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SHORT COMMUNICATION

Molecular evidence for deep phylogenetic divergence in *Mandrillus sphinx*

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Abstract

Mandrills (*Mandrillus sphinx*) are forest primates indigenous to western central Africa. Phylogenetic analysis of 267 base pairs (bp) of the cytochrome *b* gene from 53 mandrills of known and 17 of unknown provenance revealed two phylogeographical groups, with haplotypes differentiated by 2.6% comprising seven synonymous transitions. The distribution of the haplotypes suggests that the Ogooué River, Gabon, which bisects their range, separates mandrill populations in Cameroon and northern Gabon from those in southern Gabon. The haplotype distribution is also concordant with that of two known mandrill simian immunodeficiency viruses, suggesting that these two mandrill phylogroups have followed different evolutionary trajectories since separation.

Keywords: biogeography, divergence, forest refuges, haplogroups, mandrill, mtDNA

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Introduction

Mandrills and drills (*Mandrillus leucophaeus*, Papionini) are large, primarily terrestrial primates found in the tropical forests of western Central Africa from southeastern Nigeria to southwestern Republic of Congo (Kingdon 1997). The distribution of drills is disjunct, occurring on both the mainland (from southeastern coastal Nigeria through southwestern Cameroon to the Sanaga River) and on the island of Bioko. Mandrills occupy a similar coastal forest habitat with their eastern limit defined, reportedly, by the Ivindo and Ogooué rivers in Gabon (Harrison 1988).

Until recently, mandrills and drills, along with baboons, were placed in the genus *Papio* (Szalay & Delson 1979; Wolfheim 1983). However, morphological and genetic evidence supports evolution of mandrills and drills as a genus *Mandrillus* (Groves 1993), which is phylogenetically closely related to the *torquatus-galeritus* group of mangabeys of the genus *Cercocebus*, whereas baboons (*Papio*) and geladas (*Theropithecus*) are related most closely to the *albigena-aterrimus* mangabeys, of the genus *Lophocebus* (Disotell *et al*. 1992; Harris & Disotell 1998; Fleagle & McGraw 1999).

Although there has been some discussion as to whether drills and mandrills are currently sympatric (Grubb 1973; Harrison 1988), there is little disagreement that drills and mandrills represent distinct species although they can hybridize in captivity (Painter *et al*. 1993). Drills from Bioko are often considered a distinct subspecies (*M. leucophaeus poensis*) due to their geographical isolation, but to date mandrills have never been subdivided (Kingdon 1997).

Recent virological investigations reveal that mandrills are infected with two genetically and antigenically distinct but related lentiviruses: simian immune deficiency virus (SIVmnd) type-1 and SIVmnd type-2 (Tsujimoto *et al*. 1988; Souquière *et al*. 2001; Takehisa *et al*. 2001). The geographic distributions of these two viral types is disjunct, being apparently separated by the Ogooué River in Gabon. We investigated whether this separation is paralleled by divergence in the host by analysing genetic variability at the mitochondrial cytochrome *b* locus.

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Table 1 Origins of 53 mandrills of known provenance sampled throughout their distribution from southern-central Cameroon to southern Gabon

Sample ID	Geographic origin	Haplogroup	Location on Fig. 1
Yao	S. Central Cameroon	N	A
Ebo1*	Ebolowa, Cameroon	N	W
Ebo2*	Ebolowa, Cameroon	N	W
Ebo3*	Ebolowa, Cameroon	N	W
Ebo4*	Ebolowa, Cameroon	N	W
Mak	Makokou, Gabon	N	B
Coc	Cocobeach, Gabon	N	C
Lam	Lambaréné, Gabon	N	D
Ova	Ovan, Gabon	N	E
Ndj	Ndjole, Gabon	N	X
FeLope**	Lopé, Gabon	S	F
Lop2	Lopé, Gabon	S	F
Tch	Tchibanga, Gabon	S	G
Kou1	Koulamoutou, Gabon	S	H
Kou2	Koulamoutou, Gabon	S	H
Kou3	Koulamoutou, Gabon	S	H
Pou	Pouvi, Gabon	S	H
Bak	Bakoumba, Gabon	S	I
Pan	Pana, Gabon	S	J

*Takehisa *et al*. (2001). **FeLope represents 35 identical sequences from 35 faecal samples collected from two different wild mandrill groups.

Materials and methods

Sampling

Samples for total DNA extraction were collected from 49 mandrills of known provenance throughout Gabon and into southern Cameroon (Table 1, Fig. 1). Blood samples were collected from locally captured live animals (n = 11; GenBank Accession nos AY204763–AY204773), small amounts of tissue (donated by hunters) were collected from fresh cadavers (n = 3; GenBank Accession nos AY204774, AY204775, AY204776) and faecal samples were collected from wild mandrills in the Lopé Reserve, central Gabon (n = 35; GenBank Accession nos AY204793–AY204827). In addition, blood samples from captive mandrills housed at the Centre International de Recherches Médicales (n = 8; GenBank Accession nos AY204777–AY204784) and from zoos (n = 9; GenBank Accession nos AY204785–AY204792), all of unknown origin, were included. Sequences from GenBank were also included in the analyses [n = 5; GenBank Accession nos AF301616, AF301615, AF301613, AF301612 from southern Cameroon (Takehisa *et al*. 2001) and AF020423 of unknown origin (Zhang & Ryder 1998)]. This work was authorized by the Gabonese Ministry of Health and Ministry of Environment Department of Wildlife and Hunting (permit no. 00257/MEFPTE/DGEF/DFC).

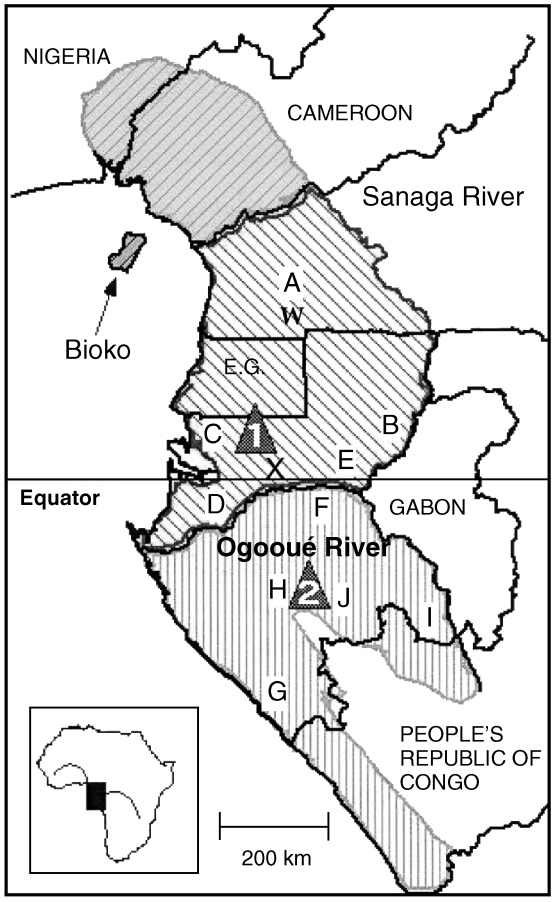

Fig. 1 Locations where mandrills were sampled; N and S indicate 'Northern Haplogroup' and 'Southern Haplogroup', respectively; numbers in parentheses are numbers of individuals at each site. A: Southwest Cameroon-N (1); W: Ebolowa, Cameroon-N (4); B: Makokou-N (1); C: Coco Beach-N (1); D: Lambaréné-N (1); E: Ovan-N (1); X: Ndjolé-N (1); F: Lopé-S (36); G: Tchibanga-S (1); H: Koulamoutou-S (4); I: Bakoumba-S (1); J: Pana-S (1). Triangle 1 indicates the Monts de Cristal; Triangle 2 the Massif du Chaillu. ▨ Drill distribution; ▧ Mandrill distribution-N; ▯ Mandrill distribution-S.

DNA extraction

DNA was extracted at CIRMF, Franceville, Gabon from either 300 µL of whole blood or from 25 mg of tissue. A QIAamp® Blood and Tissue Kit (Qiagen) was used to extract the DNA which was eluted into 60 µL of H_2O and was stored at −20 °C. Faeces were collected in RNALater (Ambion) and DNA was extracted from 100 mg sample using a QIAamp® DNA stool kit (Qiagen), according to the manufacturer's instructions. DNA from mandrills Lop2 and Kns1119 (GenBank Accession nos AY204763 and AY204785) was extracted from blood and sequenced in New York (Gabon CITES export permit no. 002426; USA CITES import permit no. 01US033594/9).

Polymerase chain reaction (PCR) amplification

A 267-base pairs (bp) region portion of cytochrome *b*, representing bases 14841–15149 of the human mitochondrial genome (Anderson *et al*. 1981), was amplified using primers L14841 and H15149 (Irwin *et al*. 1991). One μg of host DNA was used in a 100-μL PCR reaction using a Perkin Elmer PE 9700 thermocycler. The PCR conditions were 2 min at 94 °C followed by 40 cycles of 30 s at 94 °C, 30 s at 55 °C and 30 s at 72 °C, with a final extension of 5 min at 72 °C. The PCR products were cycle sequenced and analysed on an ABI-377 automated DNA sequencer, following purification with a QIAquick PCR purification kit (Qiagen).

A complete mandrill mitochondrial genome (Lop2) was amplified in three overlapping segments following the manufacturer's Long Range PCR protocol (Roche). This generated amplicons of approximately 5000, 7000 and 7500 bp, which overlapped by an average of 15% of their length. Verification of PCR fidelity was performed with two overlapping amplicons, each of approximately 10 000 bp in length. PCR products were visualized on a 0.8% agarose minigel. PCR products were cleaned of excess nucleotides and primers by an exonuclease I/shrimp alkaline phosphatase digestion protocol (Hanke & Wink 1994). A suite of catarrhine specific sequencing primers were designed. Following the manufacturer's protocol for diluted reactions, using 2 μL BigDye (Applied Biosystems) per reaction, PCR products were cycle sequenced and analysed on an ABI 377. Results were analysed with the SEQUENCING ANALYSIS software package (version 3.4, Applied Biosystems) and contigs were assembled with the SEQUENCHER program (version 4.1, AGCT Codes Corp.).

Sequence analyses

In addition to sequences from mandrills, we examined cytochrome *b* sequences from two *M. leucophaeus* (GenBank Accession nos AY204828 and AY204829), two *Cercocebus torquatus torquatus* (GenBank Accession nos AY204833 and AY204834), one *Lophocebus albigena* (GenBank Accession no. AY204830), one *Papio anubis* (GenBank Accession no. AY204836), one *P. cynocephalus* (GenBank Accession no. AY204835), one *Cercopithecus mona* (GenBank Accession no. AY204831), one *C. nictitans* (GenBank Accession no. AY204832) and one *Perodicticus potto* (as an outgroup) (GenBank Accession no. AY204837) to examine phylogenetic relationships at this locus.

Sequences were aligned using CLUSTALW 1.8. Unrooted maximum parsimony trees were inferred using PAUP version 4.0b8 (Swofford 1999) with uniformly weighted unordered characters. Distance matrix-based trees were constructed with the neighbour-joining method (Saitou & Nei 1987) using the HKY85 model of nucleotide substitution (Hasegawa *et al*. 1985). The reliability of the branching order was estimated by performing 1000 bootstrap replicates.

Results

Phylogenetic analyses inferred topologies consistent with current taxonomic classifications (Fig. 2). The genus *Mandrillus* is revealed as monophyletic and is the sister taxon to the genus *Cercocebus*, whereas *Papio* and *Theropithecus* group with the arboreal mangabeys of the genus *Lophocebus*, in agreement with Disotell *et al*. (1992) taxonomy. Mandrills are revealed as diphyletic (bootstrap values 99%), forming two distinct clades in all analyses, with a 2.6% sequence divergence between clades (Fig. 2). Each clade consists of mandrill sequences, which are partitioned geographically in a north–south distribution (Fig. 1). Mandrills sampled in northern Gabon and Cameroon belong to a haplogroup corresponding to the published sequence of Zhang & Ryder (1998), while mandrills from southern Gabon form a second haplogroup, with sequences which differ from the published and northern sequences by seven synonymous nucleotide transitions.

We define the two haplogroups based on seven specific synonymous base substitutions. The northern haplogroup reference sequence is that of Zhang & Ryder (1998) (GenBank Accession no. AF020423) and is the oldest GenBank reference to mandrill cytochrome *b* mtDNA. The southern haplogroup is defined as having the following specific substitutions in our sequences, which differentiate them from the northern haplogroup reference sequence: position 14901 (Anderson *et al*. 1981), A→G; position 14955, T→C; position 14985, T→C; position 14997, C→T; position 15027, C→T; position 15048, T→C; position 15090, T→C. Sequences from 18 other mandrills of unknown geographical origin fell into these two haplogroups. Analyses with all 70 sequences consistently produced trees showing mandrills forming two clades (data not shown).

Based on mean absolute nucleotide substitution rates ($3.5 \pm 1.5 \times 10^{-9}$ substitutions/site/year) of synonymous sites in the primate cytochrome *b* gene (Pesole *et al*. 1999), these haplogroups are estimated to have diverged approximately 800 000 years ago.

Among several groups of mammals, primate nuclear DNA may contain multiple insertions and duplications of mtDNA (Collura & Stewart 1995); however, the sequences analysed here are extremely unlikely to represent nuclear cytochrome *b* sequences, for several reasons. First, our northern haplotype sequences match those of published sequences obtained from three independent studies (Painter *et al*. 1993; Zhang & Ryder 1998; Takehisa *et al*. 2001) and Zhang & Ryder's (1998) sequences were obtained from purified mtDNA. Second, the complete mitochondrial genome of one southern mandrill was sequenced from three overlapping 5–7.5 kb amplicons which contain no

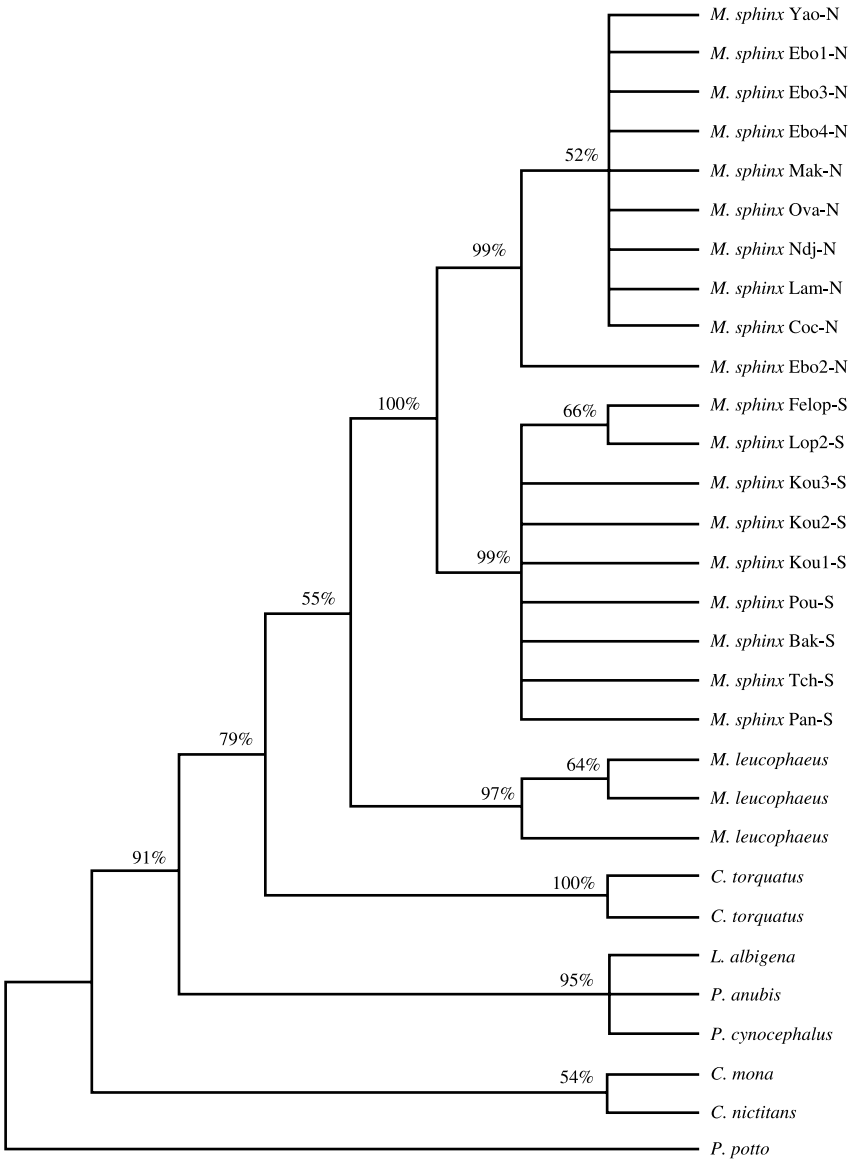

Fig. 2 Cytochrome *b* (partial sequence) phylogeny derived using neighbour-joining analysis, using the HKY85 model of nucleotide substitution (bootstrap values are percentage of 1000 replications).

frame shifts, stop codons, unanticipated insertions or deletions (data not shown). The southern sequences reported were obtained in two independent laboratories and matched that of the complete mtDNA genome. While these southern sequences are divergent from published sequences, none have the characteristics of nuclear inserts. Finally, the differences between northern and southern haplotypes are all synonymous third base changes. Thus, the consistent and geographically partitioned pattern of mtDNA segregation is the most parsimonious explanation for these data.

Discussion

We have analysed 65 new mandrill sequences and compared them with five published sequences. The cytochrome *b* gene is normally highly conserved within primates and phylogenetic analyses employing sequences from cytochrome *b*, primarily targeted within and between generic or order level divergences (Castresana 2001): therefore, little or no variation would be expected within mandrills. The importance of our results rests on the fact that mandrills sampled from south of the Ogooué river are reciprocally monophyletic with, and have a set of nucleotide substitutions that differentiate them from mandrills located north of the Ogooué River, suggesting that this geographical feature may act to restrict gene flow between northern and southern mandrills. Each haplogroup is distributed widely within its geographical range although additional sampling will localize more precisely the boundary between the two haplogroups. The high level of genetic divergence between mandrill haplotypes (2.6%) also suggests that mandrills

may be undergoing allopatric divergence. Additionally, the relative lack of variation within the clades may be indicative of population bottlenecks and/or rapid expansion but cannot be verified without further analyses with more variable markers.

The current distribution of mandrills spans an area of central African forest for which a robust, if localized, Pleistocene refuge model has been generated (Hamilton 1976; Maley 2001), supported by surveys of floral and faunal distributions (Sosef 1996; Rietkerk *et al*. 1996; Muloko-Ntoutoume *et al*. 2000; Grubb 2001), geological surveys (Nichol 1999) and palaeogeographical analyses (Maley 1996; Livingstone 2001). For approximately the last 2.5 million years the forest communities of western equatorial Africa have been subjected to periodic episodes of climatic change alternating between extended intervals of warm wet weather and colder dryer weather (Maley 1996, 2001). It is generally accepted that climatic changes mediated consecutive phases of contraction and expansion in African forests throughout the Plio-Pleistocene. The most severe and longer-lasting dry–cold periods reduced the forests to isolated remnants or 'refuges' near mountainous areas, and in low-lying river courses (Colyn *et al*. 1991; Maley 1996, 2001).

Two major mountain refuges have been identified, the first near the upland sites of the Massif Du Chaillu in southern Gabon and southern Congo and the second centred around the Monts de Cristal in northern Gabon, Equatorial Guinea and southern Cameroon (Maley 1996). Both are found to the south of the Sanaga River, which is the distribution limit for many mammals including the mandrill (Grubb 1982; Kingdon 1997), and more importantly, both are separated in Gabon by the Ogooué River.

It is therefore possible that when the western equatorial forests contracted into the forest refuges localized around the Monts de Cristal and the Massif du Chaillu, the ancestral mandrill populations became separated. Mandrills isolated in these areas would be expected to accumulate genetic differences over time, through allopatric divergence. As these forests re-extended their ranges when the climate warmed, the mandrills' range would have expanded concomitantly. The current interface between mandrill populations with different haplogroups appears to be the Ogooué River, which may impede gene flow, especially for mtDNA since female mandrills remain in their natal groups, while males migrate (Abernethy *et al*. 2002). However, no data from nuclear markers yet exist which would allow us to draw firm conclusions about population isolation. Also, we cannot say whether the two haplotypes coexisted in the ancestral population, with subsequent drift-mediated loss, or whether allopatric genetic divergence from a common ancestral haplotype has occurred.

Nevertheless, while no obvious phenotypic characteristics distinguish these populations, additional evidence for their current genetic distinctiveness is corroborated by their apparent independent infections with two unique SIV types. All mandrills found to be naturally infected with SIVmnd-1 are located south of the Ogooué while similarly, all type-2 infected mandrills are found north of the Ogooué. Both immunodeficiency viruses contain homologous mandrill-specific envelope genes. However, the SIVmnd type-1 virus belongs to a lineage derived from viruses found in *Cercopithecus lhoesti* and *C. solatus* (sun-tailed monkey), whereas the second type of mandrill virus shares a high degree of similarity with that found in *Cercocebus t. torquatus*, which in turn is related to the chimpanzee SIV and HIV-1 (Souquière *et al*. 2001). The southern type-1 virus may have originated from a cross species transmission from *C. solatus* or a *lhoesti*/*solatus* ancestor, while the northern type-2 virus appears to be the result of recombination between an ancestral mandrill–drill virus with SIVrcm from *C. t. torquatus* (Georges-Courbot *et al*. 1998; Souquière *et al*. 2001). These primates currently inhabit the same forest zone in western equatorial Africa as mandrills although *C. solatus* and *C. t. torquatus* are not sympatric. It seems plausible to hypothesize that at some point in the past, mandrills south of the Ogooué came in contact with *C. solatus* or a *solatus*/*lhoesti* ancestor and a cross-species transmission of SIVsol/l'hoesti occurred. To the north of the Ogooué a similar event seems to have taken place when mandrills came into contact with SIVrcm-infected *C. t. torquatus*, thereby giving rise to the SIVmnd type-2 virus.

A combination of detailed studies examining patterns of primate phylogenetic structure with those of retroviral evolution may, in the future, enlighten analysis of historical biogeographical processes.

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