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Defining Species and Species Boundaries in *Uroderma* (Chiroptera: Phyllostomidae) with a Description of a New Species

Front cover: *Uroderma bakeri*, new species. Illustration by Hugo Mantilla-Meluk, based upon museum voucher specimens.

Defining Species and Species Boundaries in *Uroderma* (Chiroptera: Phyllostomidae) with a Description of a New Species

Hugo Mantilla-Meluk

Abstract

A new species of Peter's tent-making bat, genus *Uroderma* (Chiroptera: Phyllostomidae), is described from Venezuela's Cordillera del Caribe and piedmonts of the Eastern Cordillera of the Colombian Andes. Cranial morphology of the new species approaches that of *U. magnirostrum*, with a notable enlargement of the nasals in the post-orbital region, giving the skull a flatter appearance in lateral profile than typical specimens of *U. bilobatum*. The new species of *Uroderma* can be distinguished easily from *U. magnirostrum* by several discrete skin and cranial characters. Taxonomic affinities among geographic variants of *U. bilobatum* were assessed through analyses of morphologic, karyotypic, and molecular variation. Although statistical support for well-defined groups was low in morphological assessments, four morphotypes were recognized based on geographic structure and previously reported karyotypic and molecular data. In addition to the newly recognized species, *U. convexum* Lyon 1902 is elevated to species status, and *U. c. molaris* is treated as a subspecies of *U. convexum*. Further, based on reciprocal monophyly of supported clades present in analyses of mitochondrial DNA data, assortment of karyotypes distinguished by three rearrangements, and reduced fitness in hybrids, *U. davisi* Baker and McDaniel 1972 is treated as a species. These taxonomic revisions result in a genus comprised of five species (*U. bilobatum*, *U. convexum*, *U. davisi*, *U. magnirostrum*, and *U. bakeri* sp. nov.).

Key words: Colombia, taxonomic revision, *Uroderma*, *U. bakeri* sp. nov., *U. bilobatum*, *U. convexum*, *U. c. molaris*, *U. davisi*, Venezuela

Resumen

Se describe una nueva especie de murciélago constructor de tiendas de Peter *Uroderma* (Chiroptera: Phyllostomidae) de la Cordillera del Caribe en Venezuela y el piedemonte oriental de la Cordillera Oriental de los Andes de Colombia. La morfología craneal de la nueva especie es cercana a aquella de *U. magnirostrum*, con un notable ensanchamiento de los nasales en la región postorbital, dándole al cráneo una apariencia más plana en perfil lateral en comparación con cráneos típicos de *U. bilobatum*. La nueva especie puede ser fácilmente diferenciada de *U. magnirostrum* por varios caracteres discretos de piel y cráneo. Las afinidades taxonómicas entre las variantes geográficas descritas para *U. bilobatum* fueron re-evaluadas teniendo en cuenta su variación morfológica, cariotípica y molecular previamente descrita. A pesar de un bajo soporte estadístico en los análisis morfológicos, cuatro grupos fueron identificados de acuerdo a su estructura geográfica e información cariotípica y molecular previamente descrita. Adicionalmente, *U. convexum* Lyon 1902, es elevada a estatus específico, y *U. c. molaris* es considerada como subespecie de *U. convexum*. De otra parte, teniendo en cuenta monofilia recíproca en clados estructurados presentes en datos de ADN mitocondrial, así como, cariotipos identificados por tres arreglos cromosómicos y éxito reproductivo reducido en híbridos, *U. davisi* Baker and McDaniel 1972 es reconocido como una especie válida. Esta revisión taxonómica resulta en un género compuesto por cinco especies (*U. bilobatum*, *U. convexum*, *U. davisi*, *U. magnirostrum*, y *U. bakeri* sp. nov.).

Palabras clave: Colombia, revisión taxonómica, *Uroderma, U. bakeri* sp. nov., *U. bilobatum*, *U. convexum*, *U. c. molaris*, *U. davisi*, Venezuela

INTRODUCTION

Tent-making bats, genus *Uroderma* (Peters 1886), are distributed from Mexico to Brazil (Simmons 2005; Gardner 2007). Presently, only two species of *Uroderma*, *U. bilobatum* and *U. magnirostrum* (Davis 1968; Baker et al. 2003; Simmons 2005), are recognized. Although *U. bilobatum* exhibits substantial karyotypic and DNA sequence variation, the use of morphology to separate karyotypic and genetic phylogroups has generated conflicting interpretations and debate (Baker and López 1970; Baker 1981; Greenbaum 1981; Barton 1982; Hafner 1982; Lessa 1990; Owen and Baker 2001; Hoffmann et al. 2003). To date, six subspecies of *U. bilobatum* have been described: *U. b. bilobatum* (Peters 1866), *U. b. convexum* (Lyon 1902), *U. b. thomasi* (Andersen 1906), *U. b. trinitatum* (Davis 1968), *U. b. molaris* (Davis 1968), and *U. b. davisi* (Baker and McDaniel 1972). Simmons (2005) recognized three phylogroups associated with the chromosomal lineages identified by Baker (1981) and molecular clades reported in Hoffmann et al. (2003). Maximum cytochrome-*b* genetic distances (< 3.7%) among phylogroups of *U. bilobatum* identified in Hoffmann et al. (2003) were lower than average percentages identified among the majority of recognized phyllostomid sister species (Bradley and Baker 2001; Baker and Bradley 2006). However, at a hybrid zone in Pacific Nicaragua, Honduras, and El Salvador between karyotypic races of *U. b. convexum* and *U. b. davisi* (Baker 1981; Owen and Baker 2001; Hoffmann et. al. 2003), the concordance of mtDNA and karyotypic geographic boundaries revealed defined geographic structure and geographic isolation maintained by negative heterosis (Barton 1982). Based on these results, Simmons (2005) encouraged further systematic revisions of *U. bilobatum* subspecies to clarify their taxonomic status. In this paper, morphologic variation in *U. bilobatum* and *U. magnirostrum* is reviewed and the evolutionary concordance of molecular and karyotypic phylogroups assessed by Hoffmann et al. (2003) is evaluated.

MATERIALS AND METHODS

Variation in skull morphology within the genus *Uroderma* was analyzed from 433 adult specimens (222 males and 211 females) representing *U. magnirostrum* and all currently recognized subspecies of *U. bilobatum* (*sensu* Gardner 2007) from most of the distribution of the genus (Appendix I). Age of specimens was determined based on the degree of ossification of phalangeal epiphyses and completeness of basisphenoid suture ossification. Specimens examined were archived in the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), the National Museum of Natural History (NMNH), and the Museum of Texas Tech University (TTU). Museum abbreviations follow Hafner et al. (1997).

Taxonomic identification.—All specimens were evaluated for each diagnostic character mentioned in the original descriptions of each recognized species and subspecies for the genus (Peters 1866 - *U. b. bilobatum*; Lyon 1902 - *U. b. convexum*; Andersen 1906 - *U. b. thomasi*; Davis 1968 - *U. b. molaris*, *U. b. trinitatum*, and *U. magnirostrum*), as well as geographic criteria depicted in Davis (1968), Baker and McDaniel (1972), and Baker and Clark (1987).

Measurements.—Originally, 16 craniodental measurements were recorded including: greatest length of skull (GLS); condylo-basal length (CBL); palatal length (PAL); zygomatic width (ZW); mastoid width (MW); brain-case width (BCW); interorbital constriction width (IOC); maxillary width (MxW); maxillary height (MxH); rostral depth (RD); distance across third upper molars (M-M); internal width between third upper molars (IMW); distance across upper canines (C-C); canine-maxillary second molar length (CM2); mandibular length (MDL); and mandibular tooth row length (cm3). All measurements were taken in millimeters to the nearest 0.1 mm with a dial caliper (Mitutoyo Absolute Snap series 573).

Selection of informative measurements.—In order to avoid redundancy among the 16 recorded measurements and to determine the minimum number of variables to be used in analyses, a preliminary principal components analysis (PCA) was performed and correlated variables were eliminated through a PCA Cattel Scree plot test in the Statgraphics 15 package (Statgrahics 2009). Multiple correlation coefficients for the analyzed variables were calculated and ordered

(low to high) for the number of variables suggested in the Scree plot. Partial correlation matrices were evaluated and those variables possessing significant differences were eliminated. In addition, values of a variance/covariance matrix from standardized data were calculated and the minimum number of variables to be included was determined based on the multiple correlation coefficient value.

Sexual dimorphism.—Sexual dimorphism was evaluated for each recognized taxon using a Hotelling's T^2 test in the statistical package PAST (Hammer et al. 2001). The 16 recorded craniodental measurements from 222 adult males and 211 adult females were used in this analysis.

Assessment of skull morphometric variation within Uroderma.—To analyze the phenetic similarities within the genus *Uroderma*, a PCA and a discriminant function analysis (DFA) were performed in the statistical packages PAST (Hammer et al. 2001) and SPSS 9.0 (SPSS Inc. 1999), respectively. The selected, informative craniodental measurements were used in these analyses.

Evaluation of an unidentified morphogroup.—Morphological differences between *U. magnirostrum* and an unrecognized morphotype, identified herein as ECNV (for eastern Colombia and northern Venezuela), also were assessed statistically using a PCA and a DFA performed on the selected craniodental variables. Both PCA and DFA were performed separately for males and females in PAST (Hammer et al. 2001) and SPSS 9.0 (SPSS Inc. 1999) softwares, respectively.

RESULTS

Selection of informative measurements.—Six craniodental measurements were selected for the morphometric analyses, as follows: GLS; MW; BCW; IOC; M-M; and MDL. Selected variables were tested for normality by the application of an Energy test in R mvnorm.etest for independent variables.

Sexual dimorphism.—Although statistically significant differences were found between measurements of males and females in three of the analyzed taxa (*U. b. bilobatum*, *U. b. convexum*, and *U. b. davisi*), all groups possessed percentages of correctly assigned individuals greater than 70% in the Hotelling's T^2-test: *U. b. bilobatum* (85%; Hotelling=58.1; F=2.03; p=0.03); *U. b. thomasi* (95%; F=2.19; p=0.06); *U. b. convexum* (71.77%; Hotelling=54.5; F=2.98; p>0.01); *U. b. davisi* (85.21%; Hotelling=124.42; F=5.7; p>0.01); *U. b. molaris* (91.67%; Hotelling=67.38; F=1.66; p=0.15); and *U. magnirostrum* (95.24%; Hotelling=80.55; F=1.81; p=0.2). The limited sample size for *U. b. trinitatum* (N=8) prevented a test for sexual dimorphism in that taxon.

Assessment of skull morphometric variation within Uroderma.—Because sexual dimorphism was depicted for some taxa, PCA and DFA were performed separately for males and females. The PCA including all taxa revealed low levels of morphometric variation within the genus *Uroderma* for the six selected variables (Fig. 1). The first principal component accounted for 80.44% and 62.52% of the variation among males and females, respectively. Loadings on the first component were all positive and relatively uniform in value for both males and females, indicating variation in general skull size for both sexes. The remaining components were variable in magnitude and sign in both datasets, indicating variation in shape (Table 1). Similarly, DFA revealed a low overall morphometric differentiation within the genus. However, *U. magnirostrum* and representatives of the unrecognized morphotype ECNV were discriminated from *U. bilobatum sensu* Davis (1968) (Fig. 2, Table 2). Although not statistically supported, the DFA revealed some differentiation between Central and South American *U. bilobatum* samples, particularly among male specimens (Fig. 2, Table 2).

Evaluation of an unidentified morphogroup.—*Uroderma magnirostrum* and the unrecognized morphotype ECNV proved to have statistically supported different skull morphologies in both male and female datasets. Skulls of *U. magnirostrum* were smaller, had wider interorbital constrictions, and possessed deeper rostri than those of the ECNV morphotype (Table 3, Fig. 3). The first principal component accounted for

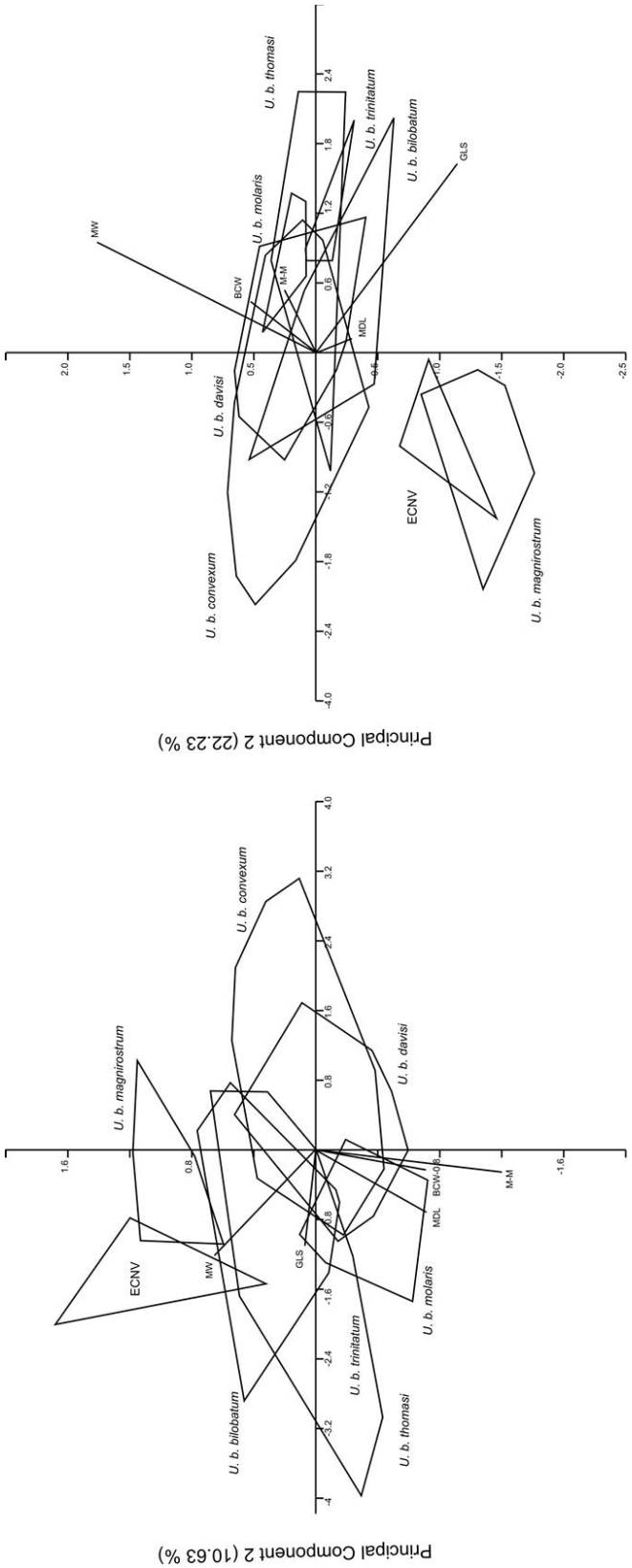

Figure 1. Principal component analysis of six craniodental measurements of 222 male (left) and 211 female (right) *Uroderma* specimens representing all recognized taxa in the genus. Abbreviations of the five measurements with the highest loadings: greatest length of skull (GLS); mastoid width (MW); brain-case width (BCW); distance across third upper molars (M-M); and mandible length (MDL).

88.95% and 76.59% of the variation among male and female datasets, respectively (Fig. 3). All analyzed individuals of both *U. magnirostrum* and ECNV were assigned correctly in the DFA (Wilks' Lambda=0.002; Chi-square=46.30; df=15; P=4.7^{-5} for male dataset; and Wilks' Lambda=0.005; Chi-square=31.14; df=12; P=0.0018 for female dataset; Table 4).

Table 1. Loading of vectors, Eigen values, and percentage of variance explained by each component in a principal component analyses (PCA) applied to six selected craniodental variables of 222 adult male and 211 adult female specimens representing eight identified phylogroups across the range of distribution of Uroderma*. Abbreviations of measurements: GLS: greatest length of skull; MW: mastoid width; IOC: interorbital constriction; BCW: braincase width; M-M: distance across first upper molars; and MDL: mandible length.*

Variable	Sex	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
GLS	♂	-0.6112	0.04605	0.1813	-0.2823	-0.6897	-0.1898
	♀	0.4250	-0.3985	0.4996	0.1339	-0.2538	-0.5733
MW	♂	-0.6652	0.3928	-0.0055	0.4954	0.3879	0.08597
	♀	0.3990	0.3948	0.0700	-0.6862	0.3842	-0.2480
IOC	♂	-0.0950	0.0564	0.6838	-0.5368	0.4251	0.2266
	♀	0.1138	-0.7334	-0.5208	-0.4200	0.0059	0.0396
BCW	♂	-0.1309	-0.7040	0.3716	0.3488	0.1486	-0.4532
	♀	0.4372	0.0727	-0.4801	0.5734	0.4479	-0.2091
M-M	♂	-0.1114	-0.4222	0.0642	0.2244	-0.2346	0.8365
	♀	0.4463	0.3362	-0.3409	-0.0424	-0.7453	0.1201
MDL	♂	-0.3812	-0.4080	-0.5978	-0.4633	0.3407	0.0090
	♀	0.5068	-0.1708	0.3572	0.06497	0.1789	0.7417
Eigen Value	♂	1.0026	0.1325	0.0390	0.0349	0.0224	0.0148
	♀	0.6680	0.2375	0.0749	0.0363	0.0307	0.0211
Variance	♂	80.4480	10.6330	3.1305	2.8030	1.7945	1.1911
	♀	62.5210	22.2310	7.0068	3.3962	2.8703	1.9740

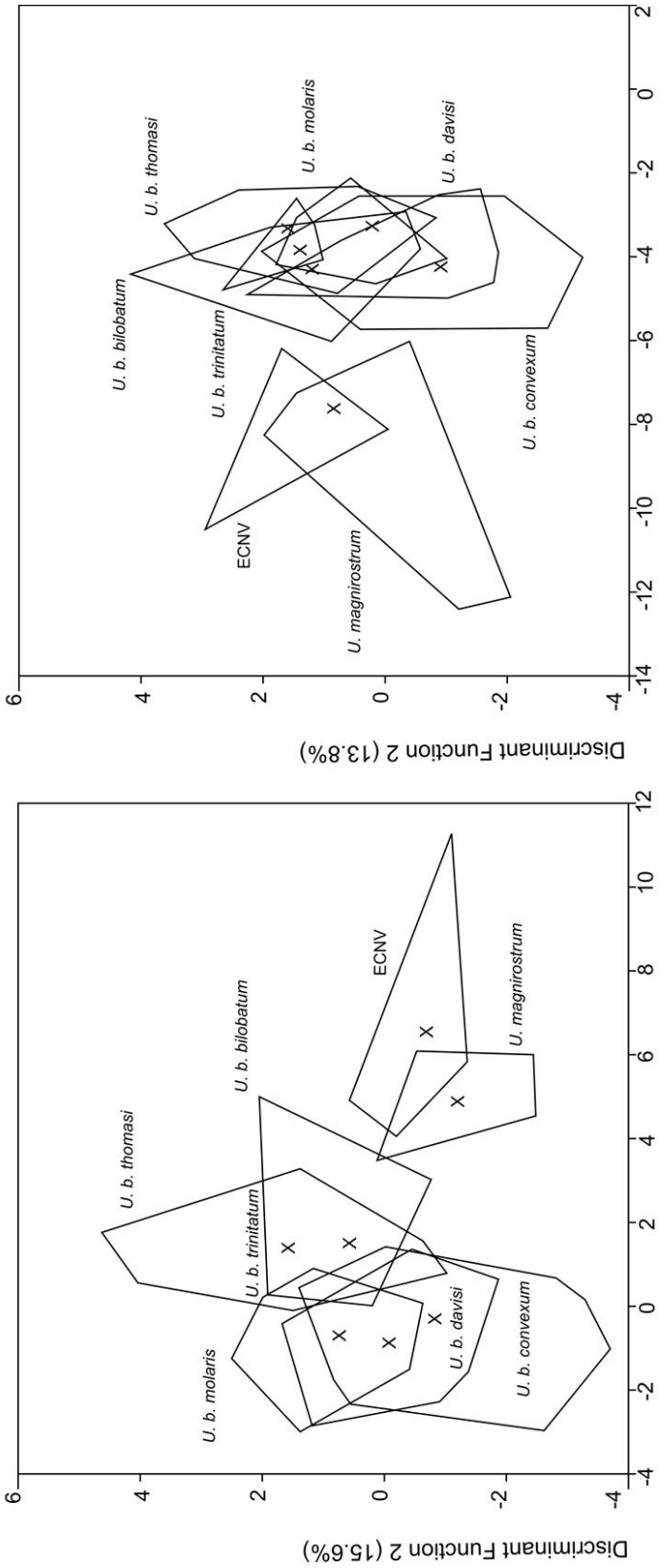

Figure 2. Discriminant function analysis performed on six selected craniodental variables of 222 male (left) and 211 female (right) *Uroderma* specimens representing all recognized taxa and the unreognized morphotype ECNV.

Table 2. Wilks' lambda values of the discriminant function analyses performed on six cranial measurements of 222 adult male and 211 adult female specimens representing eight identified phylogroups across the range of distribution of Uroderma. *Groups were discriminated a priori according to their morphology.*

Test of Function(s)	Wilks' Lambda	Chi-square	df	Sig.
	Males			
1 through 5	0.201	344.102	35	0.000
2 through 5	0.524	138.499	24	0.000
3 through 5	0.821	42.264	15	0.000
4 through 5	0.929	15.875	8	0.044
5	0.985	3.199	3	0.362
	Females			
1 through 6	0.052	583.546	42	0.000
2 through 6	0.298	239.891	30	0.000
3 through 6	0.554	117.092	20	0.000
4 through 6	0.795	45.326	12	0.000
5 through 6	0.925	15.342	6	0.018
6	0.991	1.885	2	0.390

Table 3. Loadings of principal components analysis performed on the six selected variables for U. magnirostrum *and ECNV. Abbreviations of measurements: GLS: greatest length of skull; MW: mastoid width; BCW: braincase width; IOC: interorbital constriction; M-M: distance across first upper molars; and MDL: mandible length.*

Variable	PC 1	PC2	PC 3	PC 4	PC 5	PC 6
			Males			
GLS	0.4156	0.4166	0.2727	0.0861	-0.1777	0.3455
MW	0.0676	-0.1901	-0.1377	-0.2697	-0.1112	0.5423
BCW	0.2183	0.1001	-0.2537	0.0100	-0.0444	-0.1512
IOC	-0.1400	0.2640	-0.1625	0.0899	0.0219	-0.1794
M-M	-0.3550	0.0406	0.0417	-0.6275	0.0986	-0.0646
MDL	-0.3648	-0.0597	0.1378	0.5572	0.0227	0.4179
			Females			
GLS	0.2682	0.2826	0.2731	0.0141	-0.0414	0.1156
CBL	0.2982	0.2062	0.4585	0.0870	0.1171	-0.1497
IOC	-0.3737	0.0956	0.0997	-0.4149	0.0683	-0.1059
MW	-0.3396	0.2179	0.2096	0.1943	0.2922	-0.3319
BCW	-0.1701	-0.1986	0.2046	-0.3850	-0.0059	0.2048
M-M	-0.0256	-0.1436	-0.2300	-0.1587	-0.2482	-0.0989

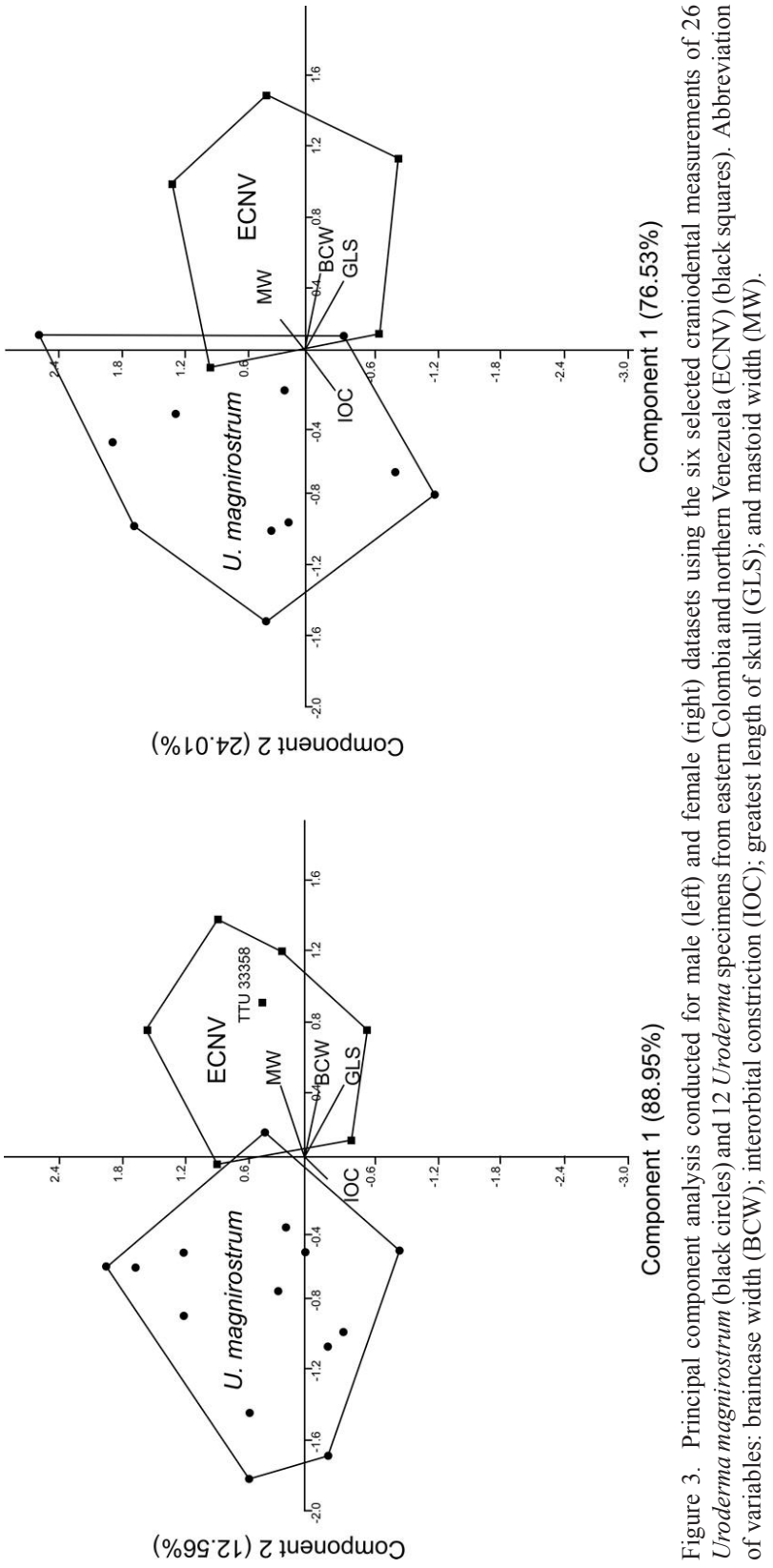

Figure 3. Principal component analysis conducted for male (left) and female (right) datasets using the six selected craniodental measurements of 26 *Uroderma magnirostrum* (black circles) and 12 *Uroderma* specimens from eastern Colombia and northern Venezuela (ECNV) (black squares). Abbreviation of variables: braincase width (BCW); interorbital constriction (IOC); greatest length of skull (GLS); and mastoid width (MW).

Table 4. Casewise results of the classification obtained from the discriminant function analyses between the unrecognized morphotype ECNV (Group 1) (N=12) and U. magnirostrum *(Group 2) (N=26). For both male and female datasets, 100% of the individuals were classified within the hypothesized groups. In column three,* P *(*D>d | G=g*) is the significance level of such a* χ^2j.

		P (D>d | G=g)	Squared Mahalanobis	Discriminant Scores
Actual Group	Predicted Group	p	Distance to Centroid	Function 1
1 ♂	1	0.79	0.07	24.84
1 ♂	1	0.52	0.41	23.93
1 ♂	1	0.76	0.09	24.88
1 ♂	1	0.30	1.08	23.53
1 ♂	1	0.97	0.00	24.53
1 ♂	1	0.20	1.65	25.85
1 ♂	1	0.89	0.02	24.43
2 ♂	2	0.97	0.00	-17.24
2 ♂	2	0.21	1.57	-15.95
2 ♂	2	0.01	7.82	-20.00
2 ♂	2	0.62	0.25	-16.70
2 ♂	2	0.63	0.23	-16.72
2 ♂	2	0.76	0.09	-17.51
2 ♂	2	0.53	0.39	-17.82
2 ♂	2	0.91	0.01	-17.09
2 ♂	2	0.27	1.19	-16.11
2 ♂	2	0.01	7.82	-20.00
2 ♂	2	0.62	0.25	-16.70
2 ♂	2	0.63	0.23	-16.72
2 ♂	2	0.76	0.09	-17.51
2 ♂	2	0.27	1.19	-16.11
2 ♂	2	0.74	0.11	-16.87
1 ♀	1	0.58	0.31	-23.14
1 ♀	1	0.98	0.00	-23.72
1 ♀	1	0.59	0.28	-24.22
1 ♀	1	0.98	0.00	-23.72
1 ♀	1	0.59	0.28	-24.22
2 ♀	2	0.93	0.01	6.37
2 ♀	2	0.93	0.01	6.37
2 ♀	2	0.93	0.01	6.37
2 ♀	2	0.93	0.01	6.37
2 ♀	2	0.93	0.01	6.37
2 ♀	2	0.93	0.01	6.37
2 ♀	2	0.20	1.65	5.18
2 ♀	2	0.13	2.25	4.96
2 ♀	2	0.16	1.95	7.86
2 ♀	2	0.79	0.07	6.20
2 ♀	2	0.87	0.03	6.62

DISCUSSION

Bats within the subfamily Stenodermatinae are part of the most recent radiation among phyllostomids and apparently have undergone a rapid process of diversification (Hoofer and Baker 2006; Larsen et al. 2007; Velazco and Patterson 2008). Velazco and Patterson (2008) suggested that the evolution of species in the subfamily Stenodermatinae is a recent event, characterized by low genetic divergence among species relative to older lineages. Velazco et al. (2010) reported genetic differences of less than 3.0% for *Cyt*b sequences between recognized species of the vampyrissine genus *Platyrrhinus* (e.g., *P. angustirostris* vs. *P. fusciventris*, 2.03%; *P. incarum* vs. *P. angustirostris*, 2.68%).

Similarly, molecular data support a rapid dispersion accompanied by low genetic differentiation for vampyrissine bats in the genus *Uroderma* (maximum *Cyt*b intra-racial differences of 1.7% and overall low morphological differentiation). Interestingly, the only sequence available for a member of the ECNV morphotype possessed the highest divergence in *Cyt*b sequences (3.7%) and clearly was differentiated from both *U. bilobatum sensu* Davis (1968) and *U. magnirostrum* (Hoffmann et al. 2003).

It also has been suggested that recent, rapid evolutionary events, such as the one exemplified by vampyrissine bats, usually result in low or incomplete morphologic divergence. Although overall morphometric resolution within *Uroderma* in this study was low, morphometric analyses revealed: 1) a greater affinity between *U. magnirostrum* and morphotype ECNV; 2) no morphometric overlap between these two forms and *U. bilobatum sensu* Davis (1968); and 3) 100% morphometric discriminations between the unrecognized morphotype ECNV and *U. magnirostrum* in both male and female data sets.

A new Uroderma *from the eastern piedmonts of the northern Andes*.—The ECNV morphotype, representing individuals from Venezuela's Cordillera del Caribe and the eastern piedmonts of Colombia's Eastern Cordillera, appears to represent an undescribed species of *Uroderma*. Recognition of this species is supported by statistically significant differences and a unique combination of discrete morphological characters, as described below.

Family Phyllostomidae Gray 1825
Stenodermatinae Gervais 1856
Uroderma Peters 1865
***Uroderma bakeri*, new species**

Holotype.—Adult male, TTU 33358, body preserved in alcohol, with extracted cranium and mandibles in excellent condition (Fig. 4) and tissues (TK 15288), collected on 25 April 1978 by Margaret O'Connell and Robert J. Baker. Measurements of the holotype and specimens in the type series are presented in Appendix II.

Type locality.—Santa Crucita, in Parque Nacional Guatopo, Miranda, Venezuela, 10°5' N, 66°33'W at an elevation of 2,480 m (Fig. 5).

Type series.—Specimens included in the type series (N=12) consist of seven males (including holotype) and five females from Colombia: adult male ICN 12917 and female ICN 12918, collected on 28 February 1993 by Juan Manuel Rengifo, in Campo Caño Limón, near Yuca oil well, inside the forest, Arauca; adult male ICN 10881 and adult female ICN 10882, collected on 22 November 1989 by a field party as part of the Introductory Mammalogy course, Universidad Nacional de Colombia, in Medina, Vereda La Sarza, Quebrada La Sarza, Cundinamarca; adult female ICN 15128, collected on 2 July 1998 by Cecilia Ramirez, Herly Zuñiga, and Héctor Lancheros, in Vereda Soya, márgen derecho del Río Zaguea, Ubalá, Cundinamarca; adult male ICN 9456, collected on 29 March 1983 by Group of Advanced Systematics, Universidad Nacional de Colombia, in Fuente de Oro, Km. 9 Road Puerto Limón - Puerto Lleras, Vereda La Esperanza, Finca La Virginia, Meta; adult males ICN 10732 and ICN 10733 and an adult female ICN 10734, collected on 23 April 1988 by María del Pilar Rivas and Pedro Sanchez Palomino, in San Juan de Arama, Caño La Curia, Meta; adult male ICN 6882 and female ICN 6884, collected on 7 May 1977 by a field party from the Universidad Nacional de Colombia, in Villavicencio, Finca El Buque, Meta. Two additional specimens of *U. bakeri* collected on the same night as the *U. bakeri* holotype were deposited with the Venezuelan authorities that provided the permits, but the museum in which they were archived has not been established.

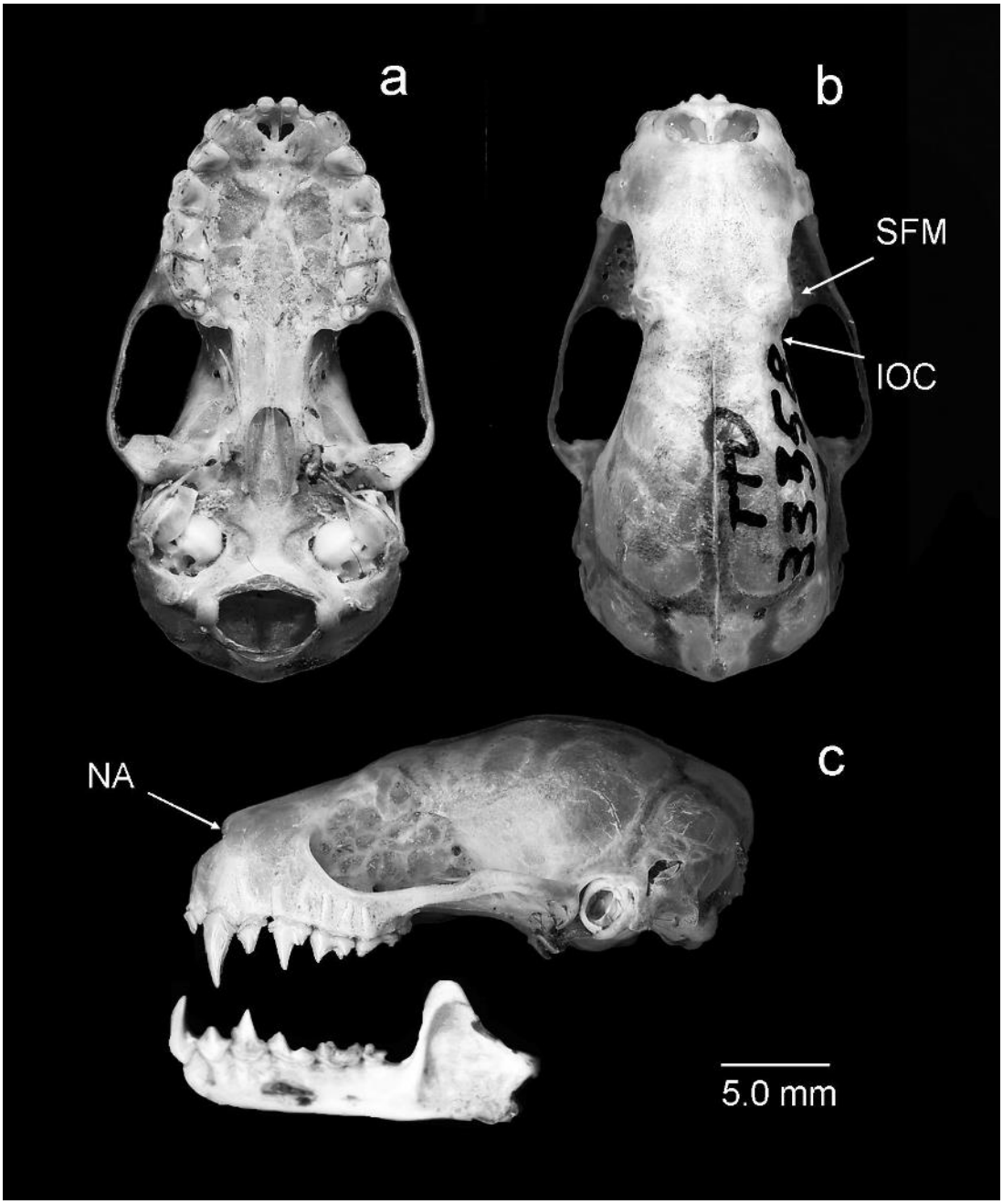

Figure 4. Ventral (a), dorsal (b), and lateral (c) profile of the holotype (TTU 33358 ♂) of *Uroderma bakeri*. Abbreviations: interorbital constriction (IOC); nasal angle (NA); and sutura frontomaxillaris (SFM).

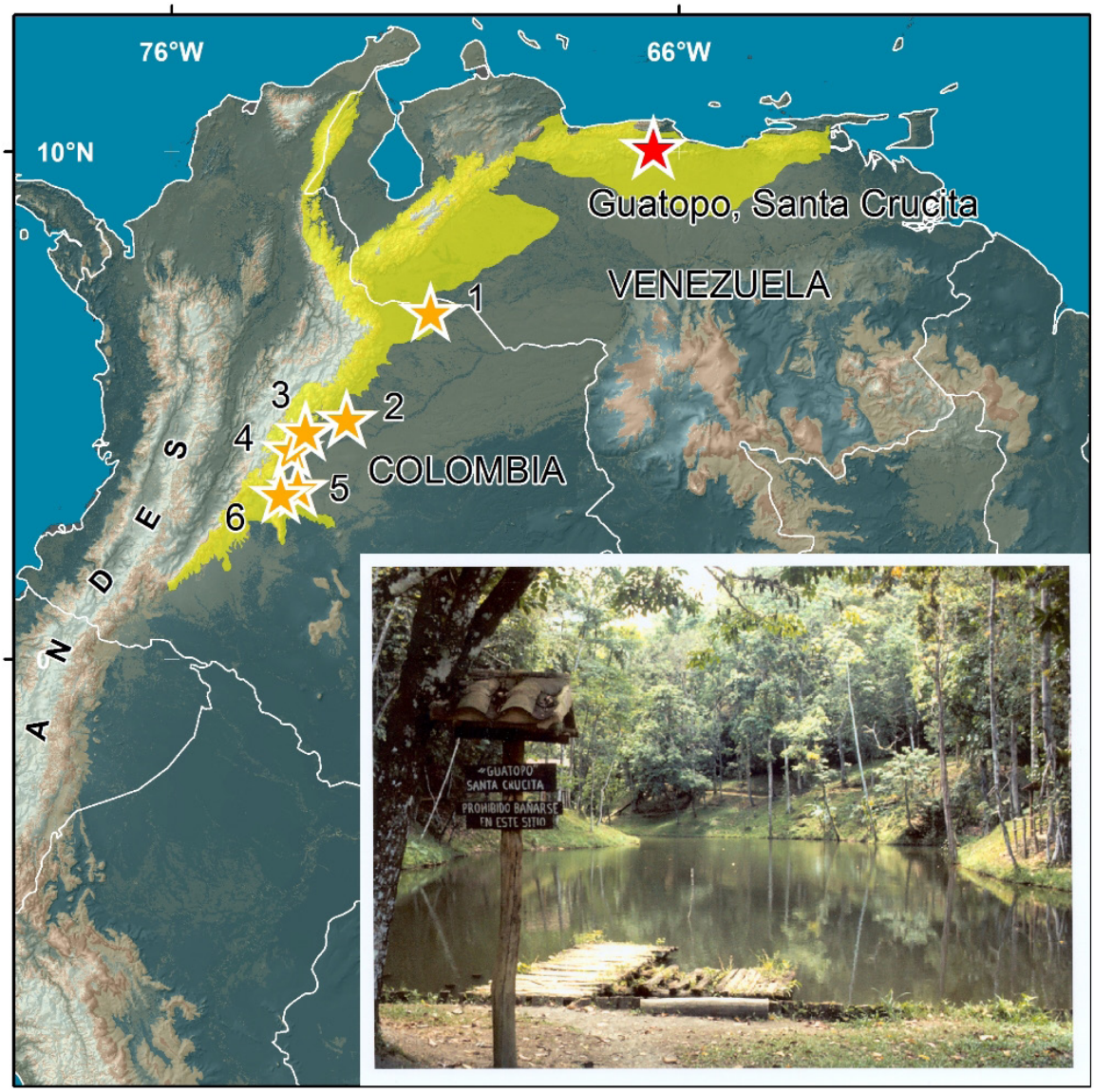

Figure 5. Type locality of *Uroderma bakeri* in Santa Crucita (red star), Parque Nacional Guatopo, Miranda, Venezuela 10º5'N, 66º33'W, at an elevation of 2,480 m. Yellow stars indicate the collecting localities associated with *U. bakeri* specimens: 1) Arauca, Campo Caño Limón, near oil drill Yuca, inside the forest (ICN 12917-18); 2) Cundinamarca, Medina, Vereda La Sarza, Quebrada La Sarza (ICN 10881-82); 3) Vereda Soya, márgen derecho del Río Zaguea, Ubalá; 4) Meta, Fuente de Oro, Km. 9 Road Puerto Limón - Puerto Lleras, Vereda La Esperanza, Finca La Virginia (ICN 9456); 5) San Juan de Arama, Caño La Curia (ICN 10732-34); 6) Villavicencio, Finca El Buque (ICN 6882-84). The area highlighted in yellow represents the potential distribution of *U. bakeri*. Inset: Photo of the collecting site, taken by Robert J. Baker the day of the capture of the holotype (25 April 1978).

Distribution.—The species is known from the piedmonts associated with the northwestern Colombian-Venezuelan Orinoco River basin of the Eastern Cordillera of the Colombian Andes and the Cordillera de Mérida and Cordillera del Caribe. This species has been recorded in an elevational range of 500 to 2,500 m (Fig. 5).

Description of the holotype.—Holotype is a general grey color. Dorsal hairs are three-quarters grey with a paler band at base, and venter is paler than dorsum. *Uroderma bakeri* has a thin, white line along the dorsal midline, well-defined white stripes across the cheek and above the eye, and well-defined black eyebrows on top of the anterior portion of the eyes. Ears have scattered hairs. Borders of the ears, horseshoe, and nose leaf possess a distinctive yellow coloration. Pelage reaches the middle of forearm, with tibia and middle part of the thigh naked. Interfemoral membrane is notched and naked with no hairs on edge. Holotype has a large and massive skull, characterized by a flat lateral profile (Figs. 4 and 6); a broader rostrum; swollen interorbital area at the sutura frontomaxillaris; and a massive dentition, with the typical formula for genus: i 2/2, c 1/1, p 2/2, m 3/3, total 32. Four upper incisors are bilobed and not in contact, with inner incisors larger and located anterior to the lateral ones. Lobes of medial incisors are subequal. Both central and lateral incisors are tilted with tips pointed bucally. Canines are massive, particularly at base, and appear straight from a lateral view. Base of first premolar is triangular. Anterior surface of mesiostyle (Osborn 1907), or anterior cingular style (Vandebroek 1961), has a flat appearance in ventral view, and half of its length is in contact with canine. Main cone (paracone) of first premolar is elongated and curved toward labial side. Curvature of first premolar, paracone, allows it to be visible behind canines in a rostral view. First upper premolar is shorter than second premolar and barely surpasses half of length of canine. From a ventral view, tip of posterior cingular style of first premolar is overlapped by mesiostyle of the paraconid of second premolar; however, teeth are not in contact as seen from a lateral view. *U. bakeri* holotype has an accessory style on first premolar and a wide contact region between second and third molar including the second molar metacone, metaconid, metastyle and its associated crista (teeth nomenclature adapted from Van Valen [1994] and Swindler [2002]).

Diagnosis.—Uroderma bakeri is diagnosed by the following characteristics: large skull (GLS > 23.00 mm); swollen interorbital area at the *sutura frontomaxillaris*; massive dentition; maxillae deflected into plane of nasals; small crest along suture joining the parietals (*sutura sagittalis*) that terminates where parietals join the temporal bones (*sutura parietointerparietalis*); projected edge of squamosal visible from a dorsal view and allowing only a small portion of the tympanic bullae to be viewed; inside the nasal aperture, ventral portion of the nasal maxilloturbinates visible, as well as the septum nasi and part of vomer septum; maxilloturbinates and superior and inferior conchas massive; joining of the nasal bones occurs caudally with respect to the maxillae, nearly forming a straight nasal angle in a lateral view (Figs. 6 and 7).

Comparisons.—The new species can be distinguished from Central American representatives of the *U. bilobatum* complex (*U. b. convexum*, *U. b. molaris*, and *U. b. davisi*) by its flat lateral profile (Figs. 4 and 7). *Uroderma bakeri* lacks the typical deflection of the nasal bones at the interorbital area, which are present in *U. b. convexum*, *U. b. molaris* and *U. davisi*. *Uroderma bakeri* has a broader rostrum, swollen interorbital area at the *sutura frontomaxillaris*, a more massive dentition, and a less arched tooth-row than *U. b. convexum* and *U. b. davisi*. In contrast with the rostrum of *U. bakeri*, rostra of *U. b. convexum*, *U. b. molaris,* and *U. b. davisi* are substantially shorter and expand abruptly from the apex to the lachrymal bone edges; therefore, the lachrymal bones are more visible from a rostral view than in *U. bakeri*. From the eastern South American forms in the *U. bilobatum* complex (*U. b. bilobatum*, *U. b. thomasi*, and *U. b. trinitatum*), *U. bakeri* also can be differentiated by its flat lateral profile, swollen interorbital constriction at the *sutura frontomaxillaris*, and by having a more massive dentition. In addition, in *U. bakeri* the union of the nasal bones with respect to the maxillae forms a straight nasal angle in a lateral view, whereas in *U. b. bilobatum*, *U. b. thomasi*, and *U. b. trinitatum*, the nasal angle is obtuse (Fig. 4c). In *U. b. bilobatum*, *U. b. thomasi*, and *U. b. trinitatum*, the edge of the maxillae (that forms the eye socket) is terminated in a rim that is less distinct in *U. bakeri.*

All museum voucher specimens in the *U. bakeri* type series had been misidentified as *U. magnirostrum*. However, these two species easily can be distinguished

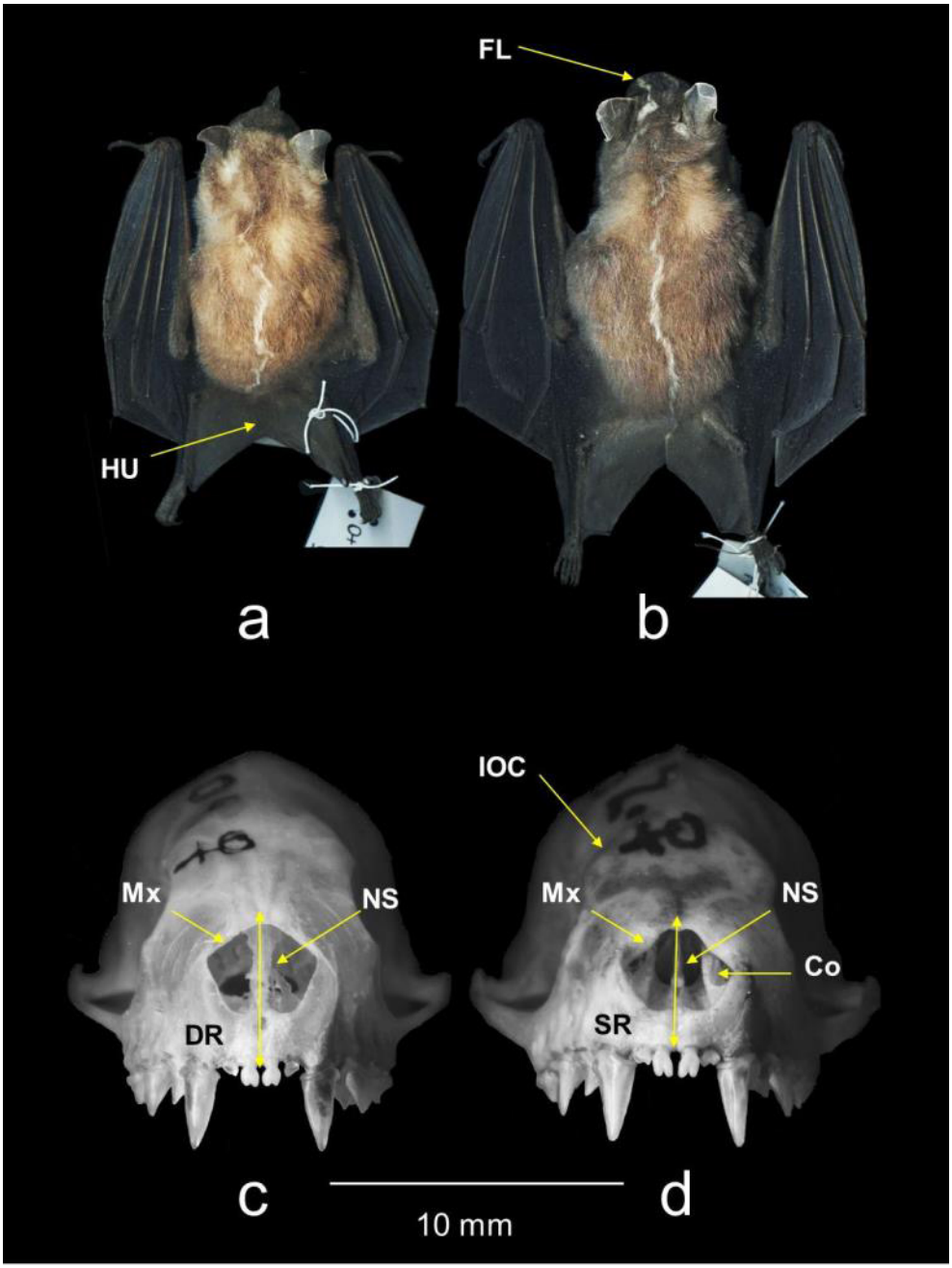

Figure 6. Comparative images of skin (a and b) and frontal view of skulls (c and d) of *Uroderma magnirostrum* (left) and *U. bakeri* (right). Abbreviations: conchas (Co); NS (septum nasi); maxilla bone (Mx); interorbital constriction (IOC); deep rostrum (DR); shallow rostrum (SR); face lines (FL); and hairy uropatagium (HU).

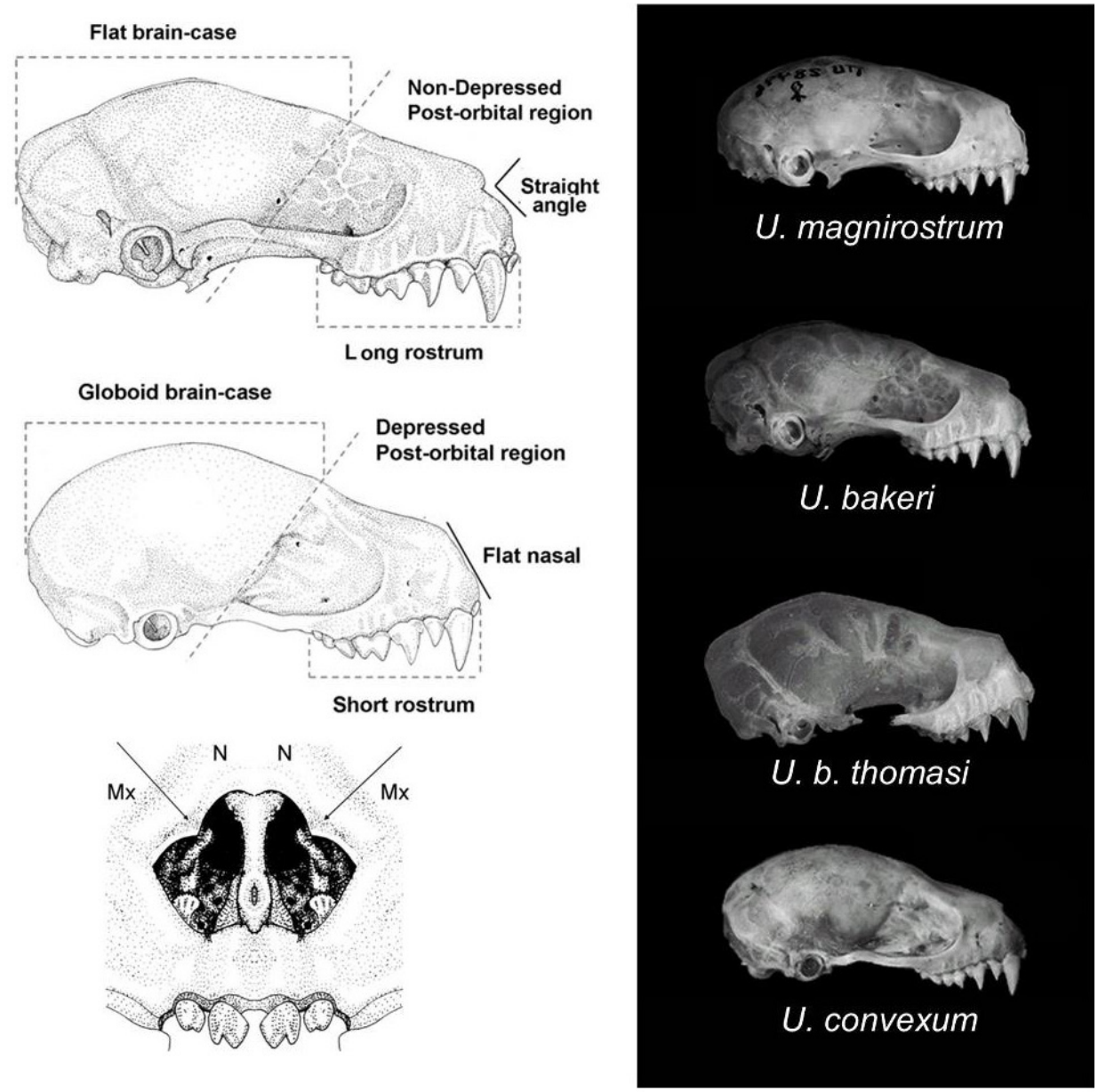

Figure 7. On the left: comparisons of cranial external characters between *Uroderma bakeri* (top) and *U. convexum* (center); detail of nasal aperture of *U. bakeri* showing the intrusion of the maxilla (Mx) into the plane of the nasals (N) (bottom). On the right: skull profiles of *U. magnirostrum* (TTU 28496); *U. bakeri* (TTU 33358); *U. bilobatum thomasi* (TTU 341912); and *U. convexum* (TTU 39139) (top to bottom).

by a suite of external and internal characters. Externally, *U. bakeri* has a dark grey general coat color contrasting the brownish coat of *U. magnirostrum*. In *U. bakeri*, rostral stripes are well-marked, whereas in *U. magnirostrum* rostral stripes are absent or only insinuated. *Uroderma bakeri* has scattered hairs on the border of the ears, contrasting the naked border of the ears of *U. magnirostrum*. In addition, the borders of the ears, the horseshoe, and the nose leaf in *U. bakeri* are distinctive yellow, contrasting the less distinctive yellow borders of the ears and nose leaf of *U. magnirostrum*. *Uroderma bakeri* has a wide uropatagium, lacking hair on both dorsal and ventral surfaces, thus differing from the uropatagium of *U. magnirostrum*, which has scattered hairs on both dorsal and ventral surfaces (Fig. 6). All specimens in the *U. bakeri* series have long, black hairs on the anterior portion of the eyes forming a brow line. This character was present in only three of 77 *U. magnirostrum* analyzed (identified based on skull characters, particularly rostrum depth [Andersen 1908]). These three specimens were collected in two localities from the northern Colombian Amazon at the department of Caquetá (ICN 11342-43 from Montañita, and ICN 12771 from Chiribiquete, department of Caquetá in Colombia). Further analysis is necessary to determine the taxonomic status of these specimens. Internally, *U. bakeri* and *U. magnirostrum* share a flattened skull profile. However, the species can be differentiated by the deeper rostrum typical of *U. magnirostrum* (Andersen 1908). In addition, in *U. bakeri* the nasal aperture has a broader appearance than in *U. magnirostrum*. The maxilloturbinates and the superior and inferior conchas of *U. bakeri* are more massive than in *U. bilobatum*, but less massive than those of *U. magnirostrum*. In *U. bakeri*, the nasal septum and the mesethmoid is formed by a thin sheet, not terminated in a shield-like structure, contrasting the wide and massive nasal septum and the shield-like structure associated with the mesethmoid of *U. magnirostrum* (Fig. 6). In *U. magnirostrum* the skull is laterally compressed and from a dorsal view, the edges of the squamosal and the tympanic bullae are hidden beneath the parietal. As in other representatives of the genus, the junction of the nasal bones occurs anterior to the junction of the maxilla in *U. bakeri*. However, in *U. bakeri* the nasal area, from a lateral view, is divided into two perpendicular planes forming an angle with the vertex marked by the tip of the septum nasi. This angle is more acute in *U. bakeri* than in other *Uroderma* (Fig. 4c). In *U. bakeri,* the protrusion of the maxillae allows the roots of the upper incisor to be more noticeable than in other *Uroderma*. The nasal aperture in *U. bakeri* is piriform, with the two upper sides deflected internally by a convergent intrusion of the maxillae into the plane of the nasal bones (Figs. 6 and 7); these intrusions are produced by the lateral projections of the nasal septi and are absent in *U. magnirostrum* where the maxillas are parallel to the nasals (Figs. 6 and 7). In *U. bakeri* the infraorbital foramen, located above the root of the second premolar, marks the inflexion point of the concave surface of the maxilla bone; in contrast, this inflexion is not noticeable in *U. magnirostrum*. In *U. bakeri*, from a rostral view, the lateral sides of the maxillae are deflected or concave and expand into the area of the anterior part of the zygomatic arches; contrasting the flat appearance of the rostrum of *U. magnirostrum* which extends within a single plane.

Genetic data.—Investigation of the molecular phylogenetic affinities between the new species and other representatives of the genus is beyond the scope of the present work. Hoffmann et al. (2003) reported that the holotype specimen TTU 33358 differed in the mtDNA *Cyt*b gene (genetic distance of 3.7%) relative to other representatives of the genus.

Karyotype.—The karyotype of *U. bakeri* is unknown.

Ecology.—The holotype of *U. bakeri* was collected at the Parque Nacional Guatopo (Fig. 5), located in northern Venezuela, southeast of the city of Caracas. The area is part of the mountainous system of Serranía del Interior. The vegetation corresponds to a tropical hyper-humid pre-montane forest. It is dominated by tree species such as *Ochoroma lagopus*, *Erythrina poeppigiana*, *Pterocarpus acapulcensis*, *Tabebuia chrysantha*, *Bursera simaruba*, and *Cecropia peltata*, and palm trees such as *Oenocarpus bataua*, *Bactris sp*. and *Asterogyne spicata*. The understory also presents a high diversity of plants including *Calathea* and *Heliconia*. Epiphytic plants also are well-represented by Araceae, Bromeliaceae, Orquidaceae, and Piperaceae (Weidmann et al. 2003).

Morphological characteristics such as larger body size and enlargement of the rostrum at the nasal area, as well as enlarged nasal conchas, may be adaptations

of *U. bakeri* to highland ecosystems. Ecological differentiation also may suggest that the divergence of *U. bakeri* can be explained by selection and adaptation (Nosil et al. 2009). Although *U. bakeri* exists across a wide range of elevational gradients (500-2,500 m), the species inhabits higher elevations than the typical maximum elevational limits of other representatives of the genus.

Etymology.—Uroderma bakeri is named for Dr. Robert J. Baker, who has dedicated his life to the study of a wide variety of aspects of the natural history and evolution of the Neotropical mammalian fauna, in particular to the study of phyllostomid bats. Dr. Baker has used *Uroderma* as a natural model in several studies since the 1970's. His ongoing research on *Uroderma* includes hybrid zones, karyotypic evolution, systematics, population genetics, and niche modeling. The proposed common name is Baker's tent-making bat.

FINAL TAXONOMIC CONSIDERATIONS

Taxonomic status of Central American Uroderma.—Trans-Andean *U. b. convexum* possess a different karyotype from typical cis-Andean *U. bilobatum* (2N=38) and are found along the Pacific coast of Panama west to Honduras and the Atlantic versant of Mexico (Fig. 8). The easternmost karyotyped record for *U. b. convexum* (2N=38) is located in Melgar, department of Tolima, in the Colombian Inter-Andean valley of the Magdalena River (Baker and López 1970). There is no evidence of cis-Andean representatives of the 2N=38 race. Although *U. b. bilobatum* (2N=42) and *U. b. convexum* could not be statistically differentiated in the current analyses, discrete morphologic characters identified in Lyon's (1902) description of *U. b. convexum* allowed discrimination of *U. b. bilobatum* from *U. b. convexum*. The molar tooth-row of *U. b. convexum* is decidedly convex and less nearly parallel compared to *U. b. bilobatum*. Teeth in *U. b. convexum* are slightly larger than corresponding teeth in *U. b. bilobatum*; most conspicuous are the greater widths of upper premolars and molars. The portion of the palate posterior to the last molar is decidedly shorter and narrower in *U. b. convexum* than in *U. b. bilobatum* (Lyon 1902:84). Lyon (1902) also reported that the rostrum of *U. b. convexum* from Panama is shorter and broader, and the nasals are more flattened compared to Brazilian specimens of *U. bilobatum*. In addition to the characters described by Lyon (1902), *U. b. convexum* has, from a lateral view, a more markedly accentuated deflection of nasal bones at the interorbital region. The more deflected appearance of the skull in *U. b. convexum* is associated with its shorter rostrum compared to other representatives of the genus (Fig. 7). Deflection of the nasal bones in *U. b. convexum* is marked by the basineurocranial plane, which is delimited by the pterigoid and the anterior portion of the basioccipital. *Uroderma b. convexum* is characterized by a higher braincase relative to *U. b. bilobatum*.

Although analyses are in agreement with the previously documented statistical support differentiating *U. b. convexum* from *U. b. davisi* (Baker and McDaniel 1972; Baker et al. 1972), the strongest evidence for specific status of *U. convexum* and *U. davisi* is defined by three unique euchromatic chromosomal rearrangements in *U. davisi* (Baker 1981) that delineate a well-defined, narrow hybrid zone thought to be maintained by negative heterosis (Barton 1982). Two chromosomally identified phylogroups, concordant with reciprocal monophyly in mtDNA, a narrow hybrid zone, and evidence of negative heterosis in hybrids merits recognition of *convexum* and *davisi* as species following the reasoning of Patton and Dingman (1968).

Similarly, based on the operational criteria of statistically supported reciprocal monophyly (Da Silva and Patton 2005), *U. davisi* is recognized as specifically distinct from *U. convexum* in both nuclear and mitochondrial markers. *Uroderma davisi* (2N=44) and *U. convexum* (2N=38) are distinguished by three unique rearrangements (Baker 1981), as well as consistent clades in the analyses of *Cyt*b sequences (Hoffmann et al. 2003). Due to the recent and rapid fixation of the observed chromosomal rearrangements in *U. convexum* and *U. davisi*, clades identified in Hoffmann et al. (2003) have low support values. In addition,

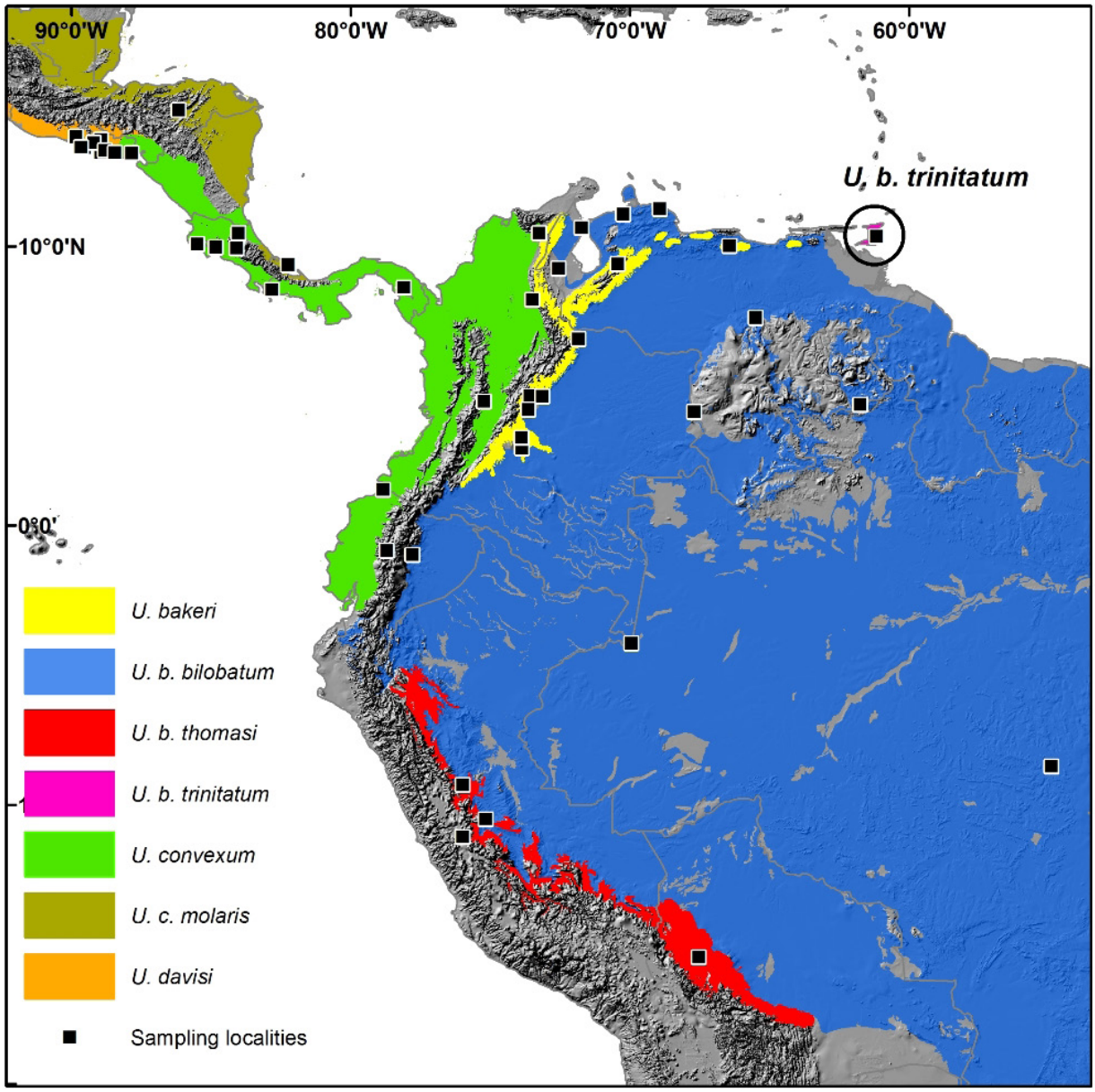

Figure 8. Distribution of taxa in the genus *Uroderma*, as recognized in this study: *U. bakeri* (yellow); *U. bilobatum bilobatum* (blue); *U. b. trinitatum* (pink, identified with label, restricted to the island of Trinidad); *U. b. thomasi* (red); *U. convexum* (light green); *U. c. molaris* (green mustard); and *U. davisi* (orange). Localities of specimens used in this study are represented by black squares.

unique allozymic alleles in *U. davisi* were proposed by Greenbaum (1981).

Concluding remarks.—The history of the taxonomy of the genus *Uroderma* is not particularly different than that of other Neotropical mammals. To discern natural diversity is not an easy task, and sometimes the complexity of the biological processes explaining diversity requires the application of more than one technique or conceptual approach. As asserted by Baker (1984) for *Rhogeesa genowaysi* and Baker et al. (2009) for *Eumops wilsoni*, there are speciation events in bats that are unaccompanied by obvious morphological changes, or in some cases, significant morphological changes are incongruent with historical patterns recovered from molecular markers. Among Neotropical bats, *Uroderma* has been one of the most intensively studied genera, including studies of multiple datasets documenting its karyotypic, molecular, and morphological variation. Hoffman et al. (2003) proposed that the divergence among the three chromosomal races would have occurred between 0.9 and 0.2 Mya. The recent origin of the *Uroderma* chromosomal races is a potential explanation for the high intraspecific variation and insipient geographic structure observed in some of the regional morphotypes. Karyotypic, molecular, and morphological geographic partitioning observed in *Uroderma* support the hypothesis of the northern Andes as an effective barrier preventing population gene flow. *Uroderma bakeri* appears to have one of the widest elevational ranges in the genus, and its distribution is associated with the piedmonts and mountainous ecosystems in northern South America. Some of the morphologically distinctive characters of *U. bakeri* can be interpreted as adaptations to highland ecosystems, such as the enlargement of the nasal area (Cortés et. al. 2003). The presence of adaptations to highland ecosystems in *Uroderma* provides new alternatives for the reconstruction of potential evolutionary scenarios for the genus.

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LITERATURE CITED

Andersen, K. 1906. Brief diagnoses of a new genus and ten new forms of stenodermatous bats. Annals Magazine of Natural History 18:419–423.

Andersen, K. 1908. A monograph of the chiropteran genera *Uroderma*, *Enchistenes*, and *Artibeus*. Proceedings of the Zoological Society of London 1908:204–319.

Baker, R. J. 1981. Chromosome flow between chromosomally characterized taxa of volant mammal, *Uroderma bilobatum* (Chiroptera: Phyllostomidae). Evolution 35:296–305.

Baker, R. J. 1984. A sympatric species of mammal: A new species of *Rhogeesa* (Chiroptera: Vespertilionidae). Systematic Zoology 33:178–183.

Baker, R. J., and R. D. Bradley. 2006. Speciation in mammals and the genetic species concept. Journal of Mammalogy 87:643–662.

Baker, R. J., and C. L. Clark. 1987. *Uroderma bilobatum*. Mammalian Species 279:1–4.

Baker, R. J., S. Hoofer, C. A. Porter, and R. A. Van Den Bussche. 2003. Evolutionary relationships and classification of New World leaf-nosed bats inferred from DNA sequence. Occasional Papers, Museum of Texas Tech University 230:1–32.

Baker, R. J., and G. López. 1970. Chromosomal variation in bats of the genus *Uroderma* (Phyllostomidae). Journal of Mammalogy 51:786–789.

Baker, R. J., and V. R. McDaniel. 1972. A new subspecies of *Uroderma bilobatum* (Chiroptera, Phyllostomidae) from Middle America. Occasional Papers, Museum of Texas Tech University 7:1–4.

Baker, R. J., W. R. Atchley, and V. R. McDaniel. 1972. Karyology and morphometrics of Peters' tent making bat, *Uroderma bilobatum* Peters (Chiroptera: Phyllostomidae). Systematic Zoology 21:414–429.

Baker, R. J., M. M.Mcdonough, V. Swier, P. A. Larsen, J. P. Carrera, and L. K. Ammerman. 2009. New species of bonneted bat, genus *Eumops* (Chiroptera: Molossidae) from lowlands of western Ecuador and Peru. Acta Chiropterologica, 11:1–13.

Barton, N. H. 1982. The structure of the hybrid zone in *Uroderma bilobatum* (Chiroptera: Phyllostomidae). Evolution 36:863–866.

Bradley R. D., and R. J. Baker. 2001. A test for the genetic species concept: cytochrome-*b* sequences in mammals. Journal of Mammalogy 82:960–973.

Cortés, A., C. Tirado, and M. Resenmann. 2003. Energy, metabolism, and thermoregulation in *Chinchilla brevicaudata*. Journal of Thermal Biology 28:489–495.

Da Silva, M. N., and J. L. Patton. 2005. Molecular phylogeography and the evolution and conservation of Amazonian mammals. Molecular Ecology 7:475–486.

Davis, W. B. 1968. Review of the genus *Uroderma* (Chiroptera). Journal of Mammalogy 49:676–698.

Gardner, A. L. 2007. Mammals of South America, Volume I: Marsupials, xenarthrans, shrews, and bats. University of Chicago Press, xx + 690 pp.

Greenbaum, I. F. 1981. Genetic interactions between hybridizing cytotypes of the tent-making bat (*Uroderma bilobatum*). Evolution 35:305–320.

Hafner, J. C. 1982. Genetic considerations at a contact zone of *Uroderma bilobatum* (Chiroptera: Phyllostomidae). Evolution 36:852–862.

Hafner, M. S., W. L. Gannon, J. Salazar-Bravo, and S. T Alvarez-Castañeda. 1997. Mammal collections in the western hemisphere: A survey and directory of existing collections. American Society of Mammalogists, Lawrence, Kansas. 93pp.

Hammer, Ø., D.A.T. Harper, and P. D. Ryan. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4:1-9.

Hoffmann, F. G., J. Owen, and R. J. Baker. 2003. mtDNA perspective of chromosomal diversification and hybridization in Peter's tent making bat (*Uroderma bilobatum*: Phyllostomidae). Molecular Ecology 12:2981–2993.

Hoofer, S., and R. J. Baker. 2006. Molecular systematics of vampyressine bats (Phyllostomidae: Stenodermatinae) with comparison of direct and indirect surveys of mitochondrial DNA variation. Molecular Phylogenetics and Evolution 39:424–438.

Larsen, P. A., S. Hoofer, M. C. Bozeman, S. Pedersen, H. Genoways, C. J. Phillips, and R. J. Baker. 2007. Phylogenetics and phylogeography of the *Artibeus jamaicensis* complex based on citochrome-*b* DNA sequences. Journal of Mammalogy 88:712–727.

Lessa, E. P. 1990. Multidimensional analysis of geographic genetic structure. Systematic Zoology 39:242–252.

Lyon, M. W. 1902. Description of a new phyllostome bat from the Isthmus of Panama. Proceedings of the Biological Society of Washington 15:83–84.

Marín-Vasquez, A., and A. V. Aguilar-González. 2005. Murciélagos (Chiroptera) del departamento de Caquetá, Colombia. Biota Colombiana 6:211–218.

Nosil, P., D. J. Funk, and D. Ortiz-Barrientos. 2009. Divergent selection and heterogeneous genomic divergence. Molecular Ecology 18:375–402.

Osborn, H. F. 1907. Evolution of mammalian molar teeth. Macmillan, New York. 250 pp.

Owen, J. G., and R. J. Baker. 2001. The *Uroderma bilobatum* (Chiroptera: Phyllostomidae) cline revisited. Journal of Mammalogy 82:1102–1113.

Patton, J. L., and R. E. Dingman. 1968. Chromosome studies of pocket gophers, genus *Thomomys*. I. The specific status of *Thomomys umbrinus* (Richardson) in Arizona. Journal of Mammalogy 49:1–13.

Peters, W. C. 1866. Machte eine Mittheilung uber neue oder ungenugend bekannte Flerthiere (*Vampyrops*, *Uroderma*, *Ametrida*, *Tylosoma*, *Vespertilio*, *Vesperugo*) und Nager (*Tylomys*, *Lasiomys*). Monatsberichtede Kurfürstlich-Brandenburgische Societät der Wissenschaften 1866:392–397.

Simmons, N. B. 2005. Order Chiroptera. Pp. 312–529 in Mammals species of the World, a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds). 3rd ed. John Hopkins University Press, Baltimore, Maryland.

SPSS Incorporated. 1999. SPSS Base 9.0 for Windows User's Guide. SPSS Inc., Chicago IL.

Statgraphics. 2009. Statgraphics XV for Windows. Statistical Graphic Corporation online manuals. StatPoint Technologies, Herndon, Virginia. 305 pp.

Swindler, D. R. 2002. Primate dentition, an introduction to the teeth of non-human primates. Cambridge University Press, United Kingdom. 296 pp.

Vandebroek, G. 1961. The comparative anatomy of the teeth of lower and non-specialized mammals. Pp. 215–320 in International colloquium on the evolution of lower and nonspecialized mammals (G. Vandebroek, ed.). Koninklijke Vlaamse Academie voor Wetenschappen, Letteren en Schone Kunsten van Belgie, Brussels.

Van Valen, L. M. 1994. Serial homology: The crests and cusps of mammalian teeth. Acta Palaeontologica Polonica 38:1451–1458.

Velazco, P. M., and B. D. Patterson. 2008. Phylogenetics and biogeography of the broad-nosed bats, Genus *Platyrrhinus* (Chiroptera: Phyllostomidae). Molecular Phylogenetics and Evolution 49:749–759.

Velazco, P. M., A. L. Gardner, and B. D. Patterson. 2010. Systematics of the *Platyrrhinus helleri* species complex (Chiroptera:Phyllostomidae), with descriptions of two new species. Zoological Journal of the Linnean Society 159:785–812.

Weidmann, K., R. Rangel, C. Todmann, and A. Reig. 2003. Parques Nacionales de Venenezuela. Oscar Todmann Eds. Editorial Arte, Caracas.

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Editor for this manuscript was Robert D. Bradley.

APPENDIX I

Specimens examined in morphometric and morphologic analyses. In capital letters are the names of the countries, followed by the departments or provinces, and the collecting localities. In parentheses is the acronym of the institution housing the specimens, followed by the museum catalogue number and sex of each individual. Acronyms follow those used in the Materials and Methods.

Uroderma bilobatum bilobatum (62: 29♂: 33♀).—BRASIL (15: 9♂: 6♀): Mato Grosso: (USNM 393686♂, USNM 393687♂, USNM 393688♀, USNM 393689♂, USNM 393690♂, USNM 393691♀, USNM 393692♂, USNM 393693♂, USNM 393694♀)); Para: (USNM 361663♂, USNM 361665♀, USNM 361667♀, USNM 361670♀, USNM 361673♂, USNM 361675♂); COLOMBIA (21: 9♂: 12♀): Amazonas: Leticia (TTU 8836♀, TTU 9044♂, TTU 9082♂, TTU 9083♀, TTU 9084♂); Caquetá (ICN 11337♂, ICN 11338♀, ICN 11339♀, ICN 11340♀, ICN 11341♀, ICN 12770♂, ICN 14631♀); Cundinamarca: Medina (ICN 10880♀); Meta: (TTU 9477♀, TTU 9511♂); (ICN 2099♀, ICN 2100♀); Putumayo: (ICN 13784♂); Vaupes: (ICN 3993♂, ICN 3994♂, ICN 3995♀); ECUADOR (8: 2♂: 6♀): East (USNM 528332♂, USNM 548156♀, USNM 548157♂, USNM 54815♀, USNM 548159♀, USNM 548160♀, USNM 548164♀); Macas: (TTU 40094♀); VENEZUELA (18: 9♂: 9♀): Bolivar: 45 Km NE Icabú (USNM 440428♀, USNM 440431♂); Bolivar: Independencia (USNM 440421♀); Santa Lucía de Surukán (USNM 440430♂); Falcón: La Pastora (USNM 440197♂, USNM 440220♀, USNM 440221♀); Mirimiré, near La Pastora (USNM 440196♂); Amazonas: Belén (USNM 389931♀, USNM 389932♂); Near Belén, W Caño Essa (USNM 389983♀); Río Cunucunuma (USNM 389943♂, USNM 389957♀); Belén, 56 Km NNW Río Cunucunuma (USNM 389951♀); Yaracuy (USNM 372041♀, USNM 372043♂, USNM 372044♂, USNM 372045♂).

Uroderma bilobatum thomasi (28: 16♂: 12♀).—BOLIVIA (13: 8♂: 5♀): La Paz: (TTU 34908♂, TTU 34909♀, TTU 34910♀, TTU 34911♀, TTU 34912 ♂, TTU 34913♂, TTU 34914♂, TTU 34915♂, TTU 34916♀, TTU 34917♀, TTU 34918♂, TTU 34919♂, TTU 34920♂); ECUADOR (3: 1♂: 2♀): Napo: (USNM 528332♂); Pastaza (USNM 54856♀, USNM 54864♀); PERU (12: 7♂: 5♀): Huánuco: (TTU 46297♀, TTU 46304♂), Junín: (USNM 507185♂, USNM 507186♂); Pasco: (USNM 364415♀, USNM 364416♀, USNM 364417♂); Pulcallpa: (USNM 461251♂, USNM 461252♂, USNM 461253♂, USNM 499090♀, USNM 499093♀).

Uroderma bilobatum trinitatum (8: 6♂: 2♀).—TRINIDAD: Saint George: (TTU 26691♂, TTU 5254♂, TTU 5327♀, TTU 5390♂, TTU 5808♂, TTU 5813♀, TTU 9018♂, TTU 9019♂).

Uroderma convexum convexum (136: 77♂: 59♀).—COLOMBIA (55: 29♂: 26♀): Antioquia: (ICN 9829♂, ICN 9830♀, ICN 9873♀); Bolivar: (ICN 16027♀, ICN 1628♂); Boyaca: (ICN 14833♂, ICN 14834♂, ICN 14835♂, ICN 14836♂, ICN 14837♀, ICN 14871♀, ICN 14872♂, ICN 14873♂, ICN 15080♀, ICN 15904♀, ICN 15908♀); Caldas: (ICN 10840♀, ICN 14297♂); Cesar: (ICN 10966♀, ICN 10967♂); Chocó: (ICN 7397♀, ICN 7398♂, ICN 7399♂, ICN 7300♀, ICN 7301♀, ICN 7302♂, ICN 7303♂, ICN 7304♂; Córdoba: (ICN 17309♂, ICN 17322♀); Huila: (ICN 8465♀, ICN 13627♀); La Guajira: (ICN 14965♂, ICN 14871♀, ICN 14872♂); Magdalena: Guaimaral (USNM 281161♂); Santa Marta (ICN 874♀, ICN 876♀, ICN 3638♂, ICN 3643♀; Sierra Negra: USNM 281165♀); Sitio Nuevo (ICN 15509♂, ICN 15516♂, ICN 15517♀); Villanueva (USNM 281159♀); Santander (ICN 4209♂); Sucre (ICN 13145♂, ICN 13146♂; ICN 17464♀); Tolima: (TTU 9322♀, TTU 9326♂, ICN 6852♂, ICN 1765♂); Valle del Cauca (ICN 4608♂, ICN 6205♀); COSTA RICA (43: 28♂: 15♀): Guanacaste: (TTU 12707♂, TTU 12708♀, TTU 12710♀, TTU 34322♂, TTU 34326♀, TTU 34328♀, TTU 34331♀, TTU 3432♀, TTU 3433♂, TTU 3434♀); Puntarenas: (TTU 12672♀, TTU 12675♂, TTU 12676♂, TTU 12678♂, TTU 12681♀, TTU 12683♂, TTU 34343♂, TTU 34344♂, TTU 34346♀, TTU 34347♂, TTU 34347♂, TTU 34348♂, TTU 34349♂); San José: (TTU 12684♂, TTU 12685♂, TTU 12689♀, TTU 12695♂, TTU 34352♂, TTU 34354♂, TTU 34356♂, TTU 34360♀, TTU 34361♂, TTU 34347♂, TTU 34348♂, TTU 34364♂, TTU 34366♀, TTU 34370♂, TTU 34374♂, TTU 34376♂, TTU 34379♂, TTU 34385♀, TTU 34388♂, TTU 34389♀);

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ECUADOR (15: 6♂: 9♀): El Oro: (USNM 513458♀, USNM 513459♀); Esmeraldas: (TTU 85375♀); Los Ríos: (USNM 522340♀, USNM 522341♂, USNM 522342♂, USNM 522343♂, USNM 522344♂, USNM 522345♀, USNM 522349♀, USNM 522351♀, USNM 522356♀; Pichincha: (USNM 528528♀, USNM 528530♂, USNM 528531♂); PANAMA (23: 14♂: 9♀): Barro Colorado Island: (USNM 576006♂); Chiriquí: Progreso (USNM 362831♂, USNM 528532♀, USNM 528533♂, USNM 528535♀, USNM 528536♂, USNM 528552♂, USNM 528553♂, USNM 362855♀, USNM 362857♂); Darién: (TTU 39138♀, TTU 39139♂); Jaque (USNM 362784♂, USNM 362785♂, USNM 362790♂, USNM 362810♀, USNM 362811♀, USNM 362812♀, USNM 362813♀, USNM 362814♂, USNM 362816♂, USNM 362817♂, USNM 362818♀).

Uroderma convexum molaris (37: 19♂: 18♀).—COSTA RICA (8: 2♂: 6♀): Heredia: (TTU 12697♂, TTU 12698♀, TTU 12699♂, TTU 12700♀, TTU 12701♀, TTU 12703♀, TTU 12704♀, TTU 12705♀); HONDURAS (17: 11♂: 6♀): Olancho: (TTU 12618♂, TTU 12619♂, TTU 12621♂, TTU 12622♀, TTU 12624♂, TTU 12625♂, TTU 12626♀, TTU 12628♂, TTU 12629♂, TTU 12631♀, TTU 12633 ♂, TTU 12635♀, TTU 12636♂, TTU 12638♂, TTU 12641♀, TTU 12642♀, TTU 12644♂); PANAMA (12: 6♂: 6♀): Bocas del Toro: Almirante (USNM 315428♀, USNM 315429♀, USNM 315441♀, USNM 315446♂, USNM 315452♀, USNM 315454♂, USNM 315472♀, USNM 315473♂, USNM 315474♂, USNM 315475♀, USNM 315476♂, USNM 315478♂).

Uroderma davisi (124: 53♂: 71♀).—EL SALVADOR: Ahuachapán (TTU 29269♀, TTU 64020♀, TTU 64021♂, TTU 64022♀, TTU 64023♂); Cuscatlán (TTU 12668♂); La Paz (TTU 12649♂, TTU 12650♂, TTU 12651♂, TTU 12652♀, TTU 12653♀, TTU 12654♂, TTU 12655♀, TTU 12656♂, TTU 12657♀, TTU 12660♂, TTU 12661♀, TTU 12662♂, TTU 12663♀, TTU 12664♀, TTU 16954♀, TTU 16955♀, TTU 16957♀, TTU16958♀, TTU 16961♂, TTU 16962♀, TTU 16963♂, TTU 16964 ♀, TTU 16965♀, TTU 16966♀, TTU 16968♀, TTU 16970♀, TTU 28321♀, TTU 28322♂, TTU 28323♂, TTU 28324♂, TTU 28325♀, TTU 28326♂, TTU 28327 ♀, TTU 28328♀, TTU 60956♀, TTU 60958♂, TTU 60959♂, TTU 60960♀, TTU 60961♀, TTU 60962♂, TTU 60963♂, TTU 60964♀, TTU 60965♀, TTU 60966♂, TTU 60967♂, TTU 60968♂, TTU 60969♂, TTU 60970♂, TTU 64029♂, TTU 64030♂, TTU 64032♀, TTU 64034♂; La Unión (TTU 64038♂, TTU 64039♀, TTU 64040♀, TTU 64042♀, TTU 64047♀); La Libertad (TTU 28342♀, TTU 64024♂, TTU 64025♂, TTU 64026♂); San Miguel (TTU 16972♂, TTU 16973♂, TTU 60971♂, TTU 60972♂, TTU 60973♂, TTU 60974♀, TTU 60975♀, TTU 60976♀, TTU 60977♂, TTU 60978♀, TTU 64042♀, TTU 64043♂, TTU 64045♂); San Salvador (TTU 12670♀, TTU 12671♂); San Vicente (TTU 64046♂), Sonsonate (TTU 64047 ♀), Usulután (TTU 16974♀, TTU 16975♂, TTU 16976♀, TTU 16977♂, TTU 16978♀, TTU 16979♀, TTU 16982♀, TTU 16983♀, TTU 16984♀, TTU 16985♀, TTU 16986♀, TTU 16987♀, TTU 16988♀, TTU 16989♀, TTU 16991♀, TTU 16992♀, TTU 16995♀, TTU 16996♀, TTU 16998♀, TTU 16999♀, TTU 17000♀, TTU 17007♂, TTU 17013♂, TTU 17027♂, TTU 17029♂, TTU 28343♂,TTU 28345♀, TTU 28347♀, TTU 28349♂, TTU 28350♀, TTU 28351♀, TTU 28353♂, TTU 28358♀, TTU 28359♀, TTU 28364♂, TTU 28367♀, TTU 28368♂, TTU 28369♀, TTU 28371♀, TTU 28372♀).

Uroderma magnirostrum (26: 15♂: 11♀).—COLOMBIA: Amazonas: Leticia, surrounding area of Leticia, borderline between Colombia and Brazil (ICN 960♂); Arauca: Campo Caño Limón, near oil drill Yuca, inside forest (ICN 12917♂, ICN 12918♀); Boyacá: Puerto Boyacá, Inspección de Policia Puerto Romero, Vereda Puerto Romero, Finca: Los Balcones (ICN 14504♂); Caquetá: La Montañita, Near School Palma Azul, La Palma Creek (ICN 11342♂, ICN 11343♀); Parque Natural Nacional Chiribiquete, western-most edge Serranía Norte (ICN 12771♀); Casanare: Maní, Hacienda La Floresta (ICN 5439♂, ICN 5440♂); Aguazul, Km. 3 Road Aguazul - Yopal, Charte River (ICN 8350♂); Cesar: La Loma de Calentura, Corregimiento Potrerillo, Finca Lusitania (ICN 18883♂); Chocó: Riosucio, Corregimiento Gilgal (ICN 7526♀); Riosucio, Vereda Sautatá, Parque Nacional Natural Los Katios (ICN 7605♀); Quibdó, San José de Bojayá, (o Alfonso López) Ciénaga, Gerujumia (ICN

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12661♀, ICN 12662♂); Huila: Baraya, Site, El Cruce, finca Las Delicias (ICN 13629♀, ICN 13631♀); Magdalena: Santa Marta, Parque Nacional Natural Tayrona, Cañaveral (ICN 7962♀); Magdalena, Santa Marta, Parque Nacional Natural Tayrona, Cinto (ICN 7963♂, ICN 7964♂); Meta: San Martín, Hacienda Los Guadules (ICN 5173♂); Restrepo, Upin River near Las Palinas (ICN 5214♂); Villavicencio, Km. 16 Road from Puerto López to El Hachón (ICN 8110♂); Puerto López, Vereda Menegua, Finca: El Lagunazo (ICN 9504♀, ICN 9505♂); Puerto López, Hacienda Mozambique (ICN 9629♀).

Uroderma bakeri sp. nov. (12: 7♂: 5♀).—COLOMBIA (11: 6♂: 5♀): Arauca: Campo Caño Limón, near oil drill Yuca, inside the forest (ICN 12917♂, ICN 12918♀); Cundinamarca: Vereda La Sarza, Quebrada La Sarza (ICN 10881♂, ICN 10882♀); Ubalá, Vereda Soya, márgen derecho del Río Zaguea (ICN 15128♀); Meta: Fuente de Oro, Km. 9 Road Puerto Limon - Puerto Lleras, Vereda La Esperanza, Finca La Virginia (ICN 9456♂); San Juan de Arama, Caño La Curia (ICN 10732♂, ICN 10733♂, ICN 10734♀); Villavicencio, Finca El Buque (ICN 6882♂, ICN 6884♀); VENEZUELA: Guárico: Miranda, Guatopo, Parque Natural Santa Crucita (TTU 3358♂ [TK 15288]).

APPENDIX II

Measurements of the holotype (*) and the eleven paratypes of *U. bakeri* sp. nov. Abbreviations of measurements: (External): forearm length (FA); (Craniodental): greatest length of skull (GLS); condylo-basal length (CBL); zygomatic width (ZW); mastoid width (MW); interorbital constriction width (IOC); brain-case width (BCW); canine-maxillary second molar length (CM2); distance across upper canines (C-C); rostral depth (RD); distance across third upper molars (M-M); mandibular length (MDL); and mandibular tooth row length (cm3). All measurements are in millimeters. ND = no data available.

	TTU 33358*	ICN 6882	ICN 9456	ICN 10732	ICN 10733	ICN 10881	ICN 12917	ICN 6884	ICN 15128	ICN 10734	ICN 10882	ICN 12918
Sex	♂	♂	♂	♂	♂	♂	♂	♀	♀	♀	♀	♀
FA	42.30	44.40	42.65	ND	ND	40.89	ND	43.60	43.80	ND	44.63	ND
GLS	24.19	23.08	23.79	23.60	23.16	23.39	23.48	23.78	23.69	22.83	23.82	22.72
CBL	22.19	23.12	21.65	21.18	21.26	21.09	21.53	21.81	21.48	20.90	21.81	20.34
ZW	13.82	13.00	12.62	12.87	12.52	13.27	ND	13.56	13.36	12.26	13.56	ND
MW	11.00	9.35	9.20	9.74	9.40	9.76	9.19	9.74	9.94	9.92	10.06	8.91
IOC	5.86	5.46	5.40	5.36	5.74	5.75	5.90	5.40	6.31	5.36	5.79	5.15
BCW	9.74	8.79	9.33	8.89	9.63	9.84	9.06	9.06	9.72	9.43	9.94	8.89
CM2	8.52	7.68	8.26	8.23	7.85	8.18	8.26	8.22	8.12	8.58	8.22	7.87
C-C	6.18	5.10	5.38	3.72	4.75	5.90	5.77	5.10	5.62	5.28	5.62	5.12
RD	5.59	4.66	5.59	5.02	5.50	4.29	5.39	5.30	5.22	5.22	5.08	5.21
M-M	9.55	8.82	8.83	8.99	8.61	9.59	9.26	8.53	9.13	8.97	9.15	9.04
MDL	15.48	14.41	14.78	14.87	14.59	14.74	14.94	14.66	14.76	14.7	15.05	14.41
cm3	8.35	ND	8.58	8.91	8.36	8.88	8.99	8.72	8.67	8.77	8.74	8.41

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