

# MORPHOMETRIC ASSESSMENT OF THE *MONDELPHIS BREVICAUDATA* GROUP (DIDELPHIMORPHIA: DIDELPHIDAE) IN VENEZUELA

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We reviewed the systematics of the *Monodelphis brevicaudata* species group in Venezuela using morphometric analyses. Results revealed that *M. b. orinoci* showed significant differences when compared to the other two Venezuelan forms of *M. brevicaudata* (*brevicaudata* and *palliolata*) and supported recognizing *M. orinoci* as a species. We find *M. brevicaudata* represented in Venezuela by two subspecies: *M. b. brevicaudata*, distributed south of the Orinoco River, and *M. b. palliolata*, found in northern Venezuela. *M. orinoci* is a small sexually monomorphic species, inhabiting lowland savanna. *M. brevicaudata* is a large sexually dimorphic species that occurs in forest habitats ranging up to elevations of 1,500 m above mean sea level.

**Key words:** *Monodelphis brevicaudata*, *Monodelphis orinoci*, marsupials, morphometrics, taxonomy, geographic distribution, neotropics

Representatives of the genus *Monodelphis* are small short-tailed opossums widely distributed in South America (cf. Corbet and Hill, 1991; Gardner, 1993; Nowak, 1991). Two species of *Monodelphis* are currently recognized in Venezuela: the cloudy short-tailed opossum, *M. adusta* (Thomas), and Seba's short-tailed opossum, *M. brevicaudata* (Erxleben). They can be distinguished on the basis of size and fur color. *M. adusta* is restricted to the states of Táchira and Mérida in northwestern Venezuela (Ramoni-Perazzi et al., 1994; Soriano, 1987). *M. brevicaudata* shows a wider distribution, which extends from the Caribbean coast to the state of Amazonas, and from the state of Zulia in the west, to the state of Bolívar in the east. Cabrera (1958) recognized three subspecies of *M. brevicaudata*: *M. b. brevicaudata*, *M. b. palliolata* (Osgood), and *M. b. orinoci* (Thomas). Reig et al. (1977) stated that *orinoci* should be considered a species because of its size and fur color but offered no empirical data

in support of their argument. Since the publication of Cabrera's (1958) monograph, the taxonomy of the *M. brevicaudata* group has not been studied in detail. Subsequent reviews of marsupials of the world contain contradictory opinions concerning taxonomic status of *orinoci*; it has been considered as either a valid species (Corbet and Hill, 1991; Honacki et al., 1982; Lee and Cockburn, 1985; Nowak, 1991) or as a subspecies of *M. brevicaudata* (Gardner, 1993).

No comprehensive taxonomic study has been published concerning morphometric variation in *M. brevicaudata* (sensu lato) from Venezuela. In this paper, we address aspects of geographic distribution, morphologic variation, and taxonomy of members of the *M. brevicaudata* species group in Venezuela.

## MATERIALS AND METHODS

We examined 99 specimens of *Monodelphis* (Appendix I): *M. b. brevicaudata* ( $n = 21$ ; 15 males, 6 females); *M. b. palliolata* ( $n = 67$ ; 42 males, 24 females, 1 ?); and *M. b. orinoci* ( $n =$

11; 8 males, 3 females). Specimens were assigned to a taxon based on their geographic origin and fur color (Pérez-Hernández, 1988, 1989).

Age-class determination was based on tooth eruption and wear criteria used by Gardner (1973) but modified slightly in accordance with criteria proposed by Tribe (1990). In contrast to larger species of didelphids, the deciduous molar (dPM3) in *M. brevicaudata* can persist while M4 is erupting (Tribe, 1990). Specimens were assigned to one of six age classes: class I—dPM3, M1, and sometimes M2 fully erupted, M3 erupting; class II—dPM3 not replaced, M3 erupting or fully erupted, M4 and m4 not erupted; class III—PM3 erupting and without M4, or dPM3 persisting while M4 is erupting, m4 can be in position; class IV—M1–M3 are functional, dPM3 shed, PM3 fully erupted, and M4 erupting; class V—all teeth erupted and M4 with little wear; class VI—all teeth erupted and M4 noticeably worn.

Measurements of 24 skull dimensions were taken (in mm) using a digital caliper to 0.01 mm (Fig. 1). Character variation in *Monodelphis* was analyzed by univariate and multivariate statistics. For each character, significance of the differences between sexes was determined using Student's *t*-test. Differences among sample means were investigated with analysis of variance (ANOVA), and Scheffé's method was used to determine significance of differences between pairs of samples (SPSS/PC+; Norusis, 1988). Data were standardized to calculate average taxonomic distances and a phenogram was constructed by the unweighted pair-group method using arithmetic averages (UPGMA; Sneath and Sokal, 1973). Distance analysis and principal-components analyses were performed using NTSYS-pc routines (Rohlf, 1994). Discriminant analysis provided linear combinations of skull variables to separate subsamples (SPSS/PC+; Norusis, 1988).

## RESULTS

*Geographic distribution and habitat.*—*Monodelphis brevicaudata* (including *orinoci* as a subspecies) occurs in Venezuela, Surinam, French Guiana, and the Amazonian slope of Brazil and Bolivia (Cabrera, 1958; Gardner, 1993). Geographic distribution (Fig. 2), and habitat requirements of the three forms of the *M. brevicaudata*

group in Venezuela are as follows (Eisenberg, 1989; Handley, 1976; Pérez-Hernández, 1989).

*Monodelphis b. brevicaudata* is found in southern Venezuela in the states of Bolívar and Amazonas. Generally it has been caught in lowland forests (95–400 m elevation) but occasionally in higher areas such as the upland forests of Serranía de los Pijiguaos (620 m), San Ignacio de Yuruaní (860 m), Santa Lucía de Surukún (900 m), and southern Prai-Tepui (1,080 m).

*Monodelphis b. palliolata* occurs in northern Venezuela. In the west, it has been found in the states of Zulia, Mérida, Barinas, Trujillo, and Táchira; Osgood (1914) placed the type locality at San Juan de Colón, Táchira. In the coastal region, *M. palliolata* extends eastward throughout the states of Falcón, Yaracuy, Carabobo, Aragua, Distrito Federal, Miranda, Sucre, and Monagas. It has been captured from sea level to 1,500 m in the mountain regions of Sierra de Perijá, the Andes, and the Central and eastern Cordillera de la Costa. These opossums have been trapped in diverse habitats, such as tropical dry forest, premontane humid and very humid forests, and tropical humid forest (forest classification system according to Holdrige in Ewel et al., 1968).

*Monodelphis b. orinoci* is found in the llanos of the state of Bolívar northward through the states of Guárico, Cojedes, and Aragua to the foothills of the Central Cordillera de la Costa (Magdaleno, 575 m elevation). It also may occur in the llanos of Colombia (A. Cadena, pers. comm.). It has been found in lowland savanna, especially in areas densely covered by grasses at elevations from 20 to 575 m.

*Nongeographic variation.*—Intersexual comparisons for each character in adults (age classes IV to VI) revealed that male and female *orinoci* differed significantly in one character (NW), whereas *brevicaudata* and *palliolata* were sexually dimorphic for 17 and 16 characters, respectively (Table 1). For *brevicaudata* and *palliolata*, males

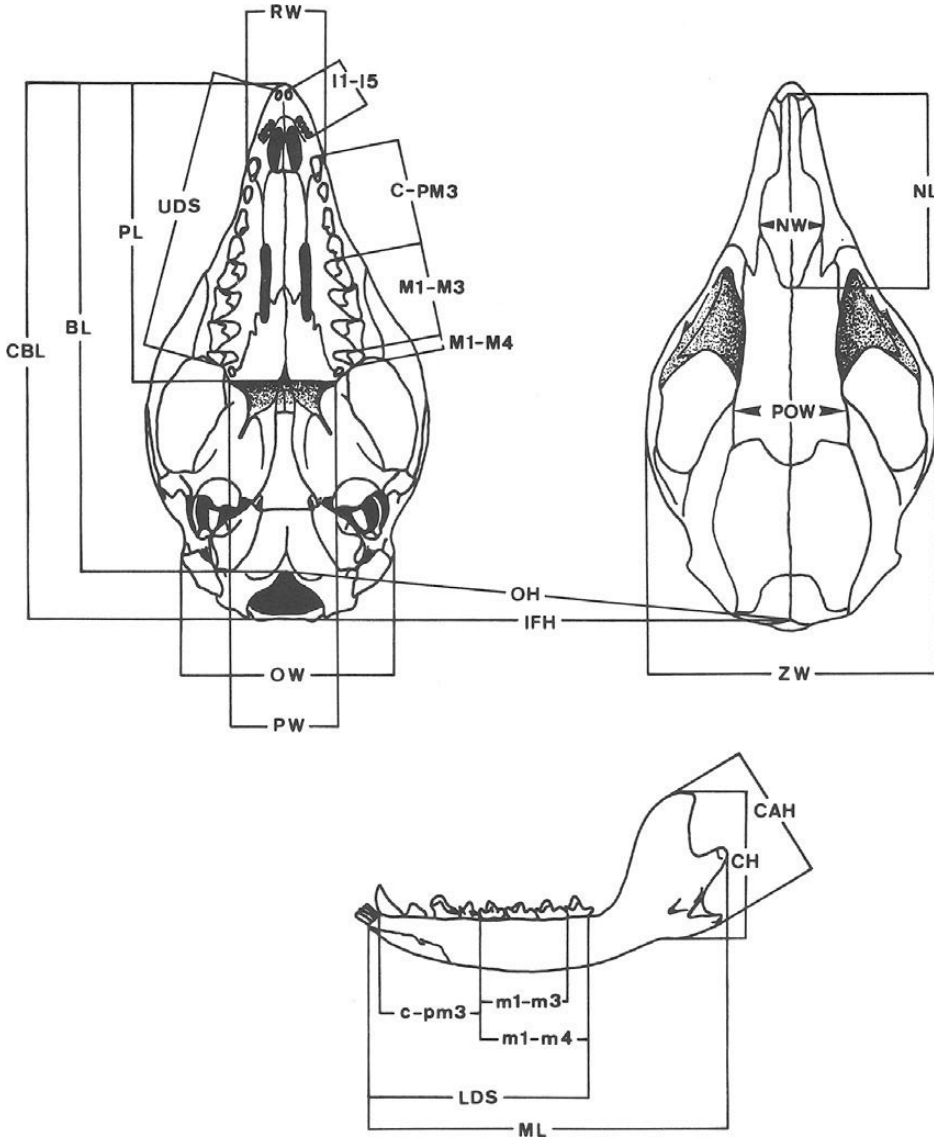


FIG. 1.—Skull measurements of *Monodelphis*: CBL, condylobasal length; BL, basal length; NL, length of nasals; PL, length of palate; I1-I5, length of I1-I5; C-PM3, length of C-PM3; M1-M3, length of M1-M3; M1-M4, length of M1-M4; UDS, length of upper dental series; PW, width of palate; NW, width of nasals; RW, width of rostrum; ZW, width of zygoma; POW, minimum postorbital width; OW, occipital width; IFH, interparietal-foramen magnum height; OH, height of occipital; ML, length of mandible; c-pm3, length of c-pm3; m1-m3, length of m1-m3; m1-m4, length of m1-m4; LDS, length of lower dental series; CAH, distance between coronoid and angular processes; CH, height of coronoid process.

showed higher mean values for each of these characters. Most of the non-significant variables were dental measurements (I1-I5, M1-M3, M1-M4, m1-m3, m1-

m4). In both taxa, skulls of males were not only larger than those of females but were also more massive, with noticeably larger canines and a longer gap between I5 and

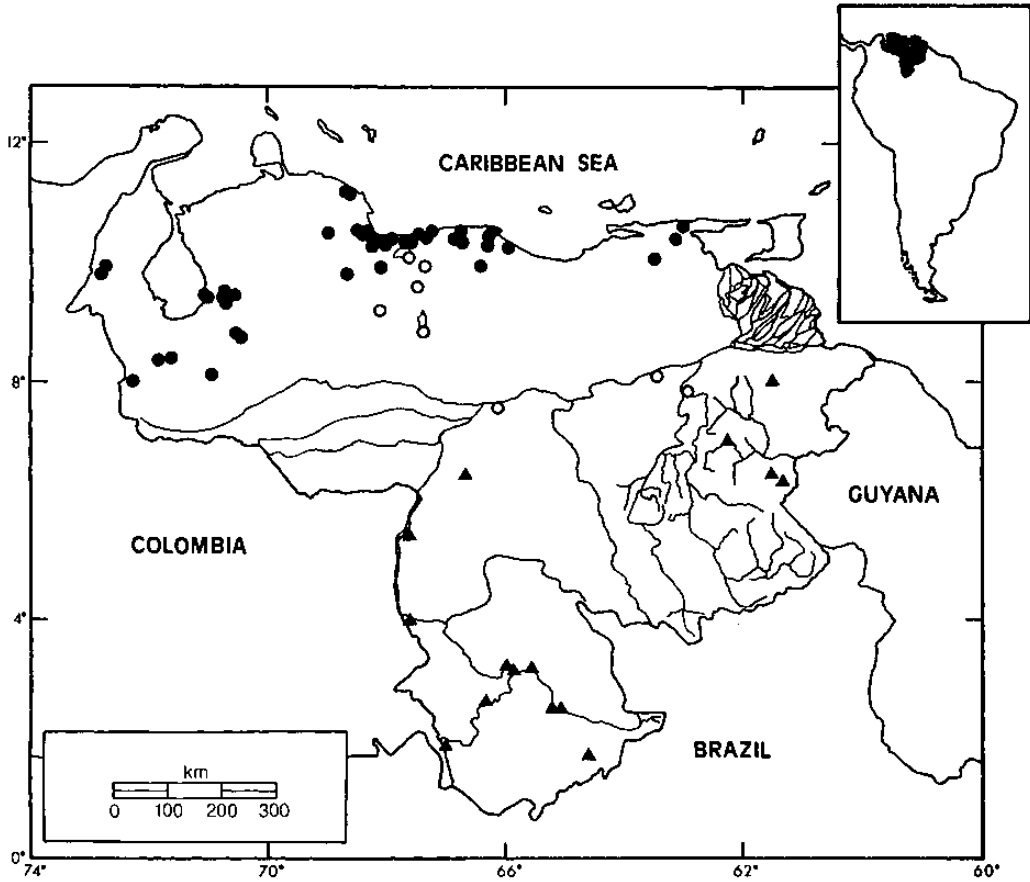


FIG. 2.—Geographic distribution of *Monodelphis* in Venezuela. (▲): *brevicaudata*; (●): *palliolata*; (○): *orinoci*.

the upper canine to accommodate the lower canine.

Due to the sample size, we were able to analyze sex and age variation only in *palliolata* (Table 2). Sexual differences were tested only in classes II, V, and VI where sample sizes were sufficiently large. Sexual differences in class II were significant for two characters (POW,  $P < 0.01$ ; IFH,  $P < 0.05$ ). Conversely, adult males of classes V and VI were larger in absolute terms than females and showed significant differences for most variables (class V, 17 characters; class VI, 18 characters).

Using all characters for specimens of classes IV, V, and VI, a discriminant function was constructed to separate males and females. Results revealed a high proportion

of the total variance attributable to differences between groups (eigenvalue = 1.5978, canonical correlation = 0.7843, Wilks' lambda = 0.3849). The difference between male and female averages on the discriminant function was significant ( $\chi^2 = 19.094$ ,  $d. f. = 6$ ,  $P < 0.005$ ). The discriminant function obtained was:  $D = -0.3738$  (NL) - 1.3392 (PW) + 2.9264 (OW) + 2.3893 (IFH) + 1.8236 (LDS) - 2.7560(CH) - 36.3714. Group centroids were: males = 0.9093 and females = -1.6166. The percentage of "grouped" cases correctly classified was 96.3%; all females ( $n = 9$ ) were classified correctly, and one male ( $n = 18$ ) was misclassified.

*Geographic variation.*—Due to sexual dimorphism found in earlier analyses, adult

TABLE 1.—Basic descriptive statistics for skull measurements of adult (classes IV, V, and VI) *Monodelphis* from Venezuela. Significance (\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ) is based on Student's *t*-test.

Character	♂♂					♀♀					P
	n	$\bar{X}$	SD	Minimum	Maximum	n	$\bar{X}$	SD	Minimum	Maximum	
Condylobasal length											
<i>brevicaudata</i>	12	38.71	2.45	35.34	42.49	4	34.7	0.68	34.00	35.74	**
<i>palliolata</i>	31	37.29	2.71	31.71	41.51	17	34.2	1.66	31.86	37.44	***
<i>orinoci</i>	7	32.74	2.86	29.62	36.95	3	33.5	1.02	32.18	34.68	
Basal length											
<i>brevicaudata</i>	11	36.21	2.42	33.11	40.16	4	32.3	0.48	31.79	32.99	**
<i>palliolata</i>	30	34.96	2.66	29.34	39.23	16	32	1.49	29.73	34.80	***
<i>orinoci</i>	7	30.71	2.87	27.53	34.91	3	31.5	1.02	30.22	32.73	
Nasal length											
<i>brevicaudata</i>	15	18.56	1.52	15.73	20.90	5	15.9	0.94	14.18	16.97	**
<i>palliolata</i>	25	17.23	1.83	14.26	21.33	11	15.9	1.34	13.71	17.79	*
<i>orinoci</i>	7	14.22	2.05	11.95	16.75	2	15.2	0.48	14.72	15.69	
Palatal length											
<i>brevicaudata</i>	15	21.30	1.08	19.48	23.10	5	19	0.30	18.70	19.51	***
<i>palliolata</i>	28	20.46	1.46	17.39	23.11	16	18.8	0.77	17.72	20.02	***
<i>orinoci</i>	7	17.89	1.63	16.37	20.23	2	18	0.26	17.76	18.29	
Length of I1–I5											
<i>brevicaudata</i>	15	3.29	0.36	2.48	3.83	5	3.18	0.25	3.00	3.67	
<i>palliolata</i>	31	3.16	0.20	2.63	3.52	17	3.11	0.10	2.94	3.28	
<i>orinoci</i>	7	2.97	0.14	2.73	3.16	3	3.01	0.05	2.94	3.06	
Length of C–PM3											
<i>brevicaudata</i>	15	7.47	0.53	6.65	8.39	5	6.73	0.33	6.22	7.21	**
<i>palliolata</i>	31	7.28	0.56	6.15	8.58	17	6.58	0.31	6.17	7.20	***
<i>orinoci</i>	7	6.52	0.63	5.83	7.28	3	6.75	0.28	6.36	7.03	
Length of M1–M3											
<i>brevicaudata</i>	15	6.50	0.34	5.89	7.03	5	6.47	0.34	5.90	6.81	
<i>palliolata</i>	31	6.16	0.30	5.10	6.66	17	6.08	0.28	5.47	6.60	
<i>orinoci</i>	7	5.75	0.25	5.41	6.24	3	5.77	0.13	5.59	5.89	
Length of M1–M4											
<i>brevicaudata</i>	15	7.74	0.33	7.14	8.31	4	7.47	0.13	7.33	7.61	
<i>palliolata</i>	31	7.38	0.29	6.65	7.94	17	7.21	0.24	6.72	7.58	
<i>orinoci</i>	6	6.86	0.27	6.53	7.25	3	6.85	0.23	6.58	7.15	
Length of upper dental series											
<i>brevicaudata</i>	15	19.61	0.96	18.18	21.37	5	18.2	0.47	17.48	18.76	**
<i>palliolata</i>	30	18.91	0.84	16.95	20.76	17	17.8	0.59	16.94	19.04	***
<i>orinoci</i>	7	17.22	1.15	15.93	19.22	3	17.3	0.36	16.94	17.75	
Palatal width											
<i>brevicaudata</i>	15	8.07	0.57	7.12	9.05	5	6.75	0.61	6.01	7.39	***
<i>palliolata</i>	26	7.46	0.43	6.61	8.41	16	7.22	0.40	6.50	8.00	
<i>orinoci</i>	7	6.47	0.77	5.42	7.49	2	6.84	0.12	6.72	6.95	
Nasal width											
<i>brevicaudata</i>	15	6.56	0.65	5.19	7.49	5	6.30	0.54	5.64	7.00	
<i>palliolata</i>	31	6.15	0.60	5.11	7.36	17	5.84	0.49	5.09	6.70	
<i>orinoci</i>	7	5.31	0.26	4.97	5.69	3	5.79	0.11	5.63	5.89	*

TABLE 1.—Continued.

Character Subspecies	♂♂					♀♀					P
	n	$\bar{X}$	SD	Mini- mum	Maxi- mum	n	$\bar{X}$	SD	Mini- mum	Maxi- mum	
<b>Rostral width</b>											
<i>brevicaudata</i>	15	6.78	0.54	5.59	7.85	5	5.78	0.33	5.23	6.20	**
<i>palliolata</i>	32	6.51	0.71	5.48	7.82	17	5.75	0.46	5.01	6.63	***
<i>orinoci</i>	7	5.70	0.80	4.87	6.80	3	5.72	0.14	5.55	5.89	
<b>Zygomatic width</b>											
<i>brevicaudata</i>	13	21.24	1.54	18.62	23.66	5	18.4	0.66	17.25	19.11	**
<i>palliolata</i>	31	20.12	1.96	17.16	23.33	17	18.4	1.22	16.42	20.44	**
<i>orinoci</i>	7	18.14	1.99	15.90	20.88	2	18.4	0.24	18.16	18.65	
<b>Minimum postorbital width</b>											
<i>brevicaudata</i>	14	6.35	0.22	5.94	6.68	5	6.34	0.23	6.13	6.75	
<i>palliolata</i>	32	6.28	0.27	5.74	6.78	17	6.17	0.15	5.88	6.43	
<i>orinoci</i>	7	5.90	0.19	5.60	6.20	3	5.79	0.15	5.66	6.00	
<b>Occipital width</b>											
<i>brevicaudata</i>	12	15.27	1.05	13.63	16.68	4	13.7	0.29	13.21	13.95	*
<i>palliolata</i>	30	14.42	0.96	12.76	15.87	17	13.4	0.72	12.38	14.98	***
<i>orinoci</i>	7	13.14	0.85	12.22	14.32	3	13.2	0.28	12.80	13.42	
<b>Height of interparietal foramen magnum</b>											
<i>brevicaudata</i>	12	4.84	0.77	3.96	6.46	4	3.75	0.22	3.46	4.01	*
<i>palliolata</i>	26	4.11	0.46	3.18	4.83	16	3.68	0.29	3.15	4.20	**
<i>orinoci</i>	6	3.59	0.22	3.26	3.87	3	3.68	0.22	3.38	3.88	
<b>Occipital height</b>											
<i>brevicaudata</i>	11	8.99	0.53	8.16	9.90	4	8.33	0.23	7.99	8.56	*
<i>palliolata</i>	29	8.41	0.50	7.52	9.31	16	7.91	0.35	7.42	8.62	**
<i>orinoci</i>	7	7.90	0.40	7.37	8.55	3	7.77	0.04	7.71	7.81	
<b>Length of mandible</b>											
<i>brevicaudata</i>	15	29.13	1.64	26.30	31.55	5	25.5	1.01	23.76	26.85	***
<i>palliolata</i>	31	28.03	2.29	23.28	32.24	17	25.5	1.58	23.28	28.34	***
<i>orinoci</i>	7	24.38	2.48	21.90	28.12	3	25.5	0.85	24.52	26.61	
<b>Length of c-pm3</b>											
<i>brevicaudata</i>	15	6.87	0.38	6.09	7.69	5	6.01	0.34	5.40	6.37	***
<i>palliolata</i>	31	6.86	0.70	5.40	8.14	17	6.16	0.41	5.54	6.90	***
<i>orinoci</i>	7	6.09	0.82	4.97	7.50	3	6.31	0.52	5.59	6.81	
<b>Length of m1-m3</b>											
<i>brevicaudata</i>	15	6.21	0.29	5.78	6.65	5	6.15	0.22	5.96	6.51	
<i>palliolata</i>	31	5.98	0.17	5.63	6.28	17	5.90	0.20	5.60	6.27	
<i>orinoci</i>	7	5.65	0.13	5.50	5.87	3	5.49	0.16	5.32	5.70	
<b>Length of m1-m4</b>											
<i>brevicaudata</i>	15	8.73	0.53	8.09	9.79	4	8.64	0.43	8.07	9.15	
<i>palliolata</i>	31	8.20	0.30	7.57	8.91	16	8.14	0.29	7.58	8.70	
<i>orinoci</i>	7	8.04	0.28	7.67	8.55	3	7.70	0.18	7.45	7.84	
<b>Length of lower dental series</b>											
<i>brevicaudata</i>	15	17.31	0.95	15.57	19.16	4	16	0.36	15.59	16.48	*
<i>palliolata</i>	31	16.97	0.75	15.61	18.37	17	16	0.57	15.16	16.95	***
<i>orinoci</i>	7	15.19	0.51	14.42	15.93	3	15.3	0.45	14.85	15.91	
<b>Distance between coronoid and angular processes</b>											
<i>brevicaudata</i>	13	10.58	0.66	9.23	11.68	5	9.25	0.43	8.65	9.99	***

TABLE 1.—Continued.

Character Subspecies	♂♂					♀♀					P
	n	$\bar{X}$	SD	Mini- mum	Maxi- mum	n	$\bar{X}$	SD	Mini- mum	Maxi- mum	
<i>palliolata</i>	30	10.28	0.87	8.80	12.13	16	9.65	0.72	8.23	10.86	*
<i>orinoci</i>	6	9.16	0.98	8.11	10.61	3	9.45	0.23	9.15	9.71	
Height of coronoid process											
<i>brevicaudata</i>	14	11.09	0.85	9.54	12.38	5	10.1	0.71	9.17	11.07	*
<i>palliolata</i>	31	10.38	1.07	8.71	12.46	16	9.56	0.71	8.40	10.67	*
<i>orinoci</i>	7	9.19	1.04	7.89	10.43	3	9.63	0.19	9.37	9.77	

males and females (age classes IV, V, and VI) were treated separately in comparisons of the three morphotypes. Statistical comparisons between males of *brevicaudata*, *palliolata*, and *orinoci* revealed significant differences in all variables (Table 3). For all characters, *orinoci* showed the lowest mean values and *brevicaudata* the highest. *M. b. orinoci* differed significantly from *brevicaudata* in all characters and from *palliolata* in 19. Conversely, *brevicaudata* and *palliolata* differed significantly in lengths of upper and lower molar series: PW, IFH, and OH (Table 3).

Results of the ANOVA performed for females indicated homogeneous dimensions for the three morphotypes, showing significant differences only for M1–M3 ( $F = 5.5281$ ,  $P < 0.02$ ; *brevicaudata* versus *orinoci*,  $P < 0.05$ ), M1–M4 ( $F = 5.551$ ,  $P < 0.02$ ; *brevicaudata* versus *orinoci*,  $P < 0.05$ ), POW ( $F = 8.98$ ,  $P < 0.002$ ; *brevicaudata* versus *orinoci*,  $P < 0.01$ ; *palliolata* versus *orinoci*,  $P < 0.01$ ), m1–m3 ( $F = 9.0483$ ,  $P < 0.002$ ; *brevicaudata* versus *orinoci*,  $P < 0.01$ ; *palliolata* versus *orinoci*,  $P < 0.05$ ), and m1–m4 ( $F = 7.2175$ ,  $P < 0.005$ ; *brevicaudata* versus *orinoci*,  $P < 0.01$ ; *brevicaudata* versus *palliolata*,  $P < 0.05$ ); for these variables *orinoci* showed the lowest means and *brevicaudata* the highest.

Two main clusters were evident in the distance phenogram (Fig. 3). One was comprised of both sexes of *orinoci* and females of *brevicaudata* and *palliolata*, the other

cluster was comprised of male *brevicaudata* and male *palliolata*. When males or females were analyzed separately, the small-sized *orinoci* were separated from the cluster formed by the large-sized *brevicaudata* and *palliolata*. This differentiation was especially marked in males. The first two principal axes explained 96.32% of variance (85.66% and 10.66%, respectively). Component I discriminated among size groups and had high positive loadings for all characters; component II was correlated mostly with dental parameters (M1–M3, c-pm3, m1–m3, m1–m4) and POW.

#### DISCUSSION

*Nongeographic variation.*—Sexual dimorphism in adults has been reported in several didelphid species, such as *Didelphis marsupialis* (Tyndale-Biscoe and Mackenzie, 1976), *D. albiventris* (Cerqueira, 1984), *Monodelphis dimidiata*, *M. sorex* (Pine et al., 1985), and *M. domestica* (Bergallo and Cerqueira, 1994). However, this is not a general feature in Didelphidae; for example, males and females of *Marmosops parvidens* do not differ significantly in size (Pine, 1981). Both patterns were observed in samples analyzed here; *brevicaudata* and *palliolata* showed noticeable sexual differences and *orinoci* was sexually invariant. These relationships were shown clearly in the distance phenogram constructed of separate male and female samples. Williams (1966) stated that high reproductive effort determines extreme sexual differences. For

several species of Didelphidae, sexual dimorphism increases following sexual maturity (Bergallo and Cerqueira, 1994; Cerqueira, 1984; Gardner, 1973; Pine et al., 1985; Tyndale-Biscoe and MacKenzie, 1976), because energy that females invest during pregnancy and lactation reduces energy available for growth (Bergallo and Cerqueira, 1994; Gardner, 1973). However, Pine et al. (1985) indicated that sexual dimorphism in *M. dimidata* might appear before sexual maturity and suggested that sexual dimorphism might be associated with semelparity. Because males have only one opportunity to mate, they may be under intense selection for large size as an advantage in agonistic encounters with other males. Lack of specimens in several age classes of *palliolata* did not allow us to determine accurately when significant differences between males and females appear. Likewise, scarce information available concerning reproductive characteristics of the species (cf. O'Connell, 1979) makes it impossible to determine age of sexual maturity. Nevertheless, it is clear that although class-II males and females were similar in skull dimensions, males and females in classes V and VI were sexually dimorphic. These results might suggest that, as in other Didelphidae, sexual dimorphism appears in adulthood. However, several variables, such as minimum postorbital width (POW) and those related to length of incisive and molar series, did not differ between adult males and females. Similar results were obtained by Pine et al. (1985) for adult specimens of *M. dimidiata*, where, except for M1-M4 and the postorbital constriction, sexual dimorphism affected skull dimensions in general. Available data do not allow us to explain this circumstance.

Absence of sexual dimorphism in *orinoci* leads us to hypothesize differences in the life-history traits between it and *brevicaudata* and *palliolata*, specifically differences in mating systems (cf. Lee and Cockburn, 1985). However, causes underlying these

patterns of sexual dimorphism remain unexplained.

*Geographic variation.*—Didelphidae are characterized by a small number of chromosomal patterns. In nine genera represented by 22 species (Reig et al., 1977), only three diploid numbers (14, 18, and 22) and four distinct karyotypes were recognized. Species of the genus *Monodelphis*, including *M. brevicaudata* and *M. orinoci*, have a karyotype of  $2n = 18$  (cf. Reig and Bianchi, 1969; Reig et al., 1977; Wainberg, 1972). In contrast to Cabrera's (1958) treatment of the genus, in which *orinoci* was considered a subspecies of *M. brevicaudata*, Reig et al. (1977:204) "... found consistent and well-marked differences in size, fur colour, and cranial features that readily distinguish typical *brevicaudata* of the mountain forest of northern Venezuela from the Calabozo lowland savanna form, which closely agrees with the holotype of *orinoci*." On the basis of this argument, they considered *orinoci* to be a separate species, pointing out that differences between it and *M. brevicaudata* are of the same magnitude as those used to separate *M. brevicaudata* from *M. dimidiata*. However, because Reig et al. (1977) did not present results of morphological analyses, separation of *brevicaudata* and *orinoci* remained unsubstantiated. Our comparative analyses of skull characters revealed significant differences between *orinoci* and similarly sized *brevicaudata* and *palliolata*. Distance analysis clearly indicated morphometric separation of *orinoci* in both males and females from the other two morphotypes. Moreover, differences in sexual dimorphism suggest differences in life-history traits between *orinoci*, and *palliolata* and *brevicaudata*. This finding also supports a specific status for sexually monomorphic *orinoci*. As for fur color, Pérez-Hernández (1988) described differences between *brevicaudata*, *palliolata*, and *orinoci*, and following observations by Reig et al. (1977), considered *orinoci* as a separate species. The latter differed from *brevicaudata* and *palliolata* in color of up-



TABLE 2.—Basic descriptive statistics for skull measurements of *Monodelphis breviceaudata pal-liolata*, grouped by sex and age class.

Sex	Age class		Character											
			Condy- lobasal length	Basal length	Nasal length	Palatal length	Length of II–I5	Length of C–PM3	Length of M1– M3	Length of M1– M4	Length of upper dental series	Palatal width	Nasal width	
♂♂	I	<i>n</i>	1	1	1	1	1					1	1	
		$\bar{X}$	21.82	19.92	8.55	11.49	2.66					4.45	4.05	
	II	<i>n</i>	9	9	8	9	9		8			9	9	
		$\bar{X}$	29.05	26.90	12.79	15.91	2.96		5.38			6.38	5.20	
		<i>SD</i>	1.98	1.85	0.99	1.06	0.17		0.98			0.48	0.36	
		Minimum	24.57	22.69	10.33	13.40	2.58		4.25			5.31	4.77	
		Maximum	31.49	29.09	13.70	17.05	3.17		6.76			7.14	5.93	
	IV	<i>n</i>	2	2	2	2	2	2	2	2	2	2	2	
		$\bar{X}$	32.49	30.24	14.38	18.02	2.78	6.31	5.70	7.24	17.45	6.89	5.38	
		<i>SD</i>	0.78	0.89	0.12	0.63	0.15	0.15	0.60	0.27	0.50	0.27	0.10	
		Minimum	31.71	29.34	14.26	17.39	2.63	6.15	5.10	6.97	16.95	6.61	5.28	
		Maximum	33.27	31.13	14.49	18.65	2.93	6.46	6.30	7.50	17.95	7.16	5.48	
	V	<i>n</i>	22	22	18	20	22	22	22	22	21	19	22	
		$\bar{X}$	36.72	34.48	17.14	20.15	3.14	7.15	6.21	7.40	18.71	7.39	5.95	
		<i>SD</i>	2.14	2.05	1.67	1.09	0.15	0.39	0.24	0.27	0.57	0.34	0.41	
		Minimum	33.01	31.00	15.35	18.29	2.88	6.39	5.83	6.77	17.82	6.65	5.11	
		Maximum	40.72	38.45	21.33	22.15	3.48	7.93	6.66	7.94	19.94	8.09	6.72	
	VI	<i>n</i>	7	6	5	6	7	7	7	7	7	5	7	
		$\bar{X}$	40.47	38.30	18.70	22.30	3.35	7.98	6.13	7.35	19.93	7.93	6.98	
		<i>SD</i>	0.54	0.52	1.14	0.38	0.17	0.30	0.18	0.35	0.47	0.37	0.33	
		Minimum	39.52	37.56	16.75	21.98	3.01	7.61	5.83	6.65	19.07	7.50	6.38	
		Maximum	41.51	39.23	20.08	23.11	3.52	8.58	6.33	7.84	20.76	8.41	7.36	
	♀♀	II	<i>n</i>	5	5	4	5	5		4			5	5
			$\bar{X}$	30.18	27.99	13.53	16.54	2.84		6.62			6.72	5.00
<i>SD</i>			0.91	0.92	0.56	0.45	0.16		0.12			0.58	0.44	
Minimum			28.61	26.41	12.98	15.75	2.60		6.45			5.66	4.67	
Maximum			31.41	29.06	14.45	17.03	3.04		6.79			7.29	5.86	
III		<i>n</i>	2	2	1	2	2		2			2	2	
		$\bar{X}$	31.65	29.46	14.00	17.34	2.97		6.71			6.66	4.88	
		<i>SD</i>	0.35	0.35	0.00	0.09	0.04		0.07			0.50	0.33	
		Minimum	31.30	29.11	14.00	17.25	2.92		6.64			6.16	4.55	
		Maximum	32.00	29.80	14.00	17.42	3.01		6.78			7.15	5.20	
V		<i>n</i>	12	12	8	12	12	12	12	12	12	12	12	
		$\bar{X}$	34.03	31.71	15.67	18.75	3.15	6.56	6.06	7.21	17.75	7.16	5.66	
		<i>SD</i>	1.64	1.46	1.46	0.76	0.08	0.27	0.30	0.26	0.61	0.36	0.36	
		Minimum	31.86	29.73	13.71	17.72	3.00	6.17	5.47	6.72	17.04	6.50	5.09	
		Maximum	37.44	34.80	17.79	20.02	3.28	7.09	6.60	7.58	19.04	7.80	6.42	
VI		<i>n</i>	5	4	3	4	5	5	5	5	5	4	5	
		$\bar{X}$	34.58	32.91	16.47	19.12	3.04	6.63	6.13	7.21	17.77	7.40	6.26	
		<i>SD</i>	1.64	1.21	0.71	0.73	0.09	0.40	0.23	0.20	0.51	0.44	0.50	
		Minimum	32.15	31.18	15.49	18.18	2.94	6.21	5.83	6.94	16.94	6.92	5.28	
		Maximum	36.58	34.09	17.13	19.94	3.19	7.20	6.45	7.42	18.36	8.00	6.70	

TABLE 2.—*Extended.*

Character												
Rostral width	Zygo-matic width	Mini-mum post-orbital width	Occipi-tal width	Height of inter-parietal foramen magnum	Occipi-tal height	Length of mandible	Length of c-pm3	Length of m1-m3	Length of m1-m4	Length of lower dental series	Distance between coronoid and angular pro-cesses	Height of coronoid process
1	1	1	1	1	1	1	1					1
4.30	11.90	5.73	10.25	1.78	5.43	15.84	4.19					5.97
9	9	9	9	8	9	9	9	9	5	5	9	9
5.09	15.42	6.30	12.08	3.18	7.34	21.10	5.37	6.17	8.43	15.80	8.02	8.12
0.19	1.00	0.22	0.57	0.27	0.37	1.51	0.23	0.17	0.27	0.48	0.56	0.63
4.66	13.03	5.82	10.75	2.80	6.70	17.75	4.99	5.87	8.04	15.36	6.64	6.81
5.32	16.54	6.64	12.77	3.67	7.89	23.34	5.78	6.46	8.83	16.70	8.51	9.31
2	2	2	2	2	2	2	2	2	2	2	2	2
5.52	17.41	6.17	12.91	3.41	7.64	24.01	5.75	6.01	8.33	15.86	8.81	8.84
0.04	0.07	0.02	0.15	0.04	0.12	0.73	0.35	0.01	0.11	0.25	0.00	0.13
5.48	17.34	6.15	12.76	3.37	7.52	23.28	5.40	6.00	8.21	15.61	8.80	8.71
5.56	17.48	6.19	13.06	3.45	7.75	24.74	6.10	6.01	8.44	16.10	8.81	8.96
23	23	23	22	18	21	22	22	22	22	22	21	22
6.31	19.71	6.28	14.23	4.00	8.32	27.48	6.72	5.97	8.21	16.80	10.10	10.14
0.54	1.65	0.29	0.77	0.37	0.42	1.68	0.56	0.18	0.34	0.60	0.74	0.93
5.51	17.16	5.74	12.93	3.18	7.54	24.50	5.94	5.63	7.57	15.67	9.08	8.71
7.33	22.77	6.74	15.85	4.59	9.31	30.68	7.82	6.28	8.91	17.93	12.13	12.46
7	6	7	6	6	6	7	7	7	7	7	7	7
7.45	22.60	6.31	15.63	4.66	8.98	30.90	7.68	5.99	8.11	17.85	11.21	11.56
0.27	0.47	0.26	0.24	0.10	0.21	0.65	0.27	0.18	0.12	0.36	0.13	0.26
7.00	21.88	5.89	15.23	4.50	8.55	30.00	7.29	5.74	7.97	17.40	10.97	11.25
7.82	23.33	6.78	15.87	4.83	9.23	32.24	8.14	6.26	8.34	18.37	11.43	12.03
5	5	5	5	4	5	5	4	5	4	4	5	5
5.03	16.29	5.97	12.30	3.53	7.68	22.23	5.27	6.17	8.57	15.61	8.29	8.44
0.19	0.93	0.12	0.45	0.22	0.29	0.67	0.12	0.17	0.16	0.12	0.30	0.46
4.69	14.98	5.78	11.55	3.29	7.27	21.07	5.10	6.04	8.33	15.45	7.83	7.56
5.22	17.79	6.13	12.96	3.81	8.00	23.06	5.40	6.51	8.76	15.76	8.70	8.90
2	2	2	2	2	2	2	2	2	2	2	2	2
5.29	16.46	6.14	12.76	3.52	7.95	23.31	5.50	6.31	8.67	15.83	8.55	8.65
0.04	0.28	0.00	0.02	0.16	0.14	0.14	0.08	0.21	0.14	0.00	0.23	0.18
5.25	16.18	6.14	12.73	3.36	7.81	23.17	5.42	6.09	8.53	15.82	8.31	8.46
5.32	16.73	6.14	12.78	3.68	8.09	23.45	5.58	6.52	8.80	15.83	8.78	8.83
12	12	12	12	11	12	12	12	12	11	12	11	11
5.64	18.09	6.19	13.28	3.67	7.87	25.20	6.08	5.88	8.18	15.93	9.47	9.37
0.37	1.11	0.14	0.62	0.27	0.34	1.49	0.37	0.20	0.30	0.58	0.68	0.66
5.01	16.42	5.88	12.46	3.18	7.42	23.28	5.54	5.60	7.58	15.16	8.23	8.40
6.39	19.75	6.43	14.52	4.20	8.60	27.21	6.70	6.27	8.70	16.95	10.64	10.35
5	5	5	5	5	4	5	5	5	5	5	5	5
6.02	18.96	6.12	13.64	3.71	8.02	26.26	6.38	5.94	8.04	16.12	10.07	9.97
0.54	1.23	0.16	0.88	0.31	0.36	1.55	0.41	0.18	0.25	0.52	0.63	0.65
5.11	17.13	5.88	12.38	3.15	7.71	23.74	5.78	5.67	7.70	15.25	9.20	8.84
6.63	20.44	6.34	14.98	4.07	8.62	28.34	6.90	6.18	8.43	16.65	10.86	10.67

TABLE 3.—Results of ANOVA and individual comparisons between pairs of samples of adult male (classes IV, V, and VI) *Monodelphis* from Venezuela. Significant differences: \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ .

Character	ANOVA		Subspecific comparisons		
	F	P	<i>brevicaudata-palliolata</i>	<i>brevicaudata-orinoci</i>	<i>palliolata-orinoci</i>
Condylobasal length	10.82	***		***	**
Basal length	9.30	***		***	**
Nasal length	13.39	***		***	**
Palatal length	13.83	***		***	***
Length of I1-I5	3.80	*		*	
Length of C-PM3	6.72	**		**	*
Length of M1-M3	14.16	***	**	***	*
Length of M1-M4	17.88	***	**	***	**
Length of upper dental series	15.02	***		***	***
Palatal width	19.99	***	**	***	***
Nasal width	10.31	***		***	**
Rostral width	5.70	**		**	*
Zygomatic width	5.90	**		**	
Minimum postorbital width	7.58	**		**	**
Occipital width	10.09	***		***	*
Height of interparietal foramen magnum	11.71	***	**	***	
Occipital height	10.06	***	*	***	
Length of mandible	11.14	***		***	**
Length of c-pm3	4.13	*		*	*
Length of m1-m3	16.24	***	**	***	**
Length of m1-m4	11.56	***	**	***	
Length of lower dental series	17.44	***		***	***
Distance between coronoid and angular processes	5.74	**		**	*
Height of coronoid process	7.83	***		**	*

per parts and sides; gray color of the upper parts of *orinoci* is much paler, and sides are cinnamon instead of reddish as occurs in *brevicaudata* and *palliolata* (Pérez-Hernández, 1988). These observations, together

with our results, corroborate the taxonomy suggested by Reig et al. (1977) and justify recognizing *orinoci* as a species. *M. brevicaudata* would be represented by two subspecies in Venezuela, the nominate subspe-

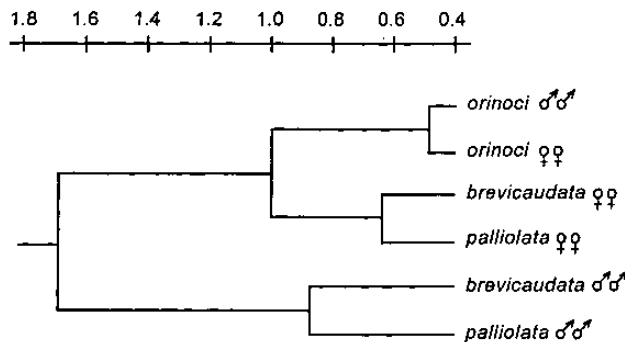


FIG. 3.—Distance phenogram showing relationships among adult specimens of *Monodelphis*. Cophenetic correlation coefficient is 0.771.

cies and *M. b. palliolata*. Ecologically, *M. orinoci* is a small savanna form, whereas both subspecies of *M. brevicaudata* are larger and occur in forests from lowlands to 1,500 m elevation. Gardner (1973) associated differences in size between *Didelphis virginiana* and *D. marsupialis* with habitat preferences, indicating that environmental diversity might favor larger size of the former. Similar circumstances might be responsible for differences observed among species of *Monodelphis* in our study. Smaller size of *M. orinoci* compared with *M. brevicaudata* could be connected with the former's more restricted habitat.

Sequences of tooth eruption used as age criteria in specimens in our study differed from the systems of age discrimination used for didelphids (cf. Gardner, 1973; Tyndale-Biscoe and Mackenzie, 1976). The basic difference involved eruption sequence of PM3 and M4 as reported by Tribe (1990) for several didelphids. Although ambiguous sequences of tooth eruption can be found, Tribe (1990) indicated two main patterns; in *Didelphis*, *Philander opossum*, *Chironectes minimus*, and the microbiotheriid *Dromiciops australis*, dPM3 is shed and PM3 erupts before the appearance of M4, but in *Caluromys*, *Glironia venusta*, and several species of *Marmosa* (sensu lato Reig et al., 1985) and *Monodelphis*, dPM3 is retained until M4 is functional. In our sample, four *M. b. palliolata* retained the dPM3 during the eruption of M4. In contrast, one specimen of *M. orinoci* (MBUCV 1761) had PM3 in eruption with M4 absent. This latter condition agrees with the *Didelphis* model in which M4 erupts only after PM3 is developed. Assuming the phylogenetic value of patterns of tooth eruption and their association with life histories in Didelphoidea (cf. Tribe, 1990), different patterns of replacement shown by *orinoci* and *palliolata* are further evidence of their specific distinctness.

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#### LITERATURE CITED

- BERGALLO, H. G., AND R. CERQUEIRA. 1994. Reproduction and growth of the opossum *Monodelphis domestica* (Mammalia: Didelphidae) in northeastern Brazil. *Journal of Zoology* (London), 232:551–563.
- CABRERA, A. 1958. Catálogo de los mamíferos de América del Sur. *Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"* e Instituto Nacional de Investigación de las Ciencias Naturales, 4:1–307.
- CERQUEIRA, R. 1984. Reproduction de *Didelphis albiventris* dans le nord-est du Brésil (Polyprotodontia, Didelphidae). *Mammalia*, 48:95–104.
- CORBET, G. B., AND J. E. HILL. 1991. A world list of mammalian species. Third ed, Natural History Museum Publications, Oxford University Press, Oxford, United Kingdom, 243 pp.
- EISENBERG, J. F. 1989. Mammals of the Neotropics. The northern Neotropics. Panamá, Colombia, Venezuela, Guyana, Suriname, French Guyana. The University of Chicago Press, Chicago, Illinois, 1:1–449.
- EWEL, J. J., A. MADRIZ, AND J. A. TOSI, JR. 1968. Zonas de vida de Venezuela. Editorial Sucre, Caracas, 265 pp.
- GARDNER, A. L. 1973. The systematics of the genus *Didelphis* (Marsupialia: Didelphidae) in North and Middle America. Special Publications, The Museum, Texas Tech University, 4:1–81.
- . 1993. Order Didelphimorpha. Pp. 15–23, in *Mammal species of the world: a taxonomic and geographic reference*. (D. E. Wilson and D. M. Reeder, eds.). Second ed. Smithsonian Institution Press, Washington, D.C., 1206 pp.
- HANDLEY, C. O., JR. 1976. Mammals of the Smithsonian Venezuelan Project. Brigham Young University Science Bulletin, Biological Series, 20:1–91.
- HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPL (EDS.). 1982. *Mammal species of the world: a taxonomic and geographic reference*. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

- LEE, A. K., AND A. COCKBURN. 1985. Evolutionary ecology of marsupials. Cambridge University Press, Cambridge, United Kingdom, 274 pp.
- NORUSIS, M. J. 1988. SPSS/PC+ advanced statistics. SPSS Inc., Chicago, Illinois, unpagged.
- NOWAK, R. M. 1991. Walker's mammals of the world. Fifth ed. The Johns Hopkins University Press, Baltimore, Maryland 1:1-642.
- O'CONNELL, M. A. 1979. Ecology of didelphid marsupials from northern Venezuela. Pp. 73-78. in Vertebrate ecology in the northern Neotropics (J. F. Eisenberg, ed.). Smithsonian University Press, Washington, D.C., 271 pp.
- OSGOOD, W. H. 1914. Four new mammals from Venezuela. Field Museum of Natural History, Zoology Series, 10:135-141.
- PÉREZ-HERNÁNDEZ, R. 1988. Notas preliminares acerca de la taxonomía de la familia Didelphidae (Mammalia-Marsupialia) en Venezuela. Memoria de la Sociedad de Ciencias Naturales (La Salle) 123: 47-76.
- . 1989. Distribution of the family Didelphidae (Mammalia-Marsupialia) in Venezuela. Pp. 363-409, in Advances in Neotropical mammalogy (K. Redford and J. F. Eisenberg, eds.). Sandhill Crane Press, Gainesville, Florida, 614 pp.
- PINE, R. H. 1981. Reviews of the mouse opossums *Marmosa parvidens* Tate and *Marmosa invicta* Goldman (Mammalia: Marsupialia: Didelphidae) with description of a new species. Mammalia, 45: 55-70.
- PINE, R. H., P. L. DALBY, AND J. O. MATSON. 1985. Ecology, postnatal development, morphometrics and taxonomic status of the short-tailed opossum, *Monodelphis dimidiata*, an apparently semelparous annual marsupial. Annals of Carnegie Museum, 54: 195-231.
- RAMONI-PERAZZI, P., G. BIANCHI, AND M. MOLINA. 1994. Hallazgo de la comadreja colicorta *Monodelphis adusta* (Thomas, 1897) en la cuenca del lago de Maracaibo, Venezuela. Acta Científica Venezolana, 45:325-326.
- REIG, O. A., AND N. O. BIANCHI. 1969. The occurrence of an intermediate didelphid karyotype in the short-tailed opossum (genus *Monodelphis*). Experientia, 25:1210-1211.
- REIG, O. A., A. L. GARDNER, N. O. BIANCHI, AND J. L. PATTON. 1977. The chromosomes of the Didelphidae (Marsupialia) and their evolutionary significance. Biological Journal of the Linnean Society, 9: 191-216.
- REIG, O. A., J. A. W. KIRSCH, AND L. G. MARSHALL. 1985. New conclusions on the relationships of the opossum-like marsupials, with an annotated classification of the Didelphimorphia. Ameghiniana, 21: 335-343.
- ROHLF, F. J. 1994. NTSYS-pc. Numerical taxonomy and multivariate analysis system. Version 1.80. Exeter Software, Setauket, New York, unpagged.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical taxonomy. W. H. Freeman and Company, San Francisco, California, 573 pp.
- SORIANO, P. 1987. On the presence of the short-tailed opossum *Monodelphis adusta* (Thomas) in Venezuela. Mammalia, 51:312-324.
- TRIBE, C. J. 1990. Dental age classes in *Marmosa incana* and other didelphoids. Journal of Mammalogy, 71:566-569.
- TYNDALE-BISCOE, C. H., AND R. B. MACKENZIE. 1976. Reproduction in *Didelphis marsupialis* and *D. albiventris* in Colombia. Journal of Mammalogy, 57: 249-265.
- WAINBERG, R. L. 1972. Cariología y carimetría de *Monodelphis dimidiata* Wagner (Marsupialia, Didelphidae). Physis, Buenos Aires, 31:327-336.
- WILLIAMS, G. C. 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. The American Naturalist, 100:687-690.

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## APPENDIX I

The specimens analyzed in this study are deposited in the following Institutions: Museo de Biología, Universidad Central de Venezuela (MBUCV); Museo de Historia Natural La Salle (MHNLS); Museo de Historia Natural, Universidad Simón Bolívar (MHNUSB); Estación Biológica Rancho Grande (EBRG); Colección Vertebrados, Universidad de Los Andes (CVU-LA). For each specimen, the following information is presented: state, locality, geographic coordinates, institution, and collection number.

*Monodelphis brevicaudata brevicaudata*.—Amazonas: Tamatama (3°08'N, 65°52'W; EBRG 3877); Alto Río Siapa (1°43'N, 64°35'W; EBRG 16909, MBUCV 5250); Acanaña, Río Cunucunuma, 48 km NW La Esmeralda (3°13'N, 65°58'W; EBRG 3875); Coromoto, 20 km S Puerto Ayacucho (5°24'N, 67°36'W; EBRG 3878); near to San Carlos de Río Negro (1°52'N, 67°00'W; MBUCV 2733); El Pozo, 10 km SE San Fernando de Atabapo (3°58'N, 67°36'W; MBUCV 4818); Koyowa-Terí (2°30'N, 65°04'W; MHNLS 7962, 7963); Cuenca alta del Río Matacuni (3°26'N, 64°39'W; MHNLS 9631). Bolívar: Serranía de los Pijiguaos (6°30'N, 66°40'W; EBRG 15756); Reserva Forestal de Imataca (8°00'N, 61°30'W; EBRG 17536); Campamento MOP, 38 km S El Dorado (6°26'N, 61°30'W; MBUCV 1404); San Martín de Turumban, Anacoco (6°42'N, 61°05'W; MHNLS 4393); 5.2 km NE San Ignacio de Yuruaní (5°02'N, 61°09'W; MHNLS 7992, 8087, 9318); Salto Uraima, Río Paragua (6°17'N, 63°37'W; MBUCV 5205); Sarisariñama (4°30'N, 64°14'W; MHNUSB p-353); Ninchare (6°10'N, 65°03'W; MHNUSB p-577). No locality data (MHNUSB 1-1529).

*Monodelphis brevicaudata palliolata*.—Aragua: Rancho Grande, Parque Nacional "Henri Pittier" (10°21'N, 67°41'W; MBUCV 6, 1406, 1440, 1441, 1442, 1444, 1559, 1560, 1561, 1650, 1719, 2436, MHNLS 1324, 7565). Barinas: Barinitas (8°45'N, 70°24'W; CVULA 366, MHNUSB 452). Carabobo: Caño Alpargatón (10°28'N, 68°15'W; MBUCV 4079, 4080, 4081); Río Abajo, Morón (10°29'N, 68°17'W; MBUCV 4096); Patanemo (10°25'N, 67°54'W; MBUCV 4156, MHNLS 3733, 3885, 4395); Camino de los Españoles, San Esteban (10°24'N, 68°05'W; MHNLS 1222). Cojedes: El Candelo (9°50'N, 68°40'W; MHNLS 4394). Distrito Federal: Canales de Naguayá, Parque Nacional El Ávila (10°35'N, 66°44'W; MBUCV 2694, 2695, 2696, 2697, 2698, 2700, 2701, 4179, MHNLS 8516, 8517, 8518, 8519, 8568, 8570, 8859, 8913); Hacienda El Limón (10°28'N, 67°17'W; MHNLS 1123); El Encantado (10°26'N, 67°16'W; MHNLS 3679); Cerro El Ávila (10°32'N, 66°52'W; MHNLS 3761). Miranda: Turgua (10°22'N, 66°45'W; MBUCV 1413); Estación Experimental Río Negro

(10°20'N, 66°17'W; MBUCV 3481, 3631); La Toma, Capaya Río Marismita (10°26'N, 66°16'W; MHNLS 3292, 3293, 3678, 3680). Monagas: Serranía del Turimiquire (10°03'N, 63°46'W; MHNLS 9911). Sucre: 9.7 km Guaraunos (10°24'N, 63°06'W; MHNLS 8167); Valle de Sartanejas (10°24'N, 66°53'W; MHNUSB 828). Yaracuy: 13 km NNW Aroa (10°32'N, 68°58'W; MHNLS 7438, 8105). Zulia: Kasmera (9°59'N, 72°43'W; MBUCV 1407, 1408, 1772); Tokuko (9°51'N, 72°47'W; MHNLS 6876, 7689, 7706, 7762, 7765, 7789, 7797).

*Monodelphis brevicaudata orinoci*.—Aragua: Magdalena, Lago de Velencia (10°06'N, 67°37'W; MHNLS 3704). Bolívar: Represa del Guri, Río Caroní (7°46'N, 62°59'W; MBUCV 1761). Cojedes: Hato Nuevo (9°12'N, 68°06'W; EBRG 415). Guárico: Cuartel Zaraza, San Juan de Los Morros (9°56'N, 67°21'W; MHNLS 1094); Estación Biológica de los Llanos, Calabozo (8°52'N, 67°23'W; MBUCV 1425, 1426, 1879, 1890, 2035, MHNUSB 531); Hato La Palmita, San Francisco de Tiznados (9°36'N, 67°29'W; MHNLS 5555).