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Molecular Phylogenetics and Evolution 36 (2005) 58–66

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AND
EVOLUTION

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X-chromosomal window into the evolutionary history of the guenons (Primates: Cercopithecini)

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Received 14 August 2004; revised 5 January 2005
Available online 16 February 2005

Abstract

Molecular studies of the guenons suggest that the arboreal *Cercopithecus* species form a monophyletic group within the tribe Cercopithecini. However, the evolutionary relationships among these arboreal congeners remain poorly resolved. The present work marks the first attempt to reconstruct the history of this group through the phylogenetic analysis of long nuclear sequences. We surveyed 19 guenons and seven outgroup taxa for a ~9.3 kb fragment of X-chromosomal DNA homologous to a portion of human Xq13.3. Parsimony and maximum likelihood analyses of these sequences consistently recover two strongly-supported patterns within the arboreal *Cercopithecus* clade: (1) a clustering of members of the *cephus* and *mitis* species groups, and (2) a monophyletic aggregate including the *mona*, *neglectus*, and *diana* species groups. Although guenons occasionally hybridize in the wild, interbreeding forms of different species groups do not cluster together as sister-taxa in the X-chromosomal tree, suggesting that the two clades inferred here are not reticulate patterns due to recent gene flow. These clades are most likely the result of either ancestral hybridization or true phylogenetic history. We advocate the latter explanation because the same two aggregates (*cephus/mitis* and *mona/neglectus/diana*) are recovered, albeit with weak support, by a number of earlier analyses. Finally, X-chromosomal divergence dates are estimated for a number of nodes in the guenon radiation. The divergence of guenon and papionin lineages at 11.5 (±1.3) MYA appears to be a particularly robust estimate since it is inferred from both mitochondrial and X-chromosomal studies, each using different fossil calibration points.

Keywords: X-chromosome; Xq13.3; Cercopithecini; Papionini; *Cercopithecus*; Guenons

1. Introduction

The Cercopithecini (guenons) is a remarkably diverse group of primates thought to have diverged from its sister-tribe, the Papionini (baboons, macaques, mandrills, and mangabeys), in the late Miocene (Delson, 1992; Raaum et al., 2005). In contrast to the grey and brown pelage of most papionins, the guenons exhibit a variety of colors and pelage patterns that are among the most elaborate in the mammalian world. They are equally as diverse in terms of habitat. Guenon species are found throughout sub-Saharan Africa in areas including woodlands, mangrove forests, swamp forests, montane forests, bamboo forests, and alpine moorland (Butynski, 2002).

The majority of cercopithecin molecular studies—including Y-chromosomal (Tosi et al., 2004, 2005) (Fig. 1A), karyotype (Dutrillaux et al., 1988) (Fig. 1C), and X-chromosomal (Tosi et al., 2004; present study) analyses—agree on four main phylogenetic subunits: (1) *Allenopithecus*, (2) *Miopithecus*, (3) a "terrestrial clade" including *Erythrocebus patas*, *Cercopithecus aethiops*,

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doi:10.1016/j.ympev.2005.01.009

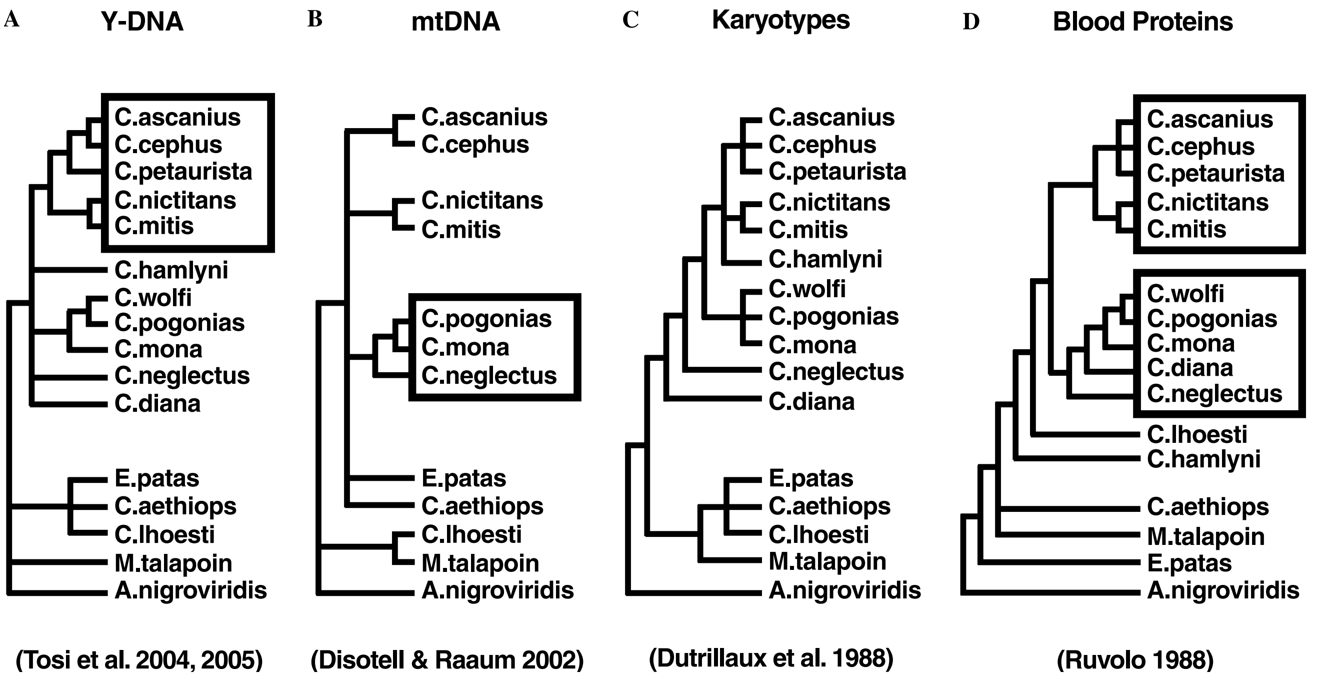

Fig. 1. Previous molecular studies of guenon evolution. Only taxa common to three or more studies are depicted. (A) Y-chromosomal DNA tree of Tosi et al. (2004, 2005). (B) Mitochondrial DNA tree of Disotell and Raaum (2002). (C) Karyotype relationships reconstructed by Disotell (2000) from the chromosomal studies of Dutrillaux et al. (1980, 1988). (D) Blood protein cladogram generated by Ruvolo (1988). The Y-chromosomal relationships depicted are the same as that of Tosi et al. (2004, 2005), with the exception that the present tree includes an additional taxon, *Cercopithecus petaurista* (GenBank Accessions # AY897616 and AY897617). Due to the inclusion of this new taxon, the Y-chromosomal dataset was reanalyzed—following the methods of Tosi et al. (2004, 2005)—however no significant change in evolutionary relationships resulted. Boxes highlight the recovery of two clusters of species groups: a *cephus*/*mitis* cluster, and a *mona*/*neglectus*/*diana* cluster. Note that the polytomous relationships of the mtDNA and karyotype trees do not argue against a *cephus*/*mitis* aggregate. Likewise, the Y-DNA tree does not argue against a *mona*/*neglectus*/*diana* aggregate.

and the *Cercopithecus lhoesti* species group, and (4) an aggregate of the "arboreal *Cercopithecus*" species. Though mitochondrial (Disotell and Raaum, 2002) (Fig. 1B) and protein (Ruvolo, 1988) (Fig. 1D) analyses do not yield a "terrestrial monophyly," the alternative patterns of (terrestrial) relationships depicted in these works seem unlikely given that they are not corroborated by any previous study (Gautier-Hion et al., 1988; Glenn and Cords, 2002).

While the outline of four main guenon divisions is steadily gaining strength, a robust phylogenetic hypothesis is lacking for lower-level relationships, particularly those within the "arboreal *Cercopithecus*" aggregate. This clade consists of six species groups (Butynski, 2002; Grubb et al., 2003): (1) the *cephus* group (*C. cephus*, *C. ascanius*, *C. petaurista*, *C. erythrotis*, *C. erythrogaster*, *C. sclateri*), (2) the *mitis* group (*C. mitis*, *C. albogularis*, *C. nictitans*), (3) the *mona* group (*C. campbelli*, *C. mona*, *C. pogonias*, *C. wolfi*), (4) the *neglectus* group (*C. neglectus*), (5) the *diana* group (*C. diana*), and (6) the *hamlyni* group (*C. hamlyni*). Y-chromosomal (Fig. 1A) and mitochondrial (Fig. 1B) topologies depict largely polytomous patterns among these aggregates, with the exception of putative sister-relationships between the *cephus* and *mitis* groups and the *mona* and *neglectus* groups. Karyotype (Fig. 1C) and protein [1] topologies (Fig. 1D) yield better resolution, but the strength of these phylogenetic patterns is somewhat dubious because statistical measures of clade support are not included.

The present work improves on these earlier studies by surveying long DNA sequences to achieve high levels of synapomorphic support within the arboreal *Cercopithecus* clade. We analyzed several guenon species and cercopithecoid outgroup taxa for a ~9.3 kb fragment of X-chromosomal DNA homologous to a portion of human Xq13.3 (Kaessmann et al., 1999). This fragment is an extension of a previously published 1.6 kb region (Tosi et al., 2004) which recovered only enough phylogenetic signal to reliably identify the four main guenon divisions (described above). The Xq13.3 homolog surveyed here consists solely of intergenic DNA and is therefore not likely to be the direct target of selective forces which could alter its ability to track guenon relationships. Moreover, X-loci are some of the best molecular markers for phylogeny reconstruction because they have a lower

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[1] Ruvolo's assumptions of basal and derived taxa automatically lead to a monophyly of the arboreal *Cercopithecus* species (plus *C. lhoesti*). However, because her *a priori* decisions did not constrain relationships within this clade, the protein tree (Fig. 1D) remains valid as a hypothesis of arboreal *Cercopithecus* phylogeny.