the degree of geographic range overlap among taxa. If interspecific gene flow was extensive within the clade or occurred at different frequencies in different data sets, we would expect no or a negative relationship between these variables.

While the data showed that allopatric speciation is the likely effect producing the positive relationship between node level and geographic range overlap, an examination of the scatterplots suggest that random range movements may have also influenced this pattern. Given the biology of guenons and the evolution of African forests, we believe that large-scale random range movements are unlikely. The majority of guenons are highly arboreal; their ranges are therefore tied to that of the African rain forest. Through regional and global climate change from the late Miocene through the Pleistocene, the range of the African forest is thought to have fluctuated numerous times. At glacial peaks, the forest probably fragmented into refugia along the coastal areas of western and West-Central Africa (Hamilton 1988, Maley 1996), along the major tributaries of the Congo river (Kingdon 1989, Colyn *et al.* 1991), and within the Albertine region of east central Africa (Hamilton 1988, Maley 1996). Guenon populations almost certainly retreated to these refugia with every glacial advance, and only recolonized formerly occupied areas with the expansion of rain forest in interglacial pluvials. During the expansion phases, guenon stocks would have repeatedly faced many of the same (semipermeable) biogeographic barriers, including belts of forest-savannah mosaic, such as the Dahomey Gap (Oates 1988; but see Maley 1996 for an opposing view), or rivers

that either impeded gene flow (*e.g.*, Congo and Sanaga rivers; Grubb 1990) or acted as a transition zone between two major ecotones, *e.g.*, Cross river (Oates 1988, Maley 1996).

**ASSUMPTIONS OF THE BIOGEOGRAPHIC METHOD.**—The ability for the comparative biogeographic method employed here to detect speciation patterns rests on several assumptions (Barracough & Vogler 2000, Losos & Glor 2003, Fitzpatrick & Turelli 2006). The first is the assumption that one particular mode of speciation is common within the clade being analyzed. If both allopatric and sympatric speciation have occurred at similar levels, then detecting speciation patterns from geographic and phylogenetic data will provide unclear results. Second, enough variation in the degree of range overlap and node ages must be present in the data set to be able to detect a relationship between these variables when one exists. Last, large shifts in the geographic ranges of species can mask detectable geographic pattern of speciation. This may be especially common with taxa that can disperse long distances (Chesser & Zink 1994, Coyne & Price 2000). These assumptions are difficult to satisfy for many taxa and are probably the reason for a lack of relationship between divergence time and geographic range overlap in numerous clades that are predicted to display allopatric speciation patterns (Barracough & Vogler 2000, Fitzpatrick & Turelli 2006). These assumptions appear to be satisfied in our current study. Although age–range correlation analyses tend to have low statistical power, we did find a significant positive correlation. In addition, most guenons are small-to medium-sized arboreal primates that are restricted to the forests of equatorial Africa (Glenn & Cords 2002). These traits likely result in most species being poor dispersers, except for vervet (*C. aethiops*) and patas monkeys (*E. patas*), which inhabit savanna and wooded regions throughout sub-Saharan Africa. Therefore, rapid and extensive range shifts were unlikely to have occurred.

In addition to the current analysis of genetic and geographic patterns, a similar comparison of morphological and geographic patterns corroborates the likely predominate allopatric speciation within the guenon clade. The guenon radiation contains a number of polytypic ‘species groups’ (*i.e.*, *mona*, *cephus*, *mitis*, *lhoesti*, and *aethiops*) whose members share a general pelage morphotype (Lernoult 1988, Kingdon 1997) and are thus considered to form distinct guenon subclades. Though sister taxa—which offer the clearest window onto the mode of speciation due to their recent divergence—have yet to be identified within the respective subclades, it is interesting to note that the members of each subclade are parapatric or have minimal overlap (Kingdon 1997). This pattern of geographic separation, in turn, suggests that sister taxa likely arose via a mechanism of allopatric speciation.

**NEW INSIGHTS AND FUTURE RESEARCH.**—Combining the results of this study with those of earlier chromosomal studies opens new insights into guenon evolution. The lack of support for the sympatric speciation model proposed by Dutrillaux *et al.* (1980, 1988) indicates that the chromosomal similarities shared by distantly related guenon taxa may be the result of ancestral hybridization (*i.e.*, post speciation). This is a reasonable idea, considering that many distinct guenon species occasionally interbreed today (Tutin 1999,

Detwiler 2002). A history of intermittent interbreeding would have opened temporary conduits for gene flow and, if beneficial alleles were exchanged, could have served as a mechanism to increase the fitness of the entire guenon species complex (Jolly 2001, Detwiler *et al.* 2005, Arnold & Meyer 2006).

The incongruence among guenon chromosomal patterns offers an excellent set of test cases for the investigation of such ancestral hybridization. While most chromosomal patterns agree with those of sequence-based phylogenies (Fig. 1), there remain six unexplained rearrangements (on chromosomes 2, 4, 7, 11, 12, and 13) that are shared among various *Cercopithecus* species (Dutrillaux *et al.* 1980, 1988). If ancestral hybridization is a viable explanation, gene trees inferred from loci across each of the six chromosomes should match the patterns inferred by Dutrillaux *et al.* (1980, 1988). More studies are needed to test this hypothesis.

Finally, it is possible that guenon speciation occasionally occurred via hybridization. During the course of guenon history, populations of divergent taxa, isolated together in a glacial-induced forest fragment or living together at a forest edge, may have undergone extensive interbreeding and produced a new form distinct from both parental stocks (Detwiler *et al.* 2005). Though speciation via hybridization is a mechanism rarely invoked for mammals (Roy *et al.* 1996; for exceptions, see Jolly 2001, Tosi *et al.* 2003), the known interbreeding among extant guenons species, coupled with their potentially reticulate chromosomal patterns, indicate that hybridization events may be closely associated with the divergence of some branches of this primate radiation.

## ACKNOWLEDGMENTS

We thank K. Detwiler for valuable discussions of guenon hybridization and speciation and J. Fleagle for insightful discussion of the evolutionary history of African primates and their habitats. T. Barracough provided methodological advice for working with phylogenies that were not fully resolved. Finally, we thank T. Di Fiore and three anonymous reviewers for providing helpful comments that improved an earlier version of the manuscript.

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