Short communication

Molecular phylogenetic affinities of the simakobu monkey (*Simias concolor*)

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1. Introduction

The simakobu (*Simias concolor*), or pig-tailed snub-nosed langur, is one of four endemic primate species on the Mentawai Islands off the west coast of Sumatra, Indonesia, and is currently considered a monotypic genus (Brandon-Jones et al., 2004; Miller, 1903). This species, like many other colobines, is a specialized folivore found in tropical rainforests. The simakobu monkey is a member of the "odd-nosed" group of Asian colobines, an informal grouping that also includes the proboscis monkey of Borneo (*Nasalis larvatus*), the snub-nosed monkeys of China and Vietnam (*Rhinopithecus* spp.), and the douc langurs of Vietnam, Laos, and Cambodia (*Pygathrix* spp.). There is no agreement, however, on the relationships among these genera, nor whether they even form a natural taxonomic or phylogenetic group (Delson, 1975; Groves, 1970, 2001; Jablonski, 1998; though see Sterner et al., in press).

Geographically, the simakobu is found closest to the proboscis monkey, and some morphological data have indicated that these species are sister taxa. Both *Simias* and *Nasalis* exhibit narrow, long-faced skulls; long narrow nasal bones; and similar hair patterns (Groves, 1970). These two species appear to share more traits than do *Rhinopithecus* and *Pygathrix*, and some researchers have suggested that *Simias* should be subsumed into the genus *Nasalis* (Delson, 1975; Groves, 1970), perhaps as a subgenus (Delson, 1975); Groves (2001; Brandon-Jones, et al., 2004) appears to have retreated from the close linkage of these genera, though is not necessarily opposed to it (Groves, pers. comm.).

Alternative hypotheses suggest that there is no evidence that *Simias* and *Nasalis* are phylogenetically linked (Napier, 1985), and that the former may be a basal colobine unrelated to other members of the "odd-nosed" group (Jablonski, 1998). Other Mentawai primates have also been suggested as basal members of their respective lineages. While Brandon-Jones (1998) considers *Simias* a member of the genus *Nasalis*, he has suggested that the other three Mentawai primate species display primitive characteristics and are basal to Southeast Asian primate lineages. According to Brandon-Jones (1998), the primates of Sumatra went extinct during Pleistocene glaciations, and the Mentawai Islands may have provided a reservoir from which primates recolonized Sumatra during interglacials (Brandon-Jones, 1998). However, this scenario is not supported by more recent biogeographic analyses of *Presbytis* and genetic analyses of the Mentawai gibbon (*Hylobates klossii*) (Meijaard and Groves, 2004; Takacs et al., 2005; Whittaker, 2005).

To date, few behavioral or ecological studies have been conducted focusing on the simakobu monkey. The proboscis monkey was previously believed to be dependent on mangrove and coastal forests, while the simakobu is typically found in inland evergreen tropical rainforest. This habitat difference has led some researchers to conclude that these species are quite distinct ecologically and thus should be separated at the genus level (Napier, 1985; Oates et al., 1994). However, more recent data have shown that proboscis monkeys are more widely distributed than previously thought, occurring throughout Borneo (Meijaard and Nijman, 2000). The odd-nosed genera *Simias*, *Nasalis*, and *Pygathrix* seem to follow a similar adaptive strategy, including the exploitation of high-quality foods during part of the year with the ability to subsist on low-quality diets at

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other times (Bennett and Davies, 1994). These three genera also appear to have some flexibility in their social systems: in the simakobu monkey, social groups contain one male and either one or several females, plus their offspring (Fuentes and Tenaza, 1995; Tenaza and Fuentes, 1995; Watanabe, 1981), while proboscis monkeys are typically found in one-male multi-female groups, but with overlapping home ranges (Bennett and Sebastian, 1988). Neither the simakobu nor the proboscis monkey have been able to out-compete sympatric colobine species, in apparent contrast to members of the genus *Pygathrix* (Bennett and Davies, 1994). These ecological data suggest many similarities between *Simias* and *Nasalis*, though no firm conclusions can be drawn without further field studies of *Simias*.

We present here the results of the first molecular study to test hypotheses regarding the phylogenetic position and taxonomic status of the simakobu monkey.

2. Methods

Hairs were collected from a wild-caught infant simakobu pet in the village of Sikakap on North Pagai Island (Fig. 1) and stored dry in a tube. The monkey was likely caught in the Pagai Islands, but its origin could have been from another Mentawai Island.

Total genomic DNA was extracted from four hairs, using the Qiagen DNA Micro Kit and manufacturer-supplied protocols for hairs without roots. We amplified and sequenced 424 bp of mitochondrial DNA using universal cytochrome *b* primers (L14724, H15149) (Kocher et al., 1989). This region includes part of the tRNA^{thr} (24 bp) and cytochrome *b* genes (400 bp). Polymerase chain reaction (PCR) was performed in 50 µl reactions containing 4 µl of template DNA, 1 µM each of primers L14724 and H15149, 0.25 mM dNTPs, 2.0 mM MgCl$_2$, and 1.25 U AmpliTaq DNA polymerase (Applied Biosystems). The PCR was run in a GeneAmp PCR System 9700 (Applied Biosystems) thermocycler with the following conditions: initial 2 min at 94 °C; followed by 45 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 2 min, and extension at 72 °C for 3 min; with a final extension at 72 °C for 7 min. A negative control containing no DNA was included in addition to the six replications of the *Simias* sample.

The PCR products were electrophoresed on an agarose gel, stained with ethidium bromide, and digitally photographed under UV light. The PCR products were purified using the QIAquick PCR Purification Kit (Qiagen) according to the manufacturer's instructions. Cycle sequencing was performed in 10 µl volume reactions, containing 0.8 µl of the purified PCR product and 0.5 µl sequencing primer in a BigDye Terminator 3.1 Cycle Sequence reaction mixture (Applied Biosystems). Cycle sequence products were purified using the ethanol/EDTA/sodium acetate protocol specified by Applied Biosystems.

Sequencing was performed on an ABI 3730XL capillary sequencer. A consensus sequence from both strands and from six replications was generated using Sequencher 3.1. The *Simias* sequence has been submitted to GenBank (Accession No. DQ143883). Comparative sequence data from other cercopithecid genera were obtained from GenBank (Table 1), including *Papio* and *Macaca* as outgroups. The sequences downloaded from GenBank were compared
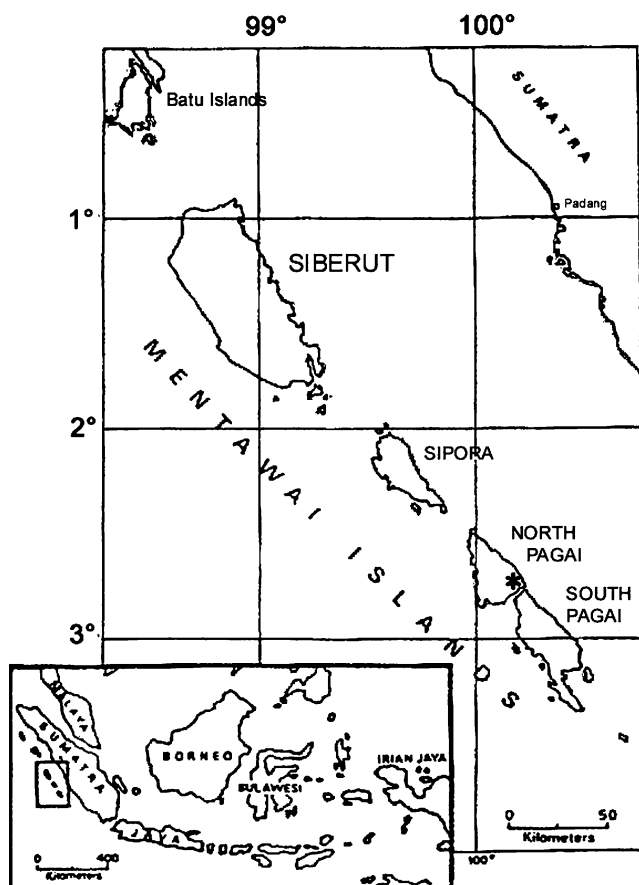

Fig. 1. Map showing location of the Mentawai Islands. Location of the village of Sikakap on North Pagai Island is indicated with an asterisk (*).

Table 1
List of samples used in study. Taxonomy follows Brandon-Jones et al. (2004)

Taxon	GenBank Acquisition Number
Simias concolor	DQ143883
Nasalis larvatus (2)	AF020418, U62663
Rhinopithecus roxellana	AF020416
Rhinopithecus avunculus	AF020415
Rhinopithecus bieti	AF020413
Pygathrix nemaeus	AF295582
Semnopithecus entellus	AF020417
Semnopithecus johnii	AF020419
Semnopithecus vetulus	AF020420
Trachypithecus francoisi	AF295578
Trachypithecus obscurus	AY863425
Colobus guereza	AY863427
Colobus angolensis	AF295583
Colobus polykomos	AF020411
Procolobus badius	AF295575
Papio hamadryas	Y18001
Macaca mulatta	NC005943

to those from unpublished mitochondrial genomes amplified in overlapping halves (Sterner et al., in press) to ensure that the analysis would not be affected by nuclear pseudogenes. The sequences were aligned using the program CLUSTALX (Jeanmougin et al., 1998).

To evaluate the relationship of *Simias* to the other colobine species, we used a Bayesian Markov Chain Monte Carlo simulation to estimate the most likely phylogenetic trees with Mr. Bayes 3.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Modeltest 3.6 (Posada and Crandall, 1998) was first run to estimate the nucleotide substitution rate and the frequency of transitions versus transversions, and these parameters were entered into Mr. Bayes. Pairwise distances (p) were generated in PAUP 4.0 (Swofford, 2002). To test whether colobine lineages are evolving in a manner consistent with a molecular clock, a relative rate test was performed using the program RRTree (Robinson-Rechavi and Huchon, 2000).

3. Results

A total of 424 bp of the cytochrome *b* and adjacent tRNA^{thr} genes were analyzed. Using the hierarchical likelihood ratio test, Modeltest 3.6 selected the Tamura-Nei (1993) model with rate variation among sites. This model assumes unequal base frequencies (observed from the data) and higher likelihood of transitions than transversions (Tamura and Nei, 1993). The parameters specify a substitution rate of 1.0 for transversions, 18.26 for A–G transitions, and 17.98 for C–T transitions. The among-site rate variation follows a gamma distribution with a shape parameter of 0.28. The Bayesian analysis was run with four chains for 500,000 generations, sampling every 100th generation, with a burn-in percentage of 25% or 1250 generations.

The phylogenetic tree produced by the Bayesian analysis (Fig. 2) strongly supports the sister taxon relationship of *Simias* and *Nasalis* with a credibility value of 100. This tree supports reciprocally monophyletic African and Asian colobine groups, as well as the monophyly of each genus for which multiple species were included. Within the Asian clade, *Semnopithecus* clusters with the odd-nosed colobines and away from *Trachypithecus* (Fig. 2A), a conclusion congruent with colobine phylogenies produced from whole mitochondrial genomes (Sterner et al., in press). An analysis of the mitochondrial ND3–ND4 region (Wang et al., 1997) further supports the separation of *Trachypithecus* from the other Asian colobines. However, in our analysis, this node has a low credibility value of 83, and collapsing this node as well as the *Rhinopithecus/Pygathrix/Semnopithecus* clade (with a credibility value of 88) results in an unresolved Asian colobine polytomy (Fig. 2B). Molecular pairwise distances (Table 2) also suggest a close relationship between the simakobu and the proboscis monkey. With the exception of *Simias* and *Nasalis*, all of the species that have a distance of about 10% or less are widely considered congeners. Pairwise distances between genera range from 10 to 25%. The molecular pairwise distance between *Simias* and *Nasalis* (about 6%) is comparable to that between congeneric species ($\leqslant 10\%$), rather than between genera (10–25%).

The relative rate test found no significant difference between the rates of change in Asian and African colobine lineages in relation to the cercopithecine outgroup taxa ($p > 0.83$), suggesting that the rate of change in these lineages is consistent with the expectations of a molecular clock.
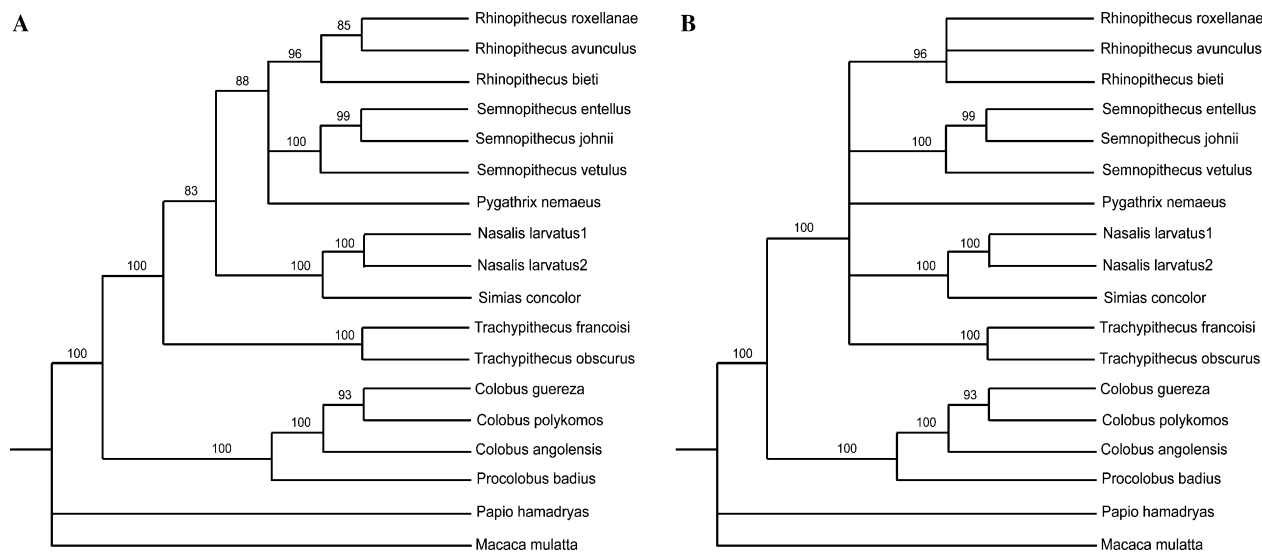

Fig. 2. Cladograms produced by Bayesian analysis. Numbers above the branches represent clade credibility scores. (A) The node supporting a *Rhinopithecus/Pygathrix/Semnopithecus* clade exclusive to *Nasalis/Simias* has low support, as does the node supporting a sister taxon relationship of *Trachypithecus* to the other Asian colobines. (B) Nodes with clade credibility values of less than 90 have been manually collapsed, resulting in an Asian colobine polytomy. Note that a close relationship between *Nasalis* and *Simias* is still supported.

Table 2
Molecular pairwise distance matrix derived from the cytochrome *b* data

Taxon	S. concolor	N. larvatus1	N. larvatus2	R. roxellana	R. avunculus	R. bieti	P. nemaeus	S. entellus	S. johnii	S. vetulus	T. francoisi	T. obscurus	C. guereza	C. angolensis	C. polykomos	P. badius	P. hamadryas	M. mulatta
S. concolor	—	**0.063**	**0.067**	0.148	0.176	0.157	0.161	0.186	0.195	0.170	0.160	0.167	0.215	0.219	0.230	0.225	0.213	0.252
N. larvatus1	**0.059**	—	**0.005**	0.159	0.165	0.178	0.211	0.202	0.184	0.179	0.153	0.155	0.256	0.252	0.261	0.247	0.210	0.236
N. larvatus2	**0.062**	**0.005**	—	0.166	0.182	0.182	0.213	0.199	0.192	0.183	0.161	0.163	0.257	0.263	0.259	0.249	0.219	0.245
R. roxellana	0.125	0.135	0.139	—	**0.060**	**0.050**	0.134	0.192	0.168	0.143	0.142	0.168	0.251	0.233	0.279	0.216	0.209	0.272
R. avunculus	0.144	0.139	0.151	**0.057**	—	**0.068**	0.167	0.212	0.194	0.169	0.165	0.185	0.275	0.281	0.292	0.225	0.202	0.279
R. bieti	0.132	0.149	0.151	**0.047**	**0.064**	—	0.143	0.183	0.161	0.156	0.167	0.182	0.250	0.214	0.280	0.222	0.211	0.278
P. nemaeus	0.136	0.170	0.172	0.116	0.141	0.124	—	0.246	0.214	0.205	0.192	0.186	0.202	0.212	0.207	0.253	0.225	0.234
S. entellus	0.156	0.168	0.166	0.158	0.173	0.154	0.195	—	**0.088**	**0.099**	0.214	0.198	0.236	0.275	0.245	0.201	0.251	0.231
S. johnii	0.161	0.154	0.158	0.142	0.161	0.137	0.175	**0.080**	—	**0.104**	0.196	0.180	0.218	0.243	0.231	0.209	0.217	0.229
S. vetulus	0.147	0.154	0.156	0.125	0.145	0.135	0.170	**0.090**	**0.095**	—	0.191	0.201	0.242	0.237	0.258	0.216	0.222	0.246
T. francoisi	0.136	0.133	0.139	0.123	0.140	0.140	0.161	0.174	0.162	0.160	—	**0.095**	0.170	0.192	0.179	0.215	0.219	0.216
T. obscurus	0.140	0.133	0.138	0.140	0.152	0.149	0.155	0.164	0.152	0.164	**0.086**	—	0.225	0.204	0.233	0.249	0.209	0.205
C. guereza	0.172	0.198	0.199	0.193	0.208	0.193	0.167	0.188	0.179	0.193	0.145	0.180	—	**0.067**	**0.010**	0.187	0.198	0.231
C. angolensis	0.173	0.195	0.201	0.181	0.208	0.171	0.172	0.210	0.193	0.190	0.158	0.165	**0.062**	—	**0.073**	0.198	0.191	0.232
C. polykomos	0.182	0.200	0.200	0.213	0.220	0.213	0.172	0.194	0.189	0.206	0.152	0.185	**0.010**	**0.068**	—	0.199	0.212	0.232
P. badius	0.179	0.193	0.194	0.174	0.181	0.178	0.199	0.168	0.173	0.178	0.175	0.192	0.155	0.162	0.165	—	0.227	0.284
P. hamadryas	0.174	0.174	0.180	0.171	0.169	0.174	0.185	0.200	0.178	0.183	0.178	0.173	0.166	0.160	0.176	0.185	—	0.170
M. mulatta	0.200	0.193	0.198	0.212	0.217	0.217	0.193	0.189	0.190	0.199	0.180	0.173	0.189	0.188	0.190	0.220	0.145	—

Figures below the diagonal are uncorrected (*p*) distances; figures above the diagonal are Tamura–Nei distances. Note that individuals differing less than 10% (shaded cells) are generally considered congenerics, with the exception of *Simias* and *Nasalis*.

4. Summary and discussion

An analysis of part of the mitochondrial cytochrome *b* gene strongly supports a sister taxon relationship between the simakobu and proboscis monkeys, and places this lineage within a monophyletic Asian colobine clade. This study is not inconsistent with the classification of the simakobu within the genus *Nasalis*, as suggested by earlier morphological analyses (Delson, 1975, 2000; Groves, 1970). Few studies have been conducted on the behavior and ecology of the simakobu, but some data indicate that *Simias* and *Nasalis* are following similar adaptive strategies (Bennett and Davies, 1994).

The hypothesis that *Simias* is a basal colobine (Jablonski, 1998) is not supported, nor is the corresponding suggestion for *Nasalis* (Groves, 1989). Recent genetic analyses of the Mentawai primates *H. klossii* and *Macaca pagensis* have consistently shown these species to be derived members of their respective clades with their closest relatives on nearby Sumatra (Roos et al., 2003; Takacs et al., 2005; Whittaker, 2005), and not primitive or ancestral as has sometimes been suggested. The phylogenetic tree presented here shows well-supported monophyletic Asian and African clades, but provides little resolution otherwise. *Nasalis* and *Simias* form a clade, but relationships among most of the Asian colobine genera appear as an unresolved polytomy. Further research is necessary to understand the phylogenetic and biogeographic history of the Asian colobines.

Currently, two subspecies are defined for *S. concolor* based on differences in pelage coloration: *S. concolor siberu* on the northernmost island of Siberut and *S. c. concolor* on the three southern islands. The same pattern is described in *P. potenziani* and *M. pagensis*, though not for *H. klossii* (Whittaker, 2005). Preliminary genetic analysis of *M. pagensis* suggests a paraphyletic origin (Roos et al., 2003). Future studies need to examine intraspecific patterns of divergence in Mentawai primates.

The simakobu monkey is among the least understood, but most endangered, of all the Asian primates. The IUCN Red List currently lists this species as "Endangered," under criteria A1cd+2c (IUCN, 2004). However, a recent reassessment of the available evidence suggests that the status of *S. concolor* should be upgraded to "Critically Endangered" based on criteria A2cd (Whittaker, 2005). The simakobu is also included in Conservation International's list of the 25 Most Endangered Primates (Mittermeier et al., 2002). Taxonomic uniqueness is sometimes used as a criterion for setting conservation priorities (Olson and Dinerstein, 1998). Should the simakobu monkey be reclassified as a member of the genus *Nasalis*, its conservation priority (or that of the Mentawai Islands as a whole) may be affected based on such methods. We believe that taxonomy should reflect phylogeny, and we do not mean to imply that this unique primate, or any of the Mentawai primates, requires any less attention or conservation action.

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