Articles

MITOCHONDRIAL DNA SEQUENCES AND THE TAXONOMIC STATUS OF *ALOUATTA SENICULUS* POPULATIONS IN NORTHEASTERN AMAZONIA

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Introduction

Red howlers (*Alouatta seniculus*) are found throughout most of the Amazon basin north of the Amazon and west of the Rios Madeira and Aripuanã, north as far as southern Panama. They occur in many types of habitat, ranging from rain forest to scrub and savanna woodland (Hill, 1962; Crockett and Eisenberg, 1987; Pope, 1992; Ferrari *et al.*, 1996). This widespread distribution and ecological flexibility is typical of a colonizing or pioneer species (Eisenberg, 1981; Crockett and Eisenberg, 1987).

The last taxonomic revision of *Alouatta seniculus* was that of Hill (1962), whose classification included nine subspecies (Fig. 1). It is still widely accepted, although recent genetic and morphological studies have begun to question its validity. In general, these studies have indicated that *Alouatta seniculus* is a complex species group rather than a single species, and that a number of Hill's subspecies are in fact true species (e.g., Minezawa *et al.*, 1985; Groves, 1993; Bonvicino *et al.*, 1995; Stanyon *et al.*, 1995).

Hill (1962) identified the red howler populations occurring between the Atlantic Ocean, to the east, and the Rios Branco and Negro, to the west, as possibly belonging to a single subspecies, *Alouatta seniculus macconnelli* Elliot, 1910; type locality - the Guyana coast. According to Hill (1962), *A. s. macconnelli* is distinguished from the other *A. seniculus* subspecies by the uniform coloration of the dorsal parts of pelage, and its orange-red underparts (Hill, 1962). He doubted, however, that it is separable from the form to the west of the Rios Negro and Branco, *A. s. stramineus* (Humboldt, 1812). Cruz Lima (1945), Cabrera (1957) and Husson (1978) all regarded *A. s. macconnelli* to be a junior synonym of *A. s. stramineus*. However, based on their cytogenetic research, Lima *et al.* (1990) argued that the red howler from the east of the Rio Trombetas was a distinct form, and attributed to *A. s. macconnelli* by Lima and Seuánez (1991). Bonvicino *et al.* (1995) identified two distinct howler species separated by the Rio Trombetas, which they referred to as *Alouatta macconnelli* (to the east) and *Alouatta straminea* (to the west), on the basis of a multivariate analysis of cranial traits. Conversely, cytogenetic and biochemical studies of these populations have also indicated that they are relatively homogeneous, consistent with the hypothesis that they belong to a single species (Sampaio *et al.*, 1996).

In recent years, mitochondrial DNA sequencing has been used extensively in phylogenetic studies of closely-related species (in the case of New World monkeys, for example: Ashley and Vaughn, 1995; Peres *et al.*, 1996; Tagliaro *et al.*, 1997). In this paper, we use sequences of the mitochondrial cytochrome oxidase subunit II (COII) gene to assess phylogenetic and taxonomic relationships among populations of red howlers from the Rios Uatumã, Trombetas and Jarí, encompassing the geographic distribution of the two species proposed by Bonvicino *et al.* (1995). We chose the COII gene sequences because, as noted in a number of publications on primates (for example, Ruvolo *et al.*, 1993; Ashley and Vaughn, 1995),

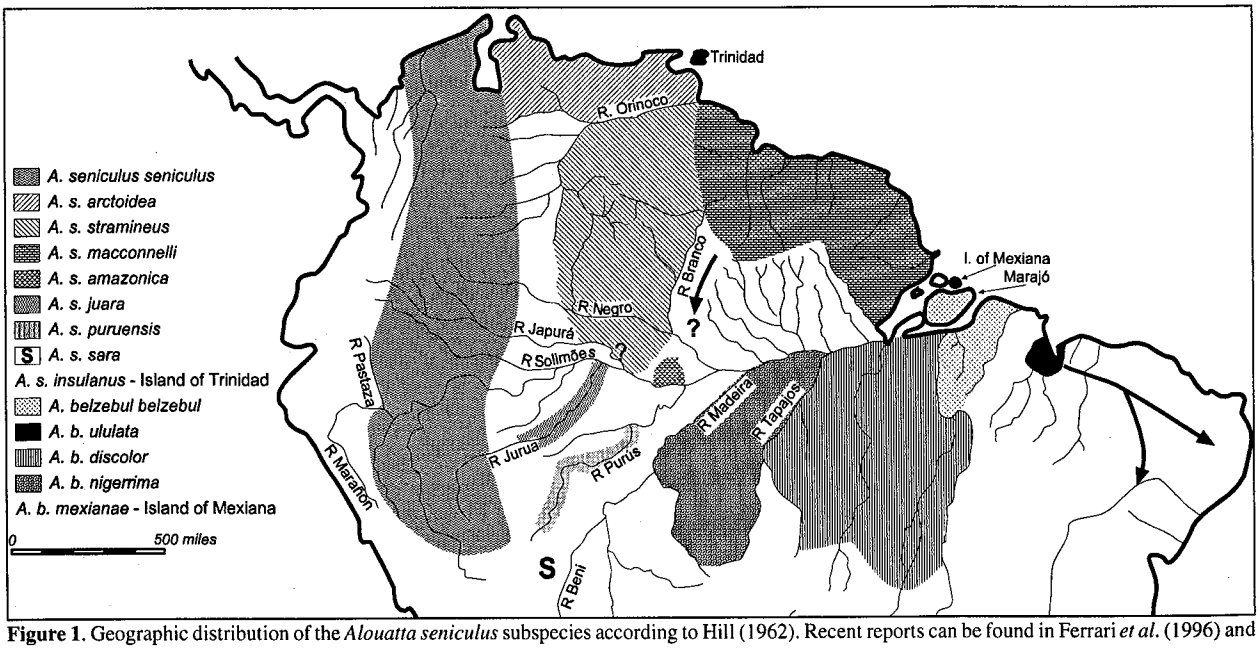

Figure 1. Geographic distribution of the *Alouatta seniculus* subspecies according to Hill (1962). Recent reports can be found in Ferrari *et al.* (1996) and Fernandes *et al.* (1995).

Cover photograph by Marc G. M. van Roosmalen: The black-crowned dwarf marmoset, *Callithrix humilis*.

Table 1: Code and collecting localities of the specimens used in the present study.

Code	Taxon	Origin
Ase JMR1	*Alouatta seniculus*	Rio Jari, Right Bank
Ase JMR2	*Alouatta seniculus*	Rio Jari, Right Bank
Ase JML1	*Alouatta seniculus*	Rio Jari, Left Bank
Ase UMR1	*Alouatta seniculus*	Rio Uatumã, Right Bank
Ase UMR2	*Alouatta seniculus*	Rio Uatumã, Right Bank
Ase UML1	*Alouatta seniculus*	Rio Uatumã, Left Bank
Ase UML2	*Alouatta seniculus*	Rio Uatumã, Left Bank
Ase UML3	*Alouatta seniculus*	Rio Uatumã, Left Bank
Ase TML1	*Alouatta seniculus*	Rio Trombetas, Left Bank
Ase TMR1	*Alouatta seniculus*	Rio Trombetas, Right Bank
Ase TMR2	*Alouatta seniculus*	Rio Trombetas, Right Bank
A. paniscus 1	*Ateles paniscus*	Rio Trombetas, Right Bank
A. paniscus 2	*Ateles paniscus*	Rio Trombetas, Right Bank

their marked variability makes them appropriate for phylogenetic studies at the specific level.

Materials and Methods

Laboratory Procedures

Blood samples were obtained from howling monkeys captured on both banks of the Rios Uatumã, Trombetas and Jari, northern tributaries of the Rio Amazonas (see Table 1), and from two spider monkeys (*Ateles paniscus*). DNA was extracted following the protocol suggested by Sambrook *et al.* (1989).

COII genes from the mtDNA of these samples were amplified using PCR (Polymerase Chain Reaction). Oligonucleotide primers were designed based on the published COII sequence of *Alouatta palliata* (Adkins and Honeycutt, 1994): primer 1, 5'C C A G C C C A A C T A G G C T T A 3', and primer 2, 5'G G C T C A T A C T T C A A A G T C T T G G 3'. The samples were subjected to 30 cycles of amplification, under the following conditions: denaturation - 94°C, 1 min; annealing -50°C, 45 sec.; extension - 72°C, 1 min., 30 sec.; final extension - 72°C, 10 min. The amplified DNA fragments were purified, cloned in p-GEM T vectors and competent cells, and single stranded DNA was obtained through infection with Helper Phage. The sequencing reactions were carried out using the dideoxy chain termination method (Sanger *et al.*, 1977).

Sequence Analysis

The sequences were aligned in relation to that published by Adkins and Honeycutt (1994) for *Alouatta palliata*, using the XESEE sequence editor (Cabot and Beckenbach, 1989). Pairwise divergence values were estimated by Kimura's 2 parameter method (Kimura, 1980) and used to compute a phylogenetic tree by the neighbor-joining method (Saitou and Nei, 1987) using the *Ateles paniscus* sequences as the outgroup. The most parsimonious tree was estimated using the DNAPARS program of Felsenstein's (1993) PHYLIP package. Bootstrap analyses of the topologies produced by these methods were conducted in order to evaluate their consistency, and "strength of grouping" values (the minimum number of additional substitutions required to break up the group defined by each node) were obtained with the SOG program (J. Czelusniak, pers. comm.).

Results

Data Analysis

The COII nucleotide sequences are deposited at the GENBANK database under the accession numbers AF054291-AF54302. One hundred and fifteen of the 620 base pairs examined were variable, and eighty-six of these were informative for parsimony analysis. Sequence variation is very low between the *A. seniculus* samples, although only two samples - Ase UMR1 and Ase UML2 - were identical. Of the eighteen variable sites in this species, thirteeen were apomorphic mutations, leaving only five informative sites. Pairwise comparisons between red howler samples revealed similar differences between haplotypes to those found in the same gene in humans. The maximum number of nucleotide substitutions in the *A. seniculus* sequences is six, the same number found in human COII sequences (Ruvolo *et al.*, 1993).

Phylogenetic Reconstruction

Genetic distances between the *A. seniculus* samples are very low, ranging from zero to 1.15%. Distances between populations are similar to those observed within populations, and some individuals from different localities are less divergent than some individuals from the same population. Genetic distances between *A. seniculus* and *A. palliata* range from 7.94% to 8.38%, while those between

Table 2: Estimated percentage of nucleotide divergence among pairwise COII sequences.

		1	2	3	4	5	6	7	8	9	10	11	12
1	*A. palliata*	-											
2	*Ase* JML1	8.38	-										
3	*Ase* JMR1	8.17	**0.49**	-									
4	*Ase* JML2	8.35	**0.65**	**0.49**	-								
5	*Ase* UMR1	7.98	**0.65**	**0.49**	**0.65**	-							
6	*Ase* UMR2	8.17	**0.82**	**0.65**	**0.81**	**0.16**	-						
7	*Ase* UML1	8.18	**0.49**	**0.33**	**0.49**	**0.49**	**0.65**	-					
8	*Ase* UML3	8.18	**0.82**	**0.98**	**1.15**	**0.49**	**0.65**	**0.98**	-				
9	*Ase* TML1	8.20	**1.15**	**0.98**	**1.15**	**0.82**	**0.98**	**0.98**	**0.98**	-			
10	*Ase* TML2	7.94	**1.07**	**0.89**	**1.07**	**0.71**	**0.89**	**0.89**	**1.07**	**0.71**	-		
11	*Ase* TMR1	8.35	**0.65**	**0.49**	**0.65**	**0.65**	**0.81**	**0.49**	**1.15**	**1.15**	**1.07**	-	
12	*A. paniscus* 1	14.19	16.68	16.39	16.61	15.74	15.96	16.20	15.99	16.46	16.37	16.61	-
13	*A. paniscus* 2	14.03	16.30	16.02	16.24	15.37	15.58	15.83	15.83	16.30	16.10	16.24	0.16

Note. Divergence values were corrected for multiple hits by the method of Kimura (1980). The pairwise comparisons among *A. seniculus* sequences are highlighted in bold.

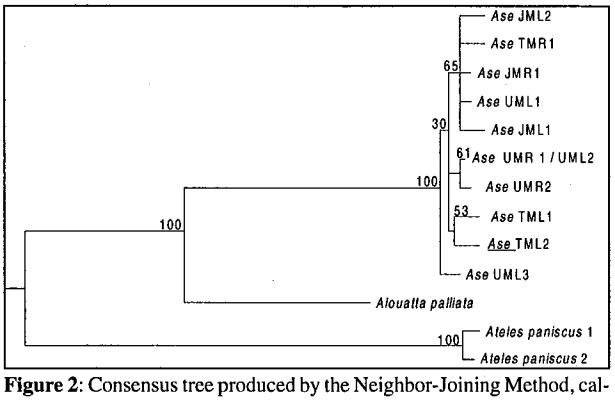

Figure 2: Consensus tree produced by the Neighbor-Joining Method, calculated with the distances corrected with the algorithm of Kimura (1980). Numbers refer to bootstrap values from 500 replications. Branch lengths are proportional to evolutionary distances between taxa.

howlers and spider monkeys are of the order of 15% (Table 2).

The tree constructed using the neighbor-joining (NJ) method (Fig. 2), grouped all *A. seniculus* samples in a single branch, separated significantly from both *Alouatta palliata* and the outgroup (*Ateles paniscus*). The topology of this branch is not coherent with the geographic distribution of the different samples, however. The bootstrap values at the node separating *Ateles* from the *Alouatta* samples, and the node separating *Alouatta palliata* from the red howlers are highly significant (100%), but all the relationships between different *Alouatta seniculus* samples are only weakly supported.

The parsimony analysis produced three most-parsimonious trees, 125 steps long (consistency index: 0.976). Figure 3 presents the 50%-majority consensus among these trees. The results obtained with the maximum parsimony (MP) method are similar to those found with NJ, with the same basic topology and similar confidence values, and with regard to the relationships of *Alouatta palliata* and *Ateles paniscus*, and the relationhsips between these and the *Alouatta seniculus* sequences. The number of substitutions needed to break up the Alouattini clade is 53 and

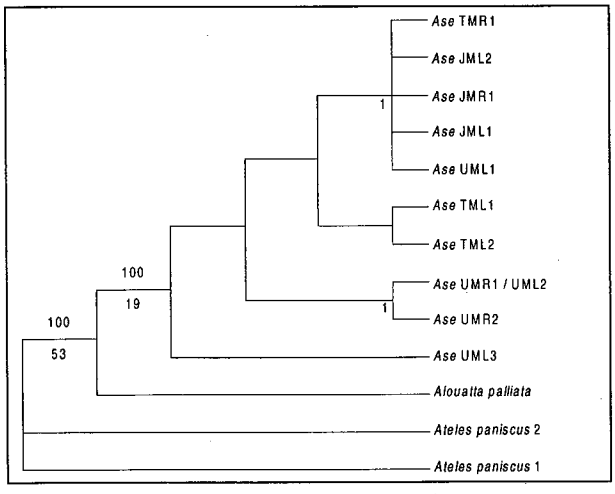

Figure 3: Fifty percent majority-rule maximum parsimony consensus tree. Numbers above branches represent bootstrap values from 500 replications. Numbers below branches are SOG values, the number of additional steps before a particular group collapses.

the grouping formed by the red howler clade is 19. However, the consensus topology supports only two groupings in the *Alouatta seniculus* clade: that between Ase UMR1/ UML2 and Ase UMR2 (supported by a single mutation), and a polytomic clade composed of the three specimens from Jari, one from Uatumã and one from Trombetas. Indeed, no synapomorphies are restricted to a single population and therefore cannot be used as genetic markers for phylogenetic distinction.

Discussion

The data presented here reveal a strong genetic homogeneity among the populations. The low number of nucleotide differences, phylogenetic continuity (tree topology), and the complete absence of any geographic partitioning of the sequences are interpreted as lending further support to the classification of the populations as belonging to a single species. According to Avise *et al.* (1987), geographic populations which exhibit the levels of sequence variability found here have had relatively extensive and recent historical interconnections through gene flow. Interestingly, the pattern of variability observed is typical of species that are both able to cross zoogeographic barriers and disperse widely (Avise *et al.*, 1987; Avise, 1994). *Alouatta seniculus* is not only one of the ecologically most flexible of Amazonian primates (Eisenberg, 1981; Crockett and Eisenberg, 1987), but is also able to disperse across major rivers, in marked contrast with most other taxa (Ayres and Clutton-Brock, 1992; Fernandes *et al.*, 1995).

Biochemical and Karyological Data

The populations analyzed here were included in the protein electrophoresis study of Sampaio *et al.* (1996). The study revealed that *A. seniculus* exhibits the highest degree of genetic variability of any neotropical primate, with an average heterozygosity (*H*) of 10%. A similar degree of heterozygosity (H = 9.9%) was encountered in *A. seniculus* populations from Venezuela (Pope, 1992). The genetic variability detected in the three populations studied here was nevertheless fairly homogeneous, and genetic distances were very similar, ranging from zero to 0.2% (Sampaio *et al.*, 1996).

The karyological data also corroborate the close similarity of these populations. *A. seniculus* from Uatumã and Jari have the same diploid number (47, 48, 49), and share similar sex chromosome structure ($X_1X_2Y_1Y_2/X_1X_1X_2X_2$). The Uatumã population, however, presents a reciprocal homozygote translocation between chromosomes 2 and 20 (Lima *et al.*, 1990; Lima and Seuánez, 1991). This chromosome translocation was interpreted by Bonvicino *et al.* (1995) to support the classification of these populations as distinct species. Interestingly, recent cytogenetic data from howler monkey specimens living on both banks of the Rio Trombetas reveal that these two populations show the same cytotypes as those found on the Uatumã (M. Lima, unpublished data). From the cytogenetic viewpoint, then, the Rio Trombetas is not a significant zoogeographic barrier for these red howler populations, as

proposed by Bonvicino *et al.* (1995).

The sum of the evidence strongly supports the existence of only a single species within the geographic area considered here. The homogeneity of the biochemical data clearly indicates continuous gene flow between the populations studied. While the chromosome translocations found in the Uatumã and Trombetas populations may constitute a reproductive barrier, further studies would be required to confirm this. Our mtDNA data are unable to discriminate these populations at any level, and indicate that any divergence between them occurred very recently. Further studies will be required in order to assess the taxonomic significance of the morphological and cytogenetic variations encountered in this area, interpreted as clinal variation by R. Gregorin (pers. comm.), on the basis of cranial measurements and pelage coloration.

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The Evolutionary History of Platyrrhines: Old Controversies and New Interpretations

Marcelo F. Tejedor

The living New World monkeys, Infraorder Platyrrhini, are represented by sixteen genera in subfamilies and families which even today are disputed (Cabrera, 1958; Hershkovitz, 1977; Rosenberger, 1981; Thorington and Anderson, 1984; Ford, 1986; Schneider *et al.*, 1995; Tejedor, 1996a). Their interrelationships have been the subject of considerable debate mainly because of the morphological diversity and the scarcity and fragmentary nature of the fossil record, that should otherwise contribute to constructing phylogenies. However, in recent years, new fossil discoveries and intensive studies of the existing evidence has led to considerable advances in our understanding of the platyrrhine radiation. South American fossil platyrrhines are known from several localities of the late Oligocene through Recent, at sites in Argentina, Bolivia, Chile, Colombia, Brazil, Cuba, Jamaica and Hispaniola. There are considerable gaps in the record between the middle Miocene (Colloncuran Land Mammal Age - LMA) and late Miocene (Huayquerian LMA), but subsequently the absence of fossil platyrrhines is notable until the Pleistocene of Brazil and the Caribbean islands. Although we now know more about the diversity of platyrrhines in the past, the record still consists of a limited number of specimens representing more than 20 extinct genera during the last 26 million years. Table 1 shows the temporal and geographic relationships between the known fossil species as well as the available sources.

The phyletic and geographic sources of platyrrhines are still a matter of speculation, but the oldest "pre-catarrhine" and "pre-platyrrhine" anthropoids are known from Africa and Asia. Therefore, platyrrhines, as anthropoids, should find their ancestral stock in Africa or Asia based on the current evidence. Dental evidence from these potential ancestors strongly favor the morphology found in the Santacrucian genera *Carlocebus* and *Homunculus* and in the living *Callicebus* as closest to the ancestral morphotype for the infraorder, for several reasons exposed elsewhere (Hartwig, 1993; Tejedor, 1997). Controversy persists because the oldest South American records, *Szalatavus* and *Branisella,* came from Bolivia and differ considerably from *Callicebus, Homunculus* and *Carlocebus,* being probably ancient representatives of the Callitrichinae (see Takai and Anaya, 1996). On other other hand, the subsequent *Chilecebus*, from the Chilean Andes (late Deseadan-Colhuehuapian LMA), shows several primitive characters not easily comparable to other fossil forms. Of course, this means that the earliest platyrrhines should have been considerably younger than the oldest Deseadan records of 26 Ma (million years ago) in Bolivia (Kay *et al.*, 1995). The absence of significant derived characters as compelling evidence for assessing early platyrrhine relationships is another unresolved problem. The similarities between *Callicebus, Homunculus* and *Carlocebus* are based largely on superficial resemblances and shared primitive characters (Tejedor, 1996b) which do not justify a phylogenetic link. But these symplesiomorphies strengthen the arguments in favor of a close common origin for the three latter genera. This would not appear to be a convincing solution, but it is also unusual to find several primitive characters shared by three genera of fossil platyrrhines together.

Soriacebus is, to date, the earliest relative of the Pitheciinae (Rosenberger *et al.*, 1990, but see Kay, 1990 for an alternative view). It is possible to argue that the lower molar structure of *Soriacebus* does not characterize the living pitheciines, but the lower premolar structures of *Cebupithecia* and *Nuciruptor* also differ from that of extant pitheciines (Meldrum and Kay, 1997), even though they are undoubtedly pitheciines. In this case, it is interesting to remember that specializations of the anterior dentition in the Pitheciinae possibly preceded those of premolars and molars, being, as Kinzey (1992) suggested, an adaptive response for sclerocarpic foraging. The shared