Morphometrics of genus *Caluromys* (Didelphimorphia: Didelphidae) in northern South America

María José López-Fuster
Universitat de Barcelona. Facultat de Biologia. Departament de Biologia Animal
Av. Diagonal, 645. E-08028 Barcelona (Spain)
e-mail: marialopez@ub.edu

Roger Pérez-Hernández
Universidad Central de Venezuela. Instituto de Zoologia Tropical
Apartado 47058. Caracas 1041-A (Venezuela)
e-mail: roperez@strix.ciens.ucv.ve

Jacint Ventura
Universitat Autònoma de Barcelona. Facultat de Biociències
Departament de Biologia Animal, de Biologia Vegetal i d'Ecologia
E-08193 Bellaterra. Barcelona. (Spain)
e-mail: jacint.ventura.queija@uab.es

Manuscript received in september 2008

Abstract

We reviewed the morphometric relationships between different forms of the woolly opossum, genus *Caluromys*, in northern South America by means of univariate and multivariate analyses of skull characters. Results revealed that specimens from Trinidad and northern Venezuela differ substantially in size and shape from other representatives of the genus. Thus, we propose that they should be attributed to *Caluromys trinitatis* rather to *C. philander*. Consequently, the specific name given by Thomas (1894, 1903) should be reapplied. The morphotype *leucurus*, also attributed by Thomas (1904) to *C. trinitatis*, has an intermediate morphology, resembling *C. philander* in size but *C. trinitatis* in shape. Therefore, we were unable to assign it to a specific taxon. Nevertheless, these differences allowed us to consider *leucurus* as a valid taxonomic entity. *Caluromys derbianus* and *C. lanatus* show similar skull sizes but these two species clearly differ in shape, the latter being more phenetically related to *C. philander* than to any other *Caluromys* form.

Key words: *Caluromys philander*, *Caluromys trinitatis*, marsupials, Neotropics, shape, size, skull.

Resumen. *Morfometría de* Caluromys philander *(Didelphimorphia: Didelphidae) en el norte de Suramérica*

Se revisan las relaciones morfométricas entre distintos morfotipos del género *Caluromys*, presentes en el norte de Suramérica, mediante análisis univariantes y multivariantes de caracteres craneales. Los resultados obtenidos indican que los ejemplares de Trinidad y del

norte de Venezuela difieren substancialmente en el tamaño y la forma del cráneo respecto a las demás muestras analizadas. En consecuencia, se sugiere atribuir dichos ejemplares a *Caluromys trinitatis* y no a *C. philander*, recuperando así el nombre específico bajo el que fueron descritos por Thomas (1984, 1903). El morfotipo *leucurus*, considerado por Thomas (1904) como una subespecie de *trinitatis*, presenta una morfología intermedia, asemejándose a *C. philander* en tamaño y a *C. trinitatis* en forma. Estas características no permiten realizar un diagnóstico específico inequívoco de los ejemplares atribuidos a dicho morfotipo. No obstante, debido a sus características craneales, se considera *leucurus* como una entidad con validez taxonómica. Los resultados obtenidos corroboran la similitud existente entre *C. derbianus* y *C. lanatus* en cuanto al tamaño craneal. Sin embargo, ambas especies difieren notablemente en forma, mostrando en este caso *C. lanatus* una mayor proximidad fenética respecto a *C. philander* que respecto a cualquier otro representante del género.

Palabras clave: *Caluromys philander*, *Caluromys trinitatis*, cráneo, forma, marsupiales, Neotrópico, tamaño.

Introduction

The New World woolly opossums of the genus *Caluromys* are nocturnal, arboreal, and solitary marsupials that inhabit lowland tropical rainforests, from southern Mexico (18º latitude N) to northern Argentina (30º latitude S). The following species have been recognized to date: *C. derbianus*, which extends from Mexico to western Colombia and Ecuador; *C. lanatus*, which occurs in northern and central Colombia, northwestern and southern Venezuela, east Ecuador, Peru, and Bolivia, eastern and southern Paraguay, northern Argentina, and western and southern Brazil; and *C. philander*, which is distributed in Trinidad and Tobago, Venezuela, Guyana, Surinam, French Guiana, and Brazil (Brown, 2004; Emmons & Feer, 1997; Gardner, 2005).

The taxonomic relationships of the distinct morphotypes of *C. philander* that occur in northern South America are controversial. Allen & Chapman (1893) reported the capture of a single, apparently adult male, of this opossum on the island of Trinidad. They provisionally assigned this specimen to *Didelphis (Philander) philander*, although they noted that it differed from this species "in its much smaller size, in the tail being hairy for only an inch and a half at the base (instead of for "from two to three inches"), and uniform grayish brown from base to tip, instead of white for its apical half, as in Brazilian examples". Further, Thomas (1894) did not hesitate in describing this Trinidadian form as a new species, *D. (P.) trinitatis*, particularly because of its smaller skull and distinct fur colour with respect to the closely related *D. philander*. Allen (1900) proposed assigning the new generic name of *Caluromys* to the taxon formerly considered as *Didelphis* (*Philander),* and reported a list of 10 species in which he included *C. trinitatis* described by Thomas (1894). Later, Thomas (1903) included a new form, *C. trinitatis venezuelae*, from northeastern Venezuela in this species. This form is similar to the nominate subspecies but paler and with longer and softer fur. According to this author, "this mainland form of *C. trinitatis* shows no approximation in size or other characters to the Guianan *C. philander*". A year later, Thomas (1904) added a new subspecies to

C. trinitatis, *C. t. leucurus*, found in the lower Orinoco (Venezuela), which was similar in size to its conspecifics but with distinctive short fur and white tail. Although some or all of these subspecies were accepted by several authors (Allen, 1904; Anduze, 1956; Cabrera, 1919; Pittier & Tate, 1932), Cabrera (1957) considered all of them as synonymies of *C. philander philander* (Type locality, Surinam). This taxonomic pattern has prevailed to date (see Gardner, 2005), although the specimens from northern Venezuela have been attributed to *C. philander* "subsp. nov" (Pérez-Hernández, 1989) or to *C. p. trinitatis* (Linares, 1998).

To our knowledge, no exhaustive study has addressed the morphological and morphometric relationships between the forms of *trinitatis* described by Thomas (1894, 1903, 1904) and between these and other *Caluromys* taxa. Here we performed comparative morphometric analyses of skull size and shape between several morphotypes of this genus, paying particular attention to the Venezuelan and Trinidadian forms currently assigned to *C. philander*.

Material and methods

We analyzed 89 skulls of adult specimens (classes IV-VI; see Gardner, 1973) of *Caluromys* from Brazil, Colombia, Ecuador, French Guiana, Panama, Peru, and *Venezuela* (Figure 1; Appendix 1). These skulls were from the following taxa: *lanatus* (n = 14; 3 males, 5 females, 6 ?), *derbianus* (n = 8; 5 males, 3 females),

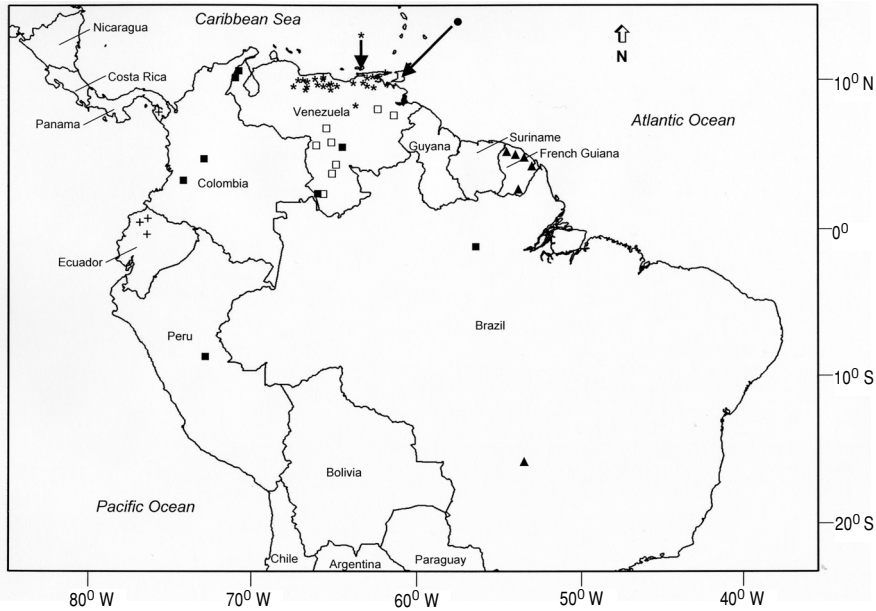

Figure 1. Localities of the *Caluromys* samples studied. Symbols: *derbianus* (+); *lanatus* (■); *philander* (▲); *trinitatis* (●); *venezuelae* (★); *leucurus* (□).

philander (n = 14; 1 male, 5 females, 8 ?), *trinitatis* (n = 2; 1 male, 1 female), *venezuelae* (n = 38; 19 males, 17 females, 2 ?), and *leucurus* (n = 13; 8 males, 5 females). Although we were able to examine only two specimens from Trinidad and Tobago, we included them in the statistical analyses in an attempt to perform an exploration of the affinities between the morphotypes formerly assigned to C. *trinitatis*, and between these forms and C. *philander* from French Guiana and Brazil.

Twenty-two skull and dental measurements were taken in each specimen using a digital caliper with an accuracy of 0.01 mm: total skull length (TSL), condylobasal length (CBL), basal length (BL), palatal length (PL), nasal length (NL), length of upper dental series (UDS), length of I1-I5 (I1-I5), length of C-PM3 (C-PM3), length of M1-M4 (M1-M4), rostral width (RW), nasal width (NW), interorbital width (IOW), width of the postorbital processes (PPW), minimum postorbital width (POW), zygomatic width (ZW), occipital width (OW), skull case height (SCH), length of mandible (ML), length of lower dental series (LDS), length of c-pm3 (c-pm3), length of m1-m4 (m1-m4), height of coronoid process (CH). A definition of these measurements can be found in Ventura et al. (1998), except TSL (see Izor & Pine, 1987), IOW (minimum skull width before the postorbital processes), and PPW (maximum width of the postorbital processes).

Data were tested for normality and homogeneity of variances by Kolmogorov-Smirnov *D*-statistic and Levene's test, respectively. A two-factor analysis of variance (ANOVA) was performed to assess the effect of group and sex. Pairwise comparisons of character means between samples were performed by Sheffé's method. For all sequential tests, P values were corrected by the Bonferroni adjustment (Rice, 1989), as modified by Chandler (1995). To evaluate variation in size and shape between samples, a multiple-group principal-component analysis was done on all the skull characters (Thorpe, 1988) of specimens for which no data was missing (n = 68). Canonical function analyses were then performed using all multiple-group component scores to analyze size and excluding the first vector to remove the effect of size.

Phenetic relationships between groups were depicted in the phenograms obtained by cluster analyses for size and shape. For size, this analysis was performed using the unweighted pair-group method (UPGMA) and the Euclidean distance matrix derived from the standardized character means. The method for size adjustment described by Burnaby (1966) was used to examine the effect of shape: scores on the first principal component axis were obtained from the total variance-covariance matrix; character means were then projected onto the hyperplane orthogonal to the first vector and the resultant adjusted data matrix was used to compute a Euclidean distance matrix, which was then clustered by the UPGMA method. Since *Caluromysiops* is the sister-group of *Caluromys* (see Voss & Jansa, 2003) we used the single species of *Caluromysiops* (*C. irrupta*) as external group in cluster analyses. Variables for this species were obtained from Izor & Pine (1987) and were selected on the basis of concordance with our measurements. These variables were total skull length, condylobasal length, basal length, palatal length, interorbital width, width of the postorbital processes, zygomatic width, occipital width, length of mandible, and length of the lower dental series. Statistical analyses were

performed with SPSS 11.0 (SPSS, Inc., Chicago, IL), except cluster analyses, which were computed by NTSYSpc (version 2.1; Rohlf, 2002).

Results

Two-way analysis of variance revealed significant geographic variation and absence of sexual dimorphism for all characters (Table 1). To increase sample sizes, males, females, and specimens of unknown sex were pooled in subsequent analyses. Descriptive statistics for the skull measurements are shown in Table 2. Except for the minimum postorbital width, morphotypes formerly assigned to *C. trinitatis* (i.e. *trinitatis*, *venezuelae*, and *leucurus*) exhibited, in general, the smallest skulls, especially *venezuelae*, while the highest mean values corresponded to *derbianus* and *lanatus*. Comparisons between pairs of samples revealed no significant difference in the following cases: *trinitatis-venezuelae*, *trinitatis-leucurus*, and *lanatus-derbianus*. The degree of morphometric divergence varied between the remaining samples (Table 3). In general terms, most variables showed significant differences in the comparisons between small-sized and large-sized taxa, especially for skull length and dental characters. Moreover, *venezuelae* diverged from *leucurus* and *philander*, except for some width dimensions. *Caluromys philander* differed significantly in several length and dental parameters (5 in each case) from *trinitatis* and *leucurus*; significance with respect to *lanatus* and *derbianus* was observed in 7 and 10 characters, respectively.

Multiple-group principal-component analysis provided 22 orthogonal components. However, because of the total sample size, we used only the first 6 vectors, which accounted for 98.67% of the total morphometric variance (eigenvalues and percentages of variance explained: PC1, 152.58, 94.65%; PC2, 3.02, 1.88%; PC3, 1.36, 0.85%; PC4, 0.79, 0.49%; PC5, 0.72, 0.44%; PC6, 0.56, 0.35%). The first vector was correlated with all skull characters ($P < 0.001$). Sign and magnitude of the components of this vector allowed us to consider it a multivariate expression of size. For the subsequent canonical function analyses, the 2 specimens of *trinitatis* were treated as "ungrouped". Canonical function analysis using the 6 components provided 4 significant discriminant functions (Wilk's lambda = 0.009; $\chi^2 = 281.472$, d.f. = 24, $P < 0.001$). The percentage of grouped cases correctly classified was 92.4%; all *philander* (n = 12) and *leucurus* (n = 10) were classified correctly, 1 *venezuelae* (n = 26) was misclassified as *leucurus*, 2 *lanatus* (n = 11) as *derbianus*, and 2 *derbianus* (n = 7) as *lanatus*. The 2 ungrouped individuals from Trinidad were assigned to the form *venezuelae*. Projection of the individual scores onto the first and second canonical functions revealed 3 major groups: one comprising the specimens formerly assigned to *C. trinitatis*, a second formed by *philander*, and a third including the large forms *lanatus* and *derbianus* (Figure 2a). Discrimination was especially clear along the first axis, which accounted for 88.4% of the total variance and was an expression of size. Within taxa assigned to *C. trinitatis*, the distribution of scores along this axis showed a clear clinal variation in size, from the small *venezuelae* to the large *leucurus*. Along the second axis, the degree of overlapping between samples was considerable, except for *phi-*

Table 1. Morphometric comparisons between *Caluromys* taxa. Results of two-way analysis of variance (ANOVA) according to group and sex.***: P <0.001; P values corrected by the Bonferroni adjustment.

		Geographic variation		Sexual dimorphism	
Character	**N**	**F**	**P**	**F**	**P**
TSL	59	57.50	***	1.70	0.199
CBL	59	57.59	***	1.91	0.174
BL	59	53.76	***	2.09	0.155
PL	59	58.79	***	1.99	0.164
NL	66	40.83	***	1.51	0.224
UDS	62	108.96	***	0.48	0.491
I1-I5	64	25.23	***	1.93	0.170
C-PM3	68	77.29	***	2.27	0.138
M1-M4	67	75.19	***	0.45	0.503
RW	65	23.49	***	0.13	0.716
NW	62	12.49	***	0.48	0.489
IOW	65	59.37	***	0.51	0.479
PPW	62	8.93	***	0.22	0.642
POW	63	11.61	***	0.50	0.480
ZW	62	30.38	***	1.14	0.290
OW	62	35.17	***	2.49	0.447
SCH	63	26.87	***	4.90	0.031
ML	69	47.92	***	1.04	0.312
LDS	68	82.47	***	0.30	0.588
c-pm3	71	68.73	***	1.18	0.281
m1-m4	72	70.24	***	2.83	0.097
CH	69	20.00	***	4.31	0.042

lander because of to its low values. This axis explained 8.3% of total variance and was related to nasal, minimum postorbital, and interorbital widths ($P < 0.001$).

Size-independent canonical function analysis (excluding the first vector) provided 4 significant discriminant functions (Wilk's lambda = 0.158; $\chi^2 = 110.698$, d.f. = 20, $P < 0.001$), which classified 81.8% of grouped cases correctly. As in the canonical analysis for size, all *philander* were classified correctly and the ungrouped *trinitatis* were assigned to *venezuelae*. Regarding the other taxa, 6 *lanatus*, 23 *venezuelae*, 9 *leucurus*, and 4 *derbianus* were classified correctly. In total 12 specimens were misclassified: 3 specimens of *lanatus* were assigned to *venezuelae*, 1 to *leucurus*, and 1 to *derbianus*; 2 individuals of *venezuelae* to *lanatus* and 1 to *leucurus*; 1 *leucurus* to *philander*; and 3 *derbianus* to *venezue-*

Table 2. Descriptive statistics for skull measurements of adult *Caluromys* taxa.

Character	Sample	n	Mean	SD	Minimum	Maximum
TSL	*lanatus*	11	58.51	1.97	54.82	61.47
	derbianus	8	59.44	1.59	57.64	61.74
	philander	12	55.30	2.54	49.32	57.89
	trinitatis	2	48.62	2.73	46.69	50.55
	venezuelae	29	47.28	2.12	43.52	51.44
	leucurus	10	51.18	2.77	48.02	55.14
CBL	*lanatus*	11	57.50	1.79	53.71	60.02
	derbianus	8	58.57	1.62	56.60	61.07
	philander	12	54.40	2.57	48.06	57.50
	trinitatis	2	47.30	2.85	45.29	49.32
	venezuelae	29	45.87	2.22	41.71	50.46
	leucurus	10	50.26	3.06	46.63	54.82
BL	*lanatus*	11	54.10	1.69	50.71	56.65
	derbianus	8	55.27	1.65	52.94	57.67
	philander	12	51.27	2.62	44.90	54.74
	trinitatis	2	44.27	2.78	42.31	46.24
	venezuelae	29	42.98	2.19	38.88	47.63
	leucurus	10	47.29	3.12	43.81	51.64
PL	*lanatus*	11	30.78	0.93	29.19	32.11
	derbianus	7	32.55	0.79	31.59	33.69
	philander	13	29.42	1.38	26.80	31.42
	trinitatis	2	25.59	1.39	24.61	26.57
	venezuelae	29	25.30	1.14	23.15	27.89
	leucurus	11	27.53	1.61	25.10	29.54
NL	*lanatus*	13	23.75	1.13	21.27	26.17
	derbianus	8	24.33	1.10	22.57	25.80
	philander	14	22.76	1.30	20.53	24.57
	trinitatis	2	17.75	0.87	17.14	18.37
	venezuelae	32	18.81	1.42	16.25	21.99
	leucurus	12	21.51	0.84	20.20	23.00
UDS	*lanatus*	11	28.08	0.65	27.32	28.99
	derbianus	7	29.35	0.48	28.95	30.35
	philander	14	26.31	0.71	25.09	27.96
	trinitatis	2	23.44	0.24	23.27	23.61
	venezuelae	30	23.08	0.69	21.63	24.97
	leucurus	12	24.96	0.87	23.73	26.02
I1-I5	*lanatus*	11	4.40	0.28	4.08	5.06
	derbianus	8	4.55	0.19	4.27	4.83
	philander	14	4.21	0.31	3.67	4.72
	trinitatis	2	3.68	0.21	3.53	3.83
	venezuelae	30	3.71	0.18	3.36	3.97
	leucurus	12	3.98	0.25	3.64	4.41

Character	Sample	n	Mean	SD	Minimum	Maximum
C-PM3	*lanatus*	11	11.20	0.50	10.00	11.76
	derbianus	7	11.70	0.33	11.30	12.10
	philander	14	10.08	0.50	9.24	10.84
	trinitatis	2	9.18	0.37	8.92	9.44
	venezuelae	36	9.01	0.41	8.15	9.91
	leucurus	12	9.64	0.35	9.23	10.34
M1-M4	*lanatus*	12	9.74	0.47	8.66	10.31
	derbianus	7	10.15	0.36	9.61	10.57
	philander	14	9.45	0.26	9.06	10.15
	trinitatis	2	8.55	0.16	8.44	8.66
	venezuelae	34	8.31	0.21	7.76	8.79
	leucurus	13	8.80	0.28	8.43	9.33
RW	*lanatus*	12	11.79	0.64	10.72	12.93
	derbianus	8	11.98	0.51	11.20	12.51
	philander	14	11.09	0.65	9.85	12.00
	trinitatis	2	10.49	0.35	10.25	10.74
	venezuelae	33	9.64	0.58	8.54	10.76
	leucurus	11	10.91	0.81	9.94	12.20
NW	*lanatus*	13	8.63	0.89	7.24	9.91
	derbianus	7	9.07	0.86	7.25	9.76
	philander	14	7.22	0.81	5.64	8.49
	trinitatis	2	7.57	0.42	7.28	7.87
	venezuelae	30	7.12	0.51	6.05	8.26
	leucurus	12	7.41	0.75	6.35	8.68
IOW	*lanatus*	13	10.53	0.76	9.60	12.05
	derbianus	8	10.88	0.58	10.00	11.61
	philander	13	8.86	0.62	7.64	9.60
	trinitatis	2	8.11	0.09	8.05	8.18
	venezuelae	33	7.81	0.53	6.79	9.14
	leucurus	12	8.53	0.52	7.82	9.35
PPW	*lanatus*	13	17.37	1.55	15.37	20.36
	derbianus	8	17.98	2.20	14.87	20.91
	philander	13	15.96	1.67	11.52	17.31
	trinitatis	2	14.90	0.35	14.65	15.15
	venezuelae	30	14.47	1.46	11.60	17.67
	leucurus	12	16.63	1.81	14.21	19.37
POW	*lanatus*	13	8.41	0.46	7.64	9.28
	derbianus	7	9.03	0.59	8.35	9.92
	philander	13	8.69	0.53	7.61	9.73
	trinitatis	2	9.11	0.66	8.64	9.58
	venezuelae	32	9.63	0.55	8.27	10.37
	leucurus	12	8.64	0.72	7.25	10.01
ZW	*lanatus*	11	33.74	1.87	30.67	36.63
	derbianus	8	33.03	1.36	31.45	35.23
	philander	13	32.02	1.35	28.76	33.69

Character	Sample	n	Mean	SD	Minimum	Maximum
ZW	*trinitatis*	2	28.29	2.10	26.81	29.78
	venezuelae	30	27.26	1.36	24.96	31.05
	leucurus	12	30.42	2.22	27.30	34.68
OW	*lanatus*	12	21.61	1.03	19.56	22.99
	derbianus	7	22.11	0.91	20.86	23.24
	philander	13	20.46	1.13	18.54	22.30
	trinitatis	2	17.84	0.71	17.34	18.35
	venezuelae	31	18.16	0.76	16.96	20.16
	leucurus	11	20.13	1.30	18.07	22.25
SCH	*lanatus*	12	15.07	1.10	13.66	16.90
	derbianus	7	15.24	0.59	14.66	16.07
	philander	13	13.62	0.49	12.97	14.53
	trinitatis	2	12.83	0.47	12.50	13.16
	venezuelae	32	12.96	0.48	11.84	13.90
	leucurus	12	13.78	0.70	12.74	15.16
ML	*lanatus*	11	43.12	1.62	40.34	45.40
	derbianus	7	44.24	1.71	41.86	46.34
	philander	14	40.70	1.74	36.75	42.43
	trinitatis	2	35.66	2.33	34.02	37.31
	venezuelae	35	34.20	1.88	30.56	38.33
	leucurus	13	38.23	2.28	34.94	41.33
LDS	*lanatus*	12	25.42	0.81	24.40	26.97
	derbianus	7	26.53	0.54	25.74	27.24
	philander	14	23.77	0.62	22.88	25.38
	trinitatis	2	20.87	0.64	20.42	21.32
	venezuelae	34	20.85	0.85	18.67	22.23
	leucurus	12	22.54	0.63	21.55	23.62
c-pm3	*lanatus*	13	12.08	0.90	10.46	14.14
	derbianus	7	12.73	0.40	12.25	13.36
	philander	14	10.63	0.46	9.78	11.28
	trinitatis	2	9.69	0.47	9.36	10.03
	venezuelae	36	9.32	0.52	8.44	10.47
	leucurus	13	10.09	0.66	9.01	11.01
m1-m4	*lanatus*	13	10.74	0.51	9.83	11.71
	derbianus	7	11.12	0.66	10.21	12.06
	philander	14	10.25	0.32	9.75	10.76
	trinitatis	2	8.91	0.11	8.84	8.99
	venezuelae	37	9.01	0.20	8.53	9.33
	leucurus	13	9.51	0.25	9.10	10.03
CH	*lanatus*	13	20.83	1.87	18.64	24.33
	derbianus	7	21.29	1.30	19.17	22.59
	philander	14	19.50	2.05	16.51	22.79
	trinitatis	2	18.57	2.11	17.08	20.06
	venezuelae	37	16.71	1.05	14.68	19.16
	leucurus	11	19.48	2.20	15.68	23.23

Table 3. Morphometric comparisons between *Caluromys* taxa. Pairwise comparisons no significant are not showed.
*: P < 0.05; **: P < 0.01; ***: P < 0.001; p-values corrected by the Bonferroni adjustment.

Character	*trinitatis, lanatus*	*trinitatis, derbianus*	*trinitatis, philander*	*venezuelae, lanatus*	*venezuelae, derbianus*	*venezuelae, philander*
TSL	***	***		***	***	***
CBL	***	***		***	***	***
BL	***	***		***	***	***
PL	***	***	***	***	***	***
NL	***	***	***	***	***	***
UDS	***	***	***	***	***	***
I1-I5		*		***	***	***
C-PM3	***	***		***	***	***
M1-M4	***	***		***	***	***
RW				***	***	***
NW				***	***	
IOW	***	***		***	***	***
PPW				***	***	
POW				***		***
ZW	*			***	***	***
OW	***	***		***	***	***
SCH	*	*		***	***	
ML	***	***		***	***	***
LDS	***	***	***	***	***	***
c-pm3	***	***		***	***	***
m1-m4	***	***	***	***	***	***
CH				***	***	***

Table 3. Continued.

Character	*venezuelae, leucurus*	*leucurus, lanatus*	*leucurus, derbianus*	*leucurus, philander*	*philander, lanatus*	*philander, derbianus*
TSL	**	***	***	*		
CBL	***	***	***			
BL	***	***	***			
PL	***	***	***			***
NL	***	*	**			
UDS	***	***	***	**	***	***
I1-I5		*	***			
C-PM3	*	***	***		***	***
M1-M4	***	***	***	***		***
RW	***					
NW		***	***		***	***
IOW		***	***		***	***
PPW						
POW	***					
ZW	***	**				
OW	***					
SCH		**	*		***	***
ML	***	***	***			
LDS	***	***	***	*	***	***
c-pm3		***	***		***	***
m1-m4	*	***	***	**		***
CH	***					

lae. A plot of the discriminant scores on the first and second canonical axes showed quite good separation of *philander*, whereas the rest of the samples overlapped (Figure 2b). These axes accounted for 69.8% and 17.3% of total variance, respectively; the first related to nasal, minimum postorbital, and interorbital widths, the second correlated positively with the width of the postorbital processes and height of the coronoid process, and negatively with upper and lower molar series.

The distant phenogram obtained by cluster analysis, including size (Figure 3a), was consistent with the geographic size variation shown by previous analyses. Thus, two main clusters appeared, one comprising the large forms, *lanatus*, *derbianus*, and *Caluromysiops*, and another constituted by the remaining samples. Within the latter, the small *venezuelae* and *trinitatis* joined, departing from the cluster formed by the intermediate forms *leucurus* and *philander*. When adjusted by size, cluster showed a very different configuration (Figure 3b). In this case, *lanatus* and *philander* joined, forming the sister branch of the group constituted by *venezuelae*, *trinitatis*, and *leucurus*. This entire cluster grouped with *derbianus*, and this latter branch with *Caluromysiops*, which showed the most divergence in phenotype.

Discussion

Our analyses revealed noticeable phenetic heterogeneity between the morphotypes currently assigned to *C. philander*. Major differences in size and shape were observed between *trinitatis-venezuelae* and *philander*. The two former morphotypes were characterized by general small dimensions of skulls, although higher minimum postorbital width, and proportionally higher nasal, postorbital processes, and interorbital widths confer to the cranium a massive aspect. The mandible, which was also smaller compared with the other forms, was robust as shown by the relatively large coronoid process. This observation is concordant with that made by Thomas (1894), according to whom the skull of adult *trinitatis* is decidedly small and exhibits the general roundedness of the younger specimens of larger species, like *C. philander*, in which it disappears with age. Likewise, in the description of *C. t. venezuelae*, Thomas (1903) notes that this subspecies is consistent with the nominate form in essential characters of size and color and differs morphologically from the Guianan *C. philander*.

Our findings agree with the comments made by Patton and Costa (2003), in that intrageneric diversity in several Neotropical marsupials could be greater than currently known. In particular, the size and shape relationships shown in our study do not support to consider *trinitatis* and *venezuelae* as subspecies of *C. philander*. In the light of these results, we suggest to include them in *C. trinitatis*, thus recovering the old specific name given by Thomas (1903) to the Trinidadian and northern Venezuelan forms of *Caluromys*. Sample size of *trinitatis* do not allow us to evaluate the taxonomic differentiation between the specimens from Trinidad and Tobago and those from northern Venezuela.

Phenetic relationships between *leucurus* and the closest forms of *Caluromys* are unclear. Thus, although *leucurus* appeared to be more related to *philander* in

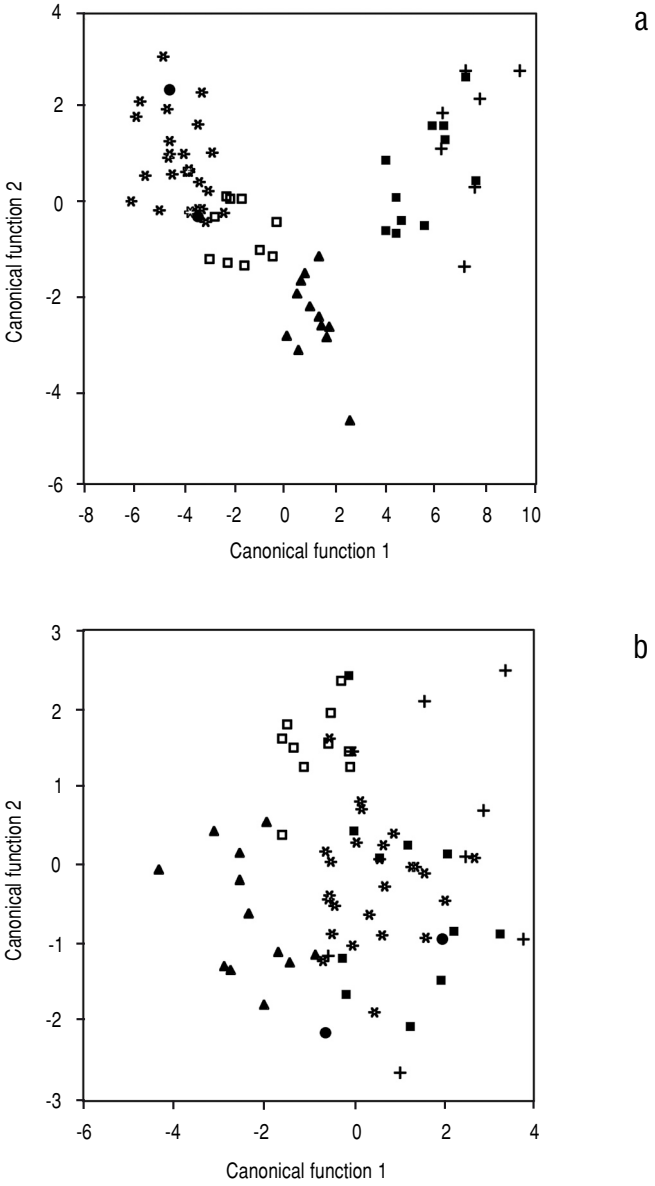

Figure 2. Projection of individual scores for the *Caluromys* samples studied onto the 2 canonical vectors (CV) for size (a) and shape (b). Symbols: *derbianus* (+); *lanatus* (■); *philander* (▲); *trinitatis* (●); *venezuelae* (★); *leucurus* (□).

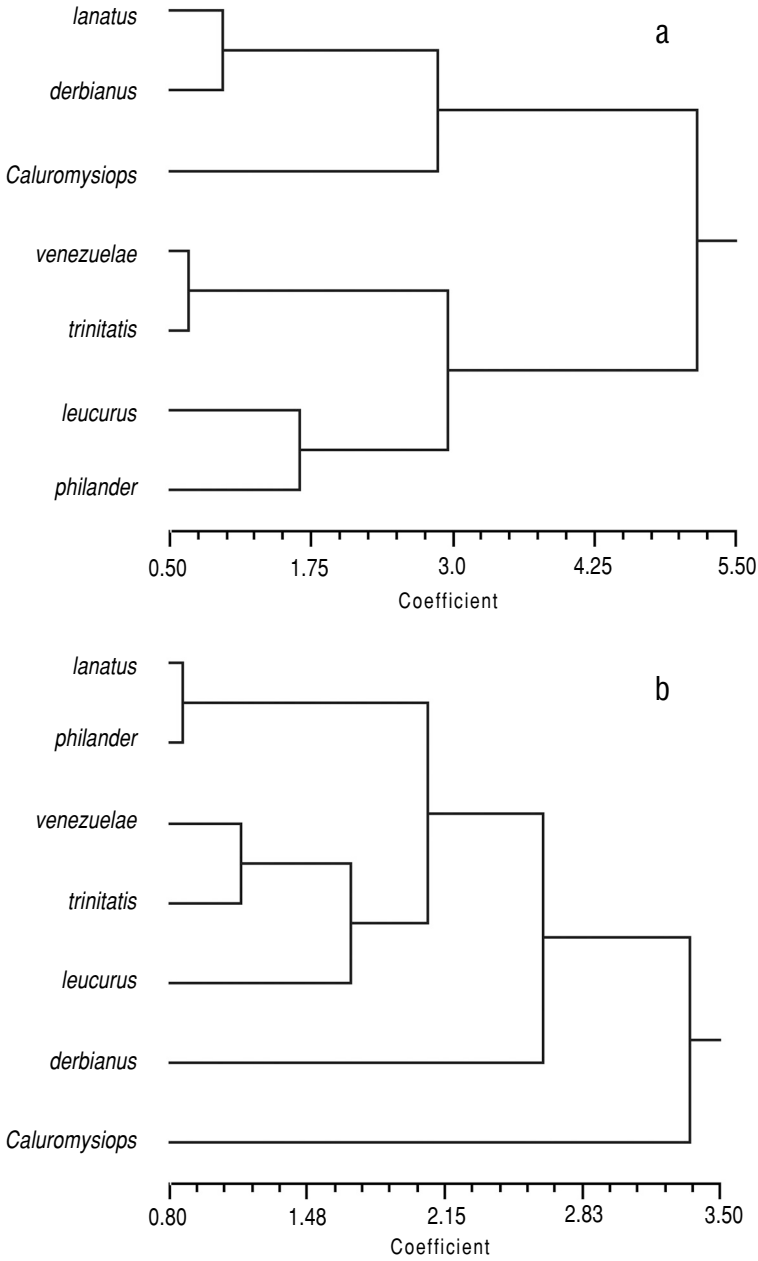

Figure 3. Distance phenograms showing relationships of *Caluromys* and *Caluromysiops* samples for size (a) and shape (b). Cophenetic correlation coefficients are 0.721 and 0.772, respectively.

size than to any other form, the two taxa showed greater differences in skull shape, specifically in the molar series, and postorbital and coronoid processes. In fact, in the size-free phenogram, *leucurus* grouped with *trinitatis* and *venezuelae* and showed a clear divergence from the remaining taxa. The uncertain relationships of *leucurus* with respect to *trinitatis-venezuelae* and *philander* can also be deduced from the description of *leucurus* by Thomas (1904). Although this author described this form as a subspecies of *C. trinitatis*, he also noted that it showed some morphological affinity to *philander*. Consequently, we cannot provide a categorical assignation to the specimens considered here as *leucurus*. Nevertheless, differences in skull size and shape with respect to *trinitatis* and *philander*, respectively, suggest that *leucurus* is a valid taxonomic entity.

Results here obtained corroborate the skull-size similarity between *derbianus* and *lanatus*, previously reported by several authors (e.g. Eisenberg, 1989). Conversely, shape analyses revealed a closer relationship between *lanatus* and *philander*, in comparison to *C. derbianus*. Moreover if, as we propose, *trinitatis* was considered a valid species, it would be more closely related phenetically to the Amazonian forms, *lanatus* and *philander*, than the trans-Andean relative, *C. derbianus*. Further research using other information sources would be fruitful avenues to improve the knowledge of the evolutional relationships within the genus *Caluromys*.

Acknowledgments

This study was funded by grants from the Instituto de Cooperación Iberoamericana, Ministerio de Educación, Cultura y Deporte (Spain). We thank the following curators for access to specimens under their care: F. Bisbal and J. Sánchez (EBRG), D. Lew (MHNLS), M. Tranier (MNHN), and J. Marinho-Filho (UNB). We also thank R. H. Pine for his helpful comments and R. Rycroft (Servei d'Assesorament Lingüístic, University of Barcelona) for improving the English.

References

Allen, J. A. 1900. Note on the generic names *Didelphis* and *Philander*. Bull. Am. Mus. Nat. Hist. 13: 185-190.

Allen, J. A. 1904. List of Mammals from Venezuela, collected by Mr. Samuel M. Klages. Bull. Am. Mus. Nat. Hist. 20: 337-345.

Allen, J. A.; Chapman, F. M. 1893. On a collection of mammals from the island of Trinidad, with descriptions of new species. Bull. Am. Mus. Nat. Hist. 5: 203-234.

Anduze, P. J. 1956. Lista de los mamíferos hasta el presente en Venezuela. Mem. Soc. Cien. Nat. La Salle. 16: 5-18.

Brown, B. E. 2004. Atlas of new world marsupials. Fieldiana Zool. New Ser. 102: 1-308.

Burnaby, T. P. 1966. Growth-invariant discriminant functions and generalized distances. Biometrics 22: 96-110.

Cabrera, A. 1919. Genera Mammalium. Monotremata, Marsupialia. Mus. Nacional Cien. Nat. Madrid.

Cabrera, A. 1957. Catálogo de los mamíferos de América del Sur. I. Metatheria, Unguiculata, Carnivora. Rev. Mus. Arg. Cien. Nat. "Bernardino Rivadavia", Cien. Zool. 4: 1-307.

Chandler, C. R. 1995. Practical considerations in the use of simultaneous inference for multiple tests. Anim. Behav. 49: 524-527.

Eisenberg, J. F. 1989. Mammals of the Neotropics. The northern Neotropics. Vol. 1. Panamá, Colombia, Venezuela, Guyana, Suriname, French Guiana. The University of Chicago Press, Chicago.

Emmons, L. H.; Feer, F. 1997. Neotropical rainforest mammals: a field guide. The University of Chicago Press. Chicago.

Gardner, A. L. 1973. The systematics of the genus *Didelphis* (Marsupialia: Didelphidae) in North and Middle America. Spec. Publ. Mus. Texas Tech Univ. 4: 1-81.

Gardner, A. L. 2005. Order Didelphimorphia. *In*: D.E. Wilson; D.M. Reeder (eds.). Mammal species of the world: a taxonomic and geographic reference. Smithsonian Institution Press. Washington, D.C. p. 15-23

Izor, R. J.; Pine, R. H. 1987. Notes on the black-shouldered opossum, *Calurpomysiops irrupta*. Fieldiana Zool. New Ser. 39: 117-124.

Linares, O. J. 1998. Mamíferos de Venezuela. Sociedad Conservacionista Audubon de Venezuela. Caracas.

Patton, J. L.; Costa, L. P. 2003. Molecular phylogeography and species limits in rainforest didelphid marsupials of South America. *In*: M. Jones; C. Dickman; M. Archer (eds.). Predators with pouches: the biology of carnivorous marsupials. CSIRO Publishing. Melbourne. p. 63-81.

Pérez-Hernández, R. 1989. Distribution of the family Didelphidae (Mammalia-Marsupialia) in Venezuela. *In*: K. H. Redford; J.F. Eisenberg (eds.). Advances in neotropical mammalogy. Sandhill Crane Press. Gainesville. p. 363-410.

Pittier, H.; Tate, G. H. H. 1932. Sobre fauna venezolana. Lista provisional de los mamíferos observados en el país. Bol. Soc. Ven. Cien. Nat. 7: 249-278.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223—225.

Rohlf, F. J. 2002. NTSYSpc: Numerical Taxonomy System, ver. 2.1. Exeter Publishing, Ltd. Setauket, New York.

Thomas, O. 1894. On two new Neotropical mammals. Ann. Mag. Nat. Hist. Ser. 6, xii: 436-439.

Thomas, O. 1903. New forms of *Sciurus, Oxymycterus, Kannabateomys, Proechimys, Dasyprocta,* and *Caluromys* from South America. Ann. Mag. Nat. Hist. Ser. 7, xi: 487-493.

Thomas, O. 1904. New *Sciurus, Rhipidomys, Sylvilagus* and *Caluromys* from Venezuela. Ann. Mag. Nat. Hist. Ser. 7, xiv: 33-37.

Thorpe, R. S. 1988. Multiple group principal component analysis and population differentiation. J. Zool. 216: 37-40.

Ventura, J.; Pérez-Hernández, R.; López-Fuster, M. J. 1998. Morphometric assessment of the *Monodelphis brevicaudata* group (Didelphimorphia: Didelphidae) in Venezuela. J. Mammal. 79: 104-117.

Voss, R. S.; Jansa, S. A. 2003. Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. Bull. Am. Mus. Nat. Hist. 276: 1-82.

Appendix 1

Specimens examined. The 89 specimens analyzed in this study are deposited in the following institutions: Estación Biológica de Rancho Grande (EBRG), Maracay, Venezuela; Museo de Biología de la Universidad Central de Venezuela (MBUCV) Caracas, Venezuela; Museo de Historia Natural La Salle (MHNLS) Caracas, Venezuela; Muséu National de Histoire Naturelle (MNHN), Paris, France, and Universidade de Brasilia D.F. (UNB), Brasilia, Brazil. The specimens from the samples here considered were from the following localities:

derbianus

PANAMÁ. Darién, 08º31'N, 78º05'W (MNHN 1877-1677); ECUADOR. Esmeraldas: río Cachabí, 00º58'N, 78º48'W (MNHN 1932-2862); río Blanco, Mindo, 00º01'S, 78º47'W (MNHN 1932-2861, 1932-2996, 1932-2997, 1932-2998, 1932-2999); río Babahoyo, Pimocha Sur, 01º49'N, 79º31'W (MNHN 1936-1441).

lanatus

BRAZIL. Manaus, 03º06'S, 60º01'W (MNHN 1898-159); COLOMBIA. Cauca: El Guamo, 02º42'N, 79º59'W (MNHN 1929-651, 1929-652, 1929-658); Tolima: Natagaima, 03º37'N, 75º05'W (MNHN 1932-29); PERÚ. Ucayali: Pulcallpa, 08º22'S, 74º32'W (MNHN 1952-809); VENEZUELA. Amazonas: Cacurí, Alto Ventuari, 04º45'N, 65º23'W (MBUCV 1390); San Carlos de Río Negro, 01º52'N, 67º00'W (MBUCV 2732, 3243); Zulia: Kunana, río Negro, Sierra de Perijá, 10º03'N, 72º47'W (MHNLS 80, 84); Misión del Tocuco, río Tocuco, km 8 camino a Santa Rosa, 09º51'N, 72º47'W (MBUCV 1388). ¿ ? Zusaga(d)uga (MNHN 1932-28, 1997-122, 1929-658).

philander

FRENCH GUIANA. Cayenne, 04º55'N, 52º19'W. (MNHN 1955-594, 1957-586, 1986-140,1986-143); Ouanary, 04º13'N, 51º40'W (MNHN 1929-555); Saint-Laurent du Maroni, 05º30'N, 54º01'W (MNHN 1909-255); Trois-Sauts, 02º15'N, 52º52'W (MNHN 1981-152); Paracou, 05º16'N, 52º55'W (MNHN 2001-1415); (MNHN 1999-1061); 1957-607; BRAZIL. Manso, Chapada dos Guimarães, 15º25'S, 55º45'W (UNB 1650, 1653, 1657,1675).

trinitatis

TRINIDAD. Caparo Valley, 10º26'N, 61º19'W (BM 97.6.7.20); Kurukai ¿? (BM 97.6.7.23).

venezuelae

VENEZUELA. Anzoátegui: Paso Bajito, río Moquete, S de El Tigre, 08º36'N, 64º13'W (MBUCV 3120); Aragua: Estación Biológica de Rancho Grande, 10º21'N, 67º41'W (EBRG 218); Estación de Piscicultura, El Limón, Maracay, 10º18'N, 67º38'W (EBRG 219, 220, 398); Estación Recursos Fitogenéticos, El Limón, 10º17'N, 67º37'W (EBRG 17505); Guacamaya, 7 km SW de Magdalena, 10º03'N, 67º39'W (MHNLS 5032); La Horqueta, vía Tiara, 10º11'N, 67º08'W (MBUCV 1549); Carabobo: Mariara, Las Brisas, 10º18'N, 67º48'W (EBRG 7561); Hacienda Saint Jean, 13 km SW de Borburata, 10º26'N, 67º57'W (EBRG 8176); Las Dos Bocas, 09º57'N, 67º59'W (MHNLS 337); San Esteban, 10º25'N, 68º04'W (BM 11.5.25.171); Montalbán, 10º09'N, 68º21'W (EBRG 3850); Miranda: Altos de Pipe, IVIC, vía San Antonio de Los Altos, 10º24'N, 66º59'W (MHNLS 3696); Turgua, 10º22'N, 66º45'W (MHNLS 42, 43, 59, 62); La Ciénaga, Baruta, 10º27'N, 66º52'W (MHNLS 20, 48, 49, 55); Baruta, 10º26'N, 66º52'W (MBUCV 1438); Estación Experimental de Río Negro, 10º20', 66º17'W (MBUCV 3483); Casupito, Parque Nacional Guatopo, 10º00'N, 66º25'W (MHNLS 1146); Caserio Salmerón, Araira, Municipio Zamora, 10º28'N, 66º22'W (EBRG 22138); Cortada del Guayabo, 10º21'N, 66º55'W (MBUCV 1037), Monagas: Cerro Papelón, al norte de La Macanilla, 10º13'N, 64º16'W (MHNLS 251); 3 km N 4 Km W Caripe, cerca de San Agustín, 10º12'N, 63º 32'W (EBRG 3842, 3843); Nueva Esparta: Fuenteidueño, E de la Isla Margarita, 11º01' N, 63º55'W (MBUCV 1601); Tacarigua adentro, Isla Margarita, 11º03'N, 63º53ºW (MHNLS 285); Sucre: San Antonio del Golfo, 10º27'N, 63º48'W (EBRG 2316); 21 Km E de Cumaná, cerca de Sotillo, 10º26'N, 64º02'W (EBRG 3836); Los Mangos, Parque Nacional Península de Paria, 10º34'N, 63º20'W (EBRG 20688, 20689); Uquire, Parque Nacional Península de Paria, 10º41'N, 61º55'W (EBRG 20690); Yaracuy: 19 KM NW Urama, 10º27'N, 68º23'W (EBRG 3833).

leucurus

VENEZUELA. Amazonas: río Manapiare, San Juan de Manapiare, 05º18'N, 66º13'W (EBRG 3841); Belén, río Cunucunuma, 03º39'N, 65º46'W (EBRG 3837, 3838, 3839, 3840); San Carlos de Río Negro, Caño Ardabo, 01º51'N, 67º03'W (EBRG 2166); San Felipe, (Raudalito) río Sipapo, 04º31'N, 67º26'W (EBRG 4464); Bolívar: río Caroní, Represa del Guri, Operación Rescate, 07º46'N, 62º59'W (EBRG 1342, 1343); 2 km carretera Tumeremo - El Dorado, 07º16'N, 61º30'W (MHNLS 3695); Serranía Los Pijiguaos, 140-160 km SW de Caicara del Orinoco, 06º35'N, 66º40'W (EBRG 15937, MHNLS 8275, 8276).