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Subspecific Variation: An Alternative Biogeographic Hypothesis Explaining Variation in Coat Color and Cranial Morphology in *Lagothrix lugens* (Primates: Atelidae)

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Abstract: In this study, I examined the skull morphology of three color phases of the Colombian Woolly Monkey *Lagothrix lugens* (Primates: Atelidae). Collecting localities of museum specimens were investigated through GIS-based modeling techniques to test for geographical and ecological patterns in *L. lugens* populations. Statistical analyses conducted on 28 cranio-mandibular measurements, in combination with the assessment of discrete characters, indicated that *L. lugens* consists of three geographic groups. The morphotype from the highlands of the Central Cordillera (>2,000 m altitude) matches in all characters the original description of *L. lugens*. There is a distinct morphotype from the lowlands of the northern Amazon (Department of Caquetá) and another from the piedmonts of the eastern versant of the Colombian Andes and the isolated mountains of the Serranía de la Macarena, herein recognized as new subspecies. The presence of an intermediate form between highland and lowland divergent lineages is also interpreted as indication of effective hybridization in a narrow contact zone at the Macizo de Garzón in the southernmost range of the Eastern Cordillera.

Key Words: Colombia, color variation, contact zone, *Lagothrix* races, skull morphology

Resumen: En este trabajo, se evaluó estadísticamente la morfología craneal de especímenes que representan tres fases de color, previamente identificadas en el primate endémico de Colombia *Lagothrix lugens* (Primates: Atelidae); al tiempo, la variación ecológica asociada a las localidades de colecta del material analizado fue investigada para probar la existencia de estructura ecológica y/o geográfica entre poblaciones de *L. lugens* mediante la aplicación de técnicas de modelamiento basadas en SIG. Los análisis estadísticos conducidos sobre 28 medidas cranio-mandibulares, en combinación con la evaluación de caracteres discretos, indicaron que la morfología craneal de *L. lugens* esta subdividida en tres grupos geográficos que incluyen un morfotipo de las tierras altas de la Cordillera Central de Colombia (>2,000 m) que coincide con todos los caracteres en la descripción original de *L. lugens*, y dos variantes geográficas que son presentadas en este estudio: un morfotipo de las tierras bajas de la Amazonía del departamento del Caquetá y un morfotipo de los piedemontes orientales de los Andes de Colombia y el sistema montañoso independiente de la Serranía de la Macarena, reconocidos en este trabajo como nuevas subespecies. Finalmente, se interpreta la presencia de una forma intermedia entre linajes divergentes de las tierras altas y bajas como indicación de hibridación en una zona de contacto estrecha en la unidad geológica del Macizo de Garzón al extremo sur de la Cordillera Oriental Colombiana.

Palabras clave: Colombia, morfología craneal, razas de *Lagothrix*, variación en color, zona de contacto

Introduction

Woolly monkeys in the genus *Lagothrix* are widely distributed in South America, occurring in distinct ecosystems from the Amazon basin to the piedmonts and highlands of the Andes of Venezuela, Colombia, Ecuador, and Peru (Fooden

1963; Groves 2001; Defler 2004). The genus presently contains four species: *L. lagothricha* (Humboldt 1812) in the Amazon and southern Orinoco basins of Brazil, Colombia, Ecuador, Peru and Venezuela; *L. cana* (É. Geoffroy 1812) with two subspecies, *L. c. tschudii* Pucheran, 1857, in the Andes and associated piedmonts of southern Peru, and *L. c.*

cana in the lowlands of the Amazon basin of Peru and Brazil; *L. poeppigii* Schinz, 1844 in the western Amazon and the Andes of Peru and Ecuador; and *L. lugens* Elliot, 1907, which has a wide ecological range from the lowlands of the Colombian Amazon, the eastern piedmonts of the Eastern Cordillera, as well as the highlands of the Central and Western Cordilleras of the Colombian Andes (Fooden 1963; Groves 2001; Defler 2004; Ruiz-García and Pinedo-Castro 2010).

Fooden (1963) identified three color phases of *L. lugens*, two of them quite distinct; one from the highlands of the Andes and the isolated Serranía de la Macarena, and the other from the lowlands of the department of Caquetá. Fooden (1963) described a third color phase represented by three individuals with an apparently restricted distribution. Although he used the subspecific epithet *lugens* for populations of *L. lagothericha* occurring north of the lower Río Guayabero (Defler 2004), only highland specimens from above 2,000 m matched the description of *L. lugens* Elliot 1907. The presence of different color phases identifying populations from ecologically contrasting habitats poses the alternative possibility that they represent independent evolutionary lineages within *L. lugens*. The presence of geographically restricted divergent specimens can also be interpreted as evidence of a contact zone between highland and lowland morphologically divergent taxa. Herein, these two hypotheses are tested through cranio-mandibular characterization of the three color phases described by Fooden (1963) and ecological analyses of their geographic ranges.

Materials and Methods

Specimens analyzed

This study was conducted in the mammal collection of the Field Museum of Natural History (FMNH), Chicago, Illinois, which holds the second largest and most geographically representative series of specimens in the genus *Lagothrix*, including all currently recognized taxa. It has the largest series of *L. lugens* of any museum, with 40 voucher specimens from nine localities, representing a significant portion of the known distribution of this taxon. All specimens analyzed were compared with the original description of *L. lugens* Elliot, 1907, in order to confirm their identity.

Morphometric variation among populations

To analyze the phenetic variation among *L. lugens* populations, a principal components analysis (PCA) was performed on 28 craniodental and mandibular measurements of adult individuals of both sexes. Males and females were analyzed separately to account for sexual dimorphism (males $n=18$; females $n=10$) (see Appendix I). The age of the specimens was estimated based on the presence of an entirely erupted and functional dentition, as well as completely fused sphenoccipital and/or ethmoid sutures.

Measurements in the present analysis included: greatest length of skull (GLS); braincase length (BCL); condylobasal length (CB); palatal length (PAL); zygomatic breadth (ZYG);

braincase width (BCW); mastoid breadth (MB); braincase height (BCH); interorbital breadth (IO); anterorbital constriction breadth (AOC); intermalar width (IM); orbital height (OH); nasomaxillary height (NMH); malar foramen diameter (MFOR); left foramen ovale width (FOROVA-L*); right foramen ovale width (FOROVA-R*); length of upper molar row (MR); length of upper premolar row (PR); first molar width (M1W*); breadth across upper canines (CC); left tooth row (LTR); right tooth row (RTR*); mandible length (ML); ramus height (RM); maximum distance between the coronoid process and the angle of the mandible (MH2); mandibular process width (Md2); mandibular tooth row (MTR); and breadth across mandibular canines (CC-1). The measurements are shown in Figure 1 except for those with an asterisk. Principal components analyses were performed in the statistical package PAST available at <<http://www.nhm.uio.no/norlex/past/download.html>>.

Selection of informative variables

Based on the PCA factorial plane, correlated variables with the lowest loadings were eliminated (variables eliminated from the male dataset: BCL, ZYG, INT-ORB, OH, MFOR, FOR-OVA-R, M1W, CC, RM, Wd1, MTR; variables eliminated from the female dataset: CB, FOR-OVA-L, ZYG, MR, BCH, M1W, INT-ORB, CC, AOC, LTR, AIM, RTR, MAXNAS, RM, MFOR, Wd1, FOR-OVA-R, CC-1). For the remaining variables the change between simple and partial correlation matrices was evaluated and the variables in which the change was significantly different were also eliminated. In addition, values of a variance/covariance matrix from standardized data were calculated and the minimum number of variables to be included was determined based on their multiple correlation coefficient value. Finally, a PCA Cattell Scree plot test in the Statgraphics 15 package was used to determine the minimum number of variables to be used in the analysis (Fig. 2). Multiple correlation coefficients for the analyzed variables were calculated and ordered (low to high) selecting the number of variables suggested in the Scree plot. Variables eliminated from the male dataset were: MR, BCW, BCH, CC-1, AIM, FOR-OVAL-L, LTR. Variables eliminated from the female dataset were: PAL, MH2, MTR, ML, PR, BCW, MB)(Fig. 2). Selected variables in male (BCW, BCH, CC-1, LTR, MR, FOR-OVAL-L) and female (PAL, BCW, MB, PR, ML, MH2, MTR) datasets were tested for normality by the application of an Energy test in R mvnorm.etest for independent variables. Selected measurements for males are marked by a single asterisk (*) and for females by a double asterisk (**) in Table 1.

The geographic subdivision proposed for *L. lugens* populations among contrasting geographic locations was: i) highlands of the Central Cordillera of the Colombian Andes; ii) Eastern piedmonts of the Eastern Cordillera of the Colombian Andes, including the Serranía de La Macarena; and iii) Amazonian lowlands in the department of Caquetá. This subdivision was statistically assessed through a discriminant function analysis (DFA) in the statistical package Statgraphics 15 performed on the seven selected cranio-mandibular

variables for males and females separately to account for sexual dimorphism (Fig. 2).

Geographic and ecological analyses

To characterize the collecting localities of the woolly monkey populations, a principal components analysis

(PCAenv) was performed on four environmental variables (elevation, precipitation, and minimum and maximum temperature) derived from raster layers of the Bioclim dataset (Fig. 3). To determine the extent of suitable conditions for *L. lugens* and to test for the presence of i) natural barriers contributing to population isolation and ii) the presence

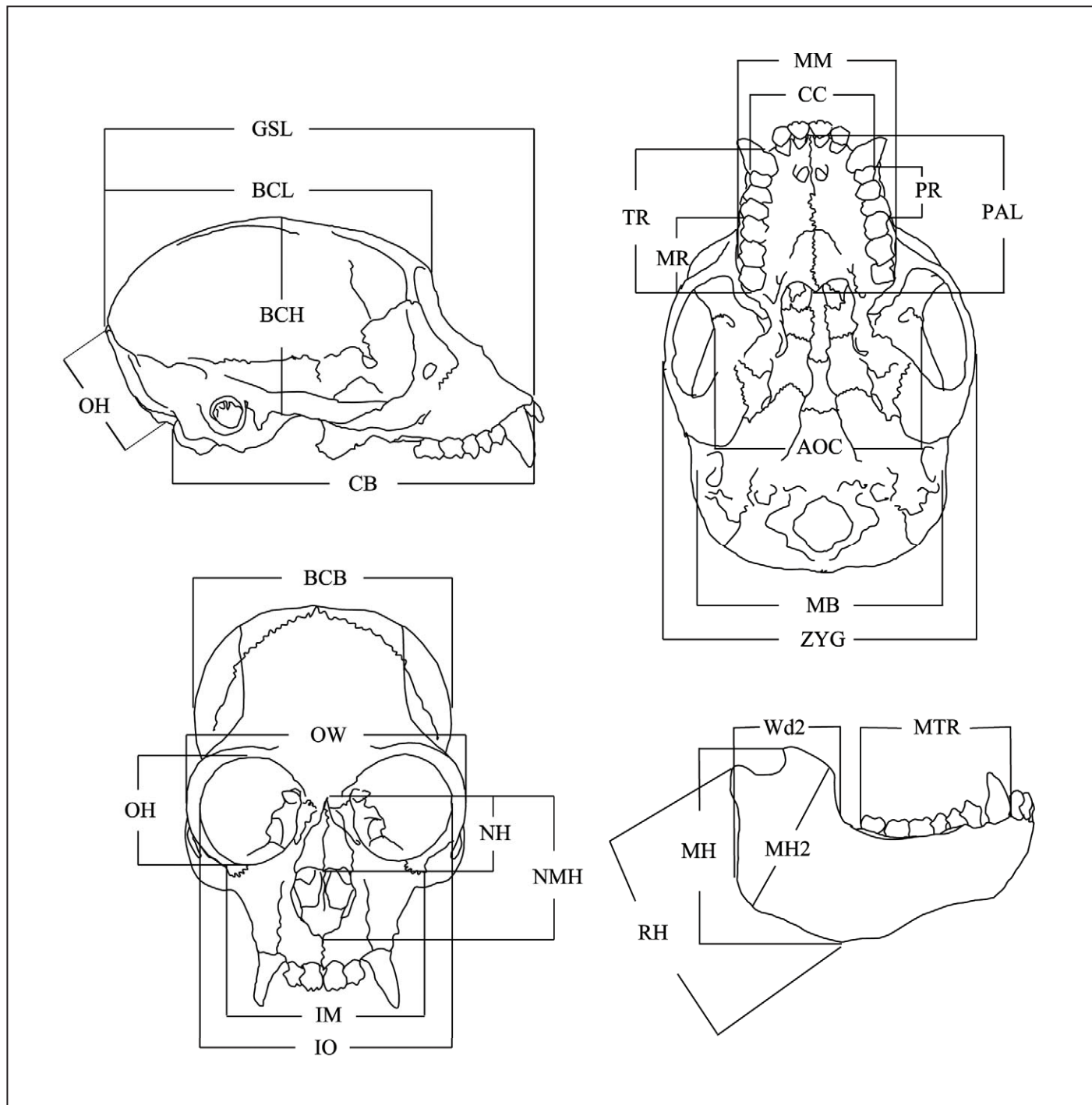


Figure 1. Visual representation of crano-mandibular measurements analyzed in this work; abbreviations described as follows: Greatest length of skull (GLS); braincase length (BCL); condylobasal length (CB); palatal length (PAL); zygomatic breadth (ZYG); braincase width (BCW); mastoid breadth (MB); braincase height (BCH); interorbital breadth (IO); anterorbital constriction breadth (AOC); intermalar width (IM); orbital height (OH); nasomaxillary height (NMH); malar foramen diameter (MFOR), not represented; left foramen ovale width (FOROVA-L), not represented; right foramen ovale width (FOROVA-R) not represented; length of upper molars row (MR); length of upper premolars row (PR); first molar width (M1W), not represented; breadth across upper canines (CC); left tooth row (LTR); right tooth row (RTR), not represented; mandible length (ML); ramus height (RM); maximum distance between the coronoid process and the angle of the mandible (MH2); mandibular process width (Md2); mandibular tooth row (MTR); breadth across mandibular canines (MCC).

Table 1. Average and standard deviation of 28 craniodental measurements among groups identified in this work. Abbreviations are given in Figure 1.

<i>Lagothrix</i> ssp.	No.		GLS	BCL	CB	PAL (**)	ZYG	BCW (*, **)	MB (**)
<i>lugens</i>	N=9 ♂	Avg	102.9	79.5	85.8	31.7	67.8	58.6	55.8
		StDv	3.2	2.2	3.2	1.7	3.9	0.8	1.3
	N=5 ♀	Avg	101.9	77.7	88.9	31.0	67.0	60.1	55.2
		StDv	1.8	0.7	5.1	1.6	0.9	1.5	1.9
<i>sapiens</i>	N=3 ♂	Avg	110.3	84.1	92.8	32.5	71.4	59.8	57.0
		StDv	3.9	2.7	3.8	0.4	4.6	1.4	0.5
	N=2 ♀	Avg	105.2	80.5	90.2	32.4	65.9	58.5	55.5
		StDv							
<i>defleri</i>	N=6 ♂	Avg	109.9	83.4	91.7	35.7	70.0	58.6	55.9
		StDv	3.3	2.2	2.7	2.3	3.7	1.4	1.4
	N=4 ♀	Avg	103.13	78.3	86.8	31.7	66.3	57.8	54.7
		StDv	4.4	4.2	2.2	1.0	1.3	1.6	2.7
			BCH (*)	INT-ORB	AOC	AIM (*)	OH	MAXNAS	MFOR
<i>lugens</i>	N=9 ♂	Avg	47.6	50.9	46.4	54.4	22.8	33.4	4.1
		StDv	1.8	2.3	1.1	2.7	1.4	1.9	0.9
	N=5 ♀	Avg	47.5	52.3	46.7	54.4	23.8	33.0	3.8
		StDv	1.1	0.9	1.1	1.0	1.1	2.5	1.0
<i>sapiens</i>	N=3 ♂	Avg	47.3	53.0	46.8	57.1	24.2	36.1	3.1
		StDv	0.4	2.5	2.0	3.3	1.6	1.6	0.8
	N=2 ♀	Avg	46.0	52.0	46.1	53.7	23.6	34.3	3.0
		StDv							
<i>defleri</i>	N=6 ♂	Avg	47.5	52.8	45.9	55.8	23.8	37.6	4.4
		StDv	0.9	2.0	1.3	2.1	1.0	1.1	0.9
	N=4 ♀	Avg	46.7	51.7	45.8	53.6	22.2	35.2	3.3
		StDv	2.8	1.2	1.5	1.5	0.6	2.6	1.0
			FOR-OVA-R	FOR-OVA-L (*)	MR (**)	PR (**)	MIW	CC	LTR (*)
<i>lugens</i>	N=9 ♂	Avg	4.0	4.0	13.9	10.6	6.1	28.2	30.2
		StDv	0.6	0.7	0.7	0.5	0.4	2.4	1.1
	N=5 ♀	Avg	3.8	4.0	15.6	11.8	6.6	26.7	30.7
		StDv	0.8	1.1	1.7	0.4	0.1	1.0	0.5
<i>sapiens</i>	N=3 ♂	Avg	4.3	4.4	14.7	10.9	6.3	30.1	31.5
		StDv	0.6	0.2	0.7	0.6	0.1	1.5	0.6
	N=2 ♀	Avg	3.7	3.8	15.1	10.8	6.8	27.1	31.0
		StDv							
<i>defleri</i>	N=6 ♂	Avg	5.4	5.3	14.7	11.2	6.3	29.2	31.6
		StDv	0.9	0.5	0.7	0.8	0.2	1.9	0.9
	N=4 ♀	Avg	5.4	5.6	14.5	10.8	6.2	27.1	30.9
		StDv	0.9	0.9	0.7	0.4	0.2	0.6	1.2
			RTR	ML	RM	MH2 (**)	Wd1	MTR (**)	CC-1 (*)
<i>lugens</i>	N=9 ♂	Avg	30.3	68.7	50.1	42.2	24.1	21.0	19.6
		StDv	0.9	3.4	5.2	5.3	2.1	1.7	1.4
	N=5 ♀	Avg	30.8	68.1	47.1	40.3	23.5	22.4	18.8
		StDv	0.7	0.7	3.2	2.0	1.0	0.4	0.6
<i>sapiens</i>	N=3 ♂	Avg	31.4	73.9	51.5	45.5	26.7	21.1	19.6
		StDv	0.55	4.0	1.8	3.2	2.2	0.4	0.4
	N=2 ♀	Avg	31.1	69.2	45.2	40.1	23.9	22.3	18.7
		StDv							
<i>defleri</i>	N=6 ♂	Avg	31.8	74.1	52.8	47.3	28.7	21.5	20.6
		StDv	0.7	3.6	4.7	4.4	2.9	0.6	0.4
	N=4 ♀	Avg	30.8	68.5	47.1	42.9	25.5	21.7	19.0
		StDv	1.3	2.4	1.2	2.6	1.3	1.4	0.6

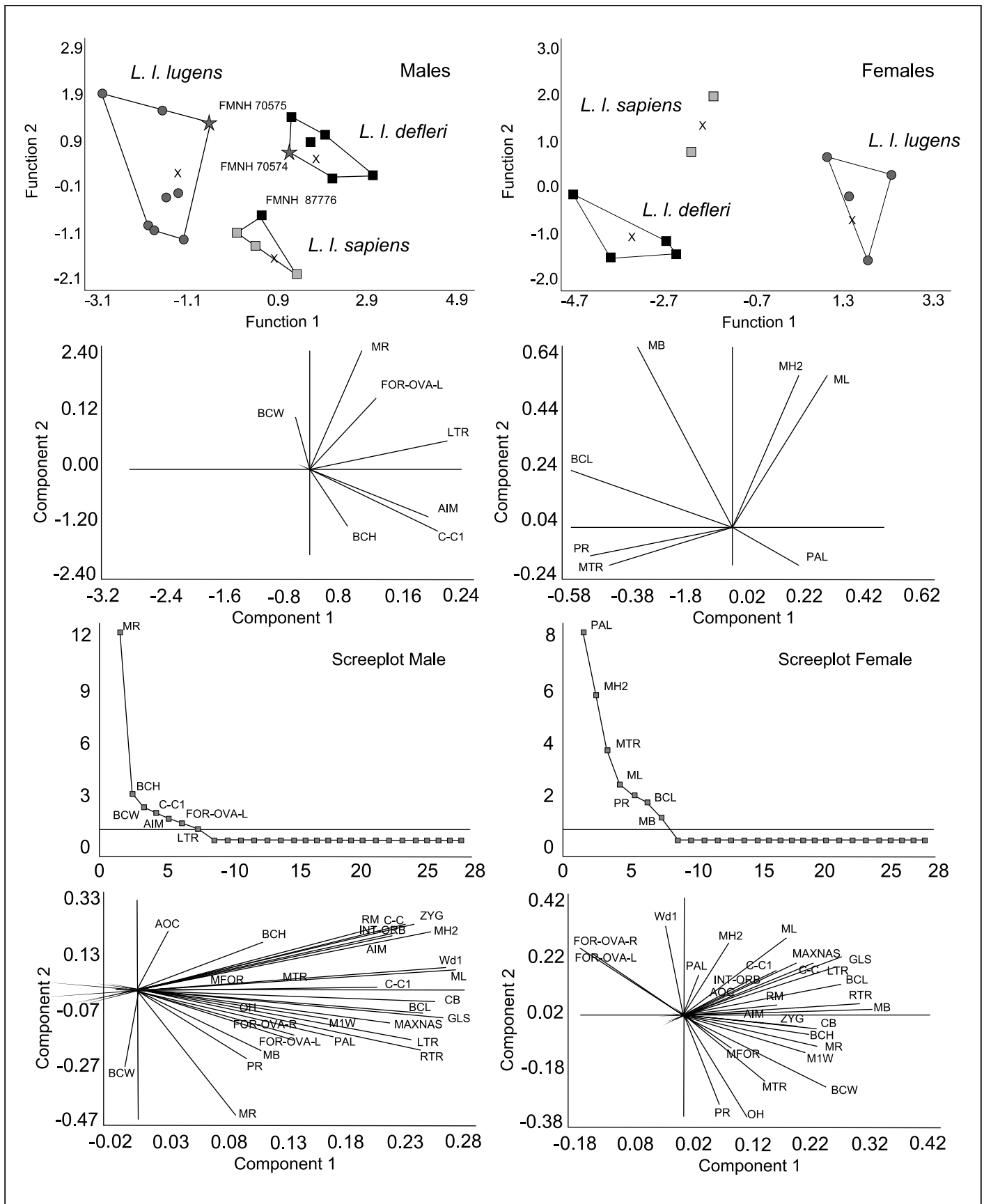


Figure 2. Discriminant function analysis (DFA) performed on seven selected craniodental variables for both male and female specimens, representing *L. lugens* populations from: 1) the lowlands of the northern Amazon in the department of Caquetá (gray squares), 2) highlands of the Andes (gray circles); and 3) the piedmonts on the eastern versant of the Eastern Cordillera and the Serranía de la Macarena (black squares) (first row); vectors of the seven selected variables in the principal components analysis (PCA) (second row); scree plot showing selected variables (third row); and preliminary PCA with the original variables (fourth row).

of potential routes of gene flow, a maximum entropy niche model (Maxent) was generated based on 19 collecting localities associated with museum voucher specimens reported by Fooden (1963) (nine of them included in the present work), following the protocols described in Phillips *et al.* (2006). Collecting localities of *L. lugens* used in the present analyses are described in Fooden (1963: pp.216–217).

In order to identify associations of environmental variables to the occurrence of *L. lugens*, a Pearson's multiple correlation test was performed between Maxent predictive values and values of 20 environmental variables derived from the Bioclim dataset in the statistical package SPSS 9.0. Descriptions of the environmental variables used in the geographic analyses of this work are available at <<http://www.worldclim.org/bioclim>>.

Results

Identity of specimens analyzed

Among the 28 analyzed adult specimens, 12 (43%) were characterized as Elliot's morphotype, matching the typical coloration attributed to *L. lugens* in Elliot's (1907) description of the species. They are referred to here as the "highland morphotype". Five specimens (18%) corresponded to the "lowland morphotype," and nine (32%) were identified as of the "piedmonts morphotype." Two specimens (7%) identified with catalogue numbers FMNH 70574 and FMNH

70575, from Aguas Claras, Huila, corresponded to an intermediate color phase between the color patterns typical of the lowland and highland populations. A detailed description of morphotypes and color phases is addressed in the "Discussion." Averages and standard deviations of cranio-mandibular measurements of identified divergent *L. lugens* morphotypes are presented in Table 1.

Normality test

Normality was proved at the 5% level of significance for both sets of variables (male and female datasets) in an Energy test of multivariate normality implemented in the statistical package R (data: males, estimated parameters, sample size 18, dimensions 7, replicates 999, E-statistic = 1.3772, *p* value = 0.09409; females, sample size 10, dimension 7, replicates 999, E-statistic = 1.2567, *p* value = 0.9259).

Principal Components Analysis (PCA)

In both PCAs (male and female datasets), the first three components accounted for most of the observed skull variation (PC1 = 36.9%, PC2 = 24.4%, and PC3 = 0% for males; and PC1 = 37.9%, PC2 = 27.6%, and PC3 = 17.1% for females) (Fig. 2). In the male dataset, MR, LTR, and CC-1, were the variables explaining most of the observed variation; while BCL, MB, and ML were the variables explaining most of the observed variation for the female dataset (Fig. 2).

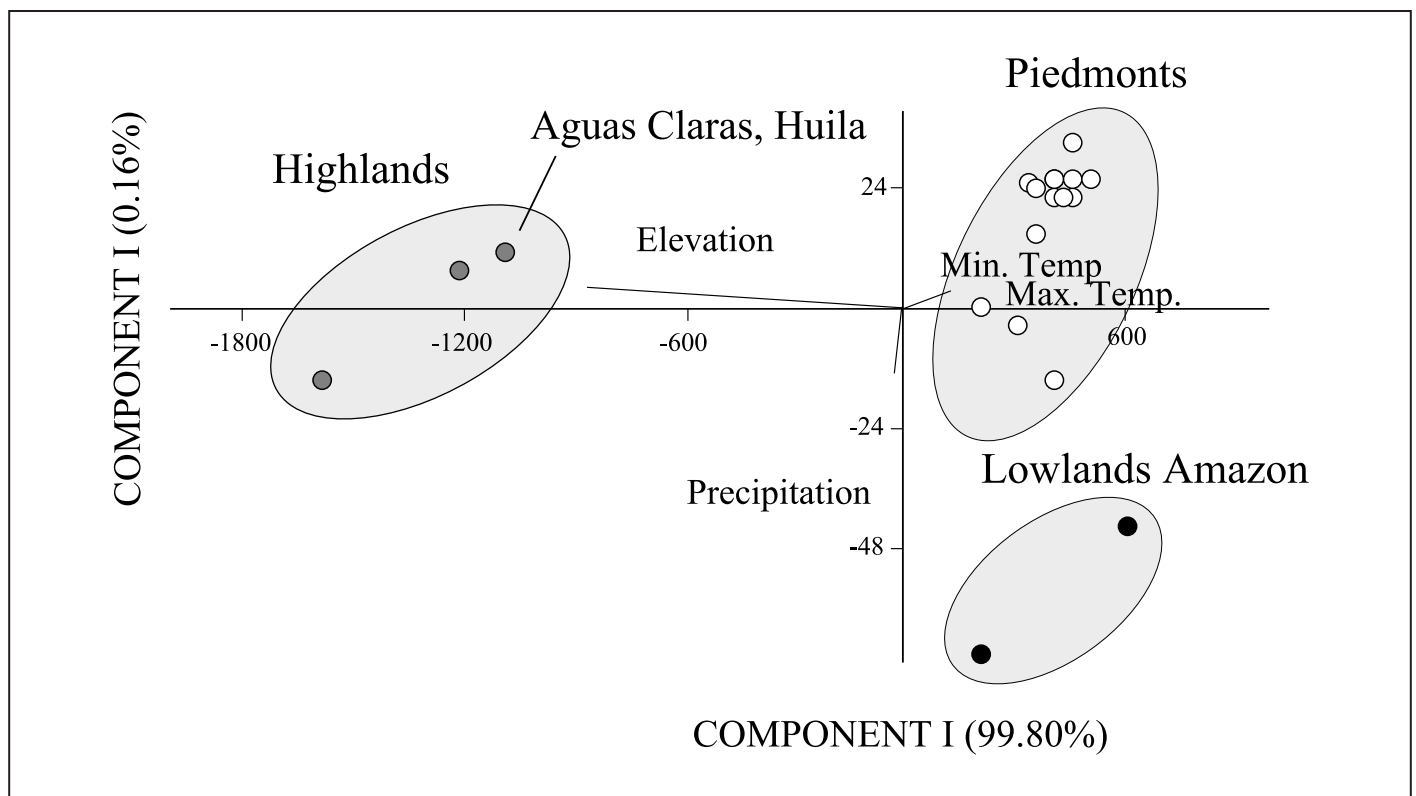


Figure 3. Principal components analysis performed on four environmental variables (elevation, precipitation, maximum temperature, and minimum temperature) associated with 19 collecting localities of *Lagothrix lugens*. Collecting localities from the highlands of the Central Cordillera (gray circles) were clearly differentiated from Eastern piedmonts localities (open circles), and from lowland localities in the Amazon (black circles).

Discriminant Function Analysis (DFA)

Female specimens from the three biogeographic regions were clearly discriminated in the DFA with 100% of specimens correctly assigned (Functions 1 and 2: Wilks' $\lambda = 0.046, 0.52$; $\chi^2 = 15.31, 3.17$; $P = 0.35, 0.7$) (Fig. 2). Male specimens from the three biogeographic regions were clearly discriminated in the DFA with 94.4% of specimens correctly assigned (Functions 1 and 2: Wilks' $\lambda = 0.188, 0.632$; $\chi^2 = 20.03, 5.49$; $P = 0.1293, 0.482$). Only two male specimens (FMNH 70574 from Aguas Claras, Huila, and FMNH 87776 from La Macarena, Meta) were incorrectly assigned (Fig. 2) (Table 2).

Collecting localities and niche modeling

Most of the ecological variation among the collecting localities analyzed was explained by the PC1 of PCAenv (99.8%) with higher loadings associated with elevation and precipitation (values of variance for elevation and precipitation: 99.78% and 0.24% respectively; Fig. 3B).

The Maximum Entropy model created for *L. lugens* (Fig. 4) failed to include all analyzed collecting localities within a single area of predictive values greater than 30%. Areas associated with high predictability (>60%) had a scattered distribution along the piedmonts of the Andes, with values greater than 80% restricted to the eastern Andes in the departments of Cundinamarca and Meta, including the Serranía de la Macarena. The Central Cordillera and the lowlands of the Amazon in the department of Caquetá were associated with lower predictive values (<40%). Finally, the distribution of *L. lugens* was positively and significantly correlated with precipitation (Pearson's correlation, $p > 0.001$: mean annual precipitation = 0.35; precipitation wettest quarter = 0.30; precipitation wettest month = 0.28).

Discussion

The stability of the alpha taxonomy of living New World monkeys, largely based on the contributions of Philip Hershkovitz in the decades of the 1950s, has experienced an extreme makeover (Rosenberger and Matthews 2008). From 67 recognized species in Napier (1976), the number of accepted platyrrhines has more than doubled at 139 (Rylands and Mittermeier 2009). The woolly monkeys, *Lagothrix* are not an exception. The last morphological revision of the genus, conducted almost half of a century ago by Fooden (1963), recognized just two species: the monotypic *L. flavicauda*, and *L. lagothricha* with four geographic variants: *L. l. cana*, *L. l. lagothricha*, *L. l. lugens*, and *L. l. poeppigii*. Groves (2001) not only resurrected the genus *Oreonax* Thomas, 1927 for the Peruvian Yellow-tailed Woolly Monkey (*O. flavicauda*), but also elevated to species rank the four subspecies of *L. lagothricha* and recognized two subspecies in *L. cana* (one from the highlands and one from the lowlands). Regardless of the debate on the validity and systematic placement of *Oreonax* (questioned by Rosenberger and Matthews 2008), the number of recognized independent lineages in *Lagothrix* has remained relatively stable. Two species of *Lagothrix* have been documented in Colombia: *L. lagothricha* and *L. lugens*. The former is a typical lowland species restricted to forested areas of the Amazon and Orinoco basins, northwest to an undetermined point in the Colombian department of Caquetá where it is replaced by *L. lugens* (see Defler 2004; Hernández-Camacho and Cooper 1976).

Lagothrix lugens evidently has a greater ecological range compared to other species in the genus (Fooden 1963; Ruiz-García and Pinedo-Castro 2010). It occurs across the lowlands of the northern Amazon, the piedmonts of the Orinoquia, as well as the highlands of the Central and Western Cordilleras of

Table 2. Classification table of Discriminant Analysis Function performed on the proposed *L. lugens* populations. 94.4% of the analyzed male specimens were correctly assigned. Only male specimen FMNH 70574, from Aguas Claras, Huila, and FMNH 87776, from La Macarena, Meta were incorrectly assigned and are marked with an asterisk.

Catalogue No.	Actual Group	High. Group	Highest value	Sq. Dist.	Prob.	2° High. Group	2° High. Value	Sq. Dist.
FMNH 70601	<i>L. l. sapiens</i>	<i>L. l. sapiens</i>	2855,41	0,792413	0,9395	<i>L. l. defleri</i>	2852,61	6,39719
FMNH 70604	<i>L. l. sapiens</i>	<i>L. l. sapiens</i>	2643,45	0,023887	0,8909	<i>L. l. defleri</i>	2640,79	5,35769
FMNH 70605	<i>L. l. sapiens</i>	<i>L. l. sapiens</i>	2654,32	0,541194	0,7630	<i>L. l. lugens</i>	2652,87	3,44328
FMNH 87775	<i>L. l. defleri</i>	<i>L. l. defleri</i>	2891,69	1,67249	0,9695	<i>L. l. sapiens</i>	2888,22	8,60618
FMNH 87776	<i>L. l. defleri</i>	<i>L. l. sapiens*</i>	2734,85	0,637566	0,6813	<i>L. l. defleri</i>	2733,64	3,06494
FMNH 87777	<i>L. l. defleri</i>	<i>L. l. defleri</i>	2789,76	0,32858	0,9782	<i>L. l. sapiens</i>	2785,76	8,31237
FMNH 87781	<i>L. l. defleri</i>	<i>L. l. defleri</i>	2624,04	1,16378	0,9580	<i>L. l. lugens</i>	2620,43	8,39185
FMNH 92331	<i>L. l. defleri</i>	<i>L. l. defleri</i>	2722,23	0,271649	0,9144	<i>L. l. sapiens</i>	2719,84	5,0705
FMNH 92332	<i>L. l. defleri</i>	<i>L. l. defleri</i>	2669,13	0,167484	0,9569	<i>L. l. sapiens</i>	2665,77	6,88185
FMNH 70574	<i>L. l. lugens</i>	<i>L. l. defleri*</i>	2682,16	0,407302	0,8841	<i>L. l. sapiens</i>	2679,67	5,37968
FMNH 70575	<i>L. l. lugens</i>	<i>L. l. lugens</i>	2634,23	0,190419	0,9217	<i>L. l. sapiens</i>	2631,67	5,30932
FMNH 70577	<i>L. l. lugens</i>	<i>L. l. lugens</i>	2604,86	1,67179	0,9317	<i>L. l. sapiens</i>	2602,23	6,92209
FMNH 70578	<i>L. l. lugens</i>	<i>L. l. lugens</i>	2623,03	2,03225	0,6432	<i>L. l. sapiens</i>	2622,42	3,24302
FMNH 70579	<i>L. l. lugens</i>	<i>L. l. lugens</i>	2590,16	1,7327	0,8761	<i>L. l. defleri</i>	2588,02	6,02033
FMNH 70580	<i>L. l. lugens</i>	<i>L. l. lugens</i>	2607,95	0,308933	0,9426	<i>L. l. sapiens</i>	2605,09	6,03392
FMNH 70585	<i>L. l. lugens</i>	<i>L. l. lugens</i>	2614,13	5,8484	0,9999	<i>L. l. defleri</i>	2604,67	24,7829
FMNH 70588	<i>L. l. lugens</i>	<i>L. l. lugens</i>	2684,56	1,94948	0,9938	<i>L. l. defleri</i>	2679,13	12,7944
FMNH 84550	<i>L. l. lugens</i>	<i>L. l. lugens</i>	2619,12	1,7559	0,9072	<i>L. l. sapiens</i>	2616,83	6,33834

the Colombian Andean system (Defler 2004). The 19 *L. lugens* collecting localities examined in this work represent nine biogeographic districts, as defined by Hernández-Camacho et al. (1992), that range from 50 to 3,000 m above sea level. Fooden (1963) documented three different color phases in the distributional range of *L. lugens*. Only one of the color variants matches all the characteristics of the specimen from the upper Río Magdalena (3,000 m above sea level) designated by Elliot (1907) as the holotype of *L. l. lugens*: “body stout, heavy, as in *L. lagothericha*, but color very different, black-purplish; fur

thick, woolly; and a tail broad at base” (p.193). Fooden (1963) interpreted the observed coat color differences among *lugens* populations as clinal intraspecific variation. From my perspective, Fooden’s (1963) interpretation was strongly influenced by assumptions in the Biological Species Concept (Mayr 1942). It is also important to mention that at the time of Fooden’s revision hybridization among mammals was considered a rare event usually discarded from systematic analyses. As a result, Fooden (1963) retained the name *L. lagothericha lugens* for all populations north of the lower Río Guayabero.

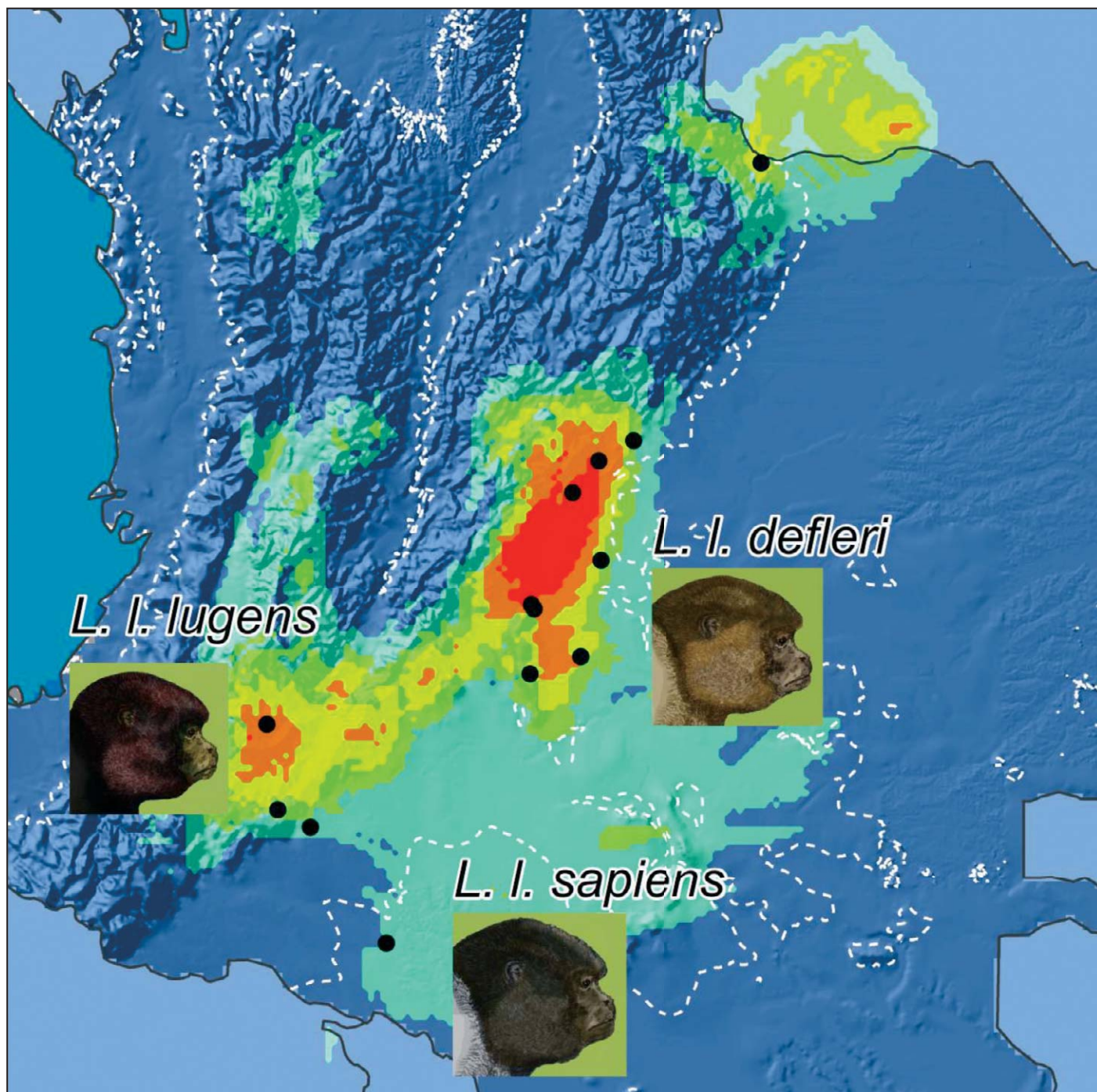


Figure 4. Predicted distribution for *L. lugens* derived from a Maximum Entropy modeling run for the 19 collecting localities of *L. lugens* analyzed by Fooden (1963) (black circles). Warm colors (red to yellow) represent probabilities greater than 50%. At 30% of predictability (aquamarine), the model succeeds in including all analyzed localities. Dashed line represents elevation of 250 m above sea level.

In my study, the skull morphology of the highland specimens, (matching all the characteristics found in Elliot's description of *L. lugens*) was clearly discriminated from lowland skulls in the DFAs of both males and females (Fig. 2). Colombian woolly monkeys from the lowlands have significantly larger skulls than the highland specimens. Lowland *L. lugens*, on the other hand, were divisible into two groups in both male and female DFAs as follows: 1) Amazon specimens, characterized by an overall silver coat color and a black cap ornate with a gray or silver mid-sagittal coronal stripe (a color phase also recognized by Fooden 1963); and 2) specimens from the piedmonts of the Eastern Cordillera and the Serranía de la Macarena, characterized by: i) a darker coloration in comparison with *L. lugens* specimens from the Amazon; ii) less defined cap and mid-sagittal stripe; iii) a larger body size compared to *L. lugens* from the highlands; iv) a shorter tail than *L. lugens* from the Amazon; and v) longer hair than in *L. lugens* from the Amazon. The above mentioned morphotype was interpreted by Fooden (1963) as a darker variant of *L. lugens* from the Amazon. In the male PCA, variables responsible for the differentiation among identified populations refer to the upper and lower molar tooth rows as well as canine separation (MR, LTR, and CC-1), all of them representing differences in dentition size; while females were differentiated by braincase length, mastoid breadth, and mandible length (BCL, MB, and ML), showing differences in skull size among identified groups. Fooden's third color phase corresponds to paler buffy-gray to brownish-gray primates, represented by one specimen from Consaya, Caquetá, and two specimens from Aguas Claras, Huila. Skull measurements in the specimen from Consaya did not differ significantly from other specimens from the same locality. On the other hand, although skulls from Aguas Claras, Huila, fell within the ranges of highland *L. lugens*, male specimen FMNH 70574 from this locality was misclassified as *L. lugens* from the Amazon in the DFA. Interestingly, specimen FMNH 7057, also from Aguas Claras, Huila, represented the most marginal point among highland samples in the DFA morphospace (Fig. 2). Aguas Claras, Huila, is part of the recently uplifted geologic unit of the Macizo de Garzón, located at the southernmost end of the Eastern Cordillera of the Colombian Andes, separating the lowlands of the Magdalena Valley from the lowlands of the Colombian Amazon and Orinoquia (Lundberg 1997). The area at the Macizo de Garzón encloses the lowest crossing points connecting the eastern and western versants of the Eastern Cordillera, and also constitutes the most likely location for intergradation between *L. lugens* from the eastern piedmonts and lowlands with individuals of *L. lugens* from the Central Cordillera of the Colombian Andes.

Ruiz-García and Pinedo-Castro (2010) examined the genetic variation of the mitochondrial marker COII for 26 putative Colombian *L. lugens* and concluded this taxon was polyphyletic encompassing higher genetic diversity than other putative species in the genus. Ruiz-García and Pinedo-Castro (2010) also mentioned that levels of genetic

divergence of COII among *L. lugens* samples were lower than those between species of *Ateles* (Collins and Dubach 2000), implying subspecific designation for the observed genetic differentiation. The same authors highlighted high historical gene flow estimates within *L. lugens*, interpreted as evidence of effective hybridization between *L. lugens* and neighboring taxa, also exemplified by individuals originated from the breeding of *L. lugens* males with *L. lagothricha* females (Ruiz-García and Pinedo-Castro 2010: p.121). Interspecific breeding among primates such as *Lagothrix*, characterized by large groups with diurnal activities that involve extensive interspecific social interaction (Defler, 2004 and cited references in pages 358–359; Defler and Defler 1996) is likely to occur.

Hybridization has been documented in 26 of the 233 Old World primate species (Phillips-Conroy and Jolly 1986; Samuels and Altman 1986; Struhsaker *et al.* 1988; Watanabe and Matsmura 1991; Bynum *et al.* 1997; Evans *et al.* 2001; Wyner *et al.* 2002), even at the intergeneric level (Dunbar and Dunbar 1974; Jolly *et al.* 1997), and in eight of the 139 New World primate taxa (Coimbra-Filho *et al.* 1993; Cortés-Ortiz *et al.* 2007; Mendes 1997; Peres *et al.* 1996). At least two hybrid speciation events have been suggested among primates: *Macaca arctoides* (see Tosi *et al.* 2003) and *Rungwecebus kipunji* (see Burrell *et al.* 2009). A common aspect in all the above mentioned studies is the presence of individuals which exhibit some combination of characters (i) an intermediate or transgressive phenotype with respect to parental species, (ii) a restricted distribution or distribution within a vegetation zone (in allopatry or parapatry) from that of parental species, and/or (iii) isolation from parental species by either allopatry or assortative mating (e.g., allochrony or mate choice), characteristics shared by *L. lugens* specimens from Aguas Claras, Huila.

The Bateson-Dobzhansky-Müller genetic speciation model (Baker and Bradley 2006) states that the absence of effective mechanisms of sexual isolation and the presence of hybrid forms are not in full disagreement with speciation produced by temporal isolation of parental populations, accompanied by the fixation of characters in a process that can be reinforced by ecological differentiation. Results in this work have demonstrated the fixation of skull morphometric traits with a clear discrimination in the DFAs of both males and females (Fig. 2), accompanied by differences in coat color patterns and a unique combination of discrete characters and supported by geographic structure.

My findings regarding the morphological and geographic components of the variation in the *L. lugens* complex, concomitantly support the hypotheses of: 1) differentiated natural groups separated by geographic and ecological barriers; and 2) the potential presence of a contact zone between highland and lowland *L. lugens* populations, as a plausible explanation for the three *L. lugens* coat-color variants previously reported in this taxon by Fooden (1963). Based on this evidence, I recognize three geographic variants, two of them introduced as new subspecies of *L. lugens*.

Family Atelidae Gray, 1825

Subfamily Atelinae Gray, 1825

Genus *Lagothrix* É. Geoffroy Saint-Hilaire, 1812

Lagothrix lugens sapiens subsp. nov.

Lagothrix lagothricha lugens of Fooden (1963)

Lagothrix lugens of Groves (2001)

Holotype: Male specimen preserved as a skin and skull in excellent condition, FMNH 70601 (Figs. 5 and 6, skull and skin), collected by Philip Hershkovitz on March 18, 1952, collector number 6146. Measurements of the holotype are included in Table 3.

Type locality: Rio Consaya, Caquetá, Colombia (0°31'59.8"N, 75°6'W, 100 m above sea level).

Type series: The type series includes five specimens, three males and two females preserved as skins and skulls, collected at the same locality and deposited in the Field Museum of Natural History, Chicago, Illinois (FMNH), identified by catalogue numbers FMNH 70602-03 ♂, FMNH 70604-05 ♀.

Diagnosis and Comparison: *Lagothrix lugens sapiens* is characterized by a smaller body and longer tail (average ratio body/tail: 0.68 ♂ n = 3; 0.62 ♀ n = 2) compared to *L. lugens* from the highlands of the Central Cordillera (0.84 ♂ n = 6; 0.77 ♀ n = 6) and *L. lugens* from the piedmonts of the eastern versant of the Colombian Andes (0.84 ♂ n = 9; 0.70 ♀ n = 6). *Lagothrix l. sapiens* can be easily identified by its paler overall coloration, gray to silver-gray trunk and darker limbs and head. It is also characterized by a blackish cap ornamented with a mid-sagittal gray or silver coronal stripe; contrasting with the overall darker coloration and a less noticeable to absent cap in typical *L. lugens* from the piedmonts of the eastern versant of the Andean system (Fig. 6). *Lagothrix l. sapiens* has shorter hair than *L. l. lugens*, particularly at the base of the tail, chest and forearms. Skulls of *L. l. sapiens* are larger than those of *L. lugens* from the highlands of the Central Cordillera, and they are within the range of *L. lugens* from the eastern piedmonts. However, skulls of *L. l. sapiens* average larger than *L. lugens* from the eastern versant of the Andes for 13 of the craniodental measurements analyzed in this work (Table 1). Mandibles of *L. l. sapiens* are larger than those of woolly monkeys from the highlands, but smaller in all measurements compared to those of woolly monkeys from the eastern piedmonts (Table 3).

Description: *External characters* – Large body (458.7 mm ♂ n = 3; 437.5 mm ♀ n = 2) and long tail (660.76 mm ♂ n = 3; 697 mm ♀ n = 2; measurements reported by Fooden 1963), general gray to silver-gray trunk; presence of contrasting darker head characterized by a blackish cap ornamented by a mid-sagittal gray or silver coronal stripe. The tail in *L. l. sapiens* is unicolored, gray to silver-gray not noticeably wider

at the base. In *L. l. sapiens*, the arms and the limbs are of the same color as the trunk, silver-gray to dark-gray, with a darker coloration, dark-gray to blackish-gray on the forearms and hands. Ventrally, long hairs on the chest, varying in color from silver gray to brown to blackish brown (Ridge-way 1912). *Skull characters* – Large skull (GSL >110 mm in males and 105 mm in females), elongated caudally; orbits enlarged; massive supraorbital arches, particularly in males; zygomatic width surpassing orbital width from a rostral view; and enlarged choanas.

Distribution: *Lagothrix l. sapiens* seems to be restricted to the lowlands of the eastern versant of Colombia's Eastern Cordillera, between the ríos Caquetá and Caguán, in a region which is

Table 3. Measurements of 28 craniodental variables in individuals of the type series of *Lagothrix lugens sapiens* and *L. lugens defleri*; holotypes.

	<i>L. l. sapiens</i> FMNH 70601 ♂	<i>L. l. defleri</i> FMNH 87775 ♂
GLS	114.74	115.09
BCL	87.15	85.42
CB	96.68	95.57
PAL	32.55	38.57
ZYG	73.5	69.74
BCW	61.43	60.29
MB	57.62	57.62
BCH	47.78	48.77
INT-ORB	55.67	51.46
AOC	49.05	45.05
AIM	59.17	56.79
OH	25.25	22.78
MAXNAS	37.88	39.3
MFOR	4.04	3.58
FOR-OVA-R	4.95	6.56
FOR-OVA-L	4.58	5.63
MR	14.3	15.36
PR	10.21	11.32
M1W	6.38	6.54
C-C	30.33	28.3
LTR	31.9	32.61
RTR	31.48	32.55
ML	77.82	76.2
RM	53.58	55.36
MH2	46.92	48.56
Wd1	27.6	30.52
MTR	21.06	21.72
C-C1	19.83	20.92



Figure 5. Skulls of holotypes of: A) *Lagothrix lugens sapiens* FMNH 70601 ♂ from Consaya, Caquetá, Colombia; B) *L. l. defleri* FMNH 87775 ♂ collected at Río Yerley, Parque Nacional Natural La Macarena, Meta, Colombia; and a specimen of *L. l. lugens*, FMNH 84550 ♂ collected at Moscopán, Huila.

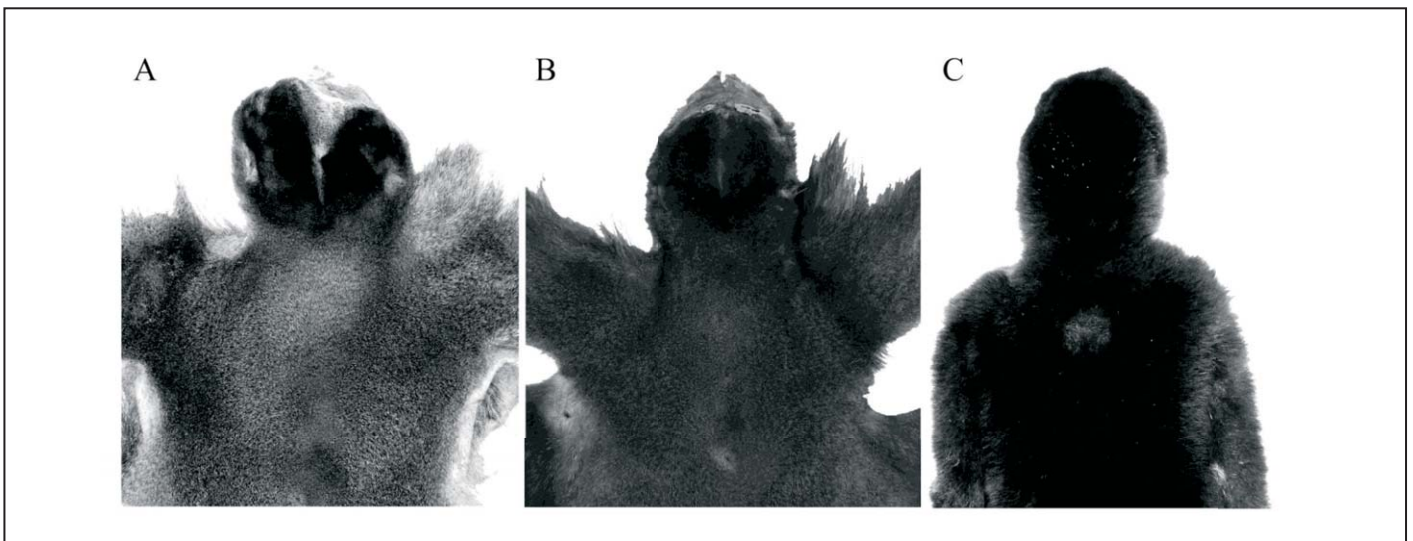


Figure 6. Detail of the upper back of *L. lugens* specimens representing color phases associated with the three skull morphotypes identified in this work and occurring in three contrasting ecosystems: A) FMNH 70601 ♂, from Río Consaya, Caquetá; B) FMNH 87775 ♂, from Río Yerley, Meta; and C) FMNH 84550 ♂, from Moscopán, Huila.

part of the biogeographic district of Caguán, in the Amazonian province (*sensu* Hernández-Camacho *et al.* 1992) (Fig. 7).

Etymology: In his visit to Colombia in 1942, Dr. Philip Hershkovitz established contact with Dr. Jorge Ignacio Hernández-Camacho, the most important figure in Colombian mammalogy in his generation (Patterson 1987). In his phonebook, Dr. Hershkovitz wrote in Spanish “El Sabio” (the wise man) beside Dr. Hernández-Camacho’s name. As a double tribute to the life of two remarkable scientists and to celebrate their meeting and all the fruits that this episode brought to the field of Primatology, the author has used the Latin translation of wise (*sapiens*) to designate the newly described taxon. The name *sapiens* highlights as well one of the most conspicuous characteristics of the subspecies; its larger skull compared to *L. l. lugens*. The author also gives tribute to the museological

endeavors of the FMNH, the institution that housed the specimens used as evidence for the description.

Common name: Woolly monkeys are called “*churucos*” or “*chulucos*” throughout their range in Colombia. I recommend “wise woolly monkey” in English and *churuco sabio* in Spanish.

***Lagothrix lugens defleri* subsp. nov.**

Lagothrix lagothricha lugens of Fooden (1963)

Lagothrix lugens of Groves (2001)

Holotype: Male specimen preserved as a skin and skull in excellent condition, FMNH 87775 (Figs. 5 and 6), collected by Kjell von Sneidern on 24 February, 1957; collector’s number 22574.

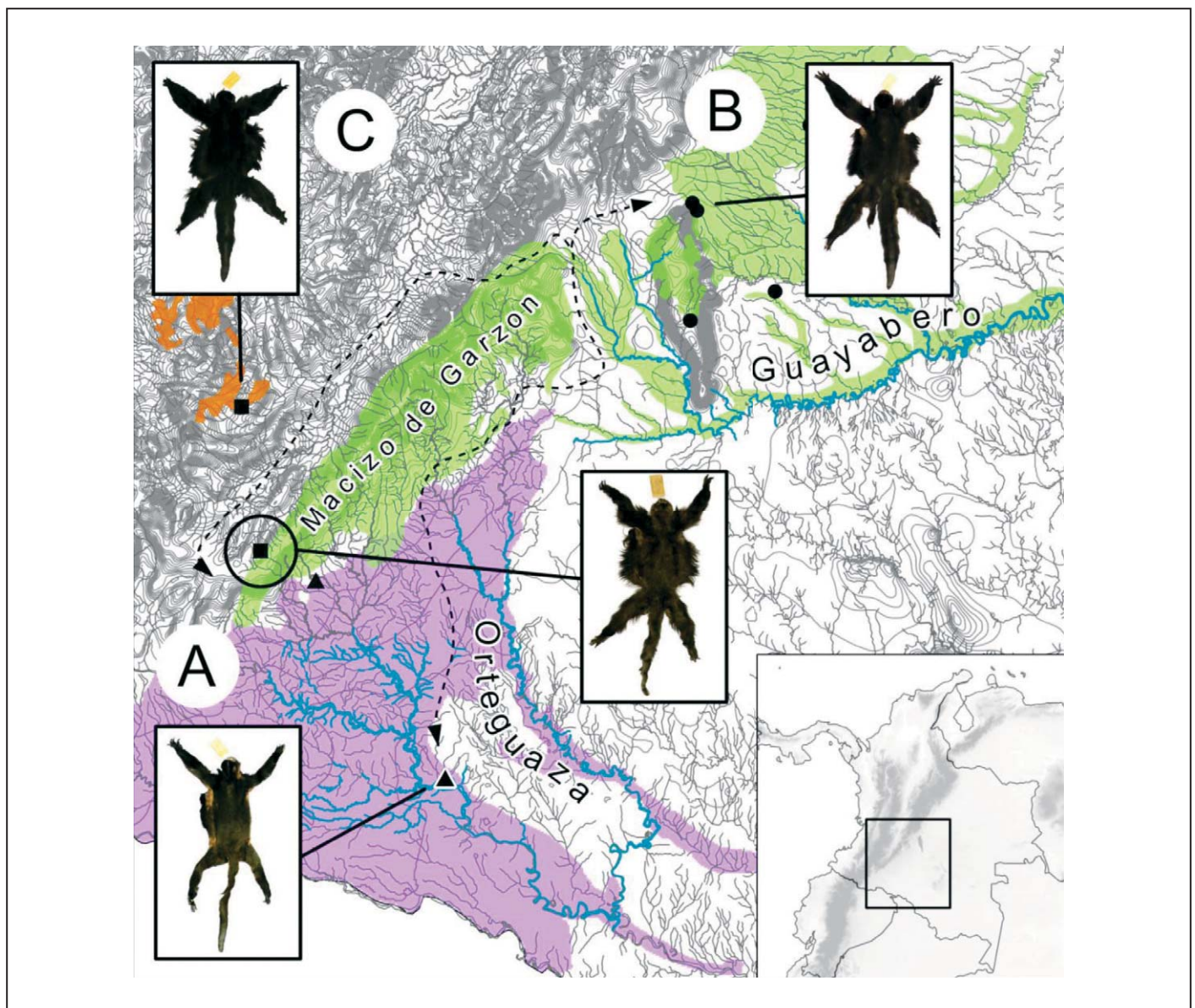


Figure 7. Geologic units associated with *Lagothrix lugens* collecting localities: Amazon Domain (purple), Andean Domain (orange), Guianan Domain (pink), and the Macizo de Garzón Unit (green); *L. l. lugens* (squares), *L. l. sapiens* (triangles); *L. l. defleri* (circles). Encircled square represents the locality of Aguas Claras, Huila, Colombia. Dashed line represents potential routes of gene flow among *L. lugens* populations.

Type locality: Río Yerley, Parque Nacional Natural La Macarena, department of Meta, Colombia (2°53'26.12"N, 75°18'W, 457.2 m [1500 ft] above sea level) (Fig. 7).

Type series: The type series includes four specimens, two males and two females preserved as skins and skulls, also collected with the holotype at Río Yerley FMNH 87776–77 ♂, FMNH 87778–79 ♀.

Diagnosis and Comparisons: *Lagothrix l. defleri* has a larger body than *L. l. lugens* and is within the morphometric range of *L. l. sapiens* in this respect (Table 3), with a shorter tail, broader at the base than in *L. l. sapiens* (see ratios body/tail in previous section). Overall coat color in *L. l. defleri* is darker than that of *L. l. sapiens*, with the hair on the chest and forearms longer than in *L. l. sapiens*. Blackish cap in *L. l. defleri* present, although contrasting less than in *L. l. sapiens*. Internally, skulls of *L. l. defleri* are larger than is typical of *L. l. lugens*; characterized by zygomatic not going beyond the orbital width in rostral view, contrasting skulls of *L. l. sapiens* specimens are FMNH 70601 ♂ FMNH 70604-05 ♂; and FMNH 70603 ♀, in which the zygomatic goes beyond the orbital width.

Description: Large (535.35 mm ♂ n = 6; 517 mm ♀ n = 6) and long tail (634 mm ♂ n = 6; 669.8 mm ♀ n = 6; measurements reported by Fooden 1963) general dark-gray to brown to brownish black trunk; darker head characterized by a blackish cap ornamented by a mid-sagittal dark gray coronal stripe. *Lagothrix l. defleri* has a broad tail, particularly at the base, that is blackish-gray to black. In *L. l. defleri*, the arms and the limbs are of the same color as the trunk, dark-gray to brownish-black. Ventrally, long hairs at the chest, varying in color from dark-gray to brown to blackish brown (Ridgeway 1912). The skull of *L. l. defleri* is larger than those of *lugens* and *sapiens* (Table 3), but slender and elongated caudally, and markedly constrained at the anteorbital constriction; orbits are enlarged with massive supraorbital arches in males; zygomatic width smaller than orbital width, particularly noticeable from a rostral view. Mandibles of *L. l. defleri* average larger than adjacent forms.

Distribution: Collecting localities of *L. l. defleri* represent five different biogeographic districts: Piedemonte Casanare-Arauca, and Piedemonte Meta, in the biogeographic province of Orinoquia; Ariari-Guayabero and Macarena in the biogeographic province of La Guayana; and Selvas Nubladas Orientales in the Norandina biogeographic province, as described by Hernández-Camacho *et al.* (1992). The subspecies is thought to occur north of the lower Río Guayabero, where populations formerly identified as *L. lugens* were reported by Klein and Klein (1976), up to the Río Apure at the border between Colombia and Venezuela, based on a record reported by Ruiz-García and Pinedo-Castro (2010) putatively assigned to *L. lugens* (Fig. 7). Most of the specimens of this taxon were collected at the Serranía de la Macarena and the piedmont of

the Uribe region (between the Serranía de la Macarena and the Eastern Cordillera).

Etymology: *Lagothrix lugens defleri* is named after Dr. Thomas R. Defler. The innumerable contributions of Dr. Defler to Colombian Primatology are the product of more than 30 years of continuous field work in the Colombian Orinoquia and Amazonia. As part of his efforts in understanding and preserving primate diversity in Colombia, Dr. Defler established the Caparú Biological Field Station (*Caparú* is the Yucuna name for the woolly monkey), dedicated to the training of young Colombian primatologists. As a former student of Dr. Defler at Caparú, I was introduced to field primate studies in 1994; since then, I have enjoyed his friendship and benefitted enormously from his extensive knowledge of primate ecology and evolution.

Common name: Woolly monkeys, genus *Lagothrix* are called “churucos” or “chulucos” throughout their distribution in Colombia. I recommend “Defler’s woolly monkey” in English and *El churucos de Defler* in Spanish.

A biogeographic hypothesis

The southern range of the Eastern Cordillera of the Colombian Andes, which marks the meeting point of the three identified *L. lugens* geographic variants, constitutes one of the most complex geological units of the country (de Porta 2003). The diverse origin of the parental material in the southern range of the Eastern Cordillera has resulted in the constitution of a mosaic of environments and vegetation types harboring a diverse fauna (Rangel 1997) that potentially promotes the ecological isolation observed among *L. lugens* populations. Genetic data in Ruiz-García and Pinedo-Castro (2010) placed the origin of the genus *Lagothrix* in the early Pleistocene (2.5 Mya), with an early isolation of *L. lugens* populations in the northern Andes of Colombia. The authors hypothesize that the high genetic diversity within this taxon, is explained by genetic drift caused by the fragmentation of suitable highland environments during glacial events (Ruiz-García and Pinedo-Castro 2010). Although the uplift of the Eastern Cordillera is placed around 12 Mya, its most active uplifting has been dated around 2.5 Mya (Adriessen *et al.* 1993; Hoorn 1994; Hoorn *et al.* 1995; Van der Hammen *et al.* 1973), suggesting that the expansion of *L. lugens* into the eastern piedmonts is a relatively recent event. This idea is also reinforced by data in Ruiz-García and Pinedo-Castro (2010) which suggested a recent divergence of the lowland species *L. lagothricha*. In addition, the complex hydrological system associated with the eastern piedmonts of the Andes seems to be an effective physical barrier preventing the dispersion of lowland populations of *L. lugens*. Rivers have been identified as effective barriers isolating natural primate populations and as the primary source of primate diversity (van Roosmalen *et al.* 2002, Hershkovitz 1963, 1979, 1982). A color variant of the titi monkey, genus *Callicebus*, in the northern part of the department of Caquetá, was first identified by Moynihan

(1976), and later formally described as an independent evolutionary lineage, *C. caquetensis*, by Defler *et al.* (2010). Defler *et al.* (2010) described the role of the Río Ortegua as an effective barrier isolating *C. caquetensis* from closely related taxa north of the Río Guayabero. The newly described taxon *L. l. sapiens*, with its type locality at Consaya, between the ríos Caquetá and Caguán, seems to follow a similar biogeographic pattern, with the Río Caguán isolating this taxon from populations of *L. l. defleri* north of the Río Guayabero.

In summary, I interpret the expansion of *L. lugens* into the piedmonts and lowlands of the eastern versant of the Andes as a recent event, followed by the isolation of lowland populations in pockets characterized by divergent ecological zones and separated by physical barriers such as rivers; a process that has led to the fixation of different external and internal characters. It is also likely that the geographic limits of divergent populations of *L. lugens*, have been fluctuating as a consequence of glacial and interglacial periods with the eventual genetic intermingle among divergent groups, resulting in hybridization in secondary contact.

Taxonomic note

As mentioned by Defler (2003), when von Humboldt (1812) wrote the holotypic description of Humboldt's woolly monkey, he spelled the species name both *lagotricha* and *lagothricha*. According to some, *lagothricha* (and its variant *lagotricha*) are incorrect Latinizations of the Greek words λάγος(ς) - lago(s) (hare) + θρίχο(ς) - thrico(s) (hair) because of the preceding vowel "o," which would require the form "trichos" rather than "thrichos". The use of the two versions was certainly a *lapsus* on von Humboldt's part. When revising the genus, however, Fooden (1963), under Article 24 (24.2) of the International Code of Zoological Nomenclature, chose the variation *lagothricha* as the "correct legal spelling" for *Lagothrix lagotricha*. I followed the determination of precedence of names or acts by the First Reviser. "If two or more names, different or identical, and based on the same or different types, or two or more nomenclatural acts, are published on the same date in the same or different works, the precedence of the names or acts is fixed by the First Reviser unless Article 24.1 applies." (International Commission on Zoological Nomenclature 1999).

Conservation remarks

Lagothrix lugens is the only member of the genus categorized as Critically Endangered (A3cd) on the IUCN Red List, and is considered a high priority for conservation due to population decline (Stevenson and Link 2008). Understanding the causes of the phenotypic variation in *L. lugens* is critical to the implementation of more realistic conservation actions to mitigate the negative effects of both anthropogenic and natural pressures. Two of the herein recognized variants of *L. lugens* are associated with Andean and sub-Andean ecosystems and it is likely that substantial changes in their distributions will take place within the next hundred years due to the predicted effects of global warming on these ecosystems

(Urrutia and Vuille 2009). Of particular concern is the situation of *L. lugens lugens* populations from Andean ecosystems (>2,000 m above sea level), which are almost entirely and in many cases completely extirpated from a substantial portion of their natural environments. The piedmonts and lowlands of the eastern versant of the Colombian Andes at the Serranía de la Macarena, habitats of the newly described subspecies, on the other hand, have experienced the devastation of unplanned anthropogenic transformation of forested areas mostly associated with the cultivation of illicit crops (Dávalos and Bejarano 2008). In Colombia, deforestation linked to drug cultivation and transport was likely responsible for more than half the forest loss during the 1990s (Alvarez 2002, 2007). To these risks we have to add the negative effects of petroleum extraction on the piedmonts of the Colombian Andes, and mining occurring across highland ecosystems in Colombia. Urgent measures are required to 1) promote comparative ecological studies among the herein described *L. lugens* variants, and 2) design a conservation plan, which takes into account the taxonomic differentiation proposed in this work.

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Appendix I. Specimens Examined

Lagothrix lugens lugens – COLOMBIA: Huila, Acevedo, FMNH 70574-75♂; FMNH 70577-80♂; FMNH 70581♀; Moscopán FMNH 84550; San Agustín, FMNH 70585♂; 70582-84♀. *Lagothrix lugens sapiens* – COLOMBIA: Caquetá, Río Consaya, FMNH 70601♂; FMNH 70604-05♂; FMNH 70602-03♀. *Lagothrix lugens defleri* – COLOMBIA: Boyacá, Bojabá, FMNH 92331-32♂; FMNH 92333-34♀; Meta, La Macarena FMNH 87775-77♂; FMNH 87781♂; FMNH 87778-79♀.