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Revisiting the taxonomic status and ecological partitioning of night monkeys genus *Aotus* in western Colombia, with notes on *Aotus zonalis* Goldman, 1914

Revisando el estatus taxonómico y la partición ecológica de los monos nocturnos del género *Aotus* en el noroccidente de Colombia, con notas sobre *Aotus zonalis* Goldman, 1914

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Abstract

As part of the project *Programa Regional de Biodiversidad, subprograma Línea Base de Conocimiento de la Biodiversidad del Chocó*, designed to document the mammalian fauna of the Biogeographic Chocó, museum voucher specimens from the Colombian Chocoan Region deposited in American institutions have been taxonomically assessed in the past three years. Herein, we review the morphological variation, distribution patterns, and taxonomy of night monkeys in the genus *Aotus* from northwestern Colombia deposited at the Field Museum of Natural History (FMNH), and GIS based analyses and Maxent modeling are used to define the geographic extent and ecological limiting factors of the analyzed taxa. Our Principal Component Analysis showed high variation in skull morphology among *Aotus* from northwestern Colombia. However, differences observed in both discrete and morphometric analyses of the interorbital region of *A. zonalis* (more depressed than that in the grographically adjacent *A. griseimembra* and *A. lemurinus*) appear as good diagnostic characters for this taxon. Our analyses on the ecological variation associated with collecting localities of *Aotus* specimens support the geographic subdivision previously proposed based on karyotypic data. Based on obtained models of potential distribution we define the location and extent of potential contact zones among species of *Aotus* from northwestern Colombia.

Keywords: *Aotus*; *A. zonalis;* Biogeographic Chocó; Ecological partitioning; Skull morphology; Taxonomy.

Resumen

Como producto del proyecto *Programa Regional de Biodiversidad, subprograma Línea Base de Conocimiento de la Biodiversidad del Chocó*, que busca documentar la biodiversidad del Chocó biogeográfico colombiano, se han revisado en los últimos tres años, especímenes museológicos depositados en colecciones americanas. En este trabajo se evalúa la variación en la morfología craneal de especímenes de monos nocturnos género *Aotus,* del noroccidente de Colombia depositados en el Field Museum of Natural History (FMNH), y se utiliza modelamiento basado en sistemas de información geográfica (SIG) y Maxent en la definición de los límites geográficos y ecológicos de los taxa analizados. El presente análisis de componentes principales mostró un alto grado de variabilidad en morfología craneal entre las poblaciones de *Aotus* del noroccidente colombiano. Sin embargo, diferencias observadas en análisis de caracteres discretos y morfométricos de la región interorbital de *A. zonalis* (caracterizada por ser más deprimida con respecto a las geográficamente adyacentes *A. griseimembra* y *A. lemurinus*), se presentan como buenos caracteres diagnósticos para este taxón. Nuestro análisis de la variación ambiental asociada con las localidades de colecta de los especímenes de *Aotus* analizados, apoya la subdivisión geográfica previamente sugerida por datos cariotípicos. Basados en los modelos de distribución obtenidos se define también la ubicación y extensión geográfica de potenciales zonas de contacto entre las especies de *Aotus* del noroccidente colombiano.

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Palabras clave: *Aotus*; *A. zonalis;* Chocó biogeográfico; Partición ecológica; Morfología craneal; Taxonomía.

Introduction

With the aim of creating a database of the mammalian species of the Biogeographic Chocó, specimens deposited in American Institutions have been documented and their systematic status has been revisited in the last three years. Our work has been focused on those groups of mammals characterized by controversial taxonomic histories such *Aotus zonalis,* Goldman, 1914 described from the Canal Zone, Gatún, Panama, which constitutes the only currently recognized Chocoan night monkey (Defler, 2003, 2004; Defler and Bueno, 2007). Difficulties in interpreting the morphological and coat color variation among night monkeys in the genus *Aotus* has resulted in controversy on the designation of appropriate taxonomic status for night monkey populations from the western versant of the Andes in Colombia (Defler and Bueno, 2007). Recent molecular and karyotipic analyses have provided important insights on the systematic relationships among geographically distinctive *Aotus* variants, supporting a greater diversity within the genus than previously documented (Defler and Bueno, 2007; Groves, 2001, 2005). Based on karyotypic data, Defler and Bueno (2007) recognized six species of *Aotus* for the Colombian territory with a suggested geographic structure (*A. brumbacki*, *A. griseimembra*, *A. jorgehernandezi*, *A. lemurinus*, *A. trivirgatus*, *A. vociferans*, and *A. zonalis*). Three of these species occur on the western versant of the Andean System distributed as follows: *A. griseimembra* (Elliot, 1912) (2N=52-54), distributed along the eastern bank of the Sinú River east across the lowlands to high elevations of the Caribbean Region up to west of the Gulf of Maracaibo in Venezuela (Defler, 2004); *A. lemurinus* (I. Geoffroy-St. Hilaire, 1843) (2N=55-56), distributed along the Andean range above 1000 m; and *A. zonalis* (Goldman, 1914) (2n=58), distributed across the lowlands of the Biogeographic Chocó north up to Costa Rica in Central America (Ford, 1994).

Herein, we revisit Chocoan specimens of *A. zonalis* deposited at the Field Museum of Natural History and present a preliminary analysis on the macroecological component of the observed morphological variation among *Aotus* species from western Colombia: *A. griseimembra, A. lemurinus*, and *A. zonalis*. In addition, models of potential distribution created for these three taxa are used to analyze the location and extent of potential zones of contact among species of *Aotus* from northwestern Colombia.

Materials and methods

Group designation. Craniodental and external characters in the descriptions of *A. lemurinus* (I. Geoffroy-St.Hilaire, 1843), *A. griseimembra* (Elliot, 1912), and *A. zonalis* (Goldman, 1914) were evaluated for the analyzed individuals. Age of the specimens was estimated based upon totally erupted and functional dentition, as well as totally fused spheno-occipital and/or ethmoid sutures.

Morphological variation. In order to assess the morphological variation among *Aotus* populations from the western versant of the Colombian Andes, a Principal Component Analysis (PCA) was performed on 30 craniodental variables (Appendix I) of 32 Colombian *Aotus* (29 adults and three juveniles (FMNH 68859, 68861, 70679, that were removed after a preliminary analysis) deposited at the scientific collections of the Field Museum of Natural History (FMNH) (Appendix I), including *A. griseimembra* (N=11), *A. lemurinus* (N=18), and *A. zonalis* (N=3) (Table 1) in the statistical package PAST, available at http://www.nhm.uio.no/norges/past/download.html. In addition, the variation of discrete skull characters included in the description of *A. zonalis* (Goldman, 1914) was also investigated for the three analyzed taxa.

Environmental variation among *Aotus* sampling localities. To determine the degree of ecological differentiation among analyzed sampling localities of *A. griseimembra*, *A, lemurinus* and *A. zonalis* (including their type localities) (N=12, Appendix II), a PCA was performed on four environmental variables (Elevation, Mean Annual Maximum Temperature, Mean Annual Minimum Temperature, and Mean Annual Precipitation). Environmental data were derived from the Bioclim data set available at http://www.worldclim. org/bioclim

Finally, to test for ecological similarities among analyzed sampling localities of *Aotus*, an ecological

niche model was created for each one of the analyzed taxon by applying the Maxent algorithm (program available at http://www.cs.princeton. edu/~schapire/maxent/) following the procedures described in (Phillips *et al.*, 2006). Overlap among obtained outputs was used to infer the location and extent of potential contact zones among species of *Aotus* from the northwestern range of Colombia.

RESULTS

Principal components analyses. Our PCA showed a relatively low degree of morphological differentiation among the three analyzed taxa in *Aotus*, with *A. lemurinus* having the greatest range of skull variation. In our PCA's morphospace, samples of *A. lemurinus* partially overlapped *A. griseimembra* and *A. zonalis* (Figure 1). Most of the observed skull variation was explained by the first two components (42.4 and 9.10%, respectively) (Table 2). Samples of *A.griseimembra* and *A. zonalis* were primarily located on the III quadrant of the morphospace of our PCA, with negative loadings suggesting a smaller size for these two taxa when compared with analyzed samples of *A. lemurinus* (Figure 1). Our PCA on measurements of the interorbital region is presented in Figure 2.

Discriminant function analysis. In our DFA only 55.2% of the samples identified as *A. griseimembra* and *A. lemurinus* were correctly assigned to predicted groups (Table 3). However, all samples of *A. zonalis* (N=3) were correctly assigned in our DFA.

Discrete characters in *A. zonalis.* Discrete characters observed in *A. zonalis* are commented in the Discussion section of this work.

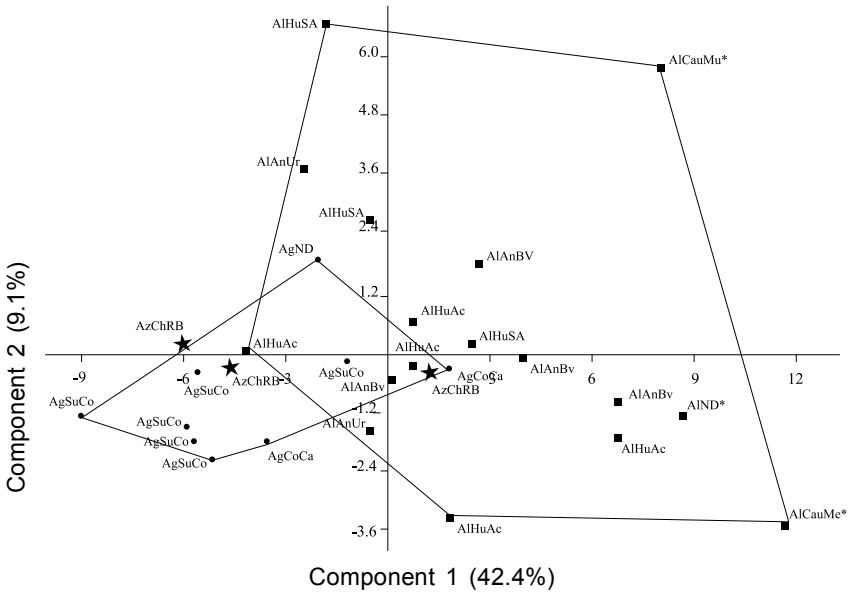
Ecological differentiation among *Aotus* from northwestern Colombia. In our PCA most of the observed

Table 1. Craniodental measurements of *Aotus* from northwestern Colombia.

	BCL	IOC*	OH	AOC*	NL*	NW*	TR	GLS	CB	PAL	ZYG	BCW	MB	BCH	OHE
A. griseimembra	50.20	42.68	31.45	21.29	12.76	5.45	17.00	59.18	42.25	17.77	38.81	33.23	32.66	26.70	12.51
(N= 9) StdD	1.88	1.03	1.29	0.55	1.40	0.54	0.86	2.51	11.97	0.89	1.46	0.97	1.22	1.69	1.24
A. lemurinus	51.39	42.54	32.68	21.04	13.47	5.70	17.69	61.19	48.94	18.29	38.79	33.87	33.75	27.11	14.66
(N= 17) StdD	2.24	2.84	2.28	1.48	1.75	0.72	0.42	2.66	4.79	1.54	2.65	0.61	1.17	1.21	1.16
A. zonalis	49.52	41.71	31.21	21.50	13.00	4.53	17.31	60.59	46.76	17.99	37.91	33.23	32.07	27.04	14.24
(N= 3) StdD	0.59	0.97	0.99	0.51	2.92	0.10	0.47	1.40	1.24	0.50	0.65	0.64	0.87	0.31	0.30

	MR	PR	M1W	C-C	AIM	MDN	TW	BOL	M-M	ML	RM	MnL1	MnL2	MTR	C-CM
A. griseimembra	8.32	6.25	3.76	15.33	36.09	20.57	24.09	9.92	19.28	36.41	22.78	26.11	17.70	18.45	10.29
(N= 9) StdD	0.76	0.38	0.19	1.13	0.99	1.66	0.87	1.69	0.83	1.67	1.37	1.18	0.96	0.75	0.65
A. lemurinus	8.63	6.62	3.88	16.05	35.95	21.48	25.02	10.33	19.29	37.90	22.73	26.13	17.42	19.42	10.63
(N= 17) StdD	0.60	0.52	0.21	1.20	3.14	1.72	1.52	0.73	1.35	2.86	3.11	3.94	4.29	0.36	0.95
A. zonalis	8.77	6.92	3.94	14.35	35.78	22.42	23.54	9.56	19.44	35.60	22.36	24.52	17.60	18.70	10.26
(N= 3) StdD	0.08	0.43	0.35	0.67	1.05	1.63	0.59	0.45	0.17	2.15	1.77	2.08	3.01	0.21	0.41

Mean and Standard Deviation (StdD) of 30 craniodental measurements analyzed among samples of *Aotus* from northwestern Colombia: Brain case length (BCL); external interorbital width (IOC); anterorbital constriction (AOC); orbit height (OH); nasal length (NL); nasal width (NW); tooth row (TR); greatest length of the skull (GLS); Condyobasal length (CB); palatal length (PAL); zygomatic (ZYG); braincase width (BCW); mastoid breadth (MB); brain case height (BCH); orbital height ext (OHE); molars row (MR); premolars row (PR); first molar width (M1W); canine to canine distance (C-C); internal width across molars (AIM); maximum distance of the nasals (MDN); temporal width (TW); basioccipital length (BOL); molar to molar length (M-M); mandibular length (ML); ramus height (RM); mandibular length 1 (MnL1); mandibular length 2 (MnL2); mandibular toothrow (MTR); and distance across mandibular canines (C-CM). Measurements marked with an asterisk (*) were used in a second PCA.



Ag: *A. griseimembra*: Al: *A. lemurinus*; and Az: *A. zonalis*; reference of collecting localities associated to analyzed samples is provided as follows: Mechenge, Cauca (CauMe); Munchique, Cauca (CauMu); Catival, Córdoba (CoCa).ND: Non determined; * Specimen FMNH 122721 assigned to *A. lemurinus*; no asterisk corresponds to specimen FMNH 123031 assigned to *A. griseimembra*); SuCo: Colosó, Sucre; AnB: Bellavista, Antioquia; AnUr Urabá, Antioquia; HuAC: Acevedo, Huila; HuSA: San Agustín, Huila; ChRB: Río Baudó, Chocó.

Figure 1. Principal Component Anaysis (PCA) of 30 craniodental variables of Colombian specimens in the genus *Aotus* from the western versant of the Andean System. Circles represent *A. griseimembra* specimens; squares represent *A. lemurinus* specimens; and stars represent *A. zonalis* specimens.

Table 2. Eigen values and percentage of variance explained by principal components in our PCA's on 30 craniodental (upper rows) variables and three interorbital variables (lower rows)

	PC	Eigenvalue	% variance
PCA 1	1	25.3	42.4
30 craniodental	2	5.4	9.1
	3	4.5	7.6
	4	3.9	6.6
	PC	**Eigenvalue**	**% variance**
PCA 2	1	3.5	65.1
3 Interorbital	2	1.6	30.2
	3	0.2	4.6

environmental variation among analyzed sampling localities was explained by the first component (98%) with elevation having positive loading among *A. lemurinus* localities and precipitation having positive loadings for *A. zonalis* localities at the department of Chocó (Figure 3). As product of our analysis we identified three clearly differentiated geographic groups as follows:

Table 3. Discriminant Analysis Functions.

Function	Wilks' Lambda		
	λ	χ^2	Significance
1	0.621	12.4	0.002

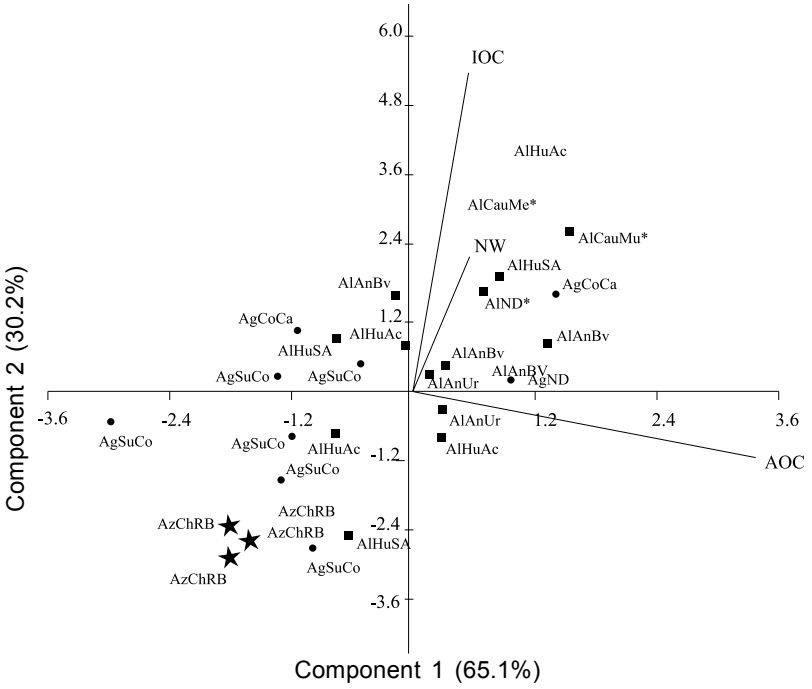
- Group 1: Andean samples and Sierra Nevada de Santa Marta (*A. griseimembra* and *A. lemurinus*).
- Group 2: Colombian Caribbean Coast, Colombian Urabá and Gatún Region in Panama (*A. griseimembra* and *A. zonalis*).
- Group 3: Chocoan locality at río Baudó (*A. zonalis*).

Ecological overlap and potential contact zones among *Aotus* species from northwestern Colombia. In our Maxent models *A. griseimem-bra* appear as the most resilient species with the widest distribution among northwestern Colombian *Aotus*. When our Maxent models constructed for *A. griseimembra* and *A. lemurinus* were evaluated at a predictive value of 50%, *A. griseimembra* distribution overlapped 100% of the predicted area for *A. lemurinus*. At probability values greater than 80% there was low overlap among

the three analyzed species of *Aotus* (Figure 4). Potential areas of overlapping among *Aotus* species from northwestern Colombia are shown in Figure 4 and commented in the Discussion section of this work.

Discussion

Morphometric analyses. In a revision of the taxonomy and the distribution of night monkeys, genus *Aotus*, Ford (1994) carried out multivariate analyses of craniodental measurements in combination with the analysis of pelage patterns and color, chromosomal data and blood protein variations. Ford (1994) concluded that there was «good support» for *A. brumbacki*, *A. lemurinus*, *A. griseimembra* and *A. zonalis* distributed in northern Colombia and the colombian Andes and Panamá. Our PCA and DFA performed on the whole set of skull measurements failed in producing a clear discrimination among analyzed population of *Aotus* from northwestern Colombia. However, most of the analyzed samples of *A. lemurinus* had positive loadings on the first component, suggesting differences in size between this taxon from the Andean region, and *A. griseimembra* and *A. zonalis* from the lowlands of the Caribbean and the Chocoan Region of Colombia respectively (Figure 1). *Aotus lemurinus* proved to have longer skulls (with greater loadings associated with condylobasal length) and broader interorbital regions (associated with greater loadings for interorbital constriction width) when compared with the two analyzed lowland forms *A. griseimembra* and *A. zonalis* (Table 1



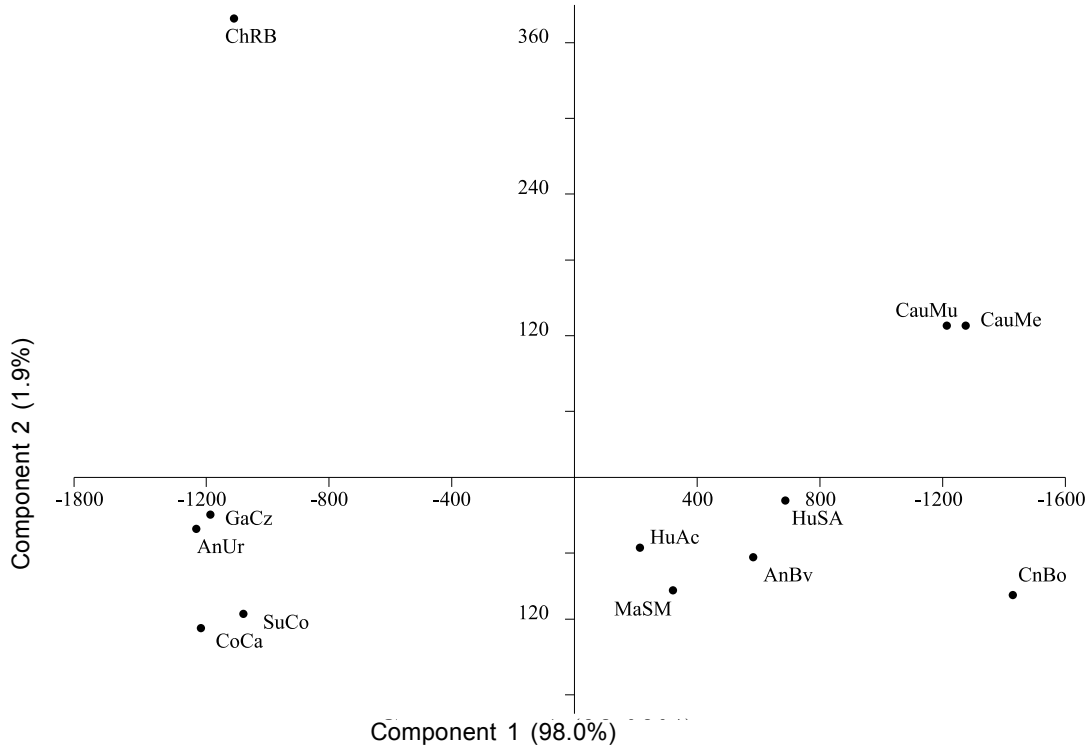
Ag: *A. griseimembra*: Al: *A. lemurinus*; and Az: *A. zonalis*; reference of collecting localities associated to analyzed samples is provided as follows: CauMe: Mechenge, Cauca; CauMu: Munchique, Cauca; CoCa: Cattival, Córdoba; ND: Non determined; SuCo: Colosó, Sucre; AnBv: Bellavista, Antioquia; AnUr: Urabá, Antioquia; HuAC: Acevedo, Huila; HuSA: San Agustín, Huila; ChRB: Río Baudó, Chocó. Individuals marked with an asterisk were originally misidentified. Acronyms for vectors: IOC: inter orbital constriction; NW: nasal width; AOC: anter-orbital constriction.

Figure 2. Principal Component Anaysis (PCA) of three nasal measurements of Colombian specimens in the genus *Aotus* from the western versant of the Andean System. Circles represent *A. griseimembra* specimens; squares represent *A. lemurinus* specimens; and stars represent *A. zonalis* specimens.

Table 3. Summary of the classification obtained in our dscriminant function analysis

		Predicted Group Membership			Total
Taxon		*A. zonalis*	*A. griseimembra*	*A. lemurinus*	
Count	*A. zonalis*	3.0	0.0	0.0	3.0
	A. griseimembra	2.0	6.0	4.0	12.0
	A. lemurinus	1.0	6.0	7.0	14.0
%	*B. zonalis*	100.0	0.0	0.0	100.0
	B. griseimembra	16.7	50.0	33.3	100.0
	B. lemurinus	7.1	42.9	50.0	100.0

55.2% of original grouped cases correctly classified



Abbreviations: CauMe: Mechenge, Cauca; CauMu: Munchique, Cauca; CoCa: Cattival, Córdoba; ND: Non determined; SuCo: Colosó, Sucre; AnBv: Bellavista, Antioquia; AnUr: Urabá, Antioquia; HuAC: Acevedo, Huila; HuSA: San Agustín, Huila; ChRB: río Baudó, Chocó; CnBo: Cundinamarca, Bogotá; Magdalena, MaSN: Sierra Nevada de Santa Marta; GaCZ: Gatún, Canal Zone, Panamá.

Figure 3. Principal Component Analysis of four environmental variables (Elevation. Mean Annual Precipitation, Mean Annual Maximum Temperature, and Mean Annual Minimum Temperature) associated with sampling localities of *Aotus*.

Table 4. PCA of environmental variables among *Aotus* sampling localities

PC	Eigenvalue	% variance
1	1.16E+06	98.049
2	22141.5	1.8654
3	775.029	0.065295
4	238.912	0.020128

and Figure 5). We analyzed measurements associated with the interorbital region in a separate PCA obtaining a better differentiation between *A. lemurinus* and *A. zonalis* with no overlap between these two forms in the morphospace. The morphometric gap between *A. lemurinus* and *A. zonalis* was filled by *A. griseimembra* (Figure 2).

Due to our low sample size, males and females were treated together in both PCA and DFA. The low differentiation in our morphometric analyses can be associated with our small sample size and skull differences associated with sexual dimorphism. In addition, the observed variation in terms developmental stages in our sampling, prevented a better differentiation among groups. Our knowledge on the allometry of members of the genus *Aotus* is still poor and to differentiate between immature and mature individuals is difficult based on skull morphology alone.

Significance of discrete characters, the case of interorbital and nasal features in A. *zonalis*. As Hershkovitz asserts, the interorbital region may have been narrow in primitive platyrrhines (Hershkovitz, 1977). Among living cebids, the interorbital region of *Aotus* and *Saimiri* agree with *Callicebus* but their orbits are wider relative to cranial breadth (Hershkovitz, 1977). Major orbital expansion in *Aotus* has been lateral but median compression is also evident in the narrowness of its interorbital region (Hershkovitz, 1977). As documented in callithichids

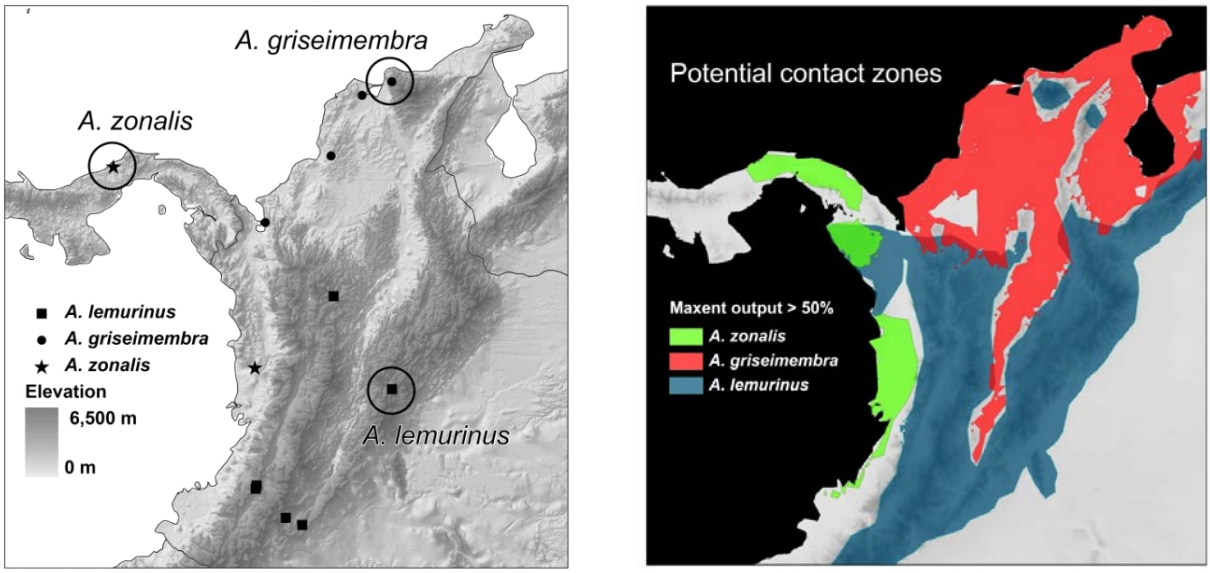


Figure 4. On the left sampling localities associated with Colombian *Aotus* museum voucher specimens analyzed and type localities (encircled). On the right, outputs of our niche models, generated in Maxent, showing the potential contact zones among the three taxa of *Aotus* in northwestern Colombia. The overlap of the model shows an evident ecological displacement of *A. zonalis* (light green) with respect to the two other species in the genus *A. griseimembra* and *A.* lemurinus, as well as a complete overlap between these last two taxa. Based on the realized model based on the suggested absence of *A. griseimembra* on the western bank of the Sinú River and on the lowlands of the Colombian Orinoquia (Defler and Bueno, 2007) proposed contact zones are delimited by the encircled areas (diagonal lines: *A. griseimembra – A. zonalis*; horizontal lines: *A. griseimembra – A. lemurinus*).

Figure 5. Skull rostral view showing differences in interorbital región width among specimens of *Aotus* from western Colombia including: *A. lemurinus* (Acevedo, Huila FMNH 70674); *A. griseimembra* (Colosó, Sucre FMNH 68855); and *A. zonalis* (río Baudó, Chocó FMNH 92622).

(Hershkovitz, 1977), the narrower interorbital septum of small species of platyrrhines (*Aotus*, *Callicebus*, and *Saimiri*) is due to relative larger eyes in smaller heads. Among higher primates the nasoturbinal is best developed in platyrrhines particularly in prehensile-tailed cebids, but most notably in pithecines. The ethmoturbinal II, as well of the ectoturbinal I are well developed in *Aotus* contrasting other platyrrhines (Hershkovitz, 1977). Although not well documented among platyrrhines, enlargements of the interorbital region and their associated turbinal systems have been linked with smell functions. Goldman (1914) mentioned that although skull of *A. zonalis* is in general broader to that of *A. griseimembra*, with the greater breath more noticeable in the braincase, the interorbital region of *A. zonalis* is «more depressed materially

altering the facial angle» (Goldman, 1914; p. 6) (Figure 1). This character was consistent among the three adult *A. zonalis* specimens analyzed in this work. In the scatter plot of our PCA on three nasal and interorbital measurements, individuals of *A. zonalis* clustered together (Figure 2). However, a depressed interorbital region was a variable character among individuals of *A. griseimembra* and *A. lemurinus*. Juvenile and sub-adult individuals of *A. griseimembra* and *A. lemurinus* presented a more depressed interorbital region when compared with adult individuals, suggesting that the presence of a depressed interorbital region in *A. zonalis* might be a neotenic characteristic in this taxon.

Distribution patterns of *Aotus* in northwestern Colombia. Hernández-Camacho and Cooper (1976) restricted *A. lemurinus* to the Colombian Andes (1000-1500 m up to 3000-3200 m) and *A. griseimembra* to the northern lowlands of the Colombian Caribbean Region, Santa Marta mountains, west to río Sinú, río San Jorge, lower río Cauca and lowlands of middle and upper río Magdalena. Same authors recognize the form *A. zonalis* as the night monkey of northwestern Colombia, in the department of Chocó, extending its distribution up to Panamá. In spite of the controversies on the taxonomic status of *Aotus* populations in northwestern Colombia, the geographic subdivision proposed by Hernández-Camacho and Cooper (1976) still accepted (Defler and Bueno, 2007). Hershkovitz (1983) recognized *lemurinus* and *griseimembra* as distinct, but considered them to be subspecies of *A. lemurinus*; he made no mention of *A. zonalis*, but as he ascribed Central American night monkeys to *A. lemurinus lemurinus*, by implication he was regarding it as a synonym of this latter form. Groves (2001) followed Hernández-Camacho and Cooper (1976) in recognizing *A. zonalis* as the typical form in Panama, and listed it as a subspecies of *A. lemurinus* along with *A. griseimembra* and *A. brumbacki*. Defler *et al*. (2001) concluded that the karyotype of *A. hershkovitzi* Ramírez-Cerquera, 1983 (from the upper río Cusiana, Boyacá, Colombia; 2n=58) was in fact that of true *lemurinus*, and they also mentioned that karyotypes considered by Hershkovitz (1983) as *lemurinus* in the northwestern distribution of the genus, were in fact of *A. zonalis*. Defler *et al.* (2001) and others (Defler, 2003, 2004; Defler and Bueno, 2007) concluded that *Aotus lemurinus* of Hershkovitz (1983) represent three karyotypically well-defined species of night monkeys as follows: 1) lowlands of Panamá and the Chocó region of Colombia represent *A. zonalis*, 2) Magdalena valley, *A. griseimembra*, and 3) those from above 1500 m *A. lemurinus*.

Potential contact zones among *Aotus* from northwestern Colombia. As shown in our Maxent model outputs (Figure 4), even at low predictive values (80%) it is possible to identify several areas of potential contact among *A. griseimembra*, *A. lemurinus*, and *A. zonalis*. *Aotus griseimembra* appears as the most ecologically resilient species of *Aotus* partially overlapping the distribution of *A. lemurinus*, and the area of the model obtained for *A. zonalis*. Intermingle between *A. griseimembra* and *A. lemurinus* is most likely to occur along the northern slopes of the Central and Western Cordilleras, as well as along the slopes of the Serranía del Perijá and the Sierra Nevada de Santa Marta (Figure 4). In the same way, *A. zonalis* and *A. griseimembra* overlap in their ecological requirements at the northwestern most corner of Colombia in the area of the Gulf of Urabá and the Colombian Darién. Although our Maxent model identified this area as part of the predictive output of *A. lemurinus*, probability values associated with this portion of the model were lower than 50%; in addition, based on morphological trends observed in the present work we consider unlikely for *A. l. lemurinus*, the typical form of the Andean region, to be present in the lowlands of the Chocó.

Conclusion

Despite of the low resolution of our PCA and DFA analyses, we agree with Defler and Bueno (2007) in the recognition of *A. griseimembra*, *A. lemurinus*, and *A. zonalis* as valid species. However, we disagree with Defler and Bueno (2007) on their argument on the validity of morphological characters to differentiate among the so called subspecies in the *A. lemurinus* group *sensu* Hershkovitz (1983). Taking into account the observed ecological overlapping and low morphological differentiation among *Aotus* from northwestern Colombia the potential presence of hybrid populations is high. The presence of hybrids and the lack of strong mechanisms of sexual isolation do not necessarily imply the absence of autopomorphic characters among karyologically distinguishable populations of *Aotus* from northern

Colombia. In our work, the three adult individuals of *A. zonalis* analyzed have a more depressed interorbital region contrasting the broad interorbital region of *A. griseimembra* and *A. lemurinus*. Based on the analysis of our niche model we agree with Hernández-Camacho and Cooper (1976) geographic subdivision among *Aotus* from northwestern Colombia.

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Appendix I

Craniodental measurements analyzed: Brain case length (BCL); external interorbital width (IOC); anterorbital constriction (AOC); orbit height (OH); nasal length (NL); nasal width (NW); tooth row (TR); greatest length of the skull (GLS); Condyobasal length (CB); palatal length (PAL); zygomatic (ZYG); braincase width (BCW); mastoid breadth (MB); brain case height (BCH); orbital height ext (OHE); molars row (MR); premolars row (PR); first molar width (M1W); canine to canine distance (C-C); internal width across molars (AIM); maximum distance of the nasals (MDN); temporal width (TW); basioccipital length (BOL); molar to molar length (M-M); mandibular length (ML); ramus height (RM); mandibular length 1 (MnL1); mandibular length 2 (MnL2); mandibular toothrow (MTR); and distance across mandibular canines (C-CM).

Appendix II

Collecting localities associated with analyzed specimens of *Aotus*: *A. griseimembra*-.- (N=11) COLOMBIA: Department of Córdoba, Catival, upper río San Jorge, 120 m (FMNH 68859 f, 68861 f, 68860 f, 68862 f); Department of Sucre, Colosó, Las Campanas, 175 m (FMNH 68850 f, 68851 f, 86652 f, 68853 f, 68855 f, 68856 f); Undetermined locality (FMNH); *A. lemurinus*. (N=18) COLOMBIA, Department of Antioquia, Bellavista (FMNH 6960 f, 69608 m, 69609 f, 69610 f); Urabá (FMNH 69612 f, 69613 f); Department of Cauca, río Mechengue (FMNH 88471 f); Munchique (FMNH 88470 m); Department of Huila, Acevedo, Aguas Claras (FMNH 70672 m, 70673 m, 70674 m, 70675 m, 70676 f); San Agustín, San Antonio 2,300 m (FMNH 70677 f, 70678 m, 70679 m, 70680 f); Undetermined locality (FMNH); *A. zonalis.* (N=3) COLOMBIA, Deparment of Chocó, río Baudó, río Sandó (FMNH 90322 f, 90323 f, 90324 f).

f = female m = male