TAXONOMIC STATUS OF *AOTUS HERSHKOVITZI*: ITS RELATIONSHIP TO *AOTUS LEMURINUS LEMURINUS*

Thomas R. Defler[1], Marta Lucia Bueno[2] and Jorge I. Hernández-Camacho[3]

[1]*Instituto Amazónico de Investigaciones, Universidad Nacional de Colombia, Apartado Aéreo 215, Leticia (Amazonas), Colombia.*
[2]*Departamento de Biología, Universidad Nacional de Colombia, Apartado Aéreo 144900, Santa Fe de Bogotá, Colombia.*
[3]*Fundación Biocolombia, Santa Fe de Bogotá, Colombia.*

Abstract

We analyze various taxonomic problems of northern *Aotus* and describe the phenotype and karyotype of specimens, which have been called *Aotus hershkovitzi* since their discovery. Karyotypes from Panama with a diploid number of 2n = 55–56 had been referred to as *Aotus lemurinus lemurinus* but actually belong to *Aotus lemurinus zonalis*, a taxon found throughout the Pacific lowlands of Colombia, extending to Panamá and the Río Sinú on the Caribbean coast of Colombia. *Aotus lemurinus zonalis* is different phenotypically and karyologically from that of the Colombian Andes population (*Aotus lemurinus lemurinus*). We correct Hershkovitz' designation of the Quindío Pass as an amended type locality for *Aotus lemurinus*. There are no solid grounds to reject the vicinity of Santa Fe de Bogotá as type locality, and this should be listed as the correct type locality. We then point out that as the karyotype of *Aotus lemurinus lemurinus* has not been described and as the specimens called *Aotus hershkovitzi* are phenotypically within the range of other *Aotus lemurinus lemurinus,* that *Aotus hershkovitzi* is a synonym for *A. lemurinus lemurinus*, which should now be recognized as having a diploid karyotype of 58 as well as the highest Fundamental Number (76) known for the genus. This interpretation is supported by the discovery of an *Aotus* (the Murrillo specimen) with 2n = 58 from the Cordillera Central. We suggest further that the karyotypes published for *Aotus lemurinus griseimembra* need to be confirmed with specimens from known collection sites and that, in fact, *Aotus* from lowland sites of the Caribbean coast may be another taxon, yet to be described. Furthermore, we clarify the unwarranted assumption that the origin of the "Quindío specimen" described karyologically by Torres *et al.* (1998) is from this region, but may represent an undescribed species from an as yet unidentified locality. Finally we suggest that in fact the "subspecies" of *Aotus lemurinus* may in fact be full species in light of their karyological differences. In order to clarify the *Aotus* species it is important to do specific systematic research, including the collection of specimens from specific localities.

Key words: *Aotus lemurinus lemurinus, Aotus hershkovitzi*, *Aotus* taxonomy, New World monkeys, Platyrrhini, Cebidae, night monkey, owl monkey

Resumen

Se analizan varios problemas taxonómicos de los *Aotus* del norte y se describe el fenotipo y cariotipo de ejemplares que han sido denominados *Aotus hershkovitzi* desde su descubrimiento. Los *Aotus* de Panamá con cariotipos (2n = 56–55) designados como *A. lemurinus lemurinus,* corresponden a *Aotus lemurinus zonalis,* taxon que puede ser diferenciado tanto en fenotipo como en cariotipo de las poblaciones andinas Colombianas de *Aotus lemurinus lemurinus. A. l. zonalis* está presente en las zonas bajas del pacifico desde Panamá hasta Colombia extendiéndose hasta el valle del río Sinú en la costa Caribe de Colombia. Proponemos una corrección de la localidad típica de *A. lemurinus.* Para Hershkovitz, la localidad tipo de esta especie fue restringida a el "Paso de Quindio." Nosotros sugerimos que no hay argumentos solidos para efectuar esta restrición en la localidad tipo de esta especie por lo cual proponemos que la localidad tipo correcta para este taxo debe ser "Santa fe de Bogotá." Según nuestro criterio, el cariotipo del verdadero *Aotus lemurinus lemurinus* aun no ha sido descrito, y los ejemplares conocidos como *Aotus hershkovitzi* corresponden en fenotipo y en rango de distribución a los *Aotus lemurinus lemurinus,* por lo cual *Aotus hershkovitzi* es un sinónimo de *Aotus lemurinus lemurinus,* que debe ser reconocido por el numero cromosómico (N = 58) y numero fundamental (NF = 76), los mas altos para el genero entre los cariotipos hasta hoy descritos. Esta interpretación esta basada en el hallazgo de un ejemplar (espécimen de Murillo) de 2N = 58 en la cordillera Central de los Andes. Es necesario determinar el numero cromosómico de *Aotus lemurinus griseimembra* a partir de ejemplares colectados en lugares cercanos a su localidad tipo, en la costa Caribe, que pueden conformar una entidad taxonómica diferente aun no evaluada. Con respecto al ejemplar del "Quindio" descrito cariológicamente por Torres *el al.* (1998) creemos que sin duda corresponde a un nuevo taxon que debe ser descrito, y definida su distribución. Finalmente, sostenemos que las "subespecies" *de Aotus lemurinus*, por sus diferencias carilógicas y fenotipicas, corresponden a especies. Es indispensable para clarificar el estado real de la diferenciación especifica de los *Aotus*, realizar un estudio sistemático, con colecciones de ejemplares en localidades especificas.

Palabras claves: *Aotus lemurinus lemurinus, Aotus hershkovitzi,* Taxonomía *de Aotus,* Primates del nuevo mundo, Platyrrhini, Cebidae, Mico de noche.

Introduction

Hershkovitz (1949: 400) first considered *Aotus* as a monotypic genus in his account of northern Colombian Primates, although he recognized several subspecies for *A. trivirgatus* (Humboldt, 1812). This scheme was followed by many authors (for example, Hill, 1960: 169–179; Cabrera, 1958). Thorington and Vorek (1976), however, pointed out that the subspecific classification of night monkeys had probably hampered any understanding of the complex geographic variation in *Aotus*. The discovery of karyotypic polymorphism in *Aotus* by Brumback *et al.* (1971) has made it necessary, during the past few years, to recognize several species of *Aotus*. Brumback (1973) recognized *Aotus griseimembra* Elliot (1912: 36; type locality, Hacienda Cincinnati [also known as Valparaíso] southeast of Santa Marta, on the northwestern slope of the massif of Sierra Nevada de Santa Marta, Magdalena, Colombia; 1,480 ft.) as a full species from northern Colombia, and he treated night monkeys from Perú as *A. trivirgatus*, although this definition of *Aotus trivirgatus* is no longer preserved in present day taxonomy according to Hershkovitz (1983). Later, Brumback (1974) distinguished a third karyotype, which he assigned to *A. azarae* (Humboldt, 1812; type locality: right bank of Río Paraguay in north-east of Argentina). However, Hershkovitz (1983: 217–223) later described this taxon as a new species *Aotus brumbacki,* and redetermined the type locality as the Villavicencio region, Department of Meta, eastern Colombia.

Work by Ma *et al.* (1976a, 1976b, 1977, 1978, 1980) described various other karyotypes of captive *Aotus*, resulting in the recognition of the polymorphic 2n = 55, 56 for animals said to be "Panamanian" and 2n = 46 for upper Amazonian specimens. They clarified the karyotype of *Aotus nigriceps* Dollman (1909: 200; type locality: Chanchamayo, Peru, 3000 ft) and *Aotus boliviensis* Elliot (1907: 189; type locality: Provincia of Sara, Bolivia), which had been described by de Boer (1974), although they continued using *Aotus trivirgatus* as a species including all members of the genus (Ma *et al.*, 1976b, 1980).

Hershkovitz (1983) described two new species, *A. brumbacki* and *A. nancymai*, and he attempted to bring order out of the chaos that had been *Aotus* taxonomy by proposing a scheme whereby a total of nine species were recognized. These were represented by the so-called "red-necked" species group, distributed almost entirely south of the Amazon River and including *A. azarae*, *A. infulatus*, *A. miconax* and *A. nancymai,* and the "gray-necked" species group, occurring almost entirely north of the Amazon River and including the species *A. brumbacki, A. lemurinus* (which he defined as including populations from Panamá and northern and Andean Colombia)*, A. trivirgatus* and *A. vociferans.*

Ford (1994) published an extensive morphometric study of the skulls of 193 *Aotus* specimens and pelage characteristics of 105 adult *Aotus*. This analysis showed "mixed variation" across almost the entire range of *Aotus.* She interpreted the cline of northern Colombian *Aotus lemurinus* (which Hershkovitz [1983] defined as including populations from Panamá as well as northern and central Colombia), *A. brumbacki* and *A. vociferans* as one clinal species, with *A. trivirgatus* being strongly separable from this clinal "*Aotus lemurinus"* (*sensu* Ford, 1994).

In 1981 Jairo Ramírez-Cerquera and Jaime Umaña collected four specimens of *Aotus* in the upper valley of the Río Cusiana (*vereda* [1, notes at end of paper] of Corinto in the Cusiana river valley, Departament of Boyacá), Colombia, in the putative geographic range of *Aotus lemurinus* (*sensu* Hershkovitz**,** 1949: 408, fig 58; *sensu* Hernández-Camacho & Cooper, 1976:46, fig. 6) or *Aotus brumbacki* (cf. Hershkovitz, 1983: 218, Fig. 2) [2]. Ramírez-Cerquera and his collaborator Marta L. Bueno studied the four specimens for karyotype. Ramírez-Cerquera (1983) reported the diploid number (2n = 58) for all of the four animals, the highest number yet reported for the genus, and he referred to these animals as *Aotus hershkovitzi* for the first time in the literature.

Giraldo *et al.* (1986) included *Aotus hershkovitzi* in their study of northern Colombian *Aotus* karyotypes, which they referred to as *Aotus* sp. They showed that all but four of the chromosomes were homologous with *A. lemurinus* (KII, KIII & KIV, *sensu* Ma *et al.*, 1976a, which correspond to populations of *A. l. griseimembra*). Hershkovitz (*verbatim*) initially thought that the four Cusiana animals represented a new karyotype for *Aotus lemurinus griseimembra.* Later, Hershkovitz (*verbatim*) changed his mind and suggested that this material represented a new species and urged the publication of a description of the new species, which Jairo Ramírez-Cerquera (1983:146) proposed be named *Aotus hershkovitzi* in a paper read at the Primate Symposium of the IX Latin American Congress of Zoology at Arequipa, Perú. Ramírez-Cerquera briefly recorded the origin of the original four specimens, giving as distinguishing characters long hair, low sensibility to experimental infection with *Plasmodium falciparum* as compared to *Aotus brumbacki* and *Aotus vociferans* and a unique diploid number. Only the diploid number of 58 was diagnostic, distinguishing the taxon from any other known karyotypic number for the genus. He mentioned, furthermore, the possibility that the species seemed to be phylogenetically closer to the populations of *Aotus* from the lowlands of eastern Colombia than to *Aotus lemurinus* from the highlands and inter-Andean valleys of Colombia, perhaps based on *Aotus hershkovitzis* lack of sensibility to *Plasmodium falciparum.*

The name *Aotus hershkovitzi* has become generally recognized by the scientific community (Rylands *et al.*, 1995, 2000) and was listed in the taxonomic reference book *Mammal Species of the World: A Taxonomic and Geographic Reference* by the author of "The Primates" (Groves, 1993: 256; type locality, department of Meta, east side of Cordillera Oriental) [3] as a full species, *Aotus hershkovitzi* Ramírez-Cerquera 1983. In this article we analyze the validity of *A. hershkovitzi* from a nomenclatural and taxonomic point of view, and its relationship with the Andean population of *Aotus* (*Aotus lemurinus lemurinus, sensu stricto*) and *Aotus brumbacki.*

Methods

We analyzed the nomenclatural and taxonomic aspects of Andean populations of *Aotus lemurinus* and *Aotus hershkovitzi* including phenotypic and karyotypic variation. In the description of pelage coloration particular attention was given to *Aotus hershkovitzi*, and we used the color nomenclature of Ridgway ("1912"=1913), capitalizing the initial letters. Standard measurements based on fresh material were taken from the specimen label.

Chromosome preparations were obtained by M. L. Bueno using standard methods for lymphocyte culture (Moorhead *et al.*, 1960). Blood samples were taken with heparinized syringes (Liquemine, Roche). Peripheral blood was cultured in Minimal Essential Medium (MEM, Sigma) with 20% of bovine fetal serum, 10% of Penicillin-streptomycin, Sigma. As mitogens, 0.35 mls P-Phytohemaglutinin (Difco, at 1:16 dilution) were used. A duplicate culture with a crude extract of *Vicia faba* lectin (the procedure of Arango and Moreno, 1977) gave the best preparations. Optimum culture time was 66 hours.

QFQ, GTG and CBG banding were carried out as described by Capersson *et al.* (1970), Seabright (1971) and Summer (1972) respectively. Late DNA replication patterns (RBG) were observed after a 5-bromodeoxyuridine (Budr) terminal pulse (see Camargo and Cervenka, 1980). CBG banding was accomplished using preparations previously analyzed with QFQ banding. Nucleolar organizer regions (NORs) were located by the procedure of Goodpasture and Bloom (1975).

The following acronyms have been used:

AMNH - American Museum of Natural History, New York.
BMNH - British Museum (Natural History) London.
FMNH - Field Museum of Natural History, Chicago.
ICN - Instituto de Ciencias Naturales, Museo de Historia Natural, la Universidad Nacional de Colombia, Santa Fé de Bogotá.
INDERENA - Instituto Nacional de los Recursos Naturales Renovables y del Medio Ambiente, Ministerio de Agricultura, Santa Fé Bogotá.
IVH - Instituto de Investigaciones de Biodiversidad Alexander von Humboldt, Ministerio del Medio Ambiente, Villa de Leyva, Boyacá, Colombia.
MCZ - Museum of Comparative Zoology, University of Harvard, Cambridge, Massachusetts.
MNHP - Muséum National d'Histoire Naturelle, Paris.
UNIFEM - Unidad Investigativa Federico Medem (INDERENA), Santa Fé de Bogotá.
USNM - National Museum of Natural History, Smithsonian Institution, Washington, DC.

Aotus lemurinus lemurinus
(I. Geoffroy-St. Hilaire, 1843)

Synonymic history: *N[yctipithecus] lemurinus* I. Geoffroy-Saint Hilaire, 1843: *Comptes Rendus Acad. Sci., Paris* 16: 1151 (original description of taxon).

Nyctipithecus lemurinus I. Geoffroy-Saint Hilaire, 1844: *Arch. Mus. Hist. Nat., Paris* 4: 24, pl.2.

Nyctipithecus villosus J. E. Gray, 1847: 6 (original description; type locality: Santa Fé de Bogotá).

Nyctipithecus hirsutus J. E. Gray, 1870: 58 (*nomen nudum*; *lapsus colanit for hirsutus*).

Aotus lanius G. Dollman, 1909: 202 (original description; holotype BMNH 1890.2.22.4, adult female, skin and skull, collected by White, "Tolima Mountains," 2°20'N, 6000 feet, now Department of Huila, Colombia). D. G. Elliot, 1913: 12-13 (type locality: "Tolima Mountains," Río Toche, 7000 feet).

Aotus aversus D. G. Elliot, 1912: 251 (original description; Fusagasugá, Cundinamarca, Colombia).

Aotus pervigilis D. G. Elliot, 1912 (La Candela, Huila, Colombia).

Aotus vociferans (*non Nyctipithecus vociferans* Spix, 1823) D. G. Elliot, "1912"[=1913]: 15-16 (*partim*; "mountains of Tolima"; *Nyctipithecus lemurinus* (original series examined; regarded as synonym).

Aotus lemurinus J. A. Allen, 1916, *Bull. Amer. Mus. Nat. Hist.* 35: 234 (Fusagasugá, type and topotype of *aversus* D. G. Elliot; *A. vociferans* Elliot, *non Nyctipithecus vociferans* von Spix, 1823, = *lemurinus* I. Geoffroy-St. Hilaire, 1843). Groves, 1993, *Primates*, in *Mammal Species of the World: A Taxonomic and Geographic Reference*, p.25 (listed type locality as Department of Caldas, Quindio, Colombia).

Aotus trivirgatus Groves and Pulido, 1982: 226 (*partim*).

Aotus lemurinus lemurinus Hershkovitz, 1983, *Am. J. Primatol.* 4(3): 209, 211, 214 (fig. 2), 233 (*partim*; Andean Colombian populations, comparisons with other taxa of *Aotus*). Rylands *et al.*, 1995, *Neotrop. Primates* 3(suppl.): 119, 122, 127, 132, 138, 149 (*partim*; Andes, Colombian populations; Neotropical primate classification and conservation). Rylands *et al.*, 2000, *Neotrop. Primates* 8(2): 62, 65, 69, 75 (*partim*; Andean Colombian populations Neotropical diversity).

Aotus trivirgatus lemurinus Hershkovitz, 1949, *Proc. U. S. Natl. Mus.* 98(3232): 405 (taxonomic revision). Hernández-Camacho and Cooper, 1976, *Neotropical Primate Field Studies and Conservation,* pp.35–69. Thorington and Vorek, 1976, *Lab. Anim. Sci.* 26(6): 1006–1021 (review of skeletal development and pelage color and patterns).

Aotus hershkovitzi Ramírez-Cerquera, 1883, *IX Congr. Latinoamer. Zool* (abstracts): 146 (first published mention of intention to name the taxon; brief diagnosis). Groves, 1993, *Mammal Species of the World,* Primates: 256 (reference to species; type locality incorrectly recorded as "Department of Meta"). Rylands *et al.*, 1995, *Neotrop. Primates* 3(suppl.): 119, 122, 127, 138, 149 (species listed according to conservation status and IUCN Mace-Lande system). Torres *et al.*, 1998, *Am. J. Primatol.* 44(4): 268, figs. 8a-b (recognize a different karyotype group for this species). Rylands *et al.*, 2000, *Neotrop. Primates* 8(2): 62, 65, 69, 75 (Neotropical diversity). Groves, 2001, *Primate Taxonomy*, p.164.

Aotus "hershkovitzi", Defler, 1994, *Trianea,* 5: 265 (species conservation). Defler, 1996, *Neotrop. Primates* 4(3): 77 (IUCN classification of Colombian primates).

[*Aotus* sp.] L1, L2, L3 and L4, Espinal *et al.*, 1984, *Amer. J. Trop. Med. and Hyg.* 33: 777–781, Table 1-2, Fig. 1-2 (report on serology and malariology of this species as compared to *A. lemurinus* and *A. vociferans*). Giraldo *et al.*, 1986, *Biomedica* 6(1-2): 11–12, fig. 6 (brief description of karyotype, included in a new group "X" following the system of Ma *et al.*, 1976a, 1978).

[*Aotus sp.*] Mittermeier *et al.*, 1988, *Ecology and Behavior of Neotropical Primates*, Vol. 2: 34 (reference to Ramirez's desire to name a new species of *Aotus* for Philip Hershkovitz).

Type locality: A problem with *Aotus lemurinus* is the lack of precision of the type locality for the species, which was first listed as "Nouvelle Grénade" by I. Geoffroy-St. Hilaire (1843: 1151), who did not designate a type specimen. In the following year the same author listed the type locality as "Santa Fé de Bogotá" (I. Geoffroy-St. Hilaire, 1844: 58). Rode (1938: 38) selected as "holotype" (= lectotype) an adult (?) male skin (mounted with skull no. 102a), purchased from Parzudaki, and another specimen designated as allotype (= lectoparatype), also purchased from Parzudaki in 1842. Designations made by Rode are fully valid, according to the International Code of Zoological Nomenclature. I. Geoffroy-St. Hilaire's (1844: 58) restriction of the type locality to "Santa Fé de Bogotá" did not take into consideration the material collected by Justine Goudot in the "Quindiu" [= Quindio region] already existing in the Paris Natural History Museum. This strengthens the case for I. Geoffroy-St. Hilaire's choice of the Bogotá region as specimens for the type series [4]. For further details about the lectotype see Hershkovitz (1949: 406).

Despite Geoffroy-St. Hilaire's designation of Santa Fé de Bogotá as type locality, Hershkovitz (1949: 407) restricted the type locality to the Quindío Pass (Cordillera Central), remarking that "this is the only authentic locality for specimens of the original series" and, further, "as *Aotus* does not occur in the Bogotá region proper, which is savanna, the type locality is here restricted to that of the Goudot specimens." Obviously the "Bogotá region proper" should include an area surrounding the city of Santa Fé de Bogotá in the Eastern Cordillera of the Andes. In a comparatively short distance from this city a wide variety of ecological conditions occur, including humid subtropical [sub-Andean] and temperate forest, as well as edaphically and climatically determined semi-arid conditions [5], so that the Bogotá region cannot be regarded as natural savanna as a whole. At the time, Hershkovitz (1949) was not acquainted personally with the Bogotá region. He probably was influenced by the fact that Chapman (1917) had classified the Bogotá plateau in the "arid temperate zone." He did not consider the fact that most of the mountains surrounding the so-called "savanna de Bogotá" actually were originally covered by humid forest where *Aotus* occurred. Furthermore, available precise records for this species include localities such as the forest adjoining the Pedro Palo lake (about 2,100 m.), Subía (*ca.* 1,700–2,500 m.), Cuchilla de Cruz Grande above Fusagasugá (2,000 m.) and the Fusagasugá type locality of *Aotus aversus* Elliot (a synonym for *A. lemurinus*). Consequently, since the original restriction "Santa Fé de Bogotá" as type locality for *A. lemurinus* and localities such as those mentioned are separated by distances that were covered in a 1–2 day mule ride, we believe that the authenticity of Santa Fé de Bogotá interpreted in a broad sense can be regarded as a valid designation of the type locality, and could be restricted even more precisely to the neighborhood of Fusagasugá (1,700–2,000 m.).

Specimens examined: Phenotypic analysis for *Aotus lemurinus* is based on an examination by JIH-C of almost all Colombian specimens held within the country (ICN, IVH = INDERENA), the United States of America (AMNH, FMNH, MCZ and USNM) as well as from the MNH (Museum National d'Histoire Naturelle, Paris) and the BMNH (British Museum of Natural History, London) totaling about 130 specimens of geographically referenced *Aotus lemurinus* collected from sites spread throughout the northern part of Colombia. A map of the origins of these specimens can be seen in Defler (in press).

Characters: According to Hershkovitz (1949: 407) distinctive characters are the following: (1) on average this is the darkest of the subspecies and (2) pelage of *Aotus lemurinus lemurinus* is extremely coarse [6], long and lax and "the majority of the specimens from the interior of Colombia are of higher altitudes than those of the coast and show, consequently, larger, coarser and laxer pelage. Beyond this, no single character serves to unite individuals here held to represent *lemurinus* in an assemblage distinct from all others. Variability in color and character of pelage is so great among these night monkeys that two discrete family groups of the same locality are apt to differ more from each other than either of them from a series of any other locality in the Colombian Andes." Thorington and Vorek (1976: 1013–1014) concur that phenotypic variation is so great as to not be useful for subspecific differentiation and that among northwestern South American *Aotus* "there is greater east-west differentiation than there is north-south."

There are two types of phenotypic variation within the area inhabited by *Aotus lemurinus lemurinus*. The first type is intrapopulational and involves more grey and less reddish and the opposite, and the development of a dark, middorsal stripe is quite variable. The second character is clinal and involves a progressive lightening of the dorsal surface of the hands and the feet and begins on the west slopes of the Cordillera Occidental and on the west slope of the Cordillera Central in the upper Magdalena valley, where the hands and feet are darkest, while on the east slope of the Cordillera Central a tendency is seen which continues south along the slope to the western slopes of the Cordillera Oriental and involves a gradual change of the hands and feet from darker to lighter. This culminates on the western slopes of the Cordillera Oriental and is due to the increasing width of the un-pigmented basal hair band.

Distribution: Hershkovitz (1949: 407; fig. 58) defined the distribution of *Aotus lemurinus lemurinus* as "forested parts of the Colombian Andes, exclusive of the northern half of the Sierra de Perijá." This distribution included the lowlands of the middle and upper Magdalena river valley and parts of the departments of Antioquia, Santander, Boyacá, Caldes, Cundinamarca, Tolima and Huila. Hershkovitz (1983: 214; fig. 2) amended this distribution to include the lowlands of the middle and upper Magdalena river valley as the distribution for *Aotus lemurinus griseimembra*. Although material is scarce for the area, phenotypes tend to support this interpretation (despite his assertion that the two subspecies were not separable phenotypically). In reality, it should be pointed out that there are no valid specimens from the highlands of the department of Norte de Santander, Santander, Boyacá or western Arauca, even though these areas were included by Hershkovitz (1949: 407, fig. 58; 1983: fig. 2) in the geographic distribution of lemurinus. Hershkovitz (1949: 407) included the eastern slope of the Cordillera Oriental in the range of his *Aotus trivirgatus lemurinus*, but in 1983, the discovery of *A. brumbacki* modified his original view. Finally, it is important to note that Hershkovitz (1949: fig. 58) included the highlands of the department of Nariño in the range of *Aotus lemurinus lemurinus*, despite the fact that there are no records for that region or for that matter for the entire department.

Hill (1960: 174) gives the distribution of this taxon precisely the same as Hershkovitz (1949: 407), but Hill (1960: map 2 between p.166–167), in his much more inaccurate map, included not only the highlands of the Andes of Nariño but also those of northern Ecuador and the piedmont on the eastern slope of the Ecuadorian Andes. Curiously there is no evidence whatsoever for the presence of *Aotus* in the Ecuadorian Andes. In this article we maintain that *A. l. lemurinus* is basically restricted to the Andean highlands of Colombia. Lowland Pacific coastal *Aotus* as well as the Panamanian and Urabá populations are *Aotus lemurinus zonalis* (see map, Defler, in press).

Supposed *Aotus lemurinus lemurinus* karyotype: An additional problem having to do with the source of the *Aotus lemurinus* karyotype is that Hershkovitz (1983: 211, Table I) chose karyotypes determined from specimens maintained in Panamá, that were collected from two known Panamanian sites and one unknown site (see Ma *et al.*, 1978: 147), as representative of *Aotus lemurinus lemurinus*. We believe that material definitely from Panamá represents another, generally unrecognized taxon *Aotus lemurinus zonalis* (Goldman, 1914) (cf. Hernández-Camacho and Cooper, 1976: 45–46) which Hershkovitz (1949) decided not to recognize. *Aotus lemurinus zonalis* is made up of populations of the Colombian Pacific coast, NW Antioquia and Córdoba as well as Panamanian animals, all of which show darker dorsal hands and feet than *griseimembra* in northern localities. The dark dorsal surface of the hands and feet is an agouti effect due to the brownish tips and light bases of the hairs (Hernández-Camacho and Cooper, 1976: 47). These are the animals which Hershkovitz (1983: 211, Table I; 214, fig. 2) decided to include with *Aotus lemurinus lemurinus*. Karyotypes for authentic Andean *Aotus lemurinus lemurinus* were unknown until now.

***Aotus lemurinus griseimembra* karyotype:** The problem of the karyotype of *Aotus lemurinus griseimembra* is that the karyotypes ascribed to this taxon came from a group of animals of uncertain origin imported from Barranquilla (department of Atlántico, Caribbean coast, Colombia) and studied by Ma *et al.* (1976b). Barranquilla at the time was a center of a widespread animal trade which gathered together primates from a wide area of northern Colombia, most coming from Magange in northern Bolívar, which also traded in animals from many regions of southern Bolívar and southern Magdalena. However, primates came from as far away as Leticia in Amazonas. Photographs were taken of all of these "Barranquilla" primates and their designated "phenotype B" was identified by Hershkovitz as coming from northern Colombia from a population ascribed by him to *griseimembra* Elliot (1912: 33; type locality Hacienda Cincinatti, formerly known as Valparaiso, on the west slope of the Sierra Nevada de Santa Marta, department of Magdalena, Colombia, 1,480 m). As we pointed out earlier, Hershkovitz (1983: 215) stated that the then recognized subspecies of *A. lemurinus* could only be distinguished "by karyotype alone," contradicting his action of identifying *griseimembra* by photo, as reported by Ma *et al.* (1976).

Since the karyotyped animals ascribed to *Aotus lemurinus griseimembra* were imported into the United States from Baranquilla, where *Aotus* specimens from many parts of Colombia arrived for the animal trade (cf. Cooper and Hernández-Camacho, 1975; Thorington and Vorek, 1976), there is no reason to accept that these animals necessarily correspond to this taxon, nor to accept that lowland *Aotus* of north central and northwestern Colombia have the same karyotype as highland forms, as suggested by Hershkovitz

(1983: 215). The lowland and highland populations are referable to several separate taxa, and Hershkovitz (1983: 215) himself has stated, “there is no certainty that the specific name *lemurinus,* based on a high-Andean night monkey of unknown karyotype, is also applicable to the Panamanian *Aotus* with known karyotype, and the holotype of *griseimembra* and its representatives from the type region in the Sierra Nevada de Santa Marta region of northern Colombia.”

From the above analysis we have concluded that *Aotus lemurinus lemurinus* is distributed only throughout the Andean region of Colombia (and perhaps Venezuela) and that the *Aotus* karyotypes used by Hershkovitz (1983) to define *Aotus lemurinus lemurinus* actually are karyotypes for *Aotus lemurinus zonalis.* This conclusion has important implications for the following description of *Aotus hershkovitzi.*

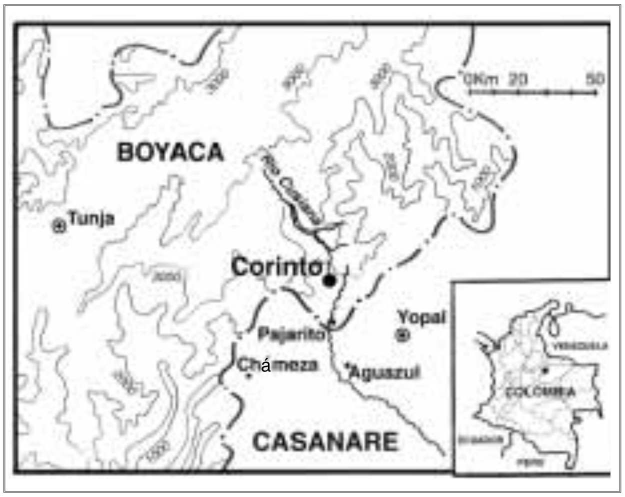

Figure 1. Map of type locality of *Aotus hershkovitzi.*

Aotus hershkovitzi Ramirez-Cerquera, 1983

Holotype: Adult female, skin and skull, ICN no. 8880 (original field numbers L-2 of the Instituto Nacional de Salud and conforming to the probable mother of L-3 and L-4); collected December, 1981, by Jairo Ramírez Cerquera and Jaime Umaña from a family group of four individuals. The skull of this specimen has fully erupted third molars, the basilar suture is closed (but not obliterated) and the skin exhibits staining of the hairs of the post-anal glands, all of which indicate that the specimen is an adult.

Type locality: Right bank of Cusiana River, upper Cusiana River valley, district (*vereda*) of Corinto, municipality of Pajarito, Boyacá department, east slope of the Cordillera Oriental de los Andes, Colombia, 5°25’35”N, 72°42’45”W, 1750 m (Fig. 1). Groves (1993: 256) incorrectly lists the type locality as “Department of Meta, east side of Cordillera Oriental.”

Paratopotype: Subadult female, skin and skull, INDERENA 4140 (No. L-4 Instituto Nacional de Salud), deposited in collection of Instituto de Investigación de Recursos Biológicos “Alexander von Humboldt” with same number as INDERENA, collected December, 1981, by Jairo Ramírez-Cerquera and Jaime Umaña from the same family group as the holotype. Entire body with stomach preserved separately from skin in 70% alchohol.

Distribution: Known with certainty only from the type locality. Karyotypes 2n = 58 have been found from two other unpreserved specimens, one of them from an unspecified locality in the department of Casanare (possibly the Cusiana river valley) and the other said to be a captive animal from Murillo on the eastern slope of the Cordillera Central de los Andes, Tolima. If the latter locality is indeed correct, this would imply sympatry of *A. hershkovitzi* with *A. lemurinus.*

Etymology: The name *Aotus hershkovitzi* first was suggested by Jairo Ramírez Cerquera to honor Philip Hershkovitz for his many contributions to Colombian and Neotropical primatology and mammalogy and for the support and friendship which he offered to many of us during his lifetime.

Diagnosis: A highland *Aotus* belonging to the gray-necked species group (*sensu* Hershkovitz, 1983: 211–212); white orbital ring of hairs interrupted by the temporal dark stripe, continuous with the lateral canthus of the eye (as in *A. lemurinus lemurinus*); broad stripe of agouti-patterned hairs below; malar stripe absent (as in *A. lemurinus lemurinus*); dark temporal stripes faintly convergent posteriorly without merging; sagittal stripe widened and fan-shaped behind and mixed with agouti-patterned hairs (as in *A. lemurinus lemurinus*); mid-dorsal stripe absent; hands and feet agouti mixed with some black hairs; buffy-yellow of throat extends to chin (in contrast to *A. lemurinus lemurinis*, which is duller and lighter with less yellow and with dark hair tips); diploid number 58 and fundamental number 76, higher than any other known for the genus.

Description of holotype: (Figs. 2, 3 a–e, 4) Dorsum with rich reddish brown (*Cinnamon Rufous*) wash extending halfway down tail; typical agouti pattern (Hershkovitz**,** 1977: 90–91) hairs proximal 2/3 (19 mm) dark brown (*Light Grayish Olive*), distal 1/3 as follows (8 mm *Cinnamon Buff* bands, 5–6 mm dark *Benzo Brown* bands, 2–3 mm *Cinnamon Rufous* bands) mixed with some black (*Sepia*) guard hairs giving overall appearance of *Cinnamon Rufous*; sides of neck and body *Cinnamon Buff* to *Cinnamon Rufous* agouti, paler than back; upper arms paler *Pinkish Buff* agouti than sides of body; upper legs agouti *Pale Pinkish Buff* and slightly more reddish than arms; dorsum of hands slightly more reddish than arms with black hairs throughout; dorsum of feet slight reddish wash on brown agouti with long black hairs throughout; neck and chest like belly dull; *Pinkish Buff*; hairs proximal half *Pinkish Buff*, distal half *Pinkish Buff*; throat becomes slightly darkened due to admixture *Sepia* tipped *Pale Pinkish* hairs (vibrissae); ventrum of arms slightly lighter agouti *Pale Pinkish Buff*; skin of hands dark pink

(*Salmon Buffy-Seashell Pink*) with blackened digits; ventrum of legs dull *Pale Pinkish Buff* and *White* on upper thighs with shorter and sparser hair than other parts of body; longer and darker agouti *Pinkish Buff* around ankles, although the base of the hairs are *Light Grayish Olive*; skin of feet dark blackish pink; digits generally darker; ventrum of tail with *Fuscous-Black* distal hair extending closer to body (1/2 tail) than on dorsum of tail; proximal half ventrum of tail rich *Ochraceous-Orange* with *Fuscous Black*-tipped hairs mixed, giving black wash effect; dark tar-like staining of hairs by post-anal glands in ellipsoid 19 mm by 10 mm; head with narrow distinct temporal stripe on right side, extending convergent towards midline of crown to position over ear; left convergent temporal stripe less distinct, more diffuse; doesn't reach ear and the two don't unite; crown same rich *Cinnamon Rufous* as back; two distinct supraocular patches of cream-colored hair with greatest length 17 mm tending towards *Pale Pinkish Buff* at outer points so that patch turns into wedge of lighter *Cartridge Buff* fur between temporal stripe and the forehead patch of basally (*Light Grayish Olive*), dark-tipped agouti hair showing black (*Fuscous Black*) patch, which extends in narrow thread down between the eyes; malar stripe absent; pelage at mid-back 26 mm length; pelage upper tail dorsum 23–24 mm length; pelage midway on sides 34 mm length; no interscapular whorl or crest.

Comparisons: Distinguished from all other known *Aotus* karyotypes by 2n = 58 (Table 1 shows two such comparisons); differentiated from all members of red-necked group by side of neck brownish agouti like side of trunk; from *A. vociferans* of the gray-necked group by absence of interscapular crest or whorl of hairs; from *A. trivirgatus* (which has no interscapular crest or whorl) by an absence of a strongly contrasting mid-dorsal stripe; from *A. lemurinus* mainly by 2n = 58 and FN = 76 although in specimens examined, in contrast to *A. lemurinus,* the *hershkovitzi* have virtually no admixture of dark hairs in gular region. Phenotypic differences between the holotype and the paratopotype are generally slightly lighter tonalities in the paratopotype as compared to the holotype. Length of hair of holotype and paratopotype are within the ranges of that measured from specimens of *A. lemurinus* (ICN 01, 02, 03, and 04) so that two color phases are identifiable (light and dark). The *hershkovitzi,* which is the dark phase, is quite comparable to the darker *A. lemurinus* de Fusagasugá. Measurements included sternum (32 mm/33 mm), interscapular (36 mm/36 mm), dorsum of tail (23–23 mm/unmeasured because of poor state), end of tail (51 mm/unmeasured because of poor state) and flanks (43 mm/44 mm); listed here with first measurement for ICN 8880 and second measurement INDERENA 4140.

Figure 2. Holotype, lateral and frontal views of *A. hershkovitzi*, Ramírez-Cerquera, 1983.

Figure 3. Holotype skull: a) frontal view; b) lateral view; c) dorsal; d) ventral view of the holotype skull; e) dorsal view of lower mandible.

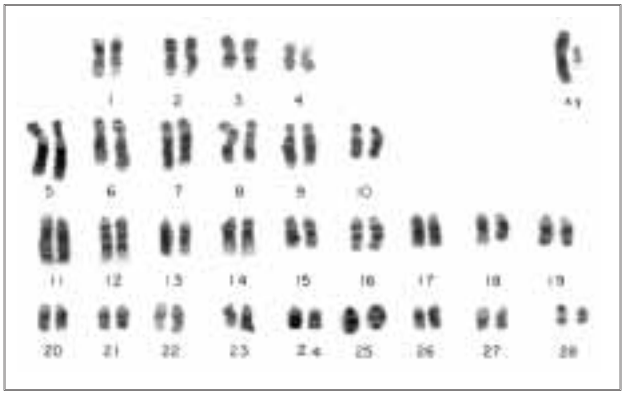

Figure 4. GTG band karyotype of L1, a male Aotus (2n = 58) from the Cusiana River, Boyacá, Colombia.

Description of paratopotype: Dorsum rich *Cinnamon Rufous* wash extending halfway down tail but slightly lighter than holotype; interscapular hairs 21 mm *Light Grayish Olive* + 8 mm *Cinnamon Buffy* band + 4 mm dark *Light Grayish Olive* band + 2–3 mm *Cinnamon Rufous* band = 36 mm in length; overall impression of *Cinnamon Rufous*; intensifying down the tail to mid-tail; side of neck and body *Cinnamon Buffy*, paler than dorsum; upper arms paler *Pinkish Buff* agouti than sides of body; upper legs agouti brown about same tone as arms; dorsum of hands slightly more reddish than arms with black hairs throughout; dorsum of feet slight *Pinkish Buff* wash on brown agouti with black hairs throughout; neck and chest like belly dull *Pinkish Buff*; color hairs half *Pale Pinkish Buff* proximally, half *Pinkish Buff* distally; throat same color throughout; ventrum of arms lighter than dorsal of arms; dried skin of hands *Salmon Buffy-Seashell Pink* with blackened digits; ventrum of legs lighter than dorsal of legs; upper thighs naked of hair (perhaps due to preparation), skin yellowish cast; feet dark yellowish skin coloration; digits black; some dark hairs around ankles; ventrum of tail *Fuscous Black* distal hair extends two-thirds up; proximal hair one-third tail rich *Ochraceous Orange*; no staining of the hairs of the post-anal gland evident and no admixture of black-tipped hairs; head with very faint temporal stripes, darker at corner of eyes and more evident fading out to slight wash and convergent to midline with left stripe slightly more pronounced; crown mixture of agouti brown and black-tipped hairs filling in area between temporal stripes with slight reddish wash; base of hairs same *Light Grayish Olive* color as black hairs + *Cinnamon Buffy* + *Cinnamon Rufous* or alternatively blackish band; two distinct supraocular patches of creamy white hairs tending slightly to more buff posteriorly; dark hairs extend down from forehead to more pronounced black between supraocular patches, no dark malar patch on either cheek; pelage at mid-back 33–35 mm length; pelage upper tail dorsum 22 mm length; pelage midway on sides 30–33 mm length; no interscapular whorl or crest evident.

Crests and whorls: No crests or whorls were detected on the two specimens (*sensu* Hershkovitz, 1977: 81; 1983: 213).

Measurements: See Table 1 for measurements.

Table 1. Homologous chromosomes in 3 taxa of *Aotus.*

Aotus l. lemurinus **2n=58**	***Aotus l. griseimembra*** **2n= 54**		***Aotus brumbacki*** **2n=50**
P.R.	**Ma *et al.* (1976)**	**Yunis *et al.* (1977)**	**Yunis *et al.* (1977)**
1	A4	9	13
2	A5	10p-	-
4	A6	11	-
5	B7	1	1
6	B12	4	3
7	B9	3	2
9	B11	6	6
11	-	-	14p+
12	B13	23	15
13	B14	24	-
14t	B10	12p+	10q
15	B16	16p+	19p+
16	B18	14	17
17	B17	15p+	18p+
18	B15	13	16
19t	A2q	8q	21
20t	A3q	5q	5q
21	B24	19	22
22	B21	20	-
23	B19	18	9
25t	A2p	8p	10p
27	B26	26	-
28t	A3p	5p	5p
X	X	X	X

P.R.: Present report.
t = Chromosomes involved in different Robertsonian translocations in other *Aotus* species.
+/-: Differences between homologues due to additions or deletions of heterochromatin.
p, q : short and long arm of chromosome, respectively. Spaces are left empty whenever chromosome homology cannot be recognized.

Karyology: The karyotype was previously superficially described by Giraldo *et al.* (1983) and placed in a new "karyotype 10 or X" according to a system defined by Ma *et al.* (1976a, 1978, 1980). Torres *et al.* (1998: 298–270) on the other hand referred to this karyotype as "karyomorph 8" (KM) of their own system and further described some of its characteristics.

In both members of the series we found a diploid number of 58 chromosomes and fundamental number (FN) of 76 (Figs. 4–8 a and b). This is the highest diploid number and fundamental number known for the genus (see Hershkovitz, 1983: 211, Table 1). The autosomes were arranged in order of decreasing size (Figs. 4, 5) according to the large groups (A and B) defined by Ma *et al.* (1976). Group A is composed of four pairs of metacentric chromosomes (Pairs 1-4). Chromosome 1 is a marker chromosome with an achromatic region in the long arm, a common finding in *Aotus* and a frequent one in many Cebidae, being the only chromosome containing a NOR (Fig. 6). Group B with pairs 5–10 is conformed of six pairs of submetacentric chromosomes. Short arms of pairs 8 and 10 are entirely heterochromatic. Pairs 11–28 are acrocentric and include a range of size from large to small. Chromosome X is metacentric and very similar to those found in other species of the genus. The holotype female (L2) showed a large telomeric block at the short arm of both X chromosomes; this region is absent in the X chromosome of male L1 but present in L3 (a male juvenile specimen) and confirms the mother-son relationship (Fig. 7).

The distribution of constitutive heterochromatin is essentially centromeric. A distinct heteromorphism in the centromeric region of chromosome 3 was observed in one specimen (L1) (Fig. 7). In addition to centromeric heterochromatin, telomeric heterochromatin blocks were observed at the short arm of chromosomes 2, 5, 7, 9 and at the long arm of chromosome 25, while the short arm of pairs 8 and 10 were

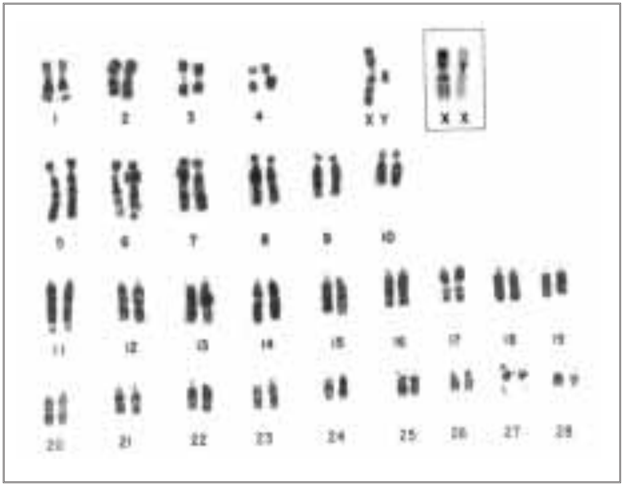

Figure 5. RBG band karyotype of a male Aotus (2n = 58) from the Cusiana River, Boyacá, Colombia. The two X chromosomes from a female specimen are shown inside the box; one X chromosome (right) shows a late replication pattern.

Figure 6. Nucleolar Organizing Region (NOR) in Aotus (2n = 58) from the Cusiana River, Boyacá, Colombia. Arrows point to silver precipitated regions on chromosome No.1.

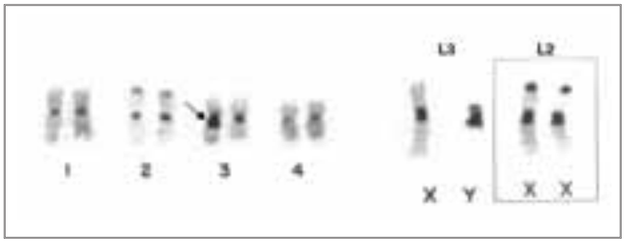

Figure 7. Partial karyotype with C-Band (CBG) showing the polymorphism of pair 3 and X Chromosome of mother (L-2) and son (L-3). Arrows point to the heterochromatic polymorphic region on chromosomes X and 3.

completely heterochromatic. Interstitial heterochromatin regions were found in the long arm of chromosomes 20 and 27. The Y chromosome was metacentric and the smallest of the chromosome complement but was the longest Y of the karyomorphs described by Torres *et al.* (1998). All chromosomes show an exact homology of complete chromosomes and chromosome arms to karyotypes known for *Aotus lemurinus griseimembra* except for the 4 pairs of extra chromosomes which had no apparent homology (Giraldo *et al.*, 1986).

Q-and G-band karyological comparisons between the specimens studied and two other previously described species of Colombian *Aotus* are shown in Table 2. Comparison is limited to euchromatic regions of karyotype II (K-II) of *A. l. griseimembra* (2n = 54; Ma *et al.*, 1976), which agrees with the one described by Yunis *et al.* (1977) for the same taxon and the karyotype assigned to *A. t. trivirgatus* (2n = 50) by Yunis *et al.*, (1977), later recognized as *A. brumbacki* (Hershkovitz, 1983).

Specimens examined: 2. COLOMBIA. Holotype ICN no. 8880 (skin and skull); paratype IVH (INDERENA) no. 4140 (stuffed skin; body preserved apart in 70% alcohol). Two other specimens from the original series, the adult male and the infant male were not preserved. Also examined for *Aotus lemurinus* 4. COLOMBIA. ICN 001, 002, 003, 004 from Fusagasugá and from Pedro Palo.

Serology: Electrophoretic analysis of the serum proteins shows a single "fast" type of albumin band not seen in other *Aotus lemurinus* specimens. Additionally a demarcated band 2 made up of three well-marked alpha-globulin bands was detected. Although three types including this type of albumin band have been identified for *A. l. griseimembra* by Reardon *et al.* (1979), three well-marked alpha-globulin bands have not been observed in any other taxon. Beta- and gamma-globulin were found as an undifferentiated wide stripe in both these specimens and *Aotus lemurinus.*

Malariology: The specimens exhibited low susceptibility to *Plasmodium falciparum.* This resulted in parasitemias of less than 5% after 14–18 days of infection. Animals referred to *Aotus lemurinus griseimembra* showed high susceptibility. Six specimens from the middle Magdalena River and referred to *Aotus lemurinus lemurinus* showed mixed susceptibility: two had low susceptibility and four had high susceptibility (Espinal *et al.*, 1984).

The systematics of *Aotus* is still far from being resolved, and Colombia is particularly difficult because of its topographic complexity, which has surely influenced the genus' evolution. The first confirmed appearance of the genus in the fossil record of La Venta (Huila, Colombia, described as *Aotus dindensis*) dates back to at least the Middle Miocene of 11.8-13.5 million years B. P. (Setoguchi and Rosenberger, 1987), although Kay (1990) has suggested synonymy with *Mohanimico hershkovitzi* described by Luchtehand, Kay and Madden (1986); Rosenberger *et al.* (1990) continue to maintain the fossil to be *Aotus.*

Not only are contemporary phenotypes unusually complicated to distinguish, but variation within populations is high, including two color phases in *A. lemurinus* (dark and light) (Hershkovitz, 1949, 1983; Hernández-Camacho and Cooper, 1976; Thorington and Vorek, 1976). Actually coat color has already proven to be unreliable as a diagnostic tool, as there are many differences which probably are not good genetic markers, as observed by Thorington and Vorek (1976). This does not seem surprising - since the species is nocturnal, there are no strong selective pressures for

Table 2. *Aotus lemurinus lemurinus (=A. hershkovitzi).* Measurements in millimeters.

Specimen No.	Head & body	Tail	Hind foot	Ear	Greatest skull length	Condylo-basal length	Zygomatic width	Biorbital breadth	Postorbital constriction
No. 8880	286	325	88	31	60.8	47.5	40.5	43.3	30.0
No. 4140	302	320	86	29					
	Braincase width	**Mastoid breadth**	**I^1-M^3**	**C–M^3**	**PM–M^3**	**$I1^{-1}$**	**$I2^{-2}$**	**C-C**	**M^{1-1}**
No. 8880	33.8	35.5	21.7	17.2	13.8	6.4	10.7	16.8	20.3
	M^{3-3}	**Mandibular length**	**Coronoidal height**	**Symphyseal angle**	**Weight***				
No. 8880	18.9	38.1	22.7	49	615				

*Datum for the weight of the adult female ICN 8880 written on the ticket of the specimen chosen as the holotype (ICN 8880) seems to be incorrect, since the weight is given as 615 g, far below the weight of a typical adult female. It seems likely that either the weight was not registered correctly or the weight belongs to the subadult female INDERENA(IVH) 4140 and was incorrectly ascribed to ICN.

differences in coat color. We should look to vocalizations, behaviors and pheromones to provide isolating mechanisms. Complicating all of this, we describe here how the taxonomic descriptions defining *Aotus lemurinus lemurinus*, *Aotus lemurinus griseimembra* and *Aotus brumbacki* (see below) have historic problems relating to the adequacy of the type specimens and associated karyotypes (which were described independently) to define the taxon.

In the case of this genus, karyology has become an indispensable tool for defining each species group, and it is particularly disappointing that so little is being done from that viewpoint to address the issues that need to be resolved. Since karyotypes used to define *Aotus l. lemurinus* and *Aotus l. griseimembra* were taken from animals obtained independently and matched by Hershkovitz to phenotypes representing the taxa, there is no certainty that high altitude *Aotus lemurinus* and the population of the holotype (if it still exists) exhibits this karyotype number (Hershkovitz, 1983: 215; Ma *et al.*, 1976a, 1978). Part of the importance of the *hershkovitzi* material is that here we have a karyotype from a known geographic locality associated with a known phenotype, a situation which has been quite rare in the history of this genus.

Other "local" karyotypes: A karyotype prepared by MLB from an animal in captivity in Armero and said to be from Murillo from the eastern slopes of Nevado de Ruíz (Tolima) also had 2n = 58. The animal perished with the village of Armero when the eruption of the Nevado de Ruíz Volcano caused the death of 20,000 inhabitants, including Jairo Ramírez-Cerquera. Another karyotype prepared by MLB from an animal in the Cali Zoo and said to have come from the department of Casanare had 2n = 58 and a phenotype resembling the two *hershkovitzi*. It could have come from the Cusiana valley in eastern Casanare. The animal died and the skin was discarded. Neither of these karyotypes was further analyzed, but if these animals were of the same taxon then the geographic distribution of *hershkovitzi* might eventually prove to be throughout the eastern and Central Cordillera of the Andes, sympatric with *Aotus lemurinus*, and probably at a higher altitude than that of *Aotus brumbacki* on the east slope of the Eastern Cordillera.

***Aotus brumbacki* karyotype:** *Aotus brumbacki* is well-founded, since Yunis *et al.* (1977) described a karyotype from animals purportedly from the Villavicencio area, which Hershkovitz (1983: 217) referred to *Aotus brumbacki.* Brumback (1974) had described the karyotype 2n = 50 as being from a Paraguayan animal and identified as *A. azarae*, but this was amended by Hershkovitz (1983: 218) as being from the area around Villavicencio (Meta, Colombia), due to the phenotype which was "gray-necked" and his assertion that "The paratype, a member of the gray-neck groups (AMNH 143756) from the Villavicencio region, Colombia, resembles the photograph of the holotype closely enough to serve equally well as phenotypic model of the species. It cannot be identified with any other species of *Aotus.*" Nevertheless, we still need additional verifying karyotypes and phenotypes from known geographic collection sites for this species as well.

Ford's (1994) conclusion that northern taxa in the gray-necked group are represented by the well-differentiated species *Aotus trivirgatus* and a clinally variable *Aotus vociferans* (including *A. lemurinus*, *A. brumbacki* and *A. vociferans*, *sensu* Hershkovitz, 1983) while provocative, seems to us to be premature in view of the extensive variability in karyomorphs and karyotypes that would be involved in such a "species," varying from 2n = 46 to 2n = 58 and FN = 58 to FN = 76. Additionally, besides chromosome variability, *Aotus* social groups and behaviors seem more likely to result in closed populations than in broad gene flow across great distances. The added factor of a complexly formed topography consisting of lowlands separated by various high mountain ranges and wide rivers would have provided many opportunities for isolation of populations with subsequent speciation. Lack of mobility in a small organism distributed across a mountainous terrain is not a situation that would lend itself to a clinal population of such magnitude as suggested by Ford (1994). And yet, her results of several clinal cranial and pelage characteristics require some explanation and future analysis.

One partial explanation might be that the clinal variation that homogenized all of the specimens analyzed for Colombia may have an uncertain origin, as Ford herself recognized. In her analysis, 33 of the specimens were clumped as being from "Baranquilla," the principal port of exportation for animal traffic for Colombia for many years. Extensive experience of one of us (JIH-C) in animal traffic control in Colombia allows us to confirm that *Aotus* from many parts of Colombia could easily have been included in this group, since it was common for animals even from as far away as Leticia, Amazonas, to arrive in Barranquilla, where they were sent by Leticia's leading animal trafficker. Nevertheless, the problem of clinal characteristics bears further analysis in the future, given that the karyotypic differences are so pronounced.

Some of the karyotypic problems mitigating against the recognition of Ford's (1994) clinal species are the five different karyomorphs described from the elements which would make up Ford's *Aotus vociferans.* These karyomorphs, four of which were previously known and which correspond to the four species lumped into Ford's clinal *A. vociferans,* and a fifth karyomorph taken from the Pereira Zoo (department of Quindío) called "Quindío" with 2n = 50, strongly suggest that reproductive barriers would exist between each of these populations of *Aotus* due to their ample karyomorphic differences (Torres *et al.*, 1998). The "Quindío" specimen actually may represent a new Colombian species, since its fundamental number (FN = 72), number of metacentric (9), submetacentric, and acrocentric (12) chromosomes are so different from *A. brumbacki,* the other northern species with a diploid number of 50. Unfortunately the location of the "Quindío" specimen's capture is unknown, so that further study will have to await the discovery of its range. The skin and skull were preserved in the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia (specimen no. ICN 14023), but a recent search for this material revealed it to be missing from the collection.

Relationship of karyotype to different species: Marks (1987) makes the interesting case that to some extent, chromosome divergence among species may be a reflection of the social system and demographic characteristics of the group. A more closed type of social group, including monogamous relationships and territorial defense, would tend to favor random inbreeding and should favor elevated genetic drift. He used the case of the six species of gibbons (*Hylobates*), which illustrate an elevated cytogenetic diversity with 2n = 38, 44, 50, 52 and exhibit a more closed social system, including territorial defense, reduced vagility and monogamy as compared to 26 papionine monkey species (macaques [*Macaca* 12 spp.], baboons [*Papio* 5 spp.; *Theropithecus* 1 spp.], mandrills [*Mandrillus* 2 spp.] and mangabays [*Cercocebus* 4 spp.; *Lophocebus* 2 spp.]), which generally exhibit a comparably more open social system including large and mobile groups that are not pair-bonded and are usually polygynous with a very uniform karyotype (2n = 42) throughout the group (Napier and Napier, 1967: 409-410). The example using *Hylobates* spp. could have been *Aotus*, with their elevated cytogenetic diversity. Furthermore, although we do not know many of the details of their social system, it is apparently more socially closed and philopatric, with pair monogamy where members of a small group do not move far and defend a small territory (Wright**,** 1978, 1981; Mittermeier *et al.*, 1999).

Callicebus would also fit into this model of elevated chromosome diversity and small, semi-closed, monogamous, philopatric groups. Although we know less about chromosome diversity in *Callicebus*, it is evident that there are wide differences. For example, *Callicebus torquatus* (2n = 20) has the lowest diploid number known for primates as compared to *Callicebus moloch* (2n = 48), *Calliceus cupreus* (2n = 46) and *Callicebus donacophilus* (2n = 50) (Hershkovitz**,** 1990: 37).

Relation of *A. hershkovitzi* karyotype to other congeneric species: The *A. hershkovitzi* karyotype shows the highest diploid number (2n = 58) so far recorded in the genus. It contains a high number of acrocentric chromosomes (nos. 14, 19, 20, 25, 28), which, in other *Aotus* species, correspond to arms of biarmed chromosomes of different Robertsonian translocations. Table 1 shows the homology between the chromosomes of *A. hershkovitzi* and the karyotypes of KII. Chromosome A-2 from KII is derived from *A. hershkovitzi* nos. 25 and 19 (Fig. 8b) and KII chromosome A-3 from *A. hershkovitzi* nos. 20 and 28. *A. hershkovitzi* and *A. brumbacki* share 15 pairs of similar chromosomes, but differ by the presence of two Robertsonian translocations. The first one involves *Aotus hershkovitzi* nos. 14 and 25 to form the chromosome 10 of *A. brumbacki*. The second one involves *Aotus hershkovitzi* nos. 20 and 28, to form chromosome 5 in *A. brumbacki*. Interestingly, *A. hershkovitzi* chromosome no. 25 is involved in two different types of Robertsonian translocations (Figs. 8a and b), either with chromosome 14 (resulting in chromosome 10 of *A. brumbacki*) or with chromosome 19, resulting in chromosome A2 in the KII, KIII and KIV karyotypes (see Ma *et al.*, 1976). This type of translocation is characteristic of *Aotus* from northern Colombia.

Comparisons between chromosomes 2, 11, 14, 15 and 17 of the *A. hershkovitzi* karyotype and their counterparts in the other species of *Aotus* (Table 1) show differences in short arm size, probably resulting from variable amounts of constitutive heterochromatin. These variations have been found to occur in different groups that have undergone drastic chromosome shuffling during radiation (Sousa Barros *et al.*, 1990). Two different types of polymorphic variation have been found by us in this taxon affecting pair no. 3 and the X chromosome. When comparing the *A. hershkovitzi* karyotype with the K-IX karyotype of "Panama" (Ma *et al.*, 1978), 24 pairs were shared between them. This finding indicated that the *A. hershkovitzi* and "Panamanian" *Aotus (A. l. zonalis)* are karyotypically more similar to each other than to the other Colombian *Aotus* suggesting a close relationship of *A. hershkovitzi* to the Panamanian *Aotus* material studied by Ma *et al.* (1978).

Our findings also indicate that fusions have been prominent in the karyotypic evolution of *Aotus,* resulting in reduction of diploid number. The alternative mechanism, *viz* fission, has been postulated by other authors (Galbreath, 1983) to

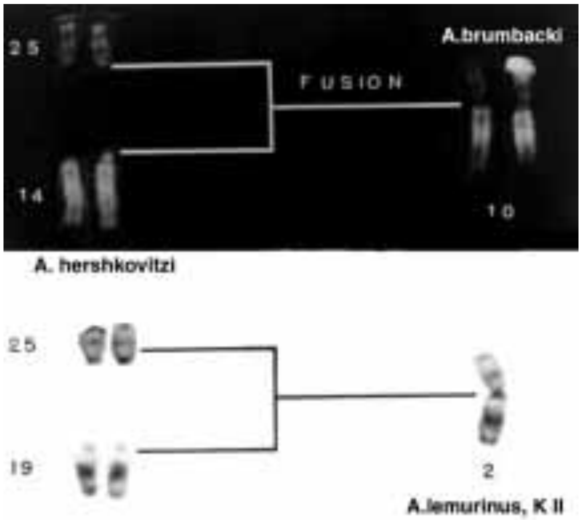

Figure 8. Presumptive chromosome rearrangements involving chromosome no. 25 of Cusiana specimens a) Robertsonian translocation between chromosome 25 and 14 of Cusiana *Aotus* resulting in chromosome 10 in *A. brumbacki* (QFQ banding); b) Robertsonian translocation between chromosomes 25 and 19 of Cusiana *Aotus* resulting in chromosome A2 of *Aotus lemurinus griseimembra* (karyotype KII). (GTG banding).

explain the occurrence of diploid numbers higher than 54, a diploid number considered by these authors to have been present in the common ancestor of the group. We suggest that the *Aotus hershkovitzi* karyotype is likely to be more similar to the ancestral karyotype because it contains at least one acrocentric chromosome that is involved in two different rearrangements, each of them being present in different species.

The sympatry of 2n = 58 individuals with *Aotus lemurinus* and their phenotypic similarity strongly suggests that the *A. hershkovitzi* described here represent Andean *Aotus lemurinus lemurinus* and not a separate species. Additionally, we believe that karyological differences between the *hershkovitzi* specimens or autocthonous *Aotus lemurinus lemurinus* and the other two *Aotus lemurinus* subspecies to which it was compared here may produce reproductive barriers between them, and that any potential hybrids may be infertile. The implication here is that the three subspecies of *Aotus lemurinus* may actually more correctly be considered separate species. More detailed cytogenetic analyses with high resolution banding, hybridization *in situ* and other molecular markers might also be needed for detecting complex rearrangements of sinteny groups which might allow us to recognize the real homology between these karyomorphs. Further karyological studies and analyses of other *Aotus lemurinus* are urgently needed to confirm these views.

In memoriam

We wish to dedicate this paper to two people, Philip Hershkovitz and Jairo Ramírez Cerquera. A first attempt at describing *A. hershkovitzi* was begun by Ramírez C. *et al.* (*mss.*) in an effort to name the taxon after Philip Hershkovitz. The effort was abandoned by the authors when Jairo was killed by the Nevado de Ruíz Volcano disaster. The present manuscript is a completely new paper, written with the desire to finally clarify the new taxon's position.

Philip Hershkovitz was well-known to many Colombians including the authors of this paper. He began field-work in Colombia with a two-year collecting trip to the Santa Marta region from 1941 to 1943. In 1948, after the Second World War, while employed by the Field Museum of Natural History in Chicago, he moved his family to Bogotá and worked in Colombia until he was obliged by his museum duties to return to Chicago in 1952. All of these collections became the heart of his subsequent work at the Field Museum, where he worked with most mammalian orders, describing many species and revising many groups of Neotropical mammals, focusing his work on their evolutionary origin, dispersal, classification, nomenclature and systematics. His impact on primatology was immense, resulting in many important revisions such as those for *Chiropotes, Pithecia, Saimiri* and *Callicebus*. Other notable achievements include his classic volume 1 of *New World Monkeys (Platyrrhini)* on the Callitrichidae and his effort to make sense out of the difficult genus *Aotus* (Hershkovitz, 1949, 1977, 1979, 1982, 1983, 1984, 1985, 1987a, 1987b, 1988, 1990). Because of Philip Hershkovitz' readiness to help and encourage all of us who work on some aspect of Neotropical mammalogy, Jairo Ramirez wanted to honor him using Hershkovitz's name as a species name for this taxon.

Jairo Ramirez-Cerquera first studied biology at the Universidad Nacional de Colombia, where he was a companion of one of us (MLB). He began his studies in primatology when he was hired as biologist of the *Aotus* colony of the Colombian National Institute of Health in Bogotá. Because of his interest in beginning a reproductive program with the animals, part of the colony was moved to the Biology Station of INS in Armero, Tolima, necessitating his move to Armero. Tragically he, along with his wife and children, were among the more than 20,000 missing in the avalanche of lahar which enveloped the town of Armero in 1985. We close this *memoria* with a quote from Russell Mittermeier and Adelmar Coimbra-Filho (1988: 34): "Jairo Ramirez, a rising star in Colombian primatology, had apparently discovered yet another species in the Colombian Andes, which because of his untimely death was never described. Ramirez' intention was to name the species after Hershkovitz in recognition of his many contributions to Neotropical primate taxonomy." It was the intention of the authors of this paper to complete Jairo's wish and at the same time honor the memory of these two men, but further analysis of the problem obliged us instead to synonymize the taxon with *Aotus lemurinus lemurinus.*

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We would like to acknowledge all those who have been interested in this problem previously, particularly the authors of the first manuscript written in the effort to formally describe *Aotus hershkovitzi*, especially Jaime A. Umaña, Marleney Montilla M., Carlos A. Espinal T. and Alejandro Giraldo. We would also like to thank Alberto Cadena (Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia) and Yaneth Muñoz (Instituto para la Investigación de la Biodiversidad "Alexander von Humboldt") for lending us the holotype and paratopotype for this hypothetical species and for other support they have given over the years towards the solution of this and other taxonomic problems. We would also like to thank Juan Manuel Renjifo for the photography of skin and skull and the National Institute of Health where the collection and preparation of the material was supported. We are grateful to Margarita Nieto for the color plate of the holotype.

Notes

[1] Subdivision of municipality in Colombia.

[2] Hill (1960: map 2) locates *A. lemurinus* throughout the region, which includes *A. hershkovitzi* and part of *A. brumbacki* and also includes northern Ecuador. We have found, however, that in general his distribution maps are

so full of distributional and geographic errors that they are practically useless for any detailed consideration of Neotropical primates.

[3] The type location identified by Groves (1993: 256) is in error, since it is located in the Department of Boyacá and not Meta.

[4] From a series of animals preserved in the MNHP. Elliot (1913: 14) did not fix a lectotype but commented that "The type of *N[yctipithecus] lemurinus* I. Geoffroy in the Paris Museum has been examined [by the author], but it is so faded from exposure to light that it is impossible to recognize its original coloring and I could only guess at it."

[5] On the plateau.

[6] Apparently a *lapsus,* since all *Aotus lemurinus* of the Cordilleras are fine-haired and not course.

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