

RESEARCH ARTICLE

Open Access

Nuclear versus mitochondrial DNA: evidence for hybridization in colobine monkeys

Christian Roos^{1,2*†}, Dietmar Zinner^{3†}, Laura S Kubatko⁴, Christiane Schwarz¹, Mouyu Yang¹, Dirk Meyer⁵, Stephen D Nash⁶, Jinchuan Xing⁷, Mark A Batzer⁸, Markus Brameier¹, Fabian H Leendertz⁹, Thomas Ziegler⁵, Dyah Perwitasari-Farajallah¹⁰, Tilo Nadler¹¹, Lutz Walter^{1,2}, Martin Osterholz^{1,12*}

Abstract

Background: Colobine monkeys constitute a diverse group of primates with major radiations in Africa and Asia. However, phylogenetic relationships among genera are under debate, and recent molecular studies with incomplete taxon-sampling revealed discordant gene trees. To solve the evolutionary history of colobine genera and to determine causes for possible gene tree incongruences, we combined presence/absence analysis of mobile elements with autosomal, X chromosomal, Y chromosomal and mitochondrial sequence data from all recognized colobine genera.

Results: Gene tree topologies and divergence age estimates derived from different markers were similar, but differed in placing *Ptilocolobus/Procolobus* and langur genera among colobines. Although insufficient data, homoplasy and incomplete lineage sorting might all have contributed to the discordance among gene trees, hybridization is favored as the main cause of the observed discordance. We propose that African colobines are paraphyletic, but might later have experienced female introgression from *Ptilocolobus/Procolobus* into *Colobus*. In the late Miocene, colobines invaded Eurasia and diversified into several lineages. Among Asian colobines, *Semnopithecus* diverged first, indicating langur paraphyly. However, unidirectional gene flow from *Semnopithecus* into *Trachypithecus* via male introgression followed by nuclear swamping might have occurred until the earliest Pleistocene.

Conclusions: Overall, our study provides the most comprehensive view on colobine evolution to date and emphasizes that analyses of various molecular markers, such as mobile elements and sequence data from multiple loci, are crucial to better understand evolutionary relationships and to trace hybridization events. Our results also suggest that sex-specific dispersal patterns, promoted by a respective social organization of the species involved, can result in different hybridization scenarios.

Background

With more than 50 species and due to some ecological adaptations, such as a ruminant-like chambered stomach to digest food rich in fiber, the Old World monkey sub-family Colobinae represents a diverse and enigmatic group of primates [1,2]. Colobines are predominantly arboreal and occur in forest and woodland habitats. They have experienced two major radiations, one in Africa with the genera *Procolobus*, *Ptilocolobus* and

Colobus, and a second in South and Southeast Asia comprising the langur genera *Semnopithecus*, *Trachypithecus* and *Presbytis*, and the odd-nosed monkey genera *Rhinopithecus*, *Pygathrix*, *Nasalis* and *Simias* [2]. However, their phylogenetic relationships are disputed [3-7], and recent molecular studies detected substantial gene tree discordance [8-10].

Traditionally, African and Asian genera are believed to form reciprocally monophyletic groups [1,2,11,12], though paraphyly has also been proposed [3-5]. Molecular investigations clearly confirm a common origin of Asian colobines and the odd-nosed monkey group [8-10], but evidence for monophyly of the langur group as well as for African colobines is still lacking.

* Correspondence: croos@dpzeu; mosterh@gwdg.de

† Contributed equally

¹Primate Genetics Laboratory, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany

Full list of author information is available at the end of the article