

Body size and form in two Neotropical marsupials, *Didelphis aurita* and *Philander opossum* (Marsupialia : Didelphidae)

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Summary. – Neotropical marsupials of the genera *Didelphis* and *Philander* differ in size but differences in body form are demonstrated herein for the first time. External measurements were taken from adults of *D. aurita* and *P. opossum*. General size was measured as the first principal component of the pooled covariance matrix (MGPC1). Body form was compared with multivariate analysis of covariance (MANCOVA). General size was the covariate for head-body, tail, and measurements of the limb elements. Foot length was the covariate for foot breadth and length of the foot claw. After accounting for the size difference, *D. aurita* has a relatively shorter tail but the foot is broader, and the arm, forearm and foot claw are longer. These differences in body form could be related to the size increase in *Didelphis* and its consequences for terrestrial and arboreal locomotion.

Résumé. – Les marsupiaux néotropicaux des genres *Didelphis* et *Philander* ont une taille différente, mais on montre ici qu'ils ont aussi des différences de la forme du corps. Les mensurations externes ont été prises sur des adultes de *D. aurita* et *P. opossum*. La taille a été mesurée comme composante principale d'une matrice d'un pool de covariance. La forme du corps a été comparée par une analyse multivariée de covariance. La taille a été la covariable pour les mensurations tête et corps et queue et celles des éléments du membre. La longueur du pied a été la covariable pour sa largeur et la longueur des griffes du pied. En tenant compte de la différence de taille, *D. aurita* a une queue relativement plus courte mais le pied est plus large, et le bras, l'avant-bras et les griffes du pied sont plus longues. Ces différences de forme du corps peuvent être reliées à l'accroissement de la taille chez *Didelphis* et ses conséquences pour la locomotion terrestre et arboricole.

INTRODUCTION

Neotropical marsupials or opossums generally are considered conservative in their morphology, especially of their postcranial skeleton (Reig *et al.* 1987 ; Szalay 1994). The most obvious differences between genera are in body size. Differences in body proportions were demonstrated only between species of contrasting life-styles, such as terrestrial vs. arboreal vs. semi-aquatic (Charles-Dominique 1983 ; Eisenberg and Wilson 1981 ; Grand 1983 ; Hildebrand 1961 ; Stein 1981 ; Works 1950).

Species of the genera *Didelphis* and *Philander* are not strictly terrestrial nor arboreal. They are usually described as « good climbers », generalists, and overlap in diet, habitat, and forest strata use (Charles-Dominique 1983 ; Emmons and Feer 1990 ; Hunsaker 1977 ; Miles *et al.* 1981 ; O'Connell 1979). The more widely distributed species of *Philander*, *P. opossum*, also overlaps in geographic distribution with species of *Didelphis* (Cerqueira 1985 ; Emmons and Feer 1990 ; Streilein 1982) : with *D. aurita* in the Atlantic forest of Brazil and southern South America, and with *D. marsupialis* in forests of Central American and the Amazon basin. The two are sister genera (Creighton 1984 ; Kirsh *et al.* 1993 ; Patton *et al.* 1996 ; Reig *et al.* 1987 ; Szalay 1994), which facilitates comparisons among them.

Size differences between these two genera are obvious, *Didelphis* being larger. However, Works (1950) and Hildebrand (1961) were not able to find conclusive differences in body proportions between them. Hildebrand (1961 : 247) suggested that *Didelphis* might have longer forelimbs relative to its size. Indeed, muscle mass is more concentrated in the hind limbs of *P. opossum* (Grand 1983), which suggests less developed forelimbs. Tail length in *Didelphis* seems to be less than or equal to head-body length (Eisenberg and Wilson 1981 ; Gardner 1973), being the shortest relative tail among the large didelphids (Creighton 1984 : 69).

On the forest floor *Philander* is more likely a scamperer (Grand 1983), more precisely a terrestrial scamperer (*sensu* Szalay 1994). For an animal of its size, the forest floor is full of obstacles, which requires jumping ability. Jumping ability is enhanced in part by longer hind limbs and reduction of the forelimbs (Emerson 1985). The same obstacles on the forest floor are smaller for *Didelphis*, jumping would not be so necessary, and hence *Didelphis* is more likely a terrestrial walker than a scamperer. Also, walking instead of scampering should be more cost-effective for *Didelphis*. Because of the higher ratio of volume/surface area of larger animals (Hildebrand 1988), jumping costs are higher and their limbs have to support and propel relatively more mass. Therefore, forelimbs should be relatively longer in *Didelphis* than in *Philander*.

My objectives in this study are to determine if there are differences in body proportions between adults of *D. aurita* and *P. opossum*, how these differences scale with body size in adults, and how they agree with expectations based on locomotory characteristics of each species. These two species are used as representatives of the genera they belong to.

MATERIAL AND METHODS

Specimens and measurements.

Animals were trapped in Rio de Janeiro (23°0'S, 43°12'W) and Teresópolis (22°25'S, 42°50'W), Brazil, as part of research programs of the Departamento de Protozoologia, Fundação Oswaldo Cruz, and of the Laboratório de Vertebrados, Universidade Federal do Rio de Janeiro. Trapping occurred in areas of secondary forests, originally part of the Atlantic Rainforest of Brazil. Voucher specimens were deposited in the Museu Nacional do Rio de Janeiro.

Only external measurements of adults were taken because animals also were used in subsequent behavioral and immunological studies. Although less precise than bone measurements, external measurements might be a more accurate measure of functional limb length. Moreover, the two species of opossums studied here are in the upper size range of small mammals, hence measurement errors will be proportionally smaller.

Animals were sedated with intramuscular Ketalar. Limb measurements were taken from the right side of the animal, parallel to the long axis of the limb, hand or foot. To obtain consistent endpoints for limb length measurements, hand, foot, distal and proximal elements of the limbs were flexed in supination, forming an angle smaller than 90° with the elements they articulate with. The following measurements were taken :

(1) Arm length - from the most proximal point of the arm at the shoulder joint (on the humeral head), to its most distal point (most proximal point on the ventral surface of the olecranon process of ulna).

(2) Forearm length - from the most proximal point of the forearm (on the posterior edge of the olecranon process of ulna), to the most anterior point at the wrist joint.

(3) Leg length - from the most proximal point of the leg at the hip joint (on the greater trochanter of the femur), to its most distal point at the knee joint (a mid point between the two lateral condyles of the femur).

(4) Foreleg length - from the most proximal point of the foreleg at the knee joint, to the most proximal point on the ventral surface of the heel (calcaneus).

(5) Tail length - from the point the tail bends when pulled and extended upwards, to the distal end of the last vertebra of the tail.

(6) Head-body - from the tip of the nose to the point the tail bends when pulled upwards. The animal was placed on its back and was straightened but not stretched.

(7) Foot length - from the most posterior point of the plantar surface (not the heel), to the tip of the longest toe, without the claw. The fingers were straightened and pressed against a flat surface.

(8) Foot and claw length - the same as before but including the claw.

(9) Foot breadth - from the tip of the hallux « abducted », forming a 90° angle with the adjacent finger, to a lateral point on the foot projected from the line of the long axis of the hallux.

Statistical methods.

Six variables obtained from the original measurements were used to estimate a general size factor : the lengths of head-body, tail, foot length and breadth, forelimb, and hind limb. Limb elements (proximal and distal) were added as a single variable because they form a single dimension of general size, limb length. The structural materials of such elements are similar, e.g., bone and muscle, hence subject to similar physical constraints. Claws may be worn or broken and factors other than general size affect their length significantly. Therefore, foot length excluding the claw was preferred.

Variables were ln-transformed and a general size factor was estimated by the first principal component of the pooled covariance matrix, MGPCI (Thorpe 1983). The pooled matrix was obtained by averaging the elements of the two species covariance matrices weighted by their sample size. Equality of covariance matrices was tested with a log-likelihood ratio chi-square (Björklund 1994 ; Flury 1988), where the null hypothesis was the pooled variance-covariance matrix, and the alternative hypothesis was that each covariance matrix is different from the rest.

With six variables, n for PCA should be at least 27 according to $n = (p2 + 3p)/2$, where p is the number of variables (Morrison 1976). Outliers were identified by Mahalanobis distances (D^2) between each individual score and the centroid of all cases (BMDP Inc. 1983). Values of $D^2/d.f. > 1$ indicate outliers. One outlier was identified in *D. aurita* and two in *P. opossum*. These three outliers also were the smallest individuals of their sample, hence excluded from subsequent analyses. Confidence intervals (C.I) for eigenvalues were calculated from asymptotic theory, determinacy of eigenvalues

lues was tested with Bartlett sphericity test, and the null hypothesis of isometry in MGPC1 was tested with Anderson's chi-square statistic (Morrison 1976).

Body size and form were examined together, using the factor model

$$X_{ijk} = I_i + Gd_i + s_i S_j + e_{ijk}$$

where X_{ijk} is the log-transformed variable X_i for specimen j of species k , I_i is the intercept of the line with slope s_i passing through the sample centroid of *D. aurita*, S_j is the size score of specimen j , G is an index of species membership that takes the value of « 0 » for *D. aurita* and « 1 » for *P. opossum*, d_i is the size-adjusted species effect (how *D. aurita* differs from *P. opossum*), s_i the common major-axis regression of variable X_i on size, and e_{ijk} is an error term for the variance unexplained by the model (Bookstein *et al.* 1985 ; Marcus and Voss 1992). Therefore, s_i is an allometric coefficient of a simple allometric model calculated after species effects (d_i s) are accounted for. Isometric variables would have an $s_i = 1/p^{1/2}$, where p is the number of variables used to calculate MGPC1 (Björklund 1994 ; Bookstein *et al.* 1985). With $p = 6$, isometric variables would have $s_i = 0.408$. This model makes more biological sense than discriminant-function analysis where the d_i discriminate species but have no biological meaning (Bookstein 1991 ; Crespi and Bookstein 1989 ; Rohlf and Bookstein 1987).

Nine variables were used to analyze body form : the lengths of head-body, tail, foot length and breadth, claw, arm, forearm, leg, and foreleg. Interspecific differences in d_i s and s_i s were determined by MANCOVA and separate ANCOVAs of each variable with general size S_j as the covariate. Foot breadth and claw length are more likely to scale with foot length than with general size because they are parts of a single structure, the foot. Therefore, these variables also were compared with foot length as a covariate.

TABLE 1. — Mean (mm) and coefficient of variation of morphological variables in the two species of opossums.

Variables	<i>Didelphis aurita</i>		<i>Philander opossum</i>	
	\bar{x}	C.V.	\bar{x}	C.V.
Head-body	38.28	7.9	26.53	8.8
Tail	31.72	9.3	26.90	9.4
Foot length	4.73	7.5	3.46	11.8
Claw	0.47	18.8	0.17	48.9
Foot breadth	3.96	9.8	2.62	6.9
Arm	6.66	7.3	4.37	7.7
Forearm	7.42	5.5	4.94	6.1
Leg	7.72	7.3	5.09	12.5
Foreleg	8.44	7.6	5.96	6.9
Forelimb	14.08	5.3	9.31	6.4
Hindlimb	16.16	6.1	11.05	8.8
<i>n</i>	25		15	

Bonferroni correction for multiple tests was applied to probabilities of separate ANCOVAs (Stevens 1992). Significance levels (α) with Bonferroni correction were obtained by dividing the usual 0.05 (α) by the number of separate tests. The hypothesis of equality of allometric coefficients between species was tested by a species by size interaction term in the MANCOVA and ANCOVAs, which also is a test of the homogeneity of slopes assumption in analysis of covariance. The assumption of multivariate normality was tested with separate Shapiro-Wilks normality tests for each variable (SAS Institute Inc. 1985) and the multivariate normality test of Mardia (1970).

RESULTS

The range of body mass was 670-1560 g for *Didelphis aurita* ($n = 25\bar{x} = 1098$, C.V. = 22.6) and 220-680 g for *Philander opossum* ($n = 15\bar{x} = 398$, C.V. = 45.2). The null hypothesis of multivariate normality of the log-transformed variables was not rejected in either species. Univariate tests did not detect any significant departure from normality as well. Variation generally was higher in the smaller species, *P. opossum* (Table 1). Coefficients of variation were close to 10 % except claw length.

Coefficients of each species PC1 coincided in their relative magnitudes (Table 2). The largest discrepancy was in foot breadth, but the covariance matrices of each species did not differ significantly from the pooled covariance matrix ($\chi^2 = 1.223$, $P > 0.99$, d.f. = 21). Therefore, MGPC1 was used as an estimate of a general size factor common to both species. Sample size for MGPCA was 40, hence appropriate. The

TABLE 2. — Principal components (unity eigenvectors) of the covariance matrices of the two species of opossums, and of their pooled covariance matrix. Isometric variables should have coefficients equal to $0.408 (= 1/p^{1/2})$, where p is the number of variables). Bartlett sphericity chi-square tests the null hypothesis of equality between a specific eigenvalue and subsequent eigenvalues of a matrix.

Variables	<i>Didelphis aurita</i>		<i>Philander opossum</i>		Pooled covariance matrix	
	PC1	PC2	PC1	PC2	MGPC1	MGPC2
Head-body	0.255	-0.899	0.382	0.398	0.372	0.277
Tail	0.549	-0.098	0.809	-0.529	0.716	-0.666
Foot length	0.368	0.171	0.142	0.593	0.255	0.525
Foot breadth	0.591	0.130	0.220	0.294	0.367	0.325
Forelimb	0.253	0.235	0.247	0.229	0.259	0.203
Hindlimb	0.292	0.286	0.265	0.268	0.288	0.239
Eigenvalue	0.020	0.006	0.048	0.021	0.030	0.012
95% C.I.	0.013-0.046	0.004-0.014	0.028-0.155	0.012-0.068	0.021-0.052	0.008-0.020
Bartlett χ^2	28.749	22.077	78.202	50.619	82.827	53.894
d.f.	14	9	14	9	14	9
P	< 0.025	< 0.010	< 0.001	< 0.001	< 0.001	< 0.001
Percentage of total variance explained	54.36	16.07	57.88	25.52	53.64	21.02

first and second eigenvalues of each species covariance matrix and of the pooled covariance matrix were well-determined, i.e., each was significantly different from the subsequent ones in Bartlett's sphericity test, and their confidence intervals did not overlap (Table 2). The proportion of the total variance explained by all first principal components was similar, greater than 50 %.

Equality of score coefficients in MGPC1, i.e., isometry, was rejected (Anderson's $\chi^2 = 14.969$, $P < 0.02$, d.f. = 5). Two allometric coefficients were close to significance, the s_i s of foot breadth and forearm length (Table 3).

Wilks λ for size and size-independent species effects were highly significant (Table 3). The tail is relatively shorter and the forelimb elements are relatively longer in *D. aurita*, indicated by their significant d_i s (Table 3). Leg and claw lengths differ significantly between the two opossums only without Bonferroni correction.

The form of the foot clearly differs when foot length was the covariate (Table 4). The foot of *D. aurita* is broader with longer claws (larger and significant d_i s in Table 4). The overall difference between species was confirmed by the low Wilks λ and associated probability of the species effect.

TABLE 3. — Size-independent coefficients of interspecific difference (d_i), allometric coefficients (s_i), probabilities of the homogeneity-of-slopes assumption of ANCOVA, and multivariate statistics of MANCOVA for the two opossums. Coefficients d_i indicate how variables change in *Didelphis aurita* compared to *Philander opossum* after adjusted for size difference. Isometric variables would have $s_i = 0.408$. Test of homogeneity of slopes corresponds to the size vs. species interaction. Asterisks indicate coefficients significant at the 0.05 level after Bonferroni correction.

Variable	ANCOVAs							
	Size-independent species effect			General size effect			Homogeneity of slopes	
	d_i	$F_{1,37}$	P	s_i	$F_{1,39}$	P	$F_{1,38}$	P
Head-body	0.120	3.364	0.075	0.351	0.433	0.514	0.578	0.452
Tail	-0.213	12.065	0.001*	0.537	2.509	0.122	1.623	0.211
Foot length	0.040	0.263	0.611	0.395	0.016	0.899	0.198	0.659
Claw	0.659	5.094	0.030	0.658	0.415	0.524	0.567	0.456
Foot breadth	0.039	0.628	0.433	0.529	3.344	0.076	0.911	0.346
Arm	0.179	10.444	0.003*	0.346	0.710	0.405	4.187	0.048
Forearm	0.199	24.492	0.000*	0.296	4.414	0.043	1.214	0.278
Leg	0.163	4.652	0.038	0.366	0.176	0.677	5.397	0.026
Foreleg	0.072	1.782	0.190	0.391	0.055	0.816	0.129	0.722

Effect	MANCOVA			
	Wilks λ	F	d.f.	P
Species	0.436	4.165	9, 29	0.002*
Size	0.002	1690.943	9, 29	0.000*
Homogeneity of slopes	0.706	1.298	9, 28	0.282

TABLE 4. – Foot-length-adjusted coefficients of interspecific difference (d_i) in foot variables, probabilities of the homogeneity-of-slopes assumption, and multivariate statistics of MANCOVA for the two opossums. Coefficients d_i indicate how variables change in *Didelphis aurita* compared to *Philander opossum* after adjusted for differences in foot length. Test of homogeneity of slopes corresponds to the species vs. foot length interaction. Asterisks indicate coefficients significant at the 0.05 level after Bonferroni correction.

ANCOVAs					
Variable	Species effect			Homogeneity of slopes (species x foot length interaction)	
	d_i	$F_{1,37}$	P	$F_{1,36}$	P
Foot breadth	0.297	34.602	0.000*	2.561	0.118
Claw	0.754	15.890	0.000*	0.316	0.577

MANCOVA				
Effect	Wilks λ	F	d.f.	P
Species	0.465	20.737	2,36	0.000*
Homogeneity of slopes	0.911	1.706	2,35	0.196

Overall homogeneity of slopes was not rejected by Wilks λ , which confirms that the relative magnitudes of PC1 score coefficients do not differ between the two species of opossums (Tables 3, 4). The probability of homogeneity of slopes in separate ANCOVAs was low for arm and leg lengths but was not significant after Bonferroni correction.

DISCUSSION

The prediction of relatively longer forelimbs in *Didelphis* was confirmed. *Philander* seems better designed for terrestrial scampering than *Didelphis*. Although scampering requires more developed hind limbs, the forelimbs are still necessary to grab, pull, and support the body after the jump, keeping balance on an uneven terrain. Besides, on trees and bushes the forelimbs also would be necessary for graspclimbing (*sensu* Szalay 1994) and bridging discontinuous substrates such as fine branches, typically used by opossums and animals with prehensile tail (Cartmill 1985). Elongation of the hind limbs moves the center of gravity upwards, increasing oscillation and reducing stability in locomotion along horizontal branches (Cartmill 1985; Hildebrand 1988). A compromise could be some elongation of the hind limbs but not as extreme as seen in more specialized terrestrial scamperers such as the brown four-eyed opossum, *Metachirus nudicaudatus*.

The forelimbs of large animals have to lift relatively more mass when climbing, because of the higher ratio of volume/surface area of large animals (Hildebrand 1988).

Therefore, climbing costs are relatively higher for large animals, such as *Didelphis* (Cartmill 1985). A combination of long claws and long forelimbs could compensate for the larger size of *Didelphis* during climbing, maintaining its generalized use of ground and trees. Besides, species of *Didelphis* are not efficient clawclimbers (*sensu* Szalay 1994) such as squirrels. Relative forelimb length increases with size in animals that do not depend on their claws to climb (Cartmill 1974, 1985 ; Jungers 1985).

Because of *Didelphis* size, its use of fine branches is certainly limited compared to *Philander*. A longer tail would not compensate for the larger size of *Didelphis*. For *Philander*, however, a longer tail could improve its ability to cross discontinuous branches. Indeed, *Philander* nests more frequently at 8 to 10 m above the ground on tree branches whereas *Didelphis* nests more frequently in trunk cavities (Miles *et al.* 1981).

The above hypotheses are just storytelling without further tests on the relationship between morphology and performance in these species. If larger size in *Didelphis* is indeed a derived character, changes in body proportions associated the size increase could test the above hypotheses.

In conclusion, *Didelphis* has a relatively shorter tail but a broader foot and longer arm, forearm, and foot claw than *Philander*. These differences in body proportions could be related to the larger size of *Didelphis* and its consequences for terrestrial and arboreal locomotion.

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BIBLIOGRAPHY

- BJÖRKLUND, M., 1994. – *Allometric relations in three species of finches (Aves : Fringillidae)*. *J. Zool.*, 233 : 657-668.
- BMDP INC., 1983. – *BMDP Statistical software*. University of California Press, Berkeley, California.
- BOOKSTEIN, F.L., 1991. – *Morphometric tools for landmark data*. Cambridge University Press, Cambridge.
- BOOKSTEIN, F.L., B. CHERNOFF, R.L. ELDER, J.M. HUMPHRIES, G.R. SMITH and R.E. STRAUSS, 1985. – *Morphometrics in evolutionary biology*. Academy of Natural Sciences of Philadelphia.
- CARTMILL, M., 1974. – Pads and claws in arboreal locomotion. Pp. 45-83. *In : Primate locomotion*. Ed. F.A. Jenkins Jr. Academic Press, New York.
- CARTMILL, M., 1985. – Climbing. Pp. 73-88. *In : Functional vertebrate morphology*. Eds M. Hildebrand, D.M. Bramble, K.F. Liem and D.B. Wake. Harvard University Press, Cambridge, Massachusetts.

- CERQUEIRA, R., 1985. – The distribution of *Didelphis* in South America (Polyprotodontia, Didelphidae). *J. Biogeogr.*, 12 : 135-145.
- CHARLES-DOMINIQUE, P., 1983. – Ecology and social adaptations in didelphid marsupials : comparison with eutherians of similar ecology. *Am. Soc. Mammal. Spec. Publ.*, 7 : 395-422.
- CREIGHTON, G.K., 1984. – *Systematics and taxonomy of the marsupial family Didelphidae*. Ph.D. Dissertation. University of Michigan, Ann Arbor.
- CRESPI, B.J. and F.L. BOOKSTEIN, 1989. – A path-analytic model for the measurement of selection on morphology. *Evolution*, 43 : 18-28.
- EISENBERG, J.F. and D.E. WILSON, 1981. – Relative brain size and demographic strategies in didelphid marsupials. *Am. Nat.*, 118 : 1-15.
- EMERSON, S.B., 1985. – Jumping and leaping. Pp. 58-72. In : *Functional vertebrate morphology*. Eds M. Hildebrand, D.M. Bramble, K.F. Liem and D.B. Wake. Belknap, Cambridge, Massachusetts.
- EMMONS, L.H. and F. FEER, 1990. – *Neotropical rainforest mammals : a field guide*. The University of Chicago Press, Chicago.
- FLURY, B., 1988. – *Common principal components and related multivariate methods*. Wiley, New York.
- 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.
- GRAND, T.I., 1983. – Body weight : its relationship to tissue composition, segmental distribution of mass, and motor function. III. The Didelphidae of French Guyana. *Aust. J. Zool.*, 31 : 299.
- HILDEBRAND, M., 1961. – Body proportions of didelphid (and some other) marsupials, with emphasis on variability. *Am. J. Anat.*, 99 : 239-249.
- HILDEBRAND, M., 1988. – *Analysis of vertebrate structure*. 3rd edition. John Wiley & Sons, New York.
- HUNSAKER, D., II, 1977. – Ecology of New World marsupials. Pp. 95-156, in : *The biology of marsupials*. Ed. D. Hunsaker II. Academic Press, New York.
- JUNGERS, W.L., 1985. – Body size and scaling of limb proportions in primates. Pp. 345-381. In : *Size and scaling in primate biology*. Ed. W.L. Jungers. Plenum Press, New York.
- KIRSH, J.A.W., R.E. BLEIWEISS, A.W. DICKERMAN and O.A. REIG, 1993. – DNA/DNA hybridization studies of carnivorous marsupials. III. Relationships among species of *Didelphis* (Didelphidae). *J. Mammal. Evol.*, 1 : 75-97.
- MARCUS, L.F. and R.S. VOSS, 1992. – Morphological evolution in muroid rodents II. Craniometric factor divergence in seven Neotropical genera, with experimental results from *Zygodontomys*. *Evolution*, 46 : 1918-1934.
- MARDIA, K.V., 1970. – Measures of multivariate skewness and kurtosis with applications. *Biometrika*, 57 : 519-530.
- MILES, M.A., A.A. DE SOUSA and M.M. POVOA, 1981. – Mammal tracking and nest location in Brazilian forest with an improved spool-and-line device. *J. Zool.*, 195 : 331-347.
- MORRISON, D.F., 1976. – *Multivariate statistical methods*. McGraw-Hill, New York.
- O'CONNELL, M.A., 1979. – Ecology of didelphid marsupials from Northern Venezuela. Pp. 73-87. In : *Vertebrate ecology in the northern Neotropics*. Ed. J.F. Eisenberg. Smithsonian Institution Press, Washington, D.C.
- PATTON, J.L., S.F. REIS and M.N.F. SILVA, 1996. – Relationships among didelphid marsupials based on sequence variation in the mitochondrial cytochrome b gene. *J. Mammal. Evol.*, 3 : 3-29.
- REIG, O.A., J.A.W. KIRSH and L.G. MARSHALL, 1987. – Systematic relationships of the living and Neocenezoic American « opossum-like » marsupials (Suborder Didelphimorphia), with comments on the classification of these and of the Cretaceous and Paleocene New World and European methaterians. Pp. 1-89. In : *Possums and opossums : studies in evolution*. Ed. M. Archer. Surrey Beatty & Sons, Sydney.

- ROHLF, F.J. and F.L. BOOKSTEIN, 1987. – A comment on shearing as a method for « size correction ». *Syst. Zool.*, 36 : 356-367.
- SAS INSTITUTE INC., 1985. – *SAS User's Guide : Basics, Version 5*. SAS Institute Inc., Cary, NC.
- STEIN, B.R., 1981. – Comparative limb myology of two opossums. *J. Morphol.*, 169 : 113-140.
- STEVENS, J., 1992. – *Applied multivariate statistics for the social sciences*. Lawrence Earlbaum Associates Publishers, Hillsdale, New Jersey.
- STREILEIN, K.E., 1982. – Behavior, ecology, and distribution of South American marsupials. Pp. 231-250. *In : Mammalian biology in South America*. Eds M.A. Mares and H.H. Genoways. University of Pittsburgh, Linesville.
- SZALAY, F.S., 1994. – *Evolutionary history of the marsupials and an analysis of osteological characters*. Cambridge University Press, Cambridge.
- THORPE, R.S., 1983. – A review of numerical methods for recognising and analysing racial differentiation. Pp. 404-423. *In : Numerical taxonomy*. Ed. J. Felsenstein. Springer Verlag, Berlin.
- WORKS, M.E., 1950. – *A morphological comparison of the Central American genera of Didelphidae (opossums)*. M.A. Thesis. University of Kansas, Lawrence, Kansas.