

# Intra and Interspecific Variation in Cranial Morphology on the Southernmost Distributed *Cebus* (Platyrrhini, Primates) Species

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**Abstract** Capuchin monkeys (*Cebus*) are one of the genera with the widest distribution among Neotropical primates (New World Monkeys, Platyrrhini), accompanied by an elevated genetic, phenotypic, behavioral, morphological, and ecological diversity, both at the interspecific and population levels. Despite being one of the most studied primate genera, this high diversity has led to a particularly complex and controversial taxonomy. In this contribution, we explored the patterns of skull size and shape variation among the southernmost distributed populations of *Cebus* using three-dimensional geometric morphometric techniques. Results showed a marked morphological differentiation (in size and shape) between previously recognized species (*C. nigrinus* and southern *C. libidinosus*), and also among *C. libidinosus* populations, which were quantitatively related with the geographic distance between them. This pattern supports a differentiation between the northwestern Argentina and southern Bolivia and Paraguay forms. Other taxonomic implications are also discussed.

**Keywords** Geometric morphometrics · Platyrrhini · *Cebus* · Populations

**Electronic supplementary material** The online version of this article (doi:10.1007/s10914-013-9249-y) contains supplementary material, which is available to authorized users.

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## Introduction

Along with howler monkeys (genus *Alouatta*), capuchins (*Cebus*) are one of the genera with the widest distribution among Neotropical primates (New World Monkeys, Platyrrhini), comprising forest habitats from Honduras in Central America to northern Argentina in the south of the continent (Wilson and Reeder 2005). Despite being one of the most studied primate genera, high biological diversity has led to a particularly complex and controversial taxonomy for *Cebus* (Hill 1960; Torres 1983; Rylands et al. 2012 and references therein). Elliot (1913) separated *Cebus* into two groups based on the presence or absence of a hair tuft or ridge on the male's heads. Hershkovitz (1949), adopting this criterion, recognized four species: *C. apella* as the only member of the tufted group and *C. albifrons*, *C. capucinus*, and *C. nigrivittatus* in the un-tufted group. More recently, Groves (2001) recognized eight species, splitting *C. apella* into four distinct taxa (*C. apella*, *C. libidinosus*, *C. xantosternos*, and *C. nigrinus*) and adding *C. kaapori* to the three pre-existing species in the un-tufted group. Silva (2001) presented an alternative taxonomic arrangement in which he recognized the un-tufted and tufted groups as subgenera (*Cebus* and *Sapajus*, respectively) and did not recognize any subspecies, contrary to Groves' arrangement (see below). Moreover, Lynch Alfaro et al. (2012a), based on evidence from molecular genetics, suggested that *Cebus* and *Sapajus* are so distinct that they should be considered different genera. Following Groves' (2001) taxonomy, *C. libidinosus* would comprise four subspecies; with *C. libidinosus paraguayanus* and *C. libidinosus pallidus* (both considered junior synonyms of *C. cay* according to Silva) jointly presenting a distribution that comprises a wide range of habitats at the margin of the southern distribution for the genus (Fig. 1). It can be found between the Paraná and Paraguay rivers in the Atlantic forest of eastern Paraguay and parts of the Cerrado and Pantanal regions in southern Mato Grosso (Brazil) and also in the cloud forests of the

Andes, the Yungas, in northwestern Argentina (Salta and Jujuy provinces), and southeastern Bolivia (Cabrera 1939, 1957; Brown 1986; Silva 2001). Along with *C. l. paraguayanus* and *C. l. pallidus*, *C. nigrinus cucullatus* - following Groves' taxonomy - comprises the southernmost distribution for the genera. However, Silva (2001), Mittermeier et al. (2013), and other authors do not recognize this subspecies, and mainly consider it as a synonym of *C. nigrinus*. According to this last criterion, this taxon inhabits the Atlantic forest of Brazil, from Rio Doce in Minas Gerais state and extending south along the coast to the northern part of Misiones province in Argentina and part of Rio Grande do Sul state, Brazil (Fig. 1). The westernmost limit is constituted by the Paraná River, which would represent a geographic barrier separating it from *C. libidinosus paraguayanus* (IUCN 2012). Both southern *C. libidinosus* and *C. nigrinus* have been the subject of several intraspecific variation studies, mainly at the cytogenetic level (e.g., Mudry 1990; Ponsà et al. 1995; Martínez et al. 2002, 2004; Nieves 2007), as well as at the molecular genetic level (Ascunce et al. 2002; Casado et al. 2010). Both approaches revealed the existence of a high degree of intraspecific polymorphism and a marked differentiation between these taxa, in agreement with external phenotype (mainly coat coloration) observations (e.g., Mantecón et al. 1984).

Morphological variation is also of potential interest in phylogenetic, evolutionary, and taxonomic studies regarding this group where some complex traits might provide further information. For instance, it is well known that the skull represents a complex structure with numerous biological functions, and therefore subjected to many selective pressures. However, skull morphology variation analyses of the above mentioned taxa are rather inexistent, with Avila (2004) the

only published work of which we are aware. In his study, Avila employed distance-based or "traditional" morphometric methods to explore the pattern of variation in skull morphology in southern *C. libidinosus* populations failing to find any significant differences between them.

The complex and disputed taxonomy of the robust group of *Cebus*, the widespread distribution of its populations, and the previous reports on the significant variability at various distinct levels make this group of primates an interesting subject for evolutionary studies in mammals. In this contribution, we explore and quantify the pattern of skull size and shape variation among the southernmost distributed populations of *Cebus* using three-dimensional geometric morphometric techniques. This approach allows size and shape to be rigorously treated as different traits (Bookstein 1991) while quantifying the morphological variation (Rohlf and Marcus 1993). Specifically, we test for differences among four skull samples from southern *Cebus* populations, and discuss these patterns in an evolutionary and taxonomic context in order to provide new data on the phenotypic variation of *Cebus* in particular and Platyrrhini in general.

## Methods

### Sample

Specimens of *Cebus* were selected from collections deposited in the Museo Argentino de Ciencias Naturales (MACN) and Museo de La Plata (MLP). Based on the indicated geographic origin and the natural distributions, each specimen was assigned either to *C. nigrinus* (CNI, specimens

**Fig. 1** Proposed natural distributions for the southernmost taxa of *Cebus* following IUCN Red List maps (IUCN 2012), which are based on Silva (2001). Groves' (2001) subspecies names for the samples used in this work are also shown. Note that Groves (2001) only gave approximate ranges. Stars show approximately the geographic origin of the samples. Question marks represent uncertainty in the presence of *Cebus* in the area



from Misiones province, Argentina) or to *C. libidinosus* without initially considering subspecies (CLI, those from Salta and Jujuy provinces, Argentina; and from Paraguay and southern Bolivia) (Fig. 1). Only adult specimens were used in the analyses. Crania were considered to be adult when they had a fully erupted and functional dentition, as well as a closed or fused speno-occipital suture. Damaged specimens or those with hardly visible anatomical landmarks were excluded. The resulting sample sizes and composition are shown in Table 1. For a complete list of the analyzed specimens, see Table S1.

### Morphological Quantification

Cranial variation was analyzed by means of geometric morphometric techniques (Adams et al. 2004). Three-dimensional coordinates were captured for 32 anatomical landmarks (following Marroig and Cheverud 2005; see Fig. S1 and Table S2) from digital images using a photogrammetry based method (Niewoehner 2001; Chiari et al. 2008). Each specimen was photographed from eleven different fixed angles covering the whole cranium surface with a 12 megapixels calibrated Canon PowerShot Sx20 IS digital camera. Photographs were then loaded into PhotoModeler Scanner 6.0 software where landmark coordinates were digitized. Morphometric analyses of the landmark data were conducted in MorphoJ software (Klingenberg 2011).

A Generalized Procrustes Analysis (GPA, Rohlf and Slice 1990) was conducted in order to eliminate variation in the dataset owing to differences in scaling, rotation, and position of the specimens (i.e., non-shape variation). GPA also provided Centroid Size (CS, computed as the square root of the sum of squared distances of a set of landmarks from the geometrical center of the figure) for each specimen, which was used as cranium size variable. In order to summarize and describe the major trends in shape variation and to reduce the dimensionality of the analyses, a Principal Components Analysis (PCA) of the dataset was conducted. Size differences were assessed using a two way ANOVA with Species and Sex as main fixed factors. A MANOVA was used to test for mean shape differences between taxa and sexes (Species and Sex as factors), using the principal components as shape variables. Also, in order to assess and control for the allometric component of

shape variation, we conducted a MANCOVA analysis with the logarithm of CS (logCS) as covariable. This allowed us to explore whether shape differences between samples were maintained once the size dependency (i.e., the allometric effects) were removed. Finally, we explored the degree of multivariate shape divergence in the whole sample by using a Canonical Analysis emphasizing the assessment of among-groups morphological differences. This analysis returned Mahalanobis (morphological) distances between group's centroids, which were employed in a UPGMA clustering analysis to further explore the pattern of morphological similarity among the *Cebus* skulls through a phenogram.

### Results

Principal Components Analysis showed that the morphological variation in the *Cebus* sample could be reduced to 18 principal components, which accounted for 95.4 % of the total variance. Using this reduced dataset, a MANOVA was performed using sex, species, and sex by species interaction as independent variables in order to determine the existence of morphological differences between the two *Cebus* taxa and between sexes (Table 2). A significant sexual dimorphism in shape was detected, while there was no significant sex by species interaction, indicating that the pattern of sexual dimorphism in shape is the same for both species. This allowed testing for differences between species pooling both sexes together. Significant shape differences were found between CNI and CLI skulls (Table 2). As for size, ANOVA showed that there is also a significant difference in skull size between species, between sexes, and no significant sex by species interaction (Table 2). These results indicate that sexual dimorphism is not only in skull shape, but also in skull size, and that the pattern of size differentiation between sexes is the same for both species. Specifically, CNI skulls were bigger than those of CLI, while males were approximately 9 % bigger than females in both species (Table 2). Furthermore, significant differences in skull size were also found between CLI samples according to their geographic origin, independently from sex (Table 2). Tukey's post-hoc test showed that the Salta-Jujuy sample presents the smallest skull size, while the Bolivia sample was the biggest ( $P < 0.05$ ). Although the sample from Paraguay had no females included, males were slightly but significantly smaller than male skulls from Bolivia ( $P < 0.05$ ).

Although size and shape were considered separately in our analyses, the allometric component of shape variation was still present (i.e., shape changes that are correlated with size variation). Thus, we decided to evaluate if the morphological differentiation observed between species and sexes was owed solely to allometric effects (given the size differences previously found) or also to an intrinsic non-allometric component. A MANCOVA using the logCS as a covariable showed that

**Table 1** Sample size and composition of analyzed *Cebus* populations

Species	Origin	Males	Females	Total
Southern <i>C. libidinosus</i>		15	12	27
	Salta-Jujuy	4	9	13
	Paraguay	5	0	5
	Bolivia	6	3	9
<i>C. nigrurus</i>	Misiones	9	5	14
Total		24	17	41

**Table 2** Multivariate analyses on skull shape variables and ANOVA on skull size variable in two *Cebus* species

Analysis		Source of variation	Wilks $\lambda$	$F$	
Shape	MANOVA	Species	0.052	20.731*	
		Sex	0.162	5.744*	
		Species $\times$ Sex	0.488	1.164	
	MANCOVA	log CS	0.121	7.673*	
		Species	0.056	17.718*	
		Sex	0.259	3.021*	
Size	ANOVA	Source of variation	MS	$F$	
		Between species	Species	0.007	4.724*
		Sex	0.068	48.969*	
	Among populations of southern <i>C. libidinosus</i>	Species $\times$ Sex	0.000	0.004	
		Population	0.009	6.024*	
		Sex	0.051	36.311*	
		Population $\times$ Sex	0.000	0.001	

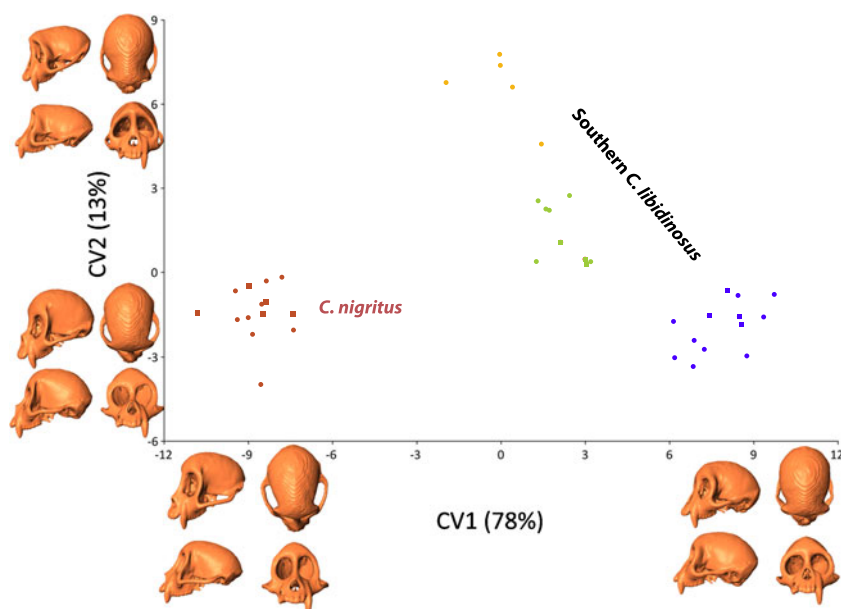
\*= $p < 0.05$ 

there is a significant effect of size on skull shape, but also revealed significant shape differences between species and sexes, and no sex-species interaction when the size effect was controlled (Table 2).

Figure 2 shows the scores plot for the first two axis of the canonical analysis on skull shape for the whole sample, which together accounted for approximately 91 % of the total variance. This analysis showed again a clear morphological separation between CNI and CLI species, mainly along the first axis (78 % of variance). The second axis (13 % of variance) separates primarily among CLI samples, although they also show differences along the first canonical axis. In morphological terms, the first axis represents changes mainly in the zygomatic arches and the maxillary bone, regions involved in the masticatory apparatus. Positive scores are associated with a more

compact general morphology, with a shorter rostrum, smaller zygomatic arches, and a more rounded cranial vault. Along the second canonical axis, morphological changes involve mainly the anterior region, with a lower frontal bone, oval orbits, and a less elongated morphology in the antero-posterior axis for higher scores in the positive direction. In Table 3 the Mahalanobis squared distances ( $D^2$ ) among CLI samples and CNI are presented. CNI is clearly divergent from all CLI samples, showing larger distances to any of them than those seen among CLI. This is also reflected by their position in the cluster analysis (Fig. 3). The Salta-Jujuy CLI sample is the most divergent from CNI, while Paraguay CLI skulls are the less distant to CNI, although their distance is slightly lower than that of Bolivian CLI. All distances were significant (permutation test with 10,000 rounds,  $P < 0.0001$ ).

**Fig. 2** Plot of first two canonical axes and associated morphological change. 3D skull models shape change is exaggerated for illustrative purposes. *Square symbols*: females; *circles*: males. *Red*: *C. nigrurus* specimens. Southern *C. libidinosus*: *Green*: Bolivia specimens; *Blue*: Salta-Jujuy specimens; *Orange*: Paraguay specimens. (For interpretation of the color references in this figure legend, the reader is referred to the online version of this article)



**Table 3** Mahalanobis morphological distances between samples from two *Cebus* species

	<i>C. nigrinus</i>	<i>C. libidinosus</i> (Salta-Jujuy)	<i>C. libidinosus</i> (Paraguay)
<i>C. libidinosus</i> (Bolivia)	12.129	8.577	9.053
<i>C. libidinosus</i> (Paraguay)	12.028	11.724	
<i>C. libidinosus</i> (Salta-Jujuy)	16.553		

## Discussion

The degree of morphological differentiation among populations results from the interaction between multiple evolutionary forces (e.g., selection, drift, etc.) that influence the genetic variability involved in the expression of morphological characters (Endler 1977). The extent of morphological divergence could be related to the geographic separation between these populations and, since cranial morphology is expected to have a strong genetic component (Marroig and Cheverud 2001), this divergence may be indicative of their evolutionary differentiation. In a recent work, Lynch Alfaro et al. (2012b) suggested that the diversification of *Cebus* unfolded as new areas were progressively invaded with the concomitant divergence of geographically separated populations. In this context, it is expected that the extensive geographic distribution of some *Cebus* species will be accompanied by high levels of variability between populations.

Accordingly, patterns of phenotypic variation are relevant in order to propose an informative and accurate taxonomy, which is ultimately the starting point in any conservation attempt or evolutionary study.

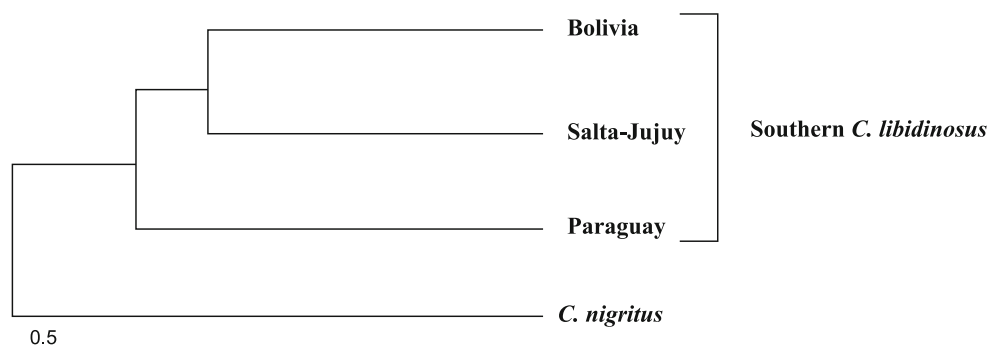
### Size and Shape Variation Between Southern *C. libidinosus* and *C. nigrinus*

Our results showed that size and shape variation among southern *C. libidinosus* and *C. nigrinus* are indicative of a marked morphological differentiation between both taxa. This is in agreement with the current knowledge that separates and defines these taxa as separate good species (Groves 2001; Silva 2001; Rylands and Mittermeier 2009; Mittermeier et al. 2013). Morphological differences were found to involve the masticatory apparatus, presenting CNI a generally more robust

morphology, an increased prognathism, larger zygomatic arches, and a bigger skull size than CLI. These results are concordant with Masterson (2001), who reported that both *C. nigrinus* and *C. robustus* were significantly larger and with an increased prognathism, among other differences involving mastication, compared to *C. libidinosus*. These results also confirm Lynch Alfaro et al.'s (2012b) suggestion that the same differentiation seen by Masterson may be also present in respect to Silva's *C. cay*, whose "adult crania (...) are so small they look like the juvenile ones in other robust species." However, differences in diet composition may be responsible for this variation as morphological differences are not always necessarily adaptive or genetically determined (e.g., phenotypic plasticity). In this sense, *C. nigrinus* eats mostly fruits and insects, relying on the tougher palm fruits during times of low food availability (Di Bitetti 2003; Ludwig et al. 2005), while southern *C. libidinosus*, specially in the Yungas region, relies extensively on fruits and Bromeliaceae stems when other high energy items become scarce (Brown 1986). The inclusion of tougher items in the diet of *C. nigrinus* and the observed morphological characteristics may be suggestive of a stronger bite force in this species.

Traditionally, size has been considered in morphometric studies as a plastic feature of organisms, while non-allometric shape changes have been regarded as adaptive (Sundberg 1989). It is interesting to test then if shape differences among compared groups are owed simply to an effect of their differences in size or if there is a "deeper" differentiation. Our analyses showed that the morphological differentiation between CLI and CNI was still evident when the effect of size variation was controlled. This may be relevant since it indicates that morphological differentiation between both species was not only attained by changes in body size, suggesting a deeper pattern of divergence and a differentiation of the proportionality among skull portions.

**Fig. 3** Relationships among studied populations of *Cebus* based on morphological similarity, obtained from an UPGMA analysis of Mahalanobis distances



## Sexual Dimorphism

*Cebus nigrinus* and southern *C. libidinosus* were found to have marked sexual dimorphism, both in size and shape. Results also indicated that the shape pattern of this dimorphism is the same for both species, suggestive of a common development pattern for these characters. This is reinforced by the fact that the size difference between sexes was the same for both species, despite the overall size difference between them. Another relevant conclusion of our analyses is that the sexes are still morphologically differentiated when size and allometric effects are accounted for, in agreement with Marroig (2007).

## Geographic Variation in Southern *C. libidinosus* Populations

Noticeably, the degree of morphological differentiation among *C. libidinosus* populations and with respect to *C. nigrinus* was qualitatively related to the geographic distance between them. Individuals from Paraguay were morphologically closer to *C. nigrinus* than any of the other two populations, even when only males were compared (data not shown). Giving the geographic proximity between Paraguay and the *C. nigrinus* distribution area, this result may be suggestive of an ongoing or recent genetic flow between the two populations, although other processes may also explain this pattern (Lynch Alfaro et al. 2012a). On the other hand, the Salta-Jujuy sample, being the farthest from the *C. nigrinus* area and from Paraguay, showed the biggest morphological distance to both populations. Ultimately, geographically closer populations resulted morphologically more similar than distant ones. This pattern may be indicative of the existence of a morphological cline, as were shown to exist in other primates (e.g., Cardini et al. 2007 in three genera of Old World Monkeys; Froehlich et al. 1991 in *Ateles*).

In respect to size variation, the Salta and Jujuy population presented a skull size strikingly smaller than that of the Bolivia population, even though they were the most closely related geographically and in shape terms. Possible explanations for this may be related to resource availability differences, since the Yungas region in Salta and Jujuy presents marked rain seasonality (Brown 1986) unlike northern Yungas. In this sense, Cardini et al. (2007) found that in the Old World monkey genera *Cercopithecus* the precipitation gradient successfully explained clinal variation in skull size, but more studies will be needed to properly address this and other questions in these *Cebus* taxa.

## Taxonomy Notes

Platyrrhine taxonomy is being intensively debated, as new genera (e.g., *Sapajus*, *Mico*, *Callibela*) and tens of species have been recently named. This has raised concerns on the effects that taxonomic instability and inflation can cause on our understanding of platyrrhine diversity and evolution (e.g., Rosenberger 2012). In this context, taxonomy is also important for our

conservation efforts, since we need to name what we think constitutes a different, biologically meaningful, thing before we can study and ultimately protect it. Groves (2001) recognized four subspecies of *C. libidinosus*: *libidinosus*, *pallidus*, *juruanus*, and *paraguayanus*. He considered the *Cebus* populations of northeast Argentina and southern Bolivia as *C. libidinosus pallidus* and those from Paraguay as *C. libidinosus paraguayanus*. Brown (1986) considered *C. libidinosus pallidus* as from Bolivia and northwestern Peru, and mentioned that *Cebus* from northeast Argentina were very similar to these forms. According to this author, biogeographic history of the Yungas region indicated that the *Cebus* populations from Bolivia and Argentina were repeatedly separated and reconnected from the Paraguayan populations. He also restricted *C. libidinosus paraguayanus* to eastern Paraguay, as did Hill (1960). Moreover, Cabrera (1957) and Vieira (1955) stated that the *Cebus* populations of Bolivia and Argentina meet with the Paraguayan populations in the Mato Grosso, Brazil (see Fig. 1). However, Casado et al. (2010) recently showed that Mato Grosso and Paraguay populations of *C. libidinosus paraguayanus* diverged at least 1.2 million years ago, making the Cabrera and Vieira statement unlikely. According to Casado et al. their results may explain “(...) the evident discontinuity between the (...) populations of western central Brazil and northeastern Paraguay from those of northwestern Argentina and southern Bolivia resulting from their separation by the Chaco (...)” region. In this direction, Avila (2004) proposed to consider, based on coat coloration characteristics, northwest Argentina and central and southern Bolivia populations as *C. libidinosus pallidus* and Paraguayan populations as *C. libidinosus paraguayanus*. Finally, Silva (2001) considered *C. libidinosus paraguayanus* as *C. cay* and *C. libidinosus pallidus* as *C. apella*; however, he assigned northwest Argentina and southern Bolivia populations to *C. cay*.

According to our results, the described skull morphological variation patterns support the differentiation between the northwest Argentina and southern Bolivia and Paraguay forms, namely *C. libidinosus pallidus* and *C. libidinosus paraguayanus*, in agreement with Hill (1960), Brown (1986), Groves (2001), Avila (2004), and Casado et al. (2010). As this is the first study on *Cebus* to use geometric morphometrics techniques, the interpretation of our results cannot be directly extended to the whole genus. Thus, more studies with a larger sample size and encompassing a wider geographic range, and especially combined with molecular and cytogenetic data will be needed not only to decide if they constitute separate species but also to extend our knowledge on diversity and evolutionary patterns in New World Monkeys.

**Acknowledgments** We thank Dr. David Flores (Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”) and Dr. Diego Verzi (Museo de La Plata) for granting us access to the collections under their care. We also thank two anonymous reviewers whose comments helped improve this work. This research was supported by grants from CONICET (MDM PIP 112) and UBACyT (X154).

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