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Aotus Diversity and the Species Problem

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Abstract: Karyotypic variability in *Aotus* suggests at least seven species in the gray-necked group (*A. brumbacki*, *A. griseimembra*, *A. lemurinus*, *A. trivirgatus*, *A. vociferans*, *A. zonalis*, and *Aotus* sp. nov.) based on six known karyomorphs, highly divergent mitochondrial cytochrome c oxidase sequences, different sensitivities to malaria, varied mitogenic and immunological responses to other diseases, and well-defined geographical distributions, and the likelihood that these species are distinctive enough to possess reproductive barriers. We discuss these karyomorphs and explain why *A. brumbacki* cannot be an *A. lemurinus* subspecies. We briefly describe a karyotype for *Aotus* from Maipures on the Río Orinoco and suggest that this represents *A. brumbacki*, extending our knowledge of that species' distribution to the Orinoco basin. We stress the presence of a new undescribed *Aotus* in Colombia from a completely unknown location, which we name *Aotus jorgehernandezii* in honor of Jorge I. Hernández-Camacho. We discuss the meaning and evolution of chromosome variability, the nature of *Aotus* as a sibling species complex and the use of the phylogenetic versus biological species concepts in primatology.

Key Words: Primates, Aotidae, *Aotus*, night monkeys, *Aotus jorgehernandezii* new species, karyotypes, Colombia

Resúmen: Las variaciones cariológicas encontradas en *Aotus* sugieren la presencia de al menos siete especies dentro del grupo de cuello gris (*A. brumbacki*, *A. griseimembra*, *A. lemurinus*, *A. trivirgatus*, *A. vociferans*, *A. zonalis* y *Aotus* sp. nov.), teniendo en cuenta los seis cariomorfos descritos, la alta divergencia en las secuencias del citocromo C oxidasa, las diferencias en las respuestas inmunológicas (a mitógenos, susceptibilidad a malaria y otras enfermedades), el aislamiento geográfico, aspectos que en conjunto sugieren la presencia de barreras reproductivas entre ellas. Basándonos en las diferencias cariológicas, se sostiene que *A. brumbacki* no puede ser una subespecie de *A. lemurinus*. Se describe el cariotipo encontrado en un ejemplar procedente de Maipures, en el Río Orinoco, con lo cual se sugiere que la distribución de *A. brumbacki* se extiende hasta el Orinoco. Se propone el nombre de *Aotus jorgehernandezii* para una nueva especie con $2N = 50$ en honor a Jorge I. Hernández-Camacho. Se discute el uso del concepto de especie filético y especie biológica, la naturaleza de los *Aotus* como un complejo de especies gemelos del género *Aotus* y el significado de la variación cromosómica en la evolución del género.

Pabras Claves: Primates, Aotidae, *Aotus*, micos nocturnos, monos nocturnos, mico de noche, mono de noche, *Aotus jorgehernandezii* especie nueva, cariotipos, Colombia

Introduction

This paper provides evidence suggesting the existence of at least seven gray-necked *Aotus* species, which we believe is well-founded due to known distinctive karyomorphs, different sensitivities to malaria, varied mitogenic and immunological responses to other diseases, and well-defined geographical distributions for most of these species. We also discuss the role of phenotypic evidence in distinguishing taxa and the possible evolutionary implications of chromosome variability

in mammals, Neotropical primates, *Aotus*, the meaning of the biological species concept for these *Aotus*, what karyotypes suggest to us about reproductive isolation, and the importance of karyological evidence.

Since the discovery of chromosome variability in *Aotus* it has become clear that there was more than one species in the genus (Ma 1981a, 1981b; Ma *et al.* 1976a, 1976b, 1977, 1978, 1980, 1981a, 1981b; Brumback 1973, 1974, 1976; Brumback and Willenborg 1973; Brumback *et al.* 1971; Hershkovitz 1983; Pieczarka *et al.* 1988, 1992; Defler *et al.* 2001). The

first attempt at proposing multi-species nomenclature, based on most of the available morphological and karyological evidence at the time, proposed nine species, consisting of five southern species (*A. azarae*, *A. miconax*, *A. nancymai*, *A. boliviensis*, and *A. nigriceps*) in a “red-necked group”, located mostly south of the Río Amazonas-Solimões, and four northern species (*A. brumbacki*, *A. lemurinus*, *A. trivirgatus*, and *A. vociferans*) in a “gray-necked group”, located north of the Río Amazonas and dividing *A. lemurinus* into two subspecies, *A. lemurinus lemurinus* and *A. lemurinus griseimembra*, and omitting the taxon *A. lemurinus zonalis* (v. Hershkovitz, 1983). After consulting with Hershkovitz, Ramírez-C. (1983) included *A. hershkovitzi* as an additional fifth northern species based on an inadequate description and considering particularly its diagnostic diploid number of 58 and fundamental number of 76, the highest known for the genus. Before Hershkovitz published his scheme in 1983, Thorington and Vorek (1976) had criticized the establishment of subspecies for the genus on the grounds that it would complicate the recognition of discrete populations and mosaic evolution, and that there did not seem to be species-wide phenotypes. We discuss this further below.

Giraldo *et al.* (1986) examined 288 Colombian *Aotus*, and found that those from the lower Río San Jorge (Bolívar Department, northern Colombia) with $2n = 52$, $2n = 53$ and $2n = 54$ (*Aotus l. griseimembra*) were a balanced polymorphism with no influence on reproduction among the three karyotypes. Observed frequencies of karyotypes were 13% ($2n = 52$), 47.6% ($2n = 53$), and 39% ($2n = 54$). Night monkeys captured in the middle Río Magdalena valley had no karyotypic differences from those of the north, confirming that this taxon extends right up the Magdalena valley. The author identified the $2n = 58$ (*A. hershkovitzi*) karyotype as something quite different from *A. lemurinus* or any other known *Aotus* and assigned it to karyotype X (*sensu* Ma 1981).

Ford (1994) did a morphometric study using data generated by Thorington and Vorek (1976) from 193 *Aotus* skulls and from her own data on pelage characteristics of 105 adult *Aotus* skins. She found mixed phenotypic variation across almost the entire range of *Aotus*. *Aotus trivirgatus* (all *sensu* Hershkovitz, 1983) was morphologically distinguishable from the other *A. vociferans*, *A. brumbacki*, and *A. lemurinus*, even though no measurable morphometric differences were found amongst the last three from the northern *Aotus* group. Ford's interpretation was that the three indistinguishable (phenotypically) species actually belonged to one clinal species, *Aotus vociferans*, that can be phenotypically distinguished from *A. trivirgatus*, suggesting only two species of gray-necked species north of the Amazon river rather than the four species distinguished by Hershkovitz (1983).

Torres *et al.* (1998) organized the known Colombian gray-necked *Aotus* polymorphs into five karyomorphs (*sensu* Reumer and De Boer 1980), referring to the cytogenetic characterization of five different populations). Thus, different karyomorphs are from different populations and show cytogenetic differences which probably are barriers to reproduction.

Karyomorphs were associated with *Aotus lemurinus griseimembra*, *Aotus brumbacki*, *Aotus vociferans*, *Aotus hershkovitzi*, and *Aotus* (Quindío specimen), an animal that they placed in a new karyomorph X, and that Torres *et al.* (1998) had found from a captive animal (in Quindío Department). Torres *et al.* (1988) also included *A. nancymai* as specimens that were obtained from “Leticia”, but Defler (2004: pp.91–92, p.274) comments on the probably fallacious inclusion of *Aotus nancymai* as part of the Colombian fauna below.

Rylands *et al.* (2000) and Groves (2001) freshly examined some of the evidence at hand and decided to accept the Hershkovitz (1983) scheme, modifying it by relegating *A. brumbacki* to a subspecies of *A. lemurinus* and accepting both *A. lemurinus zonalis* as discussed by Hernández-Camacho and Cooper (1976) and the subsequently described *Aotus hershkovitzi*. *A. brumbacki* was included in *A. lemurinus* because its pelage characters “span the gap between the two subspecies” [*A. lemurinus lemurinus* and *A. lemurinus griseimembra sensu* Hershkovitz, 1983] (Groves, 2001: p.164) without consideration of the substantial karyotypic differences.

Defler *et al.* (2001) analyzed the known facts for northern Colombian *Aotus* with the intention of describing *A. hershkovitzi* adequately, including a detailed karyological analysis. From our analysis it became clear that the karyotypes used by Hershkovitz (1983) to represent *Aotus lemurinus lemurinus* were in fact karyotypes for *A. lemurinus zonalis*, a separate lowland taxon, and that the karyotype for *A. hershkovitzi* represented the true autochthonous highland *A. lemurinus lemurinus*. The analysis also brought into question the karyotype published for *A. lemurinus griseimembra*, since the karyotypes analyzed by Ma were (according to Hershkovitz) from lowland populations of *Aotus* from northern Colombia and perhaps west of the Río Magdalena, given that most *Aotus* entered the Baranquilla animal trade from Magangué in the Department of Bolívar in central Colombia (Cooper and Hernández-Camacho 1977; Defler *et al.* 2001: p.41). The type locality of *Aotus lemurinus griseimembra* is the slopes of the Serranía de Santa Marta east of the Río Magdalena at 1,480 ft above sea level; it could very well represent a separate taxon from that of the lowlands (Hershkovitz 1983; Defler *et al.* 2001), and this is suggested by the dark-haired hands and feet of the holotype, which does not concord with the lighter brown hairs of the hands and feet of lowland specimens ascribed to *A. l. griseimembra*.

Further consideration of the karyotypes and of the putative subspecies of *A. lemurinus* led Defler *et al.* (2001) to believe that these were probably good biological species with reproductive barriers, due to chromosomal differences, which seemed to us to be sufficiently distinct to prevent successful pairing of enough alleles to allow development of fertile adult hybrids. This would allow the known gray-necked *Aotus* to be identified as follows: *Aotus brumbacki*, *A. griseimembra*, *A. lemurinus*, *A. trivirgatus*, *A. vociferans*, *A. zonalis* and *Aotus* new species (the “Quindío specimen”).

Evidence that also contradicts Ford's (1994) reduction of northern *Aotus* to two species is the discovery of highly

divergent mitochondrial cytochrome c oxidase (COII) within the genus (Ashley and Vaughn 1995). Unpublished work by Suarez *et al.* (undated) suggests that the taxa *A. griseimembra*, *A. vociferans*, *A. azarae*, *A. nigriceps*, and *A. griseimembra* are distinct from each other and that the *Aotus* radiation dates back at least 4–8 million years.

Many *Aotus* hybrids have been produced in captivity (Cicmanec *et al.* 1977; Rieckman *et al.* undated; Simpson and Jones 1982; Hershkovitz 1983; King 1995: pp.164–168), but most of them are produced from populations having similar chromosomes, especially in polymorphic populations. We deduce from laboratory attempts mentioned in the literature and from normal inferred chromosome pairing that a hybrid will be sterile in the F_1 if there is more than one rearrangement between karyotypes, as they produce sterile hybrids where the meiotic products become arrested in development, as in *Aotus*. For example, the five karyomorphs of African dik-dik antelope (*Madoqua*) produce sterile hybrids (Ryder *et al.* 1989), because the meiotic products become totally arrested in development. Interestingly, dik-diks, like *Aotus*, constitute monogamous breeding pairs which are philopatrically site-specific. Many workers believe that sterility can be induced by chromosome rearrangements which form post-mating isolating mechanisms (King 1995: pp.72–91).

Intra- and Inter-Population Chromosome Variability

Complicating interpretation of chromosome variations is the fact that there are both intra- and inter-population chromosomal differences. Thus, “considerable confusion has arisen because a large number of different karyotypes have been reported without a clear distinction between intrapopulation and interpopulation variation” (Martin 1990: p.577), there being no selection against heterozygosity in “*griseimembra*” night monkeys with diploid numbers of 54, 53 and 52. A similar situation would appear to be true for “*vociferans*” animals with diploid numbers of 46, 47 and 48 (Descailleux *et al.* 1990) and perhaps for “*zonalis*” with the polymorphisms 55 and 56 (in this species $2n = 54$ is theoretically possible but has not yet been observed). These three taxa appear to maintain their karyological identity with multiple chromosome differences. Nevertheless, a superficial perusal of the range of diploid numbers, their fundamental numbers, and their particular chromosome arrangements suggest that there would probably be no successful interbreeding among the three putative subspecies of *A. lemurinus*, nor between any of them and *A. brumbacki*, nor between *A. vociferans* and populations of *A. brumbacki* or *A. lemurinus*. Karyological differences then would establish interbreeding barriers and thus maintain these populations as species, if we are to maintain a biological species concept. But using all characters, including chromosomes, these species also fall into the phylogenetic species concept, as well (see following discussion).

Are phenotypes diagnostic?

Twenty-five years after the polyspecific nature of *Aotus* was first pointed out via chromosome differences, we are still attempting to classify night monkeys using phenotypic characters alone, often ignoring frequently striking chromosome differences. Several species have been recognized and described only through their karyotypes, since the genus actually forms a sibling species complex (Defler 2003, 2004). Being nocturnal there is very little selection for phenotypic differences, although two influential biologists, Philip Hershkovitz and Jorge Hernández-Camacho, have sustained that all *Aotus* species are phenotypically distinguishable (Hershkovitz 1949, 1983; Hernández-Camacho and Cooper 1976).

The modern generation of taxonomists have problems in distinguishing the various taxa. One analysis even pointed out the overlapping (“clinal”) nature of many characteristics in some *Aotus* groups, disqualifying them as capable of distinguishing species (Ford 1994). Species of sibling species groups are by their nature very difficult to tell apart phenotypically, although close analysis usually discovers something helpful (Mayr 1969; Bickham 1983). We are in agreement with Thorington and Vorek (1978), who argued that the subtle differences which do obtain are made up of overlapping mosaics, clines and interpopulation and intergroup variations. Some populations may be distinctive, but it seems questionable to us that all or many will have good diagnostic phenotypic characteristics, even though both Hernández-Camacho and Cooper (1976) and Hershkovitz (1983) argued to the contrary.

Hershkovitz (1983) argued that subspecies of *A. lemurinus* could not be distinguished phenotypically (Hershkovitz 1949, 1983), and his last position seemed to imply that *A. lemurinus lemurinus* (*sensu* Hershkovitz 1983) and *Aotus l. griseimembra* could only be reliably recognized from their karyotype. Hershkovitz (1983: p.209) did believe, however, that *full* species of *Aotus* were distinguishable by both phenotype and karyotype; for example, his experience allowed him to identify photos and a preserved head, previously thought to be from the Río Paraguay, as having come from Villavicencio in Colombia. He also identified photos of animals which Ma had karyotyped, as exhibiting the “*griseimembra*” phenotype or “B” phenotype (northern Colombia type, Hershkovitz 1983). He published phenotypic descriptions of *A. nancymai* and *A. brumbacki*, and reiterated Humboldt’s phenotypic description of *A. trivirgatus*. He added information on pelage growth fields in terms of crests and whorls which had not been pointed out by others (Hershkovitz 1977, 1983), although Ford (1994) subsequently denied their usefulness. Hernández-Camacho and Cooper (1976) likewise included detailed phenotypic descriptions of various northern Colombian taxa, including *A. l. zonalis* that they felt were diagnostic, and they pointed out the variability of *A. lemurinus* (*sensu* Hernández-Camacho and Cooper 1976).

Methods

We examined and compared all karyological evidence available for gray-necked northern *Aotus*, including an unpublished description of the chromosomes of an *Aotus* sp. from the left bank of the Río Orinoco, 2 km from the site of the Maipures (Maypures) village. We also tested published phenotypic descriptions of *Aotus* using museum specimens from the two major Colombian collections and attempted to place the specimens into their respective taxa using published descriptions from Hershkovitz (1949, 1983) and Hernandez and Cooper (1976).

Taxonomy of the Gray-necked *Aotus*

We list six karyomorphs in Table 1 and comparative karyological characteristics in Table 2 that correspond to six gray-necked species of *Aotus* (*A. zonalis*, *A. griseimembra*, *A. lemurinus*, *A. brumbacki*, *A. vociferans*, and *Aotus* sp. nov.). We add to these *A. trivirgatus* which has not been characterized karyologically. This gives a total of seven gray-necked species.

Aotus brumbacki as a subspecies of *A. lemurinus*?

Groves (2001) and Rylands *et al.* (2001) classified *A. brumbacki* as a subspecies of *A. lemurinus*. Groves' (2001: p.164) argument was as follows: "In pelage characters, she [Ford 1994] found it to span the gap between the two subspecies of *A. lemurinus*, which are otherwise more distinctive than hitherto recognized. In this light, it does seem likely that, as she indicated it should be placed as a subspecies of *A. lemurinus*, and that [...] the characters of the (now three) subspecies are somewhat mosaic." This seems misguided to us in view of the considerable karyological differences between these two taxa. Karyological information clearly demonstrates that *A. brumbacki* ($2n = 50$) and *A. lemurinus* ($2n = 58$) are different species, highlighting difficulties in using a phylogenetic species concept if it is based on purely phenotypic characters (see discussion below). Groves (2005) continued to list *A. brumbacki* as a subspecies of *A. lemurinus*, but he has since agreed with us, that in fact *A. brumbacki* is a separate species (C. P. Groves pers. comm. to Defler, 2006).

Aotus brumbacki and the Maipures specimen

A specimen collected live by one of us (TRD) near Maipures, Vichada, along the Orinoco River (IvH 4105) had a karyotype very similar to *A. brumbacki* ("*A. t. trivirgatus*" of Yunis *et al.* [1977]) (Table 2). One of the two Maipures specimens was karyotyped by V. Monsalve, and her interpretation was reviewed by P. Hershkovitz (letter to María Victoria Monsalve, May 9, 1989). Although there were problems resolving two of the chromosomes, Monsalve *et al.* (1989) identified 4 metacentric pairs, 7 submetacentric pairs and 11 acrocentric pairs. We have examined the poorly reproduced copy of the fotomicrograph and believe that the two poorly resolved chromosomes could be submetacentric, in which case the chromosome morphology would agree with the Yunis *et al.* (1977) description (= *A. brumbacki* of Hershkovitz (1983: p.217). It should be taken into account that none of the three previously published descriptions of chromosomal morphology for *A. brumbacki* (Brumback 1974; Yunis *et al.* 1977; Torres *et al.* 1998) agreed completely in the characteristics of the $2n=50$ chromosome types and showed considerable variation in the identification of numbers of metacentric, submetacentric and acrocentric chromosomes. *Aotus brumbacki* should thus be re-studied for chromosome morphology. Nevertheless, the Maipures karyotype is actually closer to the morphology of the karyotype published by Yunis *et al.* (1977) than are the other two published karyotypes, suggesting to us that *A. brumbacki* extends throughout the Llanos Orientales to the Río Orinoco.

Is the Maipures specimen *A. trivirgatus*?

When Hershkovitz examined color slides of the Maipures specimens he stated that he believed they were *A. trivirgatus* and that, therefore, *A. trivirgatus* had $2n = 50$ (P. Hershkovitz, letter to María Victoria Monsalve, 9 May 1989). Jorge I. Hernández Camacho did not agree with this interpretation, believing that the Maipures specimen was *A. brumbacki* or a new species (Hernández-Camacho pers. comm. to TRD). We ourselves have difficulty seeing the Maipures specimen (I.v.H. no. 4105, 4164) phenotypically as either *A. brumbacki* or *A. trivirgatus*, although it is important to note that the preserved specimens are considerably altered in color, due to the length of time they had been in captivity in Bogotá. Santos-

Table 1. Northern (gray-necked) *Aotus* karyotypes (diploid numbers) and fundamental numbers (FN).

Species	2n	FN	Reference
<i>A. vociferans</i>	46, 47, 48	70	Ma <i>et al.</i> (1976), Descailleaux <i>et al.</i> (1990)
<i>A. brumbacki</i>	50	70	Brumback (1971), Yunis <i>et al.</i> (1977)
<i>Aotus</i> (Quindío) ¹	50		Torres <i>et al.</i> (1998)
<i>Aotus</i> (Maipures)	50		Monsalve <i>et al.</i> , (unpubl.)
<i>A. griseimembra</i> ²	52, 53, 54 13%, 46%, 41% n=620	72	Ma <i>et al.</i> (1976), Giraldo <i>et al.</i> (1986)
<i>A. zonalis</i>	55, 56	72	Ma <i>et al.</i> (1976)
<i>A. lemurinus</i>	58	76	Ramírez-C. (1983), Giraldo <i>et al.</i> (1986), Defler <i>et al.</i> (2001), Torres <i>et al.</i> (1998)
<i>A. trivirgatus</i>	—	—	—

¹Is there any way this can be related to the Maipures specimen, which is $2n = 50$ as well? Maybe this is *A. trivirgatus*.

²Remains a problem whether this karyotype actually relates to *A. griseimembra* or to another lowland taxon.

Mello and Thiago de Mello (1985) published an abstract of a talk given at the 10th Congress of the Brazilian Primatological Society where they describe a karyomorph $2n = 51$ for males and $2n = 52$ for females, determined from “*Aotus* collected around Manaus” and this, according to the authors, is the true karyotype for *A. trivirgatus*. We believe that it is likely that there may be differences in karyomorphs from each side of Rio Negro, because of its size as a barrier. Karyotypes of night monkeys immediately west of the Rio Negro have yet to be described.

The so-called “Quindío” specimen as a new species: *Aotus jorgehernandezi*

Torres *et al.* (1998) karyotyped another *Aotus* specimen which proved to have $2n = 50$, possessing nine pairs of metacentric, three pairs of metacentric and 12 pairs of acrocentric chromosomes (Fig. 1). Unfortunately the preserved specimen ICN14023 could not be located, so the only phenotypic information that we could find must be taken from Figure 2, p.261 in their publication (Fig. 2). However, the karyotype illustrated in their Figure 2 must be considered diagnostic for this new species and to serve as part of the holotypic description.

The specimen was found in captivity in the Department of Quindío, Colombia, although Defler *et al.* (2001) discounted the possibility that the specimen was actually from Quindío Department itself. Chromosome morphological differences would make it very difficult for *A. brumbacki* and the Quindío *Aotus* to pair in genetic recombination, and any hybrid would

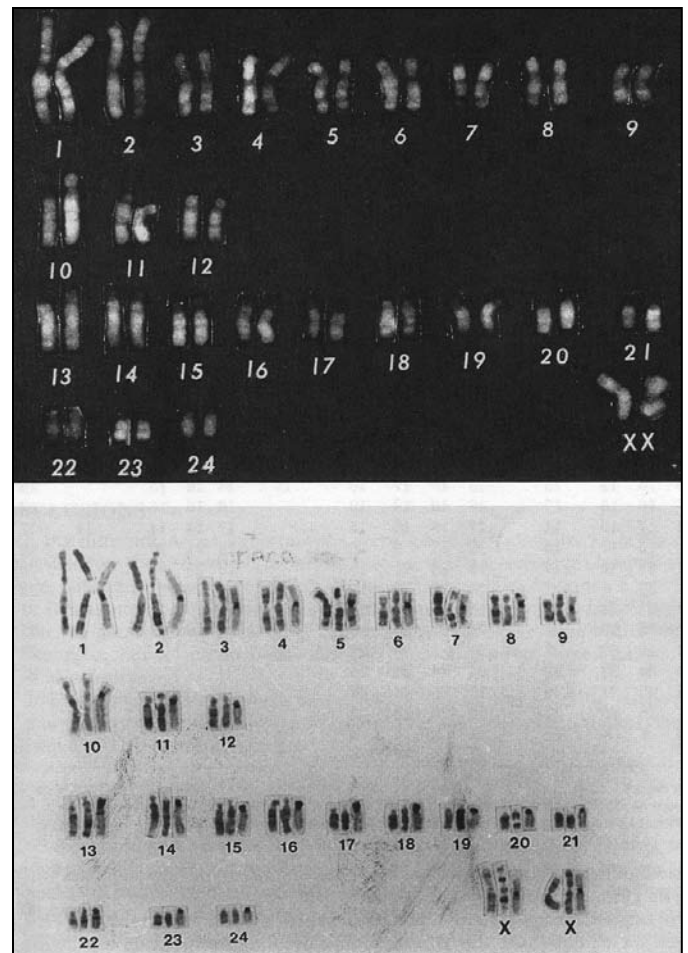


Figure 1. Karyomorph of *Aotus jorgehernandezi* (reprinted from Torres *et al.* 1998). With permission from Wiley-Liss Inc.

Table 2. Determined chromosome structure of recognized gray-necked *Aotus* karyomorphs. Revised from Torres *et al.* (1998); according to Defler *et al.* 2001 and Monsalve *et al.* (unpublished).

Species	2n ^a	Karyotype	Karyomorph	Karyomorph	Pairs of Autosomes			Chromosomes			Reference
					Ma (1981)	DeBoers and Reumer (1978)	Torres <i>et al.</i> (1998)	M ^b 1–1.9 ^c	S ^b 2–4.9 ^c	A ^b >5 ^c	
<i>A. vociferans</i>	46 47 48	V	7	7	7	5	10	M ^b	ND	-	Ma <i>et al.</i> (1976) Torres <i>et al.</i> (1998)
<i>A. brumbacki</i>	50		6	6	5	5(or 6?)	14(or 13)	M	M	0.9	Torres <i>et al.</i> (1998)
<i>A. brumbacki</i>	50		6	6	4	9	11	M			Yunis <i>et al.</i> (1977)
<i>A. brumbacki</i>	50		6	6	5(or 4?)	7(or 6?)	12(or 14)	M	Very small terminal		Brumback (1974)
<i>A. (Quindío)</i>	50			9	9	3	12	M	M	-	Torres <i>et al.</i> (1998)
<i>A. (Maipures)</i>	50			?	4	9	11	M	-	-	Monsalve <i>et al.</i> (unpubl.)
<i>A. griseimembra</i>	52 53 54	II III IV	2	2	5 6	5 5	16 14	M	M	0.8	Torres <i>et al.</i> (1998)
<i>A. griseimembra</i>	52 53 54	II III IV	2	2	5 4 4	7 7 7	14 13 15				Ma <i>et al.</i> (1976) Yunis <i>et al.</i> (1977)
<i>A. griseimembra</i>	52 53 54	II III IV	2	2	5 6	10 10	11 11	M M	Very small terminal		Brumback <i>et al.</i> (1971) Brumback (1973, 1974)
<i>A. zonalis</i>	55 56	VIII IX	1		4/4.5 4	4/4.5 4	21/23 23	M	-	-	Ma <i>et al.</i> (1976)
<i>A. lemurinus</i>	58				4	4	20	M	M	1.4	Defler <i>et al.</i> (2002)
<i>A. lemurinus</i>	58	X		8	4	5(or 6?)	18				Giraldo <i>et al.</i> (1986) Torres <i>et al.</i> (1998)

2n^a = diploid number. ^bChromosome morphology: M, metacentric; S, submetacentric; A, acrocentric. ^cRange of arm ratio (q/p). X = total X chromosome containing haploid complement length; Y = total Y chromosome; ND = not determined; RL = relative length expressed as % of Total Chromosome Length (TCL).

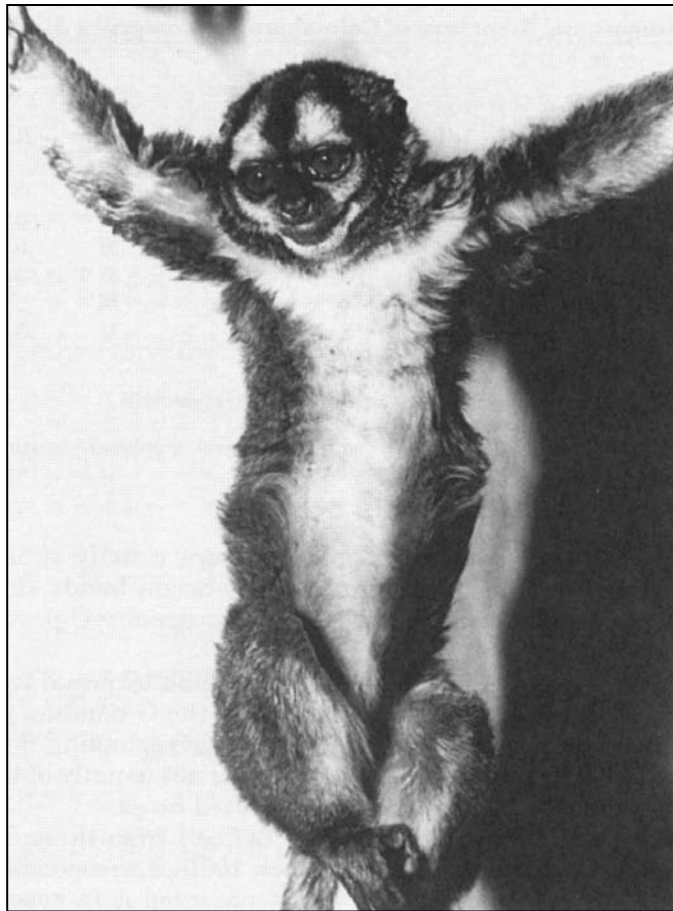


Figure 2. Live *Aotus jorgehernandezii* (reprinted from Torres *et al.* 1998). With permission from Wiley-Liss Inc.

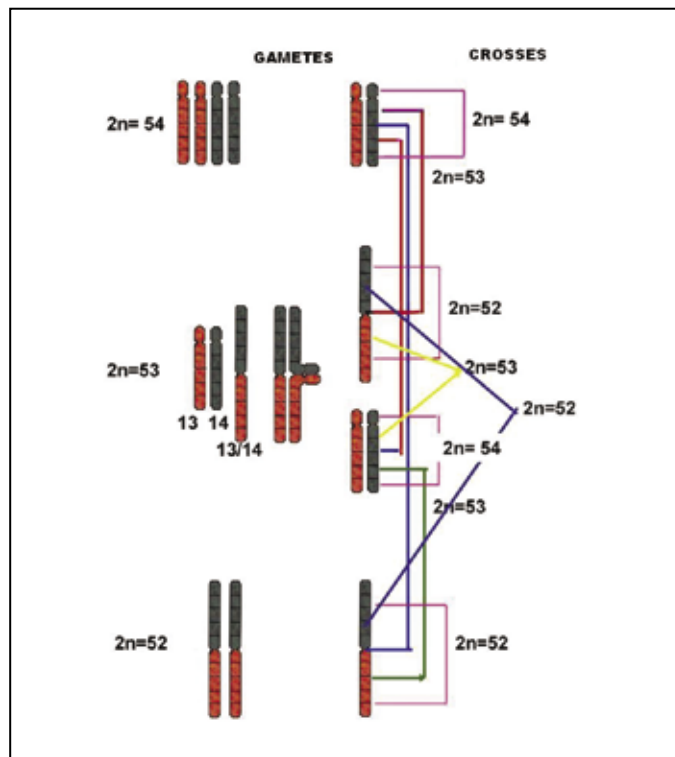


Figure 3. Hardy-Weinberg equilibrium relation between karyotypes found in *Aotus griseimembra* indicating how chromosome pairing takes place among the three different karyotypes, resulting in viable offspring rather than infertility.

certainly be sterile. Martin (1990: p.550) pointed out the superior importance of the fundamental number (i.e., the total number of chromosome arms) to the diploid number in indicating phylogenetic relationships, since the fundamental number tends to remain stable due to the inter-chromosomal rearrangements of reciprocal conversion of acrocentric and metacentric chromosomes (Matthey 1949; Bender and Metler 1958; Chu and Bender 1961; Bender and Chu 1963; White 1973; Martin 1978). We thus concur with Torres *et al.* (1998: p.270) that this karyomorph represents a new, undescribed species of *Aotus*, the exact type locality of which is unknown at this time.

Aotus jorgehernandezii new species

Type specimen: Specimen ICN 14023, a female (Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá – not located in the collection); pictured in this article (Fig. 2) and in Torres *et al.* (1998: p.261, Fig. 2).

Type locality: Uncertain. Found in captivity in Quindío Department, Colombia, but said to be from the Parque de los Nevados on the border between Quindío and Riseralda.

Diagnosis: “The previously undescribed karyomorph exhibits a diploid number of 50 chromosomes, with a chromosome constitution different from all published *Aotus* karyotypes. It was observed in a female specimen from Quindío, *Aotus* [nov. sp.]. [Figure 1] shows a QFQ karyotype, which has nine pairs of metacentric chromosomes, as well as three pairs of submetacentric and 12 pairs of acrocentric ones. Intense fluorescent terminal bands were present in the 8p, 10p, 11p, 12p, 13p, 14p, and 15p chromosomes. For chromosomes 8, 13, 14, and 15, these bands correspond to C-positive constitutive heterochromatin. [Figure 1] shows a composite karyotype representing the haploid set with G, R, and C banding. As in other karyomorphs, the X chromosome was identified by its late replication and band pattern. Chromosomes 13q and 22q show interstitial C bands, proximal to the centromere, while chromosomes 13–18 show heteromorphic whole heterochromatic short arms. The centromeric heterochromatic band of chromosome 5p is also heteromorphic.” (Torres *et al.* 1998: p.271, Fig. 9).

Description: This is a gray-necked specimen whose face shows two discrete supraocular white patches separated by a broad black frontal stripe. Sub-ocular white bands of fur are separated by a thin black malar stripe on each side of the head. The ventral part of the arms from the wrists running up into the chest and belly are of thick white fur (Fig. 2).

Comparisons: The other gray-necked *Aotus* with $2n = 50$, *Aotus brumbacki* has 4 or 5 metacentric chromosomes (instead of the 9 in the new species), has 5 or 6 submetacentrics (according to Torres *et al.* 1998), 6 or 7 submetacentrics (according to Brumback 1974) or 12 or 14 submetacentrics (according to Yunis *et al.* 1977) instead of the 3 pairs of submetacentric chromosomes reported for this new species. Finally, *A. brumbacki* is reported to have 14 pairs of acrocentrics (according to Torres *et al.* 1998), 11 acrocentrics (according to Yunis *et al.*

1977), and 12 acrocentrics (according to Brumback 1974) as compared with the 12 acrocentric chromosomes reported by Torres *et al.* (1998).

Etymology: It seems appropriate to us to name this species *Aotus jorgehernandezii* in honor of our friend and colleague, the late Jorge I. Hernández-Camacho, a person who has influenced much of Colombian organismic biology and was instrumental in influencing our latest examination of the taxonomy of *Aotus*.

Aotus vociferans

Descailleux *et al.* (1990) have indicated that *A. vociferans* has at least three diploid numbers (46, 47 and 48), and that the karyotypes 46 and 48 appear in the population with the same frequency, 47 being very rare. This suggests strong positive selective pressure for $2n = 46$ and $2n = 48$ with strong negative selection for $2n = 47$. In their study of 68 *A. vociferans* they found a total homology of all chromosomes, except for a large metacentric chromosome in $2n = 46$, which corresponded exactly with two acrocentric chromosomes of the $2n = 48$. The only individual having $2n = 47$ was a female, apparently a hybrid between the other two most common karyotypes. While the authors write that the karyotypes were all from the same “population” (Descailleux *et al.* 1990: p.573), we assume they are not using the term in a natural demographic sense but rather to refer to the sum of their gray-necked animals, which from other publications of this research group we learn had been collected from a wide area north of the Río Marañón (Aquino and Encarnación 1988: pp.377–378). Nevertheless, Aquino and Encarnación (1988: p.377) found $2n = 46$ and $2n = 48$ to be “syntopic”. One interpretation of these frequencies could be that this is an actual speciation event. Further studies of this phenomenon seem warranted.

Aotus griseimembra

The karyology of *Aotus griseimembra* has been studied much more than other karyomorphs of *Aotus* (Ma *et al.* 1976, 1978; Yunis *et al.* 1977; Miller *et al.* 1977; Giraldo *et al.* 1986). Martin (1978, 1990) and Defler and Bueno (2003) have described the behavior of the three polymorphic chromosome sets described for the taxon, and repeated calculations equaling more than 700 karyotypes have consistently shown similar values respecting the Hardy-Weinberg equilibrium, resulting in rearrangements that have neutral or mildly negative heterotic effects (Fig. 3). In this species, individuals with $2n = 53$ have 3 unpaired elements, chromosome 1 formed by a simple Robertsonian fusion of chromosomes 13 and 14 and two elements with no homologues on chromosomes 13 and 14. Karyotype $2n = 52$ has a double Robertsonian fusion on pair #1, and there are no unpaired chromosomes in this karyotype. Pairs #13 and #14 are free. The rest of the complements are the same in all three karyotypes.

Aotus zonalis

The karyology of *A. zonalis* (previously called *A. lemurinus* by Hershkovitz 1983) shows four pairs of metacentric, 4 pairs of metacentric and submetacentric, and 23 pairs of subtel- and acrocentric autosomes in the $2n = 56$ karyotype. The $2n = 55$ has 4.5 pairs of metacentric and submetacentrics and 21 pairs of subtel- and acrocentric, and two unpaired acrocentric autosomes with the sex chromosomes identical to those of the $2n = 56$. The $2n = 55$ has identical matching elements with the complement of $3n = 56$ except for three unpaired chromosomes. Actually, because this karyomorph shares 24 pairs of identical chromosomes with *A. lemurinus*, we can say that *A. zonalis* is more closely related to *A. lemurinus* than it is to other Colombian *Aotus*, including *A. griseimembra*. *Aotus zonalis* and *A. griseimembra* differ in two distinct translocations of one chromosome (Ma *et al.* 1978).

The Meaning of Chromosome Variability and its Evolution

The prevalence of a high degree of chromosome variability in *Aotus*, *Callicebus*, *Alouatta* and other genera, and in general in the Platyrrhini, requires explanation, although presently we only have hypotheses. The first question might be whether chromosome variability has some selective value or not? Does a high degree of genetic shuffling within a genus mean a “high” rate of evolution? Could high variability in *Aotus* reflect the advantages of an unfilled primate niche where the only competition is from some nocturnal non-primate mammals, and then how could such high variability be explained in diurnal genera such as *Callicebus* and *Alouatta*? Is each karyotype an adaptive block or is chromosome variability unconnected with adaptation?

The most obvious value of a high diploid number might be the increased capacity for genetic recombination (Martin 1990: p.579), and in this light it is interesting that the highest number recognized for *Aotus* ($2n = 58$; *A. lemurinus*) is a species found above 1,500 m in the Cordillera de los Andes, where much more variable habitat extremes are found than those of the lowlands. The small size of *Aotus* and the fact that other primates of this size or less drop out of the primate community at elevations above 500–600 m suggest that physiological adaptations have played a part in the success of this primate occurring up to altitudes of 3,200 m (Hernández-Camacho and Defler 1985).

Aotus has highly variable chromosomes throughout many populations, and chromosome mutation in different evolving populations has produced a series of diploid numbers varying from $2n = 46$ to $2n = 58$ with FN's 54–78. In general, primates have one of the highest mammalian speciation rates, surpassed only by the horses (Bush *et al.* 1977). The average mammalian genus has been calculated at about 6.5 million years and the average primate genus at 3.8 million years (Bush *et al.* 1977); if the fossil “*Aotus*” *didensis* is correctly placed in the genus *Aotus*, we have a primate genus at least 12–13 million years old (Sertoguchi and Rosenberger, 1987).

Perhaps this explains in part the high chromosome variability of this genus? However, the genus *Equus* (the modern horses) seems to have an age that is somewhat less than the average mammalian genus; that is 3.5 million years (since *Equus* first appears in the fossil record in the late Pliocene) and *Equus* is also karyologically highly variable (Bush *et al.* 1977: p.3944). Genus age does not seem to explain the extreme chromosome polymorphism. What do *Aotus* and *Equus* have in common, if anything?

Bush (1975), Bush *et al.* (1977), Lande (1979), Wilson *et al.* (1975), Marks (1987), Ridley (1996: pp.457–458) and others have developed the idea that high rates of karyotypic evolution may be due to certain social structures and breeding systems, which might give a higher chance of survival of chromosomal changes, so that these changes may become fixed in a population. These social structures would have to cause a subdivision of populations into small, inbred demes, giving a chance for chromosome mutation to become fixed in the homozygous state. Galbreath (1983: pp.248–249) explicitly evoked genetic drift in small *effective* populations as the mechanism most responsible for *Aotus* chromosome variability. Others go on to identify characteristics such as limited adult vagility and juvenile dispersal, patchy distribution and strong individual territoriality as characteristics of such populations subject to high chromosome evolution. Martin (1990) criticized the evocation of fixation of chromosome changes in small demes, suggesting that mammals in general do not form small inbred population units, rather one sex usually continues reproductive interchange with other social units, and that localized inbreeding is not a consistent mammalian feature. Bickham (1981) and Robbins *et al.* (1983) sustain that chromosome change is more likely to proceed to adaptive change in evolution and not to fixation in small demes. The characteristics of reproduction in the populations of many are, however, unknown and there are many potential barriers to panmictic reproduction, including social systems, population structure and habitat characteristics (Wilson *et al.* 1989).

Few details are known about *Aotus* social structure. It is known that monogamous breeders defend a territory, but the process of outbreeding is completely unknown at the present. Some comments about *Callicebus*, may be helpful here, since they also have very high chromosome variability and, like *Aotus*, are monogamous territory holders. Some species of *Callicebus* (*C. torquatus*, *C. ornatus* and certainly others) live in monogamous units and vigorously defend a territory. After the second year the territory holders' young disperse, and search for a member of the opposite sex so that they can establish a territory of their own. This is probably not easy and so at least two tactics seem to be available.

Using the first strategy, lone *C. torquatus* have been observed far from their natal groups, crossing patches of grassy savannah in northern Colombia or attempting to cross the seasonally mostly dry portion of the lake bed of an oxbow lake on the lower Río Apaporis of eastern Colombia. In all likelihood these dispersals of a small, diurnal *Callicebus* have a high degree of failure, since most successful territories are

occupied, unless one of a breeding pair happens to die. This means that philopatry is a viable option, since there are usually only patches of a few *Callicebus* pairs spread throughout the forest in a metapopulation structure. *Callicebus* densities are not high and there are large expanses of forest where titis are absent, judging by the absence of their vocalizations (Defler 2003, 2004). Dispersal in *Aotus* is even less well-known, but any long-distance dispersal is likely to be fraught with danger and the likelihood of failure is high; even more so for titis that do not have the cover of night.

A second strategy may involve unpaired *Callicebus* adults attaching themselves to a resident pair for a period of time. These adult “floaters” appear to be known to the generally aggressive territory holders; they are thus probably mature offspring that have not dispersed far and may even be enjoying the benefits of the territory where they grew up (Defler 2003, 2004). Breeding pairs vigorously defend their territory, usually via loud duetting, and occasionally with chases and same sex-attacks. We have noticed that, while displaying, *Callicebus torquatus* are visibly more aggressive towards some neighboring pairs than towards others. Neighboring territory holders that receive comparatively less aggression (cursory shout displays, then silence, as opposed to continued loud screaming with one pair finally retiring into the center of their territory or actual chases at the edges of the two territories) may include one offspring. Our interpretation is that a young animal electing to remain near its parents' territory may have resolved its breeding challenge by mating with a nearby animal that might have recently lost its mate, or it may have paired with another “floater”, with both in the process of attempting to establish a new territory nearby. If this can be confirmed, this may lend support to the possibility of the fixation of a homozygous new karyomorph.

The most likely vicariant mechanism that could facilitate fixation of a new karyomorph (i.e., a population of a particular karyotype) could be the cutting off of the neck of a meandering river bend, resulting in the isolation for a time of a small, isolated population enclave until such time as the filling in of the isolated meander would allow long-distance dispersal of group members from one bank of the cut-off river bend to the other (Hershkovitz 1983). Until it was possible to cross such a barrier the isolated population could become inbred and subject to chromosome changes becoming dominant in that population. One such formerly isolated population of *C. torquatus lugens* and of *Aotus vociferans* is known from the lower Río Apaporis in eastern Colombia, but, because of filled-in vegetation and seasonal levels in the cut-off river meander, individuals are now able to pass freely from one side to the other of what were opposite river banks (Defler pers. obs.). An *A. nancymai* enclave on the left bank of the Río Marañón is known to be surrounded by *A. vociferans* as described in Hershkovitz (1983: p.236), the two species being at least partly sympatric (Aquino and Encarnación 1986). If a cut off population had no competition on the other side of a river, then any new chromosome mutation that had become fixed in

the small population would be then spread and be diagnostic for the new population.

Observations of *Callicebus torquatus* in the Caparú Biological Station in eastern Colombia are very suggestive that not all animals disperse permanently—and if in *Callicebus*, why not in *Aotus*, which has a similar type of social structure? More detailed observations are needed on the two genera to confirm these ideas. DNA comparisons of individual animals to determine relatedness are now possible from the field, and we hope that future research might attempt using fecal material to obtain genealogical information for these species (Morin and Goldberg 2004; Woodruff 2004).

In the case of *Alouatta*, a much larger primate, the hypothesis about the causal factors leading to highly variable chromosomes would have to be modified, since the members of this genus are not monogamous. But, one male and one female are a basic social unit for at least the red howler, *A. seniculus*, and an isolated group could become inbred, and fixation of a new chromosome mutation could occur theoretically. However, a cut-off meander of a river would not be an adequate vicariant mechanism, since these animals are strong swimmers, nor do *Alouatta* balk at walking long distances over treeless expanses (Defler 2003, 2004). So of four genera with highly variable chromosome numbers and morphology, *Aotus*, *Alouatta*, *Callicebus* and *Hylobates*, three are monogamous and one is age-graded, perhaps requiring different explanations for this variability (Rylands and Brandon-Jones 1998).

Other Differences in *Aotus* Populations

Taylor and Siddiqui (1978a, 1978b, 1979) found significant mitogene differences (PHA with A and PWM) in lymphocyte cultures of *Aotus* from Panama (*A. zonalis*), Colombia (*A. griseimembra*), and Peru (*A. azarae*), and these differences were also reflected in experimental infections with *Plasmodium falciparum*. This differential sensitivity to *falciparum* infection was also studied by Espinal *et al.* (1984). Blood serum differences between populations were also pointed out by Brumback and Willenborg (1973).

Described *Aotus* Phenotypes

Most primatologists have considerable difficulties in distinguishing *Aotus* species phenotypically. Hershkovitz (1983) maintained that each species of *Aotus* is distinguishable phenotypically, karyotypically, and via serum proteins. His descriptions of color and hair patterns allow us to test his assertion (Hershkovitz 1949, 1983). Additional information provided by Hernández-Camacho and Cooper (1976) provide ample morphological descriptions for gray-necked *Aotus*. However, because *Aotus* is made up of a complex of sibling species, these phenotypes are not easy for the non-expert to apply.

Phenotypically it is of course easy to separate the “red-necked” southern species from the “gray-necked” northern species and this basic separation comes with an identifiable genetic difference as well—in the gray-necked group the

chromosome pairs 6 and 7 are discrete, while in the red-necked group the chromosomes 6 and 7 have a reciprocal translocation of arms (Hershkovitz 1983: p.211). Like Hershkovitz (1949, 1983), Hernández-Camacho and Cooper (1976) in general lumped the three northern species *A. zonalis*, *A. griseimembra*, and *A. lemurinus* phenotypically into the so-called “B-phenotype”; they distinguished *A. l. griseimembra* as having short adpressed (densely compacted) pelage and light brownish hands and feet (in actuality the holotype had blackish hands and feet), as opposed to *A. l. zonalis* with blackish hands and feet; all other characteristics being similar to *A. l. griseimembra*. They also distinguished *A. l. lemurinus* as being “only from the Cordillera de los Andes “from about 1,000–1,500 m upward to the tree line (3,000–3,500 m)” (p. 47). Hernández-Camacho and Cooper (1976) characterized *A. t. lemurinus* as follows: “It is a rather variable subspecies, appearing quite often in two color phases, which can both be found in the same family group. One is decidedly grayish-brown, and the other is a richer, more reddish-brown in the upper parts. However, a range of intermediate coloration can be found. The underparts are always a rather dull yellow, indistinguishable from *A. t. griseimembra* and *A. t. zonalis*. The hair coat is extremely long and soft and is the most valuable distinguishing characteristic.” However, pelage length is often pointed out as a poor diagnostic character, and being above about 1,500 m probably universally produces long-furred fluffy *A. lemurinus*.

Aotus are variable in color, sometimes even in the same family group and in individual specimens, but there seems to be a trend from the western Cordillera to the Eastern, although this trend should be examined in the future to confirm it. In all three species there are as well two color phases, a light overall grayish phase and a darker, reddish-brown phase with variations in between. These both are liable to appear in the same family group and there may be no trend or cline (Hernández-Camacho and Cooper 1976). The authors continue “The hands and feet of this species are remarkable in their color variation and lack of full correlation, even in individual specimens. Specimens examined from the western Andes (around Cali) and most of the specimens from the central Andes have black-tipped hairs on the hands and feet (at least reaching the distal carpus and tarsus). A few specimens from the western Andes and a number of those from the central Andes appear variably grizzled in color on the metatarsal and metacarpal regions due to reduced extent of the dark tips, thus allowing exposure of the lighter hair bases. In the eastern Andes a full range of individual variation occurs with regard to this character, i.e., from extensive black hair tips to the very reduced tips typical of *A. t. griseimembra*. Some variation has also been observed between the hands and feet of the same individuals with regard to this characteristic” (Hernández-Camacho and Cooper 1976: p.47). The most important phenotypic differences between these taxa then are the almost universal blackish hands and feet and short pelage of *A. zonalis*, the almost universal brownish feet and hands and short pelage of *A. griseimembra*, and the black or brown hands and feet and very long pelage of *A. lemurinus*.

Identifying *A. brumbacki* was no problem for Hershkovitz (1983), he identified a preserved head, which was said to be from the Río Paraguay, as in fact coming from the Villavicencio area. Hershkovitz (1983) then went on to describe *A. brumbacki* as a new species, basing his opinion especially on the karyotype ($2n = 50$), described by Brumback (1974) and Yunis *et al.* (1983). This species is also short-haired, with two temporal stripes which continue as shadowy stripes, appearing to merge into a generally dark blotch on top of and behind the crown. The body is usually some shade of grayish-buffy and there is no mid-dorsal stripe; a pale band between buffy supraorbital and suborbital patches is interrupted by an extension of the blackish temporal stripe to the outer corner of the eye; a blackish malar stripe is present. Hershkovitz (1983: p.216, p.219) distinguished *A. brumbacki* from the *A. lemurinus* complex and from *A. trivirgatus*, because *A. brumbacki* has an interscapular whorl or crest not present in the others. These characters are of questionable diagnostic value, as Ford (1994: p.26) found, since there are many exceptions, and even Hershkovitz (1983: p.216) explaining their use, noted many problems.

According to Hershkovitz (1983: p.216), *A. vociferans* has an interscapular whorl with centrifugal and a more or less circular gular gland, the surrounding hairs radiating from the center as a whorl. One helpful characteristic pointed out by Ford (1994: p.25) in this species is that the head stripes nearly always converge posteriorly.

Ford's (1994: p.25) analysis argued that *A. trivirgatus* is the most divergent and best-defined of the group of northern gray-necked *Aotus*. There are no whorls, crests or tufts and the head stripes do not unite posteriorly, this being a strongly reliable character of the species. The dorsum is usually grayish, sometimes with buffy agouti and with a narrow and strongly contrasting orange middorsal band. Morphometrically this species is easily distinguishable from the rest of the northern *Aotus* as well, with a canonical variate from cranial measurements separating *A. trivirgatus* completely from the other northern species (Ford 1994: pp.11–17).

An interpretation of Ford's (1994) discovery that *A. trivirgatus* (*sensu* Hershkovitz 1983) was morphometrically clearly distinguishable from the complex *A. vociferans*–*A. brumbacki*–*A. lemurinus* (*sensu* Hershkovitz 1983) might be that *A. trivirgatus* was the first to separate from the others of the *Aotus* species complex, allowing for the development of the more accentuated morphological differences (Mayr and Ashlock 1991: p.92). If there is no strong selection pressure on visible phenotype, easily understandable for pelage markings, and if these are fairly new species, there may not have been enough time for such phenotypical differences to become evident, although closer analysis may yet find some sharp phenological differences, as is usual after increased study of most sibling species (Mayr 1969: pp.33–58). The most fecund analyses might be made in vocalizations or pheromone cues, since these are the phenotypic characteristics that are most important to a nocturnal animal (Mayr 1969: pp.33–58).

Many problems arose when we actually studied collection skins, because of strong similarities among these species. Perhaps *Aotus* species are so similar because they are nocturnal, and selection for coat patterns may be very weak. It may be that blocks of balanced adaptations maintain themselves in an essentially homogeneous habitat throughout the range of the genus, and that the "*Aotus* adaptation" for nocturnal forest living is reflected via similar phenotypes. Patton and Smith (1980) described genetic and morphological divergence among pocket gopher species, where two species (operationally defined as clearly maintaining two genetically different populations through reproductive isolation maintained by a sterile F_1 hybrid zone) have no distinguishable morphological difference except for size and that also show no substantive degree of genetic differentiation (as measured by electrophoresis). Other gopher species of this complex (*Thomomys*) show considerable genetic differences. Morphological differentiation appears to have occurred much more slowly than genetic differentiation in the sibling species complex, and may be due mostly to genetic drift in color and skull characteristic rather than any selective force.

Thorington and Vorek (1976) make some interesting observations on variation in coat color in *Aotus*. They felt that Hershkovitz' designations of the subspecies *A. lemurinus lemurinus* and *A. l. griseimembra* would only complicate a real appreciation of the variability in *Aotus* populations. Van Roosmalen *et al.* (2002) believe that the use of the subspecies category has "minimal value" when describing Neotropical primate diversity. Although Hershkovitz (1949, 1983) and Hernández-Camacho and Cooper (1976) confidently identified and described various *Aotus* populations in their publications; we find the task to be much more difficult, especially because different characters vary independently across the species' range and many characters do not seem to exhibit regular variations. It is possible Hershkovitz and Hernández-Camacho had special abilities that come from many years of study of *Aotus*.

The fact that Ford's (1994) work defined one phenetic unit made up of *A. vociferans*, *A. brumbacki*, and *A. lemurinus* (*sensu* Hershkovitz, 1983) is not surprising, given the nature of sibling species complexes. But it is important to realize that a phenetic unit (or a phenetic "species") is not the same as a biological species. Biological species require reproductive barriers and these are strongly suggested by the karyotypic differences. Although differences in karyotype do not inevitably mean reproductive barriers, as evidenced by the balanced polymorphism of *A. griseimembra*, the level of karyotypic differences found in *A. lemurinus*, *A. zonalis* and *A. brumbackii* would most probably result in pre-zygotic barriers due to problems of chromosome pairing, resulting in sterility at the F_1 or F_2 generation or drastically reduced fertility (Torres *et al.* 1998; Defler *et al.* 2001).

Similarities and lack of truly cogent differences in *Aotus* phenotypes may be due to the fixation of chromosome differences in small, isolated populations. If *Aotus* has an established phenotype adapted to a nocturnal feeding niche, there

would be little pressure for new feeding adaptations, which are often the basis for many morphological differences, especially in teeth. A speciation event, due to a pre-zygotic mechanism such as a chromosome change, very possibly would allow the two sister clades to continue to exist parapatricly in a very similar niche. If the new species was successful enough to quickly expand its population, only gene drift would define differences between the populations, not new adaptations. If the genus (as seems likely) was well-adapted to its nocturnal existence, balanced co-adapted gene clusters could maintain themselves even in reproductively isolated populations, as has been discussed in the pocket gopher species complex, where many morphologically very similar or identical species exist (Patterson and Smith 1989). Many mosaic characters of *Aotus* such as pelage coloration may be the results of genetic drift (Thorington and Vorek 1976; Ridley 1996).

Despite the difficulties of determining the various phenotypes, we include here a key (Table 3) that has been constructed based on the comments of Hernández-Camacho and Cooper (1976), Hershkovitz (1983) and Ford (1994), in their efforts at recognizing appropriate phenotypes for some of the gray-neck species that we recognize. Although these authors in several cases do not agree with each other (for example, Ford lumps all species together except for *A. trivirgatus*), it seems helpful to us to organize this information in such a way that it can be used by other workers.

It should be appreciated that from the first time that a second species was distinguished from *A. trivirgatus*, the division was appreciated because of karyotypic differences not phenotypic. Further species have been identified, each time because of their karyotype, not because of phenotype.

Aotus Origin and Evolution

Aotus may have had its origin in central Colombia, if “*Aotus dindensis*” described from 12–13 million-year-old deposits of the La Venta formation near the Río Magdalena in Colombia (Setoguchi and Rosenberger 1987) truly belongs to this genus. This was well before the appearance of the Cordillera de los Andes about 5 million years ago. Two other lines of evidence suggest a northern origin. First, following the theory of metachromism (Hershkovitz 1977, 1983), the red-necked *Aotus* species had to have derived from the gray-necked species in the north. According to the model, these pigment changes are one-way and always proceed from the loss of eumelanin.

Secondly, the *Aotus* karyotype appears to have evolved generally through fusion, as the highest diploid numbers are among the gray-necked northern group, the lowest numbers among the animals to the south. Ma (1981) and Galbreath (1983) had posited an ancestral *Aotus* of $2n = 54$, before a published description of the karyomorph $2n = 58$ (Defler *et al.* 2001; Torres *et al.* 1998; Giraldo *et al.* 1986). Our analysis

Table 3. Phenetic key to species of gray-necked *Aotus* (according to Hernández-Camacho and Cooper 1976; Hershkovitz 1983; Ford 1994).

1.1	Part or entire side of neck including area behind and below ear, and not less than medial portion and posterior half of throat orange or buff like chest. Red neck species group (south of Río Amazonas)
1.2	Entire side of neck including area behind and below ear, grayish agouti or brownish agouti like flank or outer side or arm; throat from entirely grayish or brownish agouti to entirely orange or buff. Gray-neck species group (north of Río Amazonas)
Gray-neck species group	
2.1	Inner side of limbs entirely grayish agouti like outer side or with orange or buffy of chest and belly extending to or slightly beyond midarm or midleg rarely to ankle; pelage of dorsum short and adpressed to long and lax; coloration of upper parts of body variable; middorsal band, if present, broad, blackish, brown or orange and not well defined, temporal stripes separate or united behind (Hershkovitz [1983] added that the interscapular whorl or crest is absent in all specimens of this group; Ford [1994] found that this is unreliable). 3
2.2	Interscapular whorl or crest present with raised hairs directed backward and laterally; gular gland long (5 cm), thin, the surrounding hairs extending outward from sides (according to Hershkovitz (1983). Ford (1994) rejected this and distinguished <i>A. brumbacki</i> as belonging phenotypically to 4.1 and 4.2; Hernández-Camacho and Cooper (1976) identified <i>A. brumbacki</i> as <i>A. trivirgatus</i> , and described the taxon as “short-to-medium hair coat usually of a rather pure gray color with comparatively light-colored hands and feet due to rather short, dark, apical hair tips slightly more apparent than those of <i>A. t. griseimembra</i> ”. 5
3.1	Long fluffy hair (long and lax), feet may or may not have black hairs. <i>Aotus lemurinus</i>
3.2	Hair of dorsum short and adpressed. 4
4.1	Feet with black hairs (Hernández-Camacho and Cooper 1976). <i>Aotus zonalis</i>
4.2	Feet with light brown hairs (Hernández-Camacho and Cooper 1976). <i>Aotus griseimembra</i>
5.1	With raised hairs directed backward and laterally; gular gland long (5 cm), thin, the surrounding hairs extending outward from sides (according to Hershkovitz [1983], but Ford [1994] rejected this). <i>Aotus brumbacki</i>
5.2	Temporal stripes nearly always united behind (Hershkovitz [1983] and Ford [1994] both agreed that this is an important diagnostic character for this species); Hershkovitz (1983 also wrote “malar stripe well defined to absent; pedal digital tufts thin, not extending beyond unguis; size smaller, tail length 340(308-363)38 N. <i>Aotus vociferans</i>

suggests that in fact the ancestral *Aotus* was probably $2n = 58$, due to the acrocentric chromosome that is involved in two different rearrangements, in *A. brumbacki* and *A. griseimembra* (Defler *et al.* 2001: p.48, Fig. 8).

During the late Miocene, the paleo-Amazon River emptied into the Pacific Ocean, creating a historic barrier to the south. Later, perhaps due to the rising Cordillera, *Aotus* was able to extend south of the great river and, in the process, bleaching of the blackish-brown eumelanin and the acquisition of the reddish pheomelanin hairs of its ventrum and neck took place, thus producing the “red-necked” group, which became isolated south of the great river with the continuing rise of the Cordillera.

Chromosome evolution takes place not by addition or subtraction so much as rearrangement of genetic material, so that animals with large karyotypic differences still retain their phylogenetic inheritance somewhere upon the chromosome arms (Martin 1990: 548). If the chromosome arms are rearranged, difficulties start to arise because of pericentric inversions, centric rearrangements or fission or fusion (perhaps via Robertsonian translocations) in attempts at meiotic synapsis, and it becomes impossible for genetic recombination to occur.

Some interpopulational (inter-karyomorphic) polymorphs, which surmount problems of chromosome differences (though the known polymorphic karyomorphs are only present in a one-step series of three karyotypes, not in wide differences, as exist between many karyomorphs), are able to maintain a polymorphic condition within the karyomorph. Examples of these are *Aotus vociferans* ($2n = 46, 47, 48$), *Aotus griseimembra* ($2n = 54, 55, 56$), and *Aotus zonalis* ($2n = 52, 53$, although one expects that 54 will be discovered in the future), but most crosses between different species should cause problems of infertility or reduced fertility in F_1 or F_2 generations. Each of these polymorphisms seems to maintain itself and population samples from each have contained each of these karyotypes (Giraldo *et al.* 1986). These chromosome differences then become species isolating mechanisms which then work to maintain the integrity of the species and its karyomorph. It is probable that other pre-mating isolating mechanisms have evolved, most likely in the form of such as displays, vocalizations, and pheromones—anything that would be effective at night to allow two animals to recognize each other as the same species.

It seems doubtful that extensive chromosome variation in *Aotus* is a reflection of active phenotypic evolution, since morphological differences in *Aotus* are quite difficult to determine. Many authors have taken the view that chromosomal rearrangements do not have special adaptive significance and only contribute to reproductive isolation (White 1973, 1978; Martin 1990), although it has been justly pointed out that there have been many linked clusters of genes recognized in mammals, and this suggests that the order that is found of genes upon the chromosome could have selective differences (Bodmer 1975, 1981). Chromosome number should be adaptive in as much as it affects the level of recombination that can occur, so that large diploid numbers have greater capacities

for genetic recombination than small diploid numbers (Martin 1990). Possible recombinations vary exponentially with an increase in haploid number, so that even an increase in diploid number from 56 (lowland *Aotus*) to 58 means a vast increase in possibilities for recombination (Dutrillaux 1986; Martin 1990). It is, then, significant that the autochthonous *Aotus lemurinus* with a karyomorph of $2n = 58$ (the highest known diploid number in the genus) inhabits the Cordillera de los Andes above 1,500 m to 3,200 m, where it must be adapted to many different habitat types, while lower diploid numbers are found in karyomorphs from lowland and more homogeneous habitat.

Species Concepts

Recently Groves (2001: pp.30–31) has suggested that primatologists should accommodate to the “phylogenetic species concept (PSC)” as defined by Cracraft (1983), replacing entirely the “biological species concept (BSC)”, because of various criticisms of the older view of species that include: the indeterminate status of geographic isolates, the overreliance on reproductive barriers to define species, and difficulties in demonstrating reproductive isolation, hybridization between putative species, the difficulties in highlighting discrete variation. Cracraft (1983) defined his species concept as “the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent”, and argued that “Species possess, therefore, only unique combinations of primitive and derived characteristics, that is, they simply must be diagnosable from all other species. This does not mean, however, that such a definition is predicated on reproductive disjunction as is the BSC, but only on an acknowledgment that all species definitions must have some notion of reproductive cohesion within some definable cluster of individual organisms.” Cracraft (1983: p.170). He criticized the BSC especially on the basis of a recognized conflict of taxonomic practices with systematic analysis and his belief that “the pattern of reproductive disjunction among taxa does not necessarily correlate with the history of their differentiation”, thus making any speciation analysis incomplete (Cracraft 1983: p.160).

We believe that it is true that modern biology has not developed adequate tools for the analysis and description of phylogenetic history. Molecular analysis is, after all, very recent, and classificatory criteria are still being considered and taxonomies often ignore karyological, and other, information. Thus, real evolutionary variation is often not reflected in the taxonomic scheme that is in use; but, we do not think that a PSC model will solve these problems, especially if it ignores reproductive barriers.

A taxonomist who was just “conscientious and spread the net as widely as possible, taking osteodental, soft anatomy, external, ethological, karyological, and molecular features into account *to the extent that they are available* [our emphasis]” (Groves 2001: p.31), would be describing a taxon that might accord with a biological species. But such

taxonomies are few and far between. Instead we have “species” on the basis of differences in hand color, black or white (*v. Callicebus medemi*), or other “species” (for example of the *C. torquatus* complex) that have been described as subspecies first, then just bumped up (revision of Van Roosmalen *et al.* 2002). Species are often described on the basis of some sharply distinct feature. This is the argument of the separation of *Lagothrix lugens* and *L. lagothricha*, (even though they actually have much phenotypic overlap and *L. l. lugens, sensu* Fooden [1963], actually contains at least 2–3 distinctive phenotypes of which we are aware [Groves 2001: pp.176–177, pp.190–192]). To upgrade all subspecies to species because “we increasingly find the concept of subspecies to be of minimal value in describing the diversity of Neotropical primates”, we see as only moving the problem up one level, and obscures the reality of a real evolutionary unit, the biological species, without actually solving the problem of the description of diversity (Van Roosmalen *et al.* 2002). If separate lineages are identified using all possible criteria, including karyological and molecular, many such “species” will be identical to a biological species. However, ignoring karyological evidence in favor of phenotypic and the use of small pelage differences alone only takes us back to the typological species concept of 150 years ago. The biological species concept should not be ignored just because it is not easily translated into an operational definition. The “subspecies” concept is useful to classify phenotypic diversity within a polytypic species, but the fact that we now recognize so many other levels of diversity, especially genetic polymorphism, only points to the need to find new methods of classifying the diversity within a species, and these methods are only now being formulated.

Possible Future Research

More *Aotus* karyotypes must be collected from individuals of known provenance to better understand their geographic distribution. This need not result in the death of the individuals which could be photographed and released at the capture site. High altitude *Aotus* karyotypes from the Cordillera de los Andes are needed to confirm the karyotype of *A. lemurinus*, and in the Sierra Nevada to confirm the karyotype of *Aotus griseimembra*. More *A. zonalis* karyotypes are needed which we predict will result in the discovery of individuals with a diploid number of 54. It would be of great interest to locate any hybrids in *Aotus* colonies between *A. zonalis* and *A. griseimembra* and to identify whether they are sterile or fertile. The poorly-understood distributions of *A. brumbacki* and other night monkeys east of the Colombian Andes need to be plotted using karyotypes of individuals. New Maipures karyotypes need to be analyzed to be certain of the phylogeny of the populations there. *Aotus* in eastern Colombia need to be studied for karyotype, especially since phenotypes seem to be related to *A. trivirgatus*, and the true karyotype for *A. trivirgatus* needs to be established. The distribution of *Aotus jorgehernandezii* needs to be determined.

In Memoriam

We dedicate this paper to the memory of our colleague and friend, Professor Jorge Ignacio Hernández-Camacho, who passed away on 15 September 2001. Jorge was an inspiration to us both and showed us many paths that needed to be trod, one of them being detailed consideration of the northern *Aotus*. He accompanied us along this path for part of the way (see Defler *et al.* 2001). Jorge’s dedication to the Colombian biota and to the unfinished journey provoked us to extend the arguments in our previous paper, which we present here.

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