

MORPHOLOGICAL VARIATION BETWEEN TWO SUBSPECIES OF *CEBUS LIBIDINOSUS* (PRIMATES: CEBIDAE)

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Abstract.- The Paraguayan tufted capuchin, *Cebus libidinosus paraguayanus*, lives in two different areas in South America: one is the forest of eastern Paraguay to the south of the Matto Grosso in Brazil and the other is the most southern cloud Andean Forest known as Yungas of northwest Argentina and south of Bolivia. The Tambopata tufted capuchin, *Cebus libidinosus pallidus* lives in the north to the center of Bolivia and northwest of Matto Grosso. The objective of this study was to evaluate the phenotypic and craneometric differences between three allopatric populations, assigned to the two different subspecies: one population of *C. l. paraguayanus* from the Yungas region of northwest Argentina, an other one of the same subspecies from eastern Paraguay, and a population of *C. l. pallidus* from the south central Bolivia region of Buena Vista. The study consisted of phenotypic observation of museum's skins and a multivariate analysis of 21 cranial measurements of specimens housed in the collections of the Museo Argentino de Ciencias Naturales and Museo Nacional de Historia Natural del Paraguay. Two phenotypes are found in the Yungas and south central Bolivian specimens each, and one for the Paraguayan population, two phenotypes were similar to each other: the Yungas *C. l. paraguayanus* and Bolivian *C. l. pallidus*. The multivariate analysis denoted light craneometric differences between the three populations. Because the Yungas capuchin shares at least one phenotype with the Buena Vista Bolivian population, and the allopatric distribution of the *paraguayanus* subspecies which are about 800 km apart one each other. It is proposed to name all the northwest Argentina and south of Bolivia Yungas forest Capuchin as *C. l. pallidus*.

Resumen.- El mono cai, *Cebus libidinosus paraguayanus*, vive en dos diferentes áreas en Sudamérica: una población desde las selvas del este de Paraguay al sur del Matto Grosso en Brasil y la otra en las selvas de neblina del los Andes conocido como las Yungas en el noroeste de la Argentina y sur de Bolivia. El mono cai *Cebus libidinosus pallidus* vive en el norte y centro de Bolivia y en el noroeste del Matto Grosso. El objetivo de este estudio fue evaluar las diferencias fenotípicas y craneométricas entre tres poblaciones alopatricas, asignados a dos diferentes subspecies: una población de *C. l. paraguayanus* de la región de las Yungas Argentinas, y otra de la misma subespecie proveniente del este paraguayo, y una población de *C. l. pallidus* de la región de Buena Vista en el centro sur boliviano. El estudio consistió en observaciones fenotípicas de pieles y de análisis multivariados de 21 medidas craneales, de especímenes depositados en el Museo Argentino de Ciencias Naturales y en el Museo Nacional de Historia Natural del Paraguay. Dos fenotipos fueron identificados en las pieles provenientes de la yungas, dos de las provenientes del centro sur de Bolivia y solo un fenotipo único para las pieles provenientes del Paraguay. Dos fenotipos fueron similares entre sí: uno proveniente de las yungas de la subespecie *C. l. paraguayanus* y otro de la subespecie *C. l. pallidus* de Bolivia. El análisis multivariado muestra pequeñas diferencias craneométricas entre las tres poblaciones. Debido a que los monos kai de la Yungas argentinas comparte por lo menos un fenotipo con la población proveniente de la región de Buena Vista, Bolivia, y la distribución alopatrica de la subespecie *paraguayanus*, la cual están separadas por una franja de aproximadamente 800 km, se propone denominar a todos los especímenes de las Yungas del noroeste argentino y sur boliviano como *C. l. pallidus*.

The Paraguayan tufted capuchin, *Cebus libidinosus paraguayanus* Fisher 1829, has two allopatric distribution: one is between the Parana and Paraguay rivers in the forest of eastern Paraguay to the south of the Matto Grosso, Brazil, and the other in the cloud forest of the Andes, known as Yungas, of northwestern Argentina and south of Bolivia (Cabrera 1939, 1957; Brown & Rumiz, 1986; Zunino & Mudry 1993) (Fig. 1). Between these

two separated populations is the extensive and xeric Chaco plateau in which no species of capuchin monkey occur (Mantecon et al, 1984, Brown & Rumiz, 1985; Anderson, 1997). Mantecon et al. (1984) and Zunino & Mudry (1993) hypothesize a forest running just north of the Chaco plateau in Bolivia connecting the populations of southern Bolivia with the south of Matto Grosso in Brazil. This could be the subhumid rainforest of 'Bosques Chiquitanos'



Fig. 1. Distribution map: light grey: *C. l. paraguayanus*; dark grey: *C. l. pallidus*.

of central Bolivia, but according to Brown & Rumiz (1985) and Anderson (1997) this area is inhabited by a different subspecies: The Tambopata tufted capuchin, *Cebus libidinosus pallidus* Grey, 1965, which inhabits the jungles of northern and central Bolivia and northeast of Matto Grosso (Cabrera, 1957; Brown & Rumiz, 1985) (Fig. 1).

The taxonomy of these monkeys is very complex and confusing. Elliot (1913) described *Cebus azarae* from Paraguay and Matto Grosso, and *C. azarae pallidus* from Santa Ana, Peru, into Bolivia, with its complete range referred to “unknown”, he denoted the similarity between the two forms and pointed out the variability he found in the species; however, he described the *pallidus* form as generally darker.

Cabrera (1917) described *Cebus paraguayanus* as a full species including two subspecies: *C. p. paraguayanus* from Paraguay and Matto Grosso and *C. p. pallidus* as an occidental darker race of *C. paraguayanus*. Cabrera (1939) reported for the first time the occurrence of *Cebus paraguayanus* in the

northwest Argentinean region; he also noted that the forms *paraguayanus* and *pallidus* are closely related but gave them full species status. Later on, Cabrera (1957) recognized 11 subspecies for *Cebus apella*, among them he named *C. a. pallidus* from North and Central Bolivia and northeast of Matto Grosso and *C. a. paraguayanus* from Paraguay to Matto Grosso and southeast Bolivia and northwest Argentina.

The revision of the species made by Hill (1960), recognizing 16 subspecies, among them: *Cebus apella pallidus* and *Cebus apella kay* (= *paraguayanus*). He found them very similar, but in contrast with the descriptions made by Elliot (1913) and Cabrera (1917), he found *C. a. paraguayanus* “...darker in general colour, differing in the form of the black cap and the coloration of hands, feet and digits...”, but he describes phenotypic variation in both subspecies.

Mantecon et al (1984) confirmed the absence of *Cebus* in the Chaco plateau and described the specimens from the northwest Argentina and eastern Paraguay as similar and specimens from southeast Bolivia as reddish compared to the others.

Brown and Rumiz (1985) mentioned that the allopatric distribution together with some phenotypic differences found in specimens from the Yungas of Argentina and south Bolivia compared to specimens from Paraguay captive in the Centro Argentino de Primates (CAPRIM); and suggested that both populations could be different; unfortunately they did not describe any of these differences.

Mudry (1990) and Zunino & Mudry (1993) did not find significant differences in the study of the standard, G-banded and C-banded karyotype from specimens collected in Paraguay and the Yungas of northwestern Argentina. At the phenotypic level, they found that both populations exhibit the characteristics of coat colour and distribution described by Cabrera (1939) and Crespo (1950), for these reasons, they referred all the specimens collected in Paraguay

and northwest Argentina as *C. a. paraguayanus*.

Groves (2001) had separated the *Cebus apella* group complex in four species, turning *Cebus a. paraguayanus* and *Cebus a. pallidus* as subspecies of *Cebus libidinosus*.

The aim of this study was to evaluate the phenotypic and craneometric differences between three allopatric populations assigned to two different subspecies: one from the Yungas region of northwest Argentina, and other from eastern Paraguay both referred as *C. l. paraguayanus*, and the third one from south central Bolivia referred as *C. l. pallidus*.

MATERIALS AND METHODS

Phenotypic analysis

The phenotypic study was made on the pelage coloration of skins from specimens of northwest Argentina, eastern Paraguay and Buena Vista region of south central Bolivia, the collections are housed at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN). Only adult specimens were used.

Morphometric analysis

The morphometric study was based on 46 preserved skulls from the collections at MACN, and the Museo Nacional de Historia Natural del Paraguay (MNHNPy), comprising 9 males and 14 females from northwest Argentina, 10 males and 7 females from eastern Paraguay and 4 males and 2 females from south central Bolivia.

Only adult specimens with reasonable well preserved skulls were used, considering specimens to be adults if the spheno-occipital suture was closed and the permanent dentition complete (Zunino & Mudry, 1993). Twenty one cranial and dental characters were measured with a digital caliper of 0.01 mm precision, with bilateral characters always measured on the right side.

Measurements are as follows: 1- skull length (SL); 2- maximum cranial width at parietal

bones (MCWP); 3- condylobasal length (CL); 4- maximum width between zygomatic arches (MWZA); 5- orbital width (OW); 6- postorbital width (PW); 7- interorbital width (IO); 8- width between postglenoid process (WPP); 9- maximum width of foramen magnum (MWFm); 10- mandibular length (ML); 11- length between $C^1 - M^3$; 12- coronoidal height (CH); 13- coronoidal width (CW); 14- width between $C^1 - C^1$; 15- length between $M^1 - M^3$; 16- width between $M^1 - M^1$; 17- width between $I^2 - I^2$; 18- width between $I_2 - I_2$; 19- M^1 transverse diameter; 20- M^2 transverse diameter; 21- width between $M_1 - M_1$.

Multivariate analysis

Two multivariate techniques were performed: Principal Components Analysis (PCA), to study the inter-relationships of all specimens, and Discriminant Function Analysis (DFA) to test if the specimens can be classified within their own population and sex.

For the PCA analysis, both sexes were separated 'a priori' in difference groups following Zunino and Mudry (1993) results which show significant sexual dimorphism in the subspecies. NTSYS-pc 1.70 (Rohlf 1992) software packages was used to perform all the analyses.

RESULTS

Phenotypic analysis

The coat colour phenotype of all the adults specimens is dark brown to black in the tail, feet and hands, white cheeks and black cap always with tuft. The Paraguayan specimens are dorsally brown and ventrally reddish light brown; the Yungas specimens shows two phenotypes, one grayish brown in the dorsal region and ventrally reddish light brown but lighter than Paraguayan ones and the other, dorsally pale brown and ventrally reddish light brown similar to Paraguayans. The Bolivian specimens also present two phenotypes, one pale brown similar to one of the phenotypes from the Yungas and another dorsally reddish

Variables	Males		Females	
	Factor I	Factor II	Factor I	Factor II
SL	-247.465	-138.329	-253.936	-0.11520
MCWP	-0.95486	0.59674	-179.928	0.62018
CB	-263.151	-0.40496	-244.152	0.21628
MWZA	-336.996	148.527	-211.110	0.31684
OW	-223.558	-0.25155	-125.631	-113.973
PW	-0.11600	0.00111	-0.63376	-0.37043
IW	-0.31418	0.09159	-0.11967	-0.18625
WPP	-162.621	0.90897	-277.957	113.481
MWFM	-0.11049	0.30042	-0.43761	0.01585
ML	-256.994	-0.20975	-156.724	-0.81263
C ¹ - M ³	-0.66714	-183.601	-0.65987	0.04897
CH	-229.285	-0.33686	-109.802	-136.826
CW	-140.590	-0.21948	-0.79674	-0.75092
C ¹ - C ¹	-0.59187	-0.28615	-0.70156	0.10741
M ¹ - M ³	-0.05290	-0.07841	-0.12673	0.31387
M ¹ - M ¹	-0.49021	-0.34856	-0.38466	-0.28315
I ² - I ²	-0.43453	-0.29659	-0.50507	-0.09755
I ² - I ²	-0.29356	0.09117	-0.02933	-0.01351
M ¹	-0.00454	-0.23722	0.06322	-0.04943
M ²	-0.06035	-0.17071	-0.00560	0.03684
M ₁ - M ₁	-0.88432	140.053	-0.45914	-0.24076

Table I. Variable loadings on the first two principal components for the males and females group PCA.

brown and golden brown in the ventral region.

Morphometric analysis

The first two factors of the PCA analysis cumulate 70.2 % of total variance in males and 73.48 % in females (Table I). From the female data set analysis neither the first or second factor clearly separate any populations (Fig. 2B); instead the males data set shows some population differences (Fig. 2A): factor I separates 3 of the 4 Bolivian specimens from the rest and factor II slightly separates most Paraguayan and Yungas specimens. To factor I the characters that contribute most are condylobasal length, maximum width between

zygomatic arches and mandibular length; and to factor II the length between C¹ - M³ (Table I).

DFA analysis was highly significant (Wilks' lambda= 0.00032; p < 0.0000). All specimens were classified 100 % correct (Table II). The first function clearly confirms the sexual dimorphism and also separates the Yungas females from the others (Fig. 3); function II discriminates the Paraguayan males and most of Paraguayan females (Fig. 3). The characters which contribute most variation to function I are the width between C¹ - C¹, width between zygomatic arches and coronoidal width and to function II is the width between C¹ - C¹ (Table III).

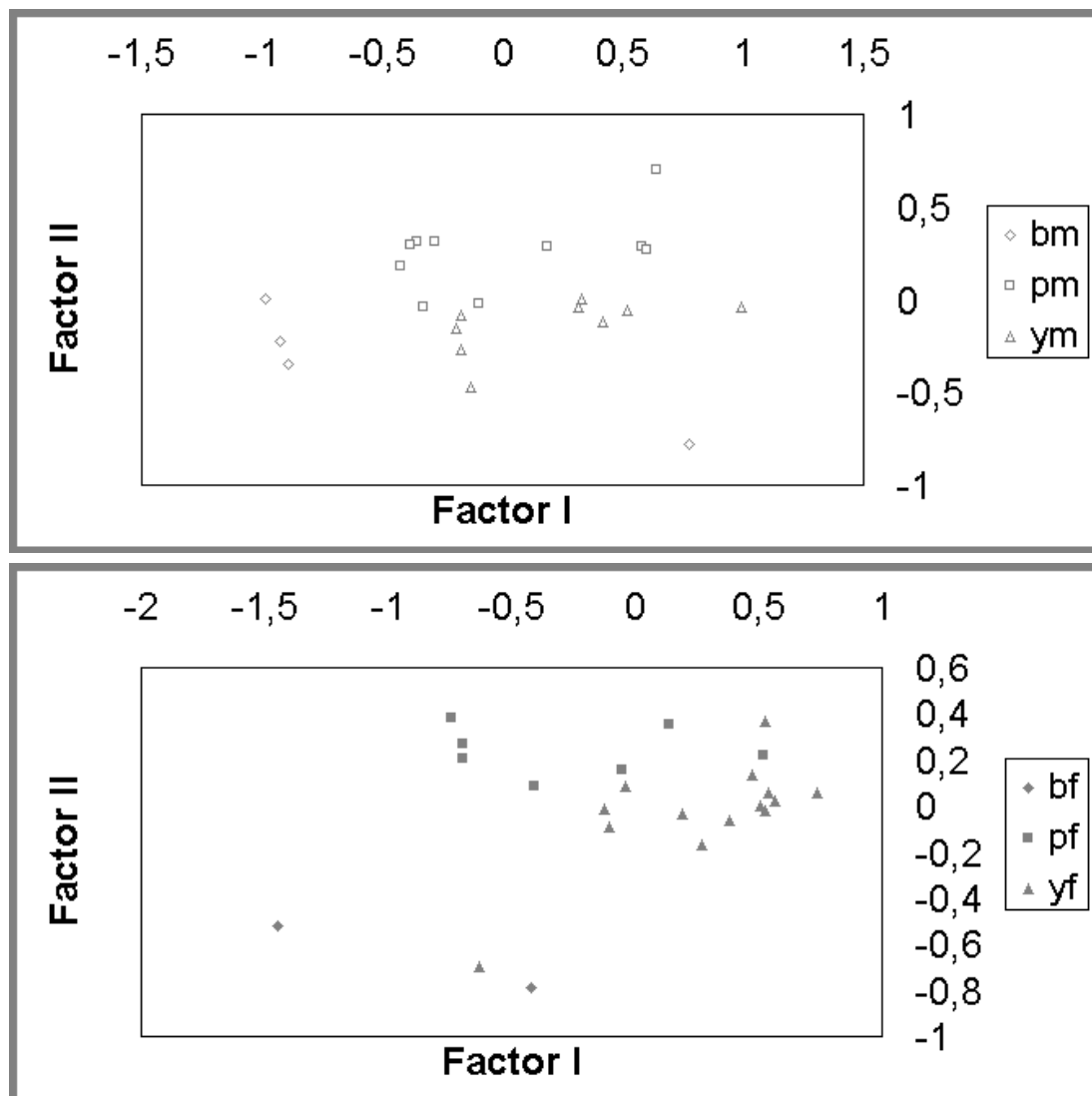


Fig. 2. Results of the PCA analysis: A from the males data matrix, B from the females data matrix.

DISCUSSION

Phenotypic analysis shows a tendency of colour variability within the populations, with the exception of Paraguayan specimens where only one phenotype could be described, but in fact from personal observation of *Cebus* in the wild of eastern Paraguay I could also observe slight colour variability. These results are in agreement with Elliot (1913) and Hill (1960) who also denote phenotypic variability within the subspecies. The phenotypes described by them are so similar and variable that there are

some specimens housed at the British Museum (Natural History) collected by A. Robert in Santa Anna de Chapada (15° 00' S; 55° 00' W) near Cuyaba, Matto Grosso, Brazil (Fig. 1) (Thomas, 1904) which are identified by Elliot (1913) as *Cebus azarae azarae* (=paraguayanus) and by Hill (1960) as *Cebus apella pallidus*. It is interesting to denote that for Elliot (1913) and Cabrera (1917) the *pallidus* forms are darker than *paraguayanus* opposite to Hill (1960) description of the subspecies.

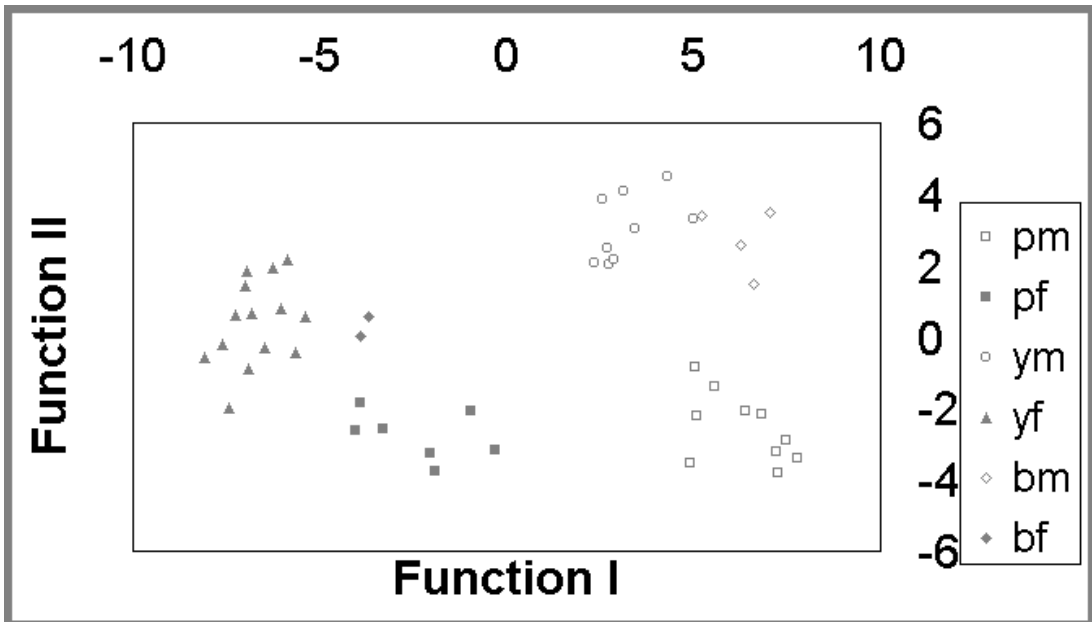


Fig. 3. Results of the DFA analysis. Eastern Paraguay: pm: males, pf: females. Northwestern Argentina: ym: males, yf: females. South central Bolivia: bm: males, bf: females.

	%	N
East Paraguay males	100	10
East Paraguay females	100	7
Central Bolivia males	100	4
Central Bolivia females	100	2
Northwest Argentina males	100	9
Northwest Argentina females	100	14

Table II. DFA Classification matrix.

Multivariate analysis results were rather ambiguous and not at all concluding. PCA analysis denoted just a slight population grouping from the males data set, but in females analysis the distribution of the specimens in the multivariate space was quite homogeneous (Fig. 2); however the DFA analysis suggested that all the specimens could be classified into the own population group and sex (Fig. 3) but we have to take into account that what DFA does, is to force the classification through the optimization of the variables that optimize the differences between the groups 'a priori' applied to each specimens.

It is evident that there are some craneometric

differences between the three population studied, but the main problem in this study, to fully clarify the taxonomy of these two highly variable subspecies, is the low number of specimens from Bolivia and none from the Matto Grosso region of Brasil. All the 6 crania and 3 of the 6 skin from Bolivia became from only one site, Buena Vista (17° 27' S; 63° 40' W) and other 3 skins from Cerro Amboro (17° 44' S; 63° 39' W) about 40 km south of Buena Vista (Fig. 1); this location, according to Anderson (1997), are one of the most southern distribution of the *pallidus* form in Bolivia. For all of these reasons mentioned, further studies may resolve the taxonomic problem more conclusively.

Due to the fact that some of the northwestern Argentinean *Cebus* specimens studied share identical phenotypes with the *Cebus* from Buena Vista, Bolivia, and the northwestern Argentinean and south of Bolivia Yungas region are around 800 km away from the eastern Paraguayan region, which is the closer *C. l. paraguayanus* habitat, it is propose to name all the northwest Argentina and south of Bo-

Variables	Function I	Function II	Function III
SL	0.2794204	0.1887423	-0.1380727
MCWP	0.1413328	-0.1932888	-0.1275229
CB	0.2838164	0.1338168	-0.1193164
MWZA	0.3907948	0.0135012	-0.0879781
OW	0.2424619	0.1906357	-0.2679709
PW	0.1353156	0.0726099	0.0616362
IW	0.1535273	0.0990584	0.0059112
WPP	0.3409705	-0.1628599	-0.0740753
MWFM	0.1147453	-0.1716935	-0.0246978
ML	0.3684347	0.2486358	-0.0985552
$C^1 - M^3$	0.1258427	0.1820421	-0.1536101
CH	0.2932611	0.3536642	-0.0645914
CW	0.3811379	0.3032593	-0.1349273
$C^1 - C^1$	0.5015099	0.4297594	0.2840820
$M^1 - M^3$	0.0405863	-0.0411409	-0.0009310
$M^1 - M^1$	0.1191773	0.2629687	-0.0256084
$I^2 - I^2$	0.1748673	0.1008605	-0.2198531
$I^2 - I^2$	0.0577625	0.0324714	-0.0488629
M^1	0.0315219	0.2998144	0.0426290
M^2	0.0593411	0.2416680	0.1072016
$M_1 - M_1$	0.0371276	-0.0077748	0.2145652

Table III. Canonical loadings for the first three discriminant functions.

livia Yungas forest *Cebus* monkeys as *C. lividinosus pallidus*.

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