

MORPHOMETRICS AND TAXONOMY OF BATS OF THE GENUS *PTERONOTUS* (SUBGENUS *PHYLLODIA*) IN VENEZUELA

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In Venezuela, bats of the subgenus *Phyllodia* of the genus *Pteronotus* (Mormoopidae) are divided into 3 taxa, *Pteronotus parnellii fuscus*, *P. p. paraguayensis*, and *P. p. rubiginosus*. We compare them with respect to body size and shape by means of principal components analyses and cluster analyses applied to 26 craniodental and 7 appendicular (fore and rear limbs) measurements of 267 Venezuelan specimens. The analyses indicate that the subspecies endemic to the Península de Paraguaná, *P. p. paraguayensis*, differs from the other 2 taxa in being considerably smaller and in having markedly distinct craniodental and appendicular shapes; and, although to a lesser degree, *P. p. fuscus* and *P. p. rubiginosus* also differ notably from each other in these morphometric aspects. Our results justify raising *P. p. paraguayensis* to species rank. The tight dependence of members of *Phyllodia* on forest may explain the high levels of morphometric (this paper) and molecular (previous studies) variability of the subgenus. The reduced geographic distribution, small population, and full species status of the *Phyllodia* of Península de Paraguaná justify special conservation measures.

Key words: conservation, endemism, forest dependence, Mormoopidae, morphometrics, Península de Paraguaná, *Phyllodia*, *Pteronotus*, taxonomy, Venezuela

Mormoopidae is a family of neotropical insectivorous bats that presently ranges from the southwestern United States to southern Brazil, and is also found in the Greater Antilles, Lesser Antilles, Dutch West Indies, Trinidad, and Tobago (Simmons and Conway 2001; Smith 1972). Traditionally, Mormoopidae includes 2 genera (*Mormoops* and *Pteronotus*), 8 extant species, and 2 species only known from fossils (Silva-Taboada 1974, 1976; Simmons 2005; Simmons and Conway 2001; Smith 1972).

Although the phylogenetic relationships of the family Mormoopidae have received attention in recent years (Lewis-Oritt et al. 2001; Simmons and Conway 2001; Van Den Bussche and Hofer 2004; Van Den Bussche et al. 2002; Van Den Bussche and Weyandt 2003), the α -level taxonomy of mormoopid bats has remained relatively stable since the revisionary contribution of Smith (1972). Since then, the only taxonomic changes in the family have been the descriptions of

2 extinct species (*Mormoops magna*† and *Pteronotus pristinus*†—Silva-Taboada 1974) and an extant subspecies (*P. parnellii paraguayensis*—Linares and Ojasti 1974), and the recognition of *Chilonycteris fuliginosus* and *Dermonotus suapurensis* as junior synonymns of *Lobostoma quadridens* (currently *P. quadridens*—Silva-Taboada 1976) and *C. gymnonotus* (currently *P. gymnonotus*—Smith 1977), respectively (Simmons 2005). Nevertheless, based on DNA sequence data from mitochondrial ribosomal and cytochrome-*b* genes and the nuclear recombination activating gene-2, some authors (Dávalos 2006; Lewis-Oritt et al. 2001; Van Den Bussche et al. 2002; Van Den Bussche and Weyandt 2003) have suggested that more species exist in the family than those recognized by Smith (1972).

The traditional classification of *Pteronotus* (Simmons and Conway 2001; Smith 1972) recognizes 3 subgenera, *Pteronotus* (*P. davyi* and *P. gymnonotus*), *Chilonycteris* (*P. personatus*, *P. macleayii*, and *P. quadridens*), and *Phyllodia* (*P. parnellii* and *P. pristinus*†). Among these subgenera, *Phyllodia* is the most widely distributed and morphometrically variable (Smith 1972), with 9 taxa recently treated as subspecies of *P. parnellii* (Simmons 2005). In addition, a form not yet described from Saint Vincent, Lesser Antilles, is likely to be added to this list

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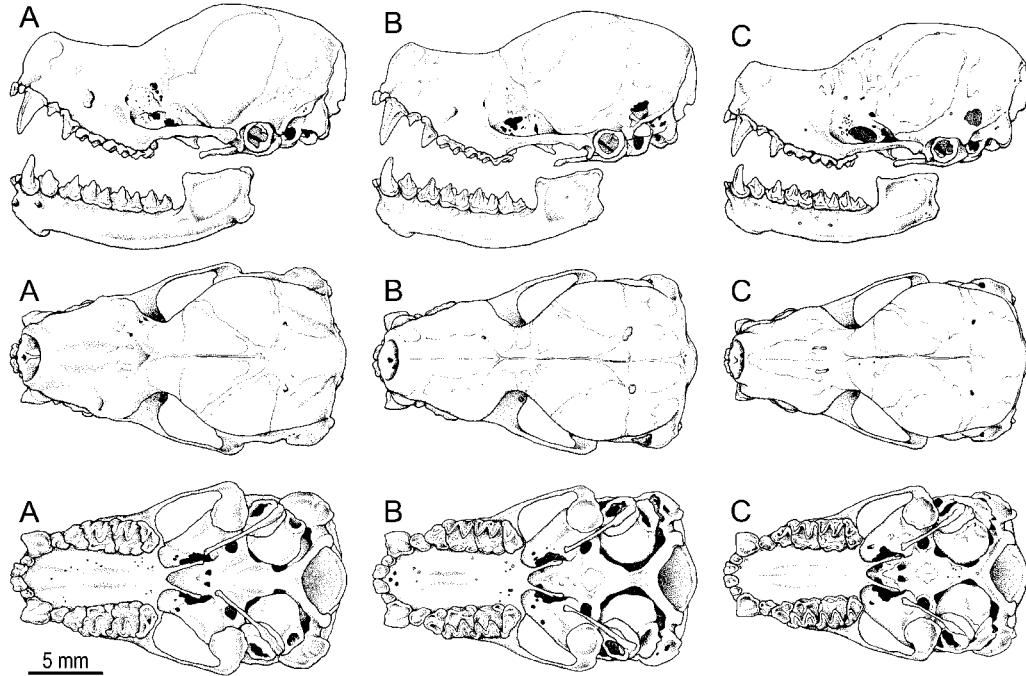


FIG. 1.—Lateral (top), dorsal (middle), and ventral (bottom) views of crania, and lateral views of mandibles, of the 3 taxa of the genus *Pteronotus* subgenus *Phyllodia* occurring in Venezuela: *rubiginosus* (A; MBUCV 3724), *fuscus* (B; CVULA 8122), *paraguayensis* (C; CVULA 8145).

(Vaughan and Hill 1996). Five of these taxa occur on the mainland: *P. parnellii mexicanus* in Mexico north of Istmo de Tehuantepec; *P. p. mesoamericanus* in Mexico south of Istmo de Tehuantepec, Central America north of Honduras, western Honduras, Pacific coasts of Nicaragua, Costa Rica, and Panamá; *P. p. rubiginosus* in eastern Honduras, Atlantic coasts of Nicaragua, Costa Rica, Panamá, South America south of the

Río Orinoco, Trinidad, the Guayanas, and Matto Grosso do Sul in Brazil; *P. p. fuscus* in Caribbean regions of Colombia and Venezuela, except for the Península de Paraguaná; and *P. p. paraguayensis* in the Península de Paraguaná (Simmons 2005; Simmons and Conway 2001; Smith 1972). These taxa differ substantially in size (Linares and Ojasti 1974; Smith 1972; Fig. 1) and, based on genetic, morphological, and distributional data it has been argued that mainland *Phyllodia* represent several “cryptic” species that are not conspecific with West Indian *Phyllodia* (Dávalos 2006; Van Den Bussche and Weyandt 2003).

Here, we evaluate the morphometric variation among Venezuelan samples of *Phyllodia*, including *Pteronotus p. rubiginosus*, *P. p. fuscus*, and *P. p. paraguayensis* (Fig. 1). In Venezuela, these taxa have allopatric distributions (Fig. 2): *P. p. fuscus* is found north of the Río Orinoco (including the Isla de Margarita) but is absent from the Península de Paraguaná and the Llanos (savannas); *P. p. paraguayensis* is endemic to the Península de Paraguaná; and *P. p. rubiginosus* is known in the country only from localities south of the Río Orinoco, with the exception of 2 localities, just north of that river in Estado Apure (localities 11 and 12, Appendix I). Additionally, we discuss the conservation status of the form endemic to the Península de Paraguaná and suggest actions that should be carried out in order to guarantee the persistence of its populations.

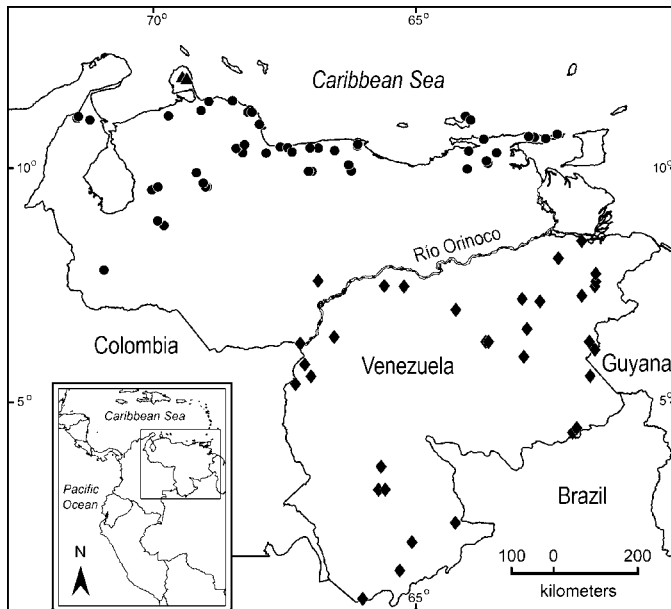


FIG. 2.—Map of Venezuela showing the position of geographic samples of *Pteronotus parnellii rubiginosus* (diamonds), *P. parnellii fuscus* (dots), and *P. p. paraguayensis* (triangles) used in this study. See Appendix I for localities and museum catalog numbers.

MATERIALS AND METHODS

Morphometric data.—In our procedures on animal care and use, we followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

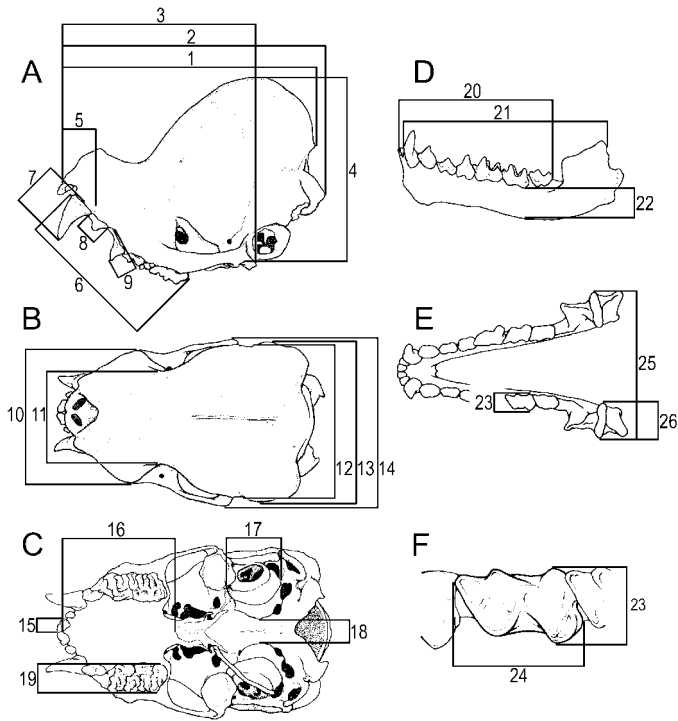


FIG. 3.—A) Lateral, B) dorsal, and C) ventral views of a cranium, and D, E) views of mandible and F) 2nd lower molar of *Mormoops megalophylla* (drawings taken from Gutiérrez 2004) showing the method used for obtaining craniodental measurements on mormoopid bats. Measurements: 1 = occipitonasal length, 2 = condylobasal length, 3 = zygorostr length, 4 = braincase depth, 5 = premaxillae–infraorbital foramen length, 6 = maxillary tooththrow length, 7 = upper canine height, 8 = upper PM3 length, 9 = upper PM4 height, 10 = rostral breadth, 11 = interorbital breadth, 12 = anterior braincase breadth, 13 = posterior braincase breadth, 14 = zygomatic breadth, 15 = upper 1st incisor breadth, 16 = palatal length, 17 = ectotympanic bulla length, 18 = basioccipital breadth, 19 = M3 breadth, 20 = mandibular tooththrow length, 21 = mandibular condylocanine length, 22 = mandibular depth, 23 = m2 breadth, 24 = m2 length, 25 = intercondylar breadth, 26 = mandibular condyle breadth.

We examined 267 specimens of adult *Pteronotus* (151 males and 116 females) from Venezuela (*P. p. rubiginosus*, $n = 125$; *P. p. fuscus*, $n = 117$; *P. p. paraguayensis*, $n = 25$; see Appendix I). For each specimen, we took 33 skeletal measurements, 26 craniodental (Fig. 3), 7 appendicular, and 4 standard external measurements. Most measurements have been previously used in taxonomic studies of small mammals (Anderson 2003; Handley 1988; McLellan 1984; Simmons and Handley 1998; Smith 1972; Velazco and Solari 2003), but others (identified with asterisks below) are probably used here for the 1st time. We employed digital calipers to take the occipitonasal length, condylobasal length, and the appendicular measurements to the nearest 0.01 mm. For all other skeletal measurements we used a micrometer in a Leica MZ-8 stereomicroscope ($10\times$ – $40\times$) to the nearest 10^{-4} mm. For specimens preserved as skin and skull, our only option was to record the standard external measurements from the specimen tag. For specimens preserved in alcohol, we retook standard external measurements (following Handley 1988) in order to

minimize measurement errors frequently associated with data on specimen tags (Blackwell et al. 2006). For all specimens, we recorded mass and geographic information regarding collection locality from either the specimen tag, museum catalog, or field notes. All measurements are expressed in millimeters, with the exception of mass, which is in grams.

The craniodental, mandibular, appendicular, and standard external measurements (Fig. 3; Appendix II) considered in this study are: occipitonasal length, greatest distance from the anteriormost projection of the nasal bones to the posteriormost portion of the occipital bone; condylobasal length, distance from the anteriormost projection of the premaxillae to the posteriormost projection of the exoccipital condyles; zygorostr length, distance from the anteriormost projection of the premaxillae to the posteriormost projection of the postglenoid process; braincase depth, distance from the juncture of the midline and frontal–parietal sutures to the inferiormost point of the glenoid fossae; premaxillae–infraorbital foramen length*, distance from the anteriormost projection of the premaxillae to the middle of the infraorbital foramen; maxillary tooththrow length, greatest crown length of the maxillary tooththrow measured from the anteriormost surface of the canine to the posteriormost surface of M3; upper canine height, the greatest height of the tooth, from its tip to the margin of the alveolus with the dentary bone; upper PM3 length*, the greatest length between the anterior and posterior margins of the premolar; upper PM4 height*, the greatest height of the premolar, from its crown to the margin of the alveolus with the dentary bone; rostral breadth, greatest breadth across the rostrum at a right angle to the longitudinal axis of the cranium; interorbital breadth, least width across the interorbital constriction at a right angle to the longitudinal axis of the cranium; anterior braincase breadth, greatest breadth across the lateral margins of the parietal at the anterior region to the suture coronalis (measured at a right angle to the longitudinal axis of the cranium); posterior braincase breadth, greatest breadth across the lateral margins of the parietal at the posterior region to the suture coronalis (measured at a right angle to the longitudinal axis of the cranium); zygomatic breadth, greatest distance across the zygomatic arches at right angle to the longitudinal axis of the cranium; upper 1st incisor breadth*, greatest breadth across the lateral margins of 1 of the upper 1st incisors at right angle to the longitudinal axis of the tooth; palatal length, distance from the anteriormost point of the premaxilla (excluding incisors) to the posterior margin of the horizontal process of the palatine, just in the midline of the horizontal process of the palatine; ectotympanic bulla length, greatest length across the anterior and posterior margins of 1 ectotympanic bulla; basioccipital breadth, least breadth across the lateral margins of the basioccipital; M3 breadth, greatest breadth across the lateral margins of M3 at a right angle to the longitudinal axis of the tooth; mandibular tooththrow length, greatest distance from the anteriormost surface of i1 to the posteriormost surface of m3; mandibular condylocanine length, greatest distance from the anteriormost point of the lip of the alveolus of 1 of the lower canines to the posteriormost point of 1 of the mandibular condyles; mandibular depth, greatest depth of the corpus at the level of m2 taken at the point of greatest depth; m2 breadth,

greatest breadth across the lateral margins of m2 at a right angle to the longitudinal axis of the tooth; m2 length, greatest length from the anteriormost point to the posteriormost point of m2; intercondylar breadth, greatest breadth across the external margins of the mandibular condyles; mandibular condyle breadth, greatest breadth across the lateral margins of 1 mandibular condyle; forearm length, distance from the elbow (measured from the tip of the olecranon process) to the wrist (including the carpals); 3rd metacarpal length, distance between the proximal and distal ends of the 3rd metacarpal; 1st phalanx of digit III length, distance between the proximal and distal ends of the 1st phalanx of digit III; 2nd phalanx of digit III length, distance between the proximal and distal ends of the 2nd phalanx of digit III; 4th metacarpal length, distance between the proximal and distal ends of the 4th metacarpal; 5th metacarpal length, distance between the proximal and distal ends of the 5th metacarpal; tibia length, distance from the proximal end of the tibia to the posterior (outer) base of the calcar; total length, distance from the tip of the snout to the tip of last caudal vertebra; tail length, distance from the base (dorsal flexure of tail) to the tip of the last caudal vertebra; hind-foot length, distance from the inner (anterior) edge of the base of calcar at its junction with the tibia to the tip of the claw of the longest toe; ear length, distance from the notch at the base of the ear to the tip of the ear.

Statistical analyses.—We conducted 2 principal component analyses (PCAs), 1 based on the craniodental measurements, and another on the appendicular measurements, in both cases using SPSS for Windows, version 11. To give equal weight to all variables, we used the correlation matrix of the respective data set (i.e., craniodental measurements or appendicular measurements) for these analyses (e.g., McGarigal et al. 2000). Because multivariate analyses require data sets to be complete, we estimated missing values (those not possible to measure because of partially broken bones). We performed such estimation through multiple regressions, using known values of other measurements as predictors (Bekele et al. 1993; De Marinis 1995; De Marinis et al. 1990; Fandos and Reig 1993; Giannico and Nagorsen 1989; Wiig 1989). We conducted multiple regression analyses using Microsoft Excel 2003 (Microsoft Corp., Redmond, Washington). Using data from the 3 taxa pooled together, we centered and standardized data for each measurement by subtracting its corresponding mean and dividing by its standard deviation.

In contrast with most other studies, our main objective in conducting PCAs was not to reduce dimensionality by discarding lower variance components, but to dissect variation in size from variation in shape, which requires taking into account all components. When a PCA is performed on linear body measurements, the 1st component (PC1) represents a size factor, and each of the remaining components represents a unique shape factor (e.g., Anderson 2003; Chase et al. 2002; De Marinis 1995; Jolicoeur and Mosimann 1960; Lorenzo et al. 2004; Molina and Molinari 1999; Rohlf and Bookstein 1987; Schonewald et al. 1985). However, there are exceptions (e.g., Anderson and Jarrín-V. 2002; Pardiñas et al. 2005). Hence, only after inspecting PCA variable loadings, we interpreted the 1st component of each PCA as a size factor, and subsequent

components as shape factors (see “Results” for the criteria that we used). As a rule of thumb, when sample size exceeds 200, as is the case for both our craniodental and appendicular data, PCA variable loadings greater than or equal to ± 0.14 and ± 0.18 are recommended, respectively, for the 5% and 1% significance levels (McGarigal et al. 2000).

To visualize size differences among taxa, we plotted PCA scores for specimens on a scatter graph using as axes the craniodental PC1 and the appendicular PC1. We used standard deviations to equalize the units and lengths of both axes. We tested for significance of differences in size among taxa comparing means of scores for specimens on PC1 of each PCA through 2-tailed *t*-tests. Additionally, we conducted 2-tailed *t*-tests to compare means of measurements among taxa. Descriptive statistics of measurements are shown in Appendix II.

To classify specimens according to shape, we performed a cluster analysis for each data set. Each cluster analysis was based on scores for specimens in all components of PCA except the 1st (i.e., PC2–PC n , where n = number of measurements), which was excluded for being a size factor. We used average linkage as an agglomerative technique and Euclidian distance as a measure of dissimilarity. We performed cluster analyses using SPSS for Windows, version 11, and we represented the results of such analyses in the form of dendrograms. We used standard deviations to equalize the units and lengths of dendrogram scales. We joined all the specimens in each main ramification of each dendrogram into a single group. We use the term “branch” to refer to each of such groups.

To quantify the proportional contribution of each variable to overall differences in shape, we calculated its communality, which equals the sum of the squared loadings of the variable in the components of interest (McGarigal et al. 2000), in our case PC2–PC n . In PCAs based on the correlation matrix, the total communality of any variable (i.e., the sum of its squared loadings in all components) equals unity (McGarigal et al. 2000). Therefore, the proportional contribution of each variable to differences in size (i.e., communality in PC1 = squared loading of the variable in PC1) is simply the complement of its communality in PC2–PC n .

RESULTS

Analyses of size.—For each PCA, the loadings of PC1 are all of the same sign (Tables 1 and 2). Hence, we interpret PC1 to represent a size axis, with larger specimens having higher scores because the signs of the loadings are all positive (see Anderson 2003). These components explain 59.56% of the variance of craniodental measurements and 76.95% of the variance of appendicular measurements (Tables 1 and 2). Sample dispersion along the 2 axes, which represent craniodental (x-axis) and appendicular (y-axis) sizes, indicate differences among taxa (Fig. 4), with a remarkable separation of *Pteronotus parnellii paraguayensis* from the larger *P. p. fuscus* and *P. p. rubiginosus*, and with some overlap between the latter 2 taxa.

Two-tailed *t*-tests comparing mean scores for specimens in the craniodental PC1 (Table 1) indicate that *Pteronotus*

TABLE 2.—Results of the principal components (PC) analysis of appendicular measurements of Venezuelan *Phyllodia* ($n = 245$). Components 6 and 7 are omitted because together they represent less than 10% of total shape variance. Figures in bold indicate significant ($P \leq 0.05$) loadings within each shape-relevant component. The single italic communality (≥ 0.5) corresponds to the only variable that is more important in determining shape differences than in determining size differences.

	Loadings					Communality (PC2–PC7)
	PC1	PC2	PC3	PC4	PC5	
Forearm length	0.95	–0.08	–0.05	–0.18	–0.04	0.10
Third metacarpal length	0.84	–0.20	0.46	0.15	0.15	0.29
First phalanx of digit III length	0.88	0.06	–0.17	0.40	–0.15	0.23
Second phalanx of digit III length	0.60	0.79	0.03	–0.03	0.10	<i>0.64</i>
Fourth metacarpal length	0.97	–0.04	0.04	–0.11	–0.13	0.06
Fifth metacarpal length	0.96	–0.05	0.06	–0.18	–0.12	0.08
Tibia length	0.87	–0.23	–0.34	–0.01	0.26	0.24
% total variance	76.95	10.44	5.16	3.76	2.19	
% cumulative total variance	76.95	87.39	92.54	96.31	98.50	
% shape (PC2–PC7) variance	0	45.29	22.37	16.31	9.52	
% cumulative shape variance	0	45.29	67.66	83.97	93.49	

parnellii paraguayensis is significantly smaller than same-sex *P. p. fuscus* ($P \leq 0.001$) or *P. p. rubiginosus* ($P \leq 0.001$), and that *P. p. fuscus* is significantly smaller than same-sex *P. p. rubiginosus* ($P \leq 0.001$). In the 3 taxa, males are significantly larger than females (*P. p. paraguayensis*, $P \leq 0.01$; *P. p. fuscus* and *P. p. rubiginosus*, $P \leq 0.001$).

Two-tailed *t*-tests comparing mean scores for specimens in the appendicular PC1 (Table 2) indicate that *Pteronotus parnellii paraguayensis* is significantly smaller than same-sex *P. p. fuscus* ($P \leq 0.001$) or *P. p. rubiginosus* ($P \leq 0.001$), and

that *P. p. fuscus* is significantly smaller than same-sex *P. p. rubiginosus* ($P \leq 0.001$). In *P. p. fuscus*, females are significantly larger than males ($P \leq 0.01$). In both *P. p. paraguayensis* and *P. p. rubiginosus*, we did not find significant differences between the sexes.

Two-tailed *t*-tests comparing separately the mean of each of the 26 craniodental and 7 appendicular measurements (Appendix II) indicate that *Pteronotus parnellii paraguayensis* is significantly smaller ($P \leq 0.05$) than same-sex *P. p. fuscus* in most measurements (exceptions for males are premaxillae–infraorbital foramen length, ectotympanic bulla length, upper PM3 length, and mandibular condyle breadth; exceptions for females are premaxillae–infraorbital foramen length, basioccipital breadth, upper 1st incisor breadth, upper PM3 length, M3 breadth, mandibular condyle breadth, and the 3rd metacarpal length). In equivalent comparisons, we found both *P. p. paraguayensis* and *P. p. fuscus* to be significantly smaller ($P \leq 0.05$) than same-sex *P. p. rubiginosus* in all measurements.

Analyses of shape.—Excluding PC1 (=size) from each PCA, subsequent components explain 40.44% of the variance in craniodental, and 23.05% of the variance in appendicular measurements (Tables 1 and 2). These components (PC2–PC n) represent axes that compare shape because loadings are both positive and negative (Tables 1 and 2). Dendrograms based on Euclidian distances in these components (PC2–PC n) are shown in Fig. 5A (craniodental PCA) and Fig. 5B (appendicular PCA). These dendrograms classify specimens according to shape.

Our results show an exceptionally clear-cut shape differentiation of *Pteronotus parnellii paraguayensis* with respect to the other 2 *Phyllodia* taxa occurring in Venezuela. Regarding craniodental shape (Fig. 5A), the 25 specimens of *P. p. paraguayensis* clustered together in a separate major branch (composed of the lower rank branches *j*–*l*), in which none of the 222 specimens of the other 2 taxa were included. Regarding appendicular shape (Fig. 5B), all but 1 of the 25 specimens of *P. p. paraguayensis* clustered together in a separate major branch (composed of the lower rank branches *i*–*k*) in which only 1 of the 98 specimens of *P. p. fuscus* and none of the 122

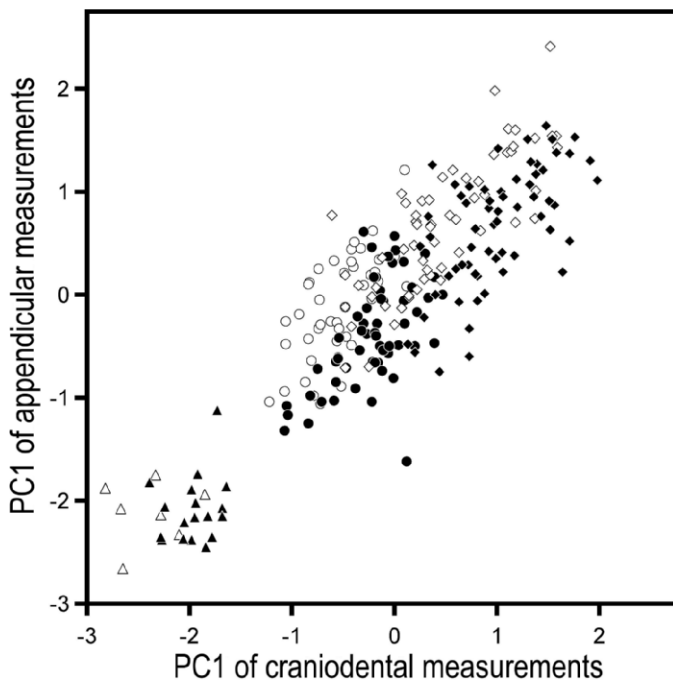


FIG. 4.—Scores of specimens on the 1st components of the principal component analyses performed with craniodental (x axis) and appendicular (y axis) measurements. *Pteronotus parnellii rubiginosus* (males, solid diamonds; females, open diamonds), *P. parnellii fuscus* (males, solid dots; females, open dots), and *P. p. paraguayensis* (males, solid triangles; females, open triangles).

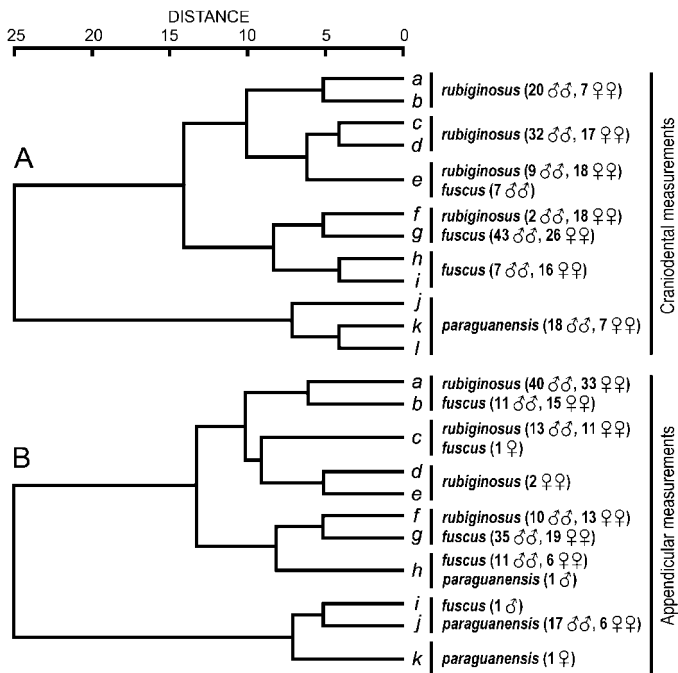


FIG. 5.—Dendrograms showing shape similarities among specimens of *Pteronotus parnellii rubiginosus*, *P. parnellii fuscus*, and *P. p. paraguayensis* according to A) craniodental and B) appendicular measurements. Dendrograms resulted from cluster analysis based on specimen scores in all components of principal components analysis, except principal component 1. Average linkage was used as an agglomerative technique and Euclidian distance as a measure of dissimilarity.

specimens of *P. p. rubiginosus* were included. The remaining branches of both dendrograms (Figs. 5A and 5B) contain mixtures of specimens of *P. p. fuscus* and *P. p. rubiginosus*, indicating that these taxa are not easily distinguished from each other on the basis of craniodental and appendicular shapes. However, mixtures are uneven. In the craniodental dendrogram (Fig. 5A), 103 of the 123 specimens of *P. p. rubiginosus* are in the 1st (composed of lower rank branches a–e) and 92 of the 99 specimens of *P. p. fuscus* are in the 2nd (composed of lower rank branches f–i) of 2 major branches. In the appendicular dendrogram (Fig. 5B), 99 of the 122 specimens of *P. p. rubiginosus* are in the 1st (composed of lower rank branches a–e) and 71 of the 98 specimens of *P. p. fuscus* are in the 2nd (composed of lower rank branches f–h) of 2 major branches.

The segregation of *Phyllodia* taxa according to craniodental shape (Fig. 5A) is a consequence of relatively numerous components of rather similar importance because variance decays slowly as component rank increases (Table 1). Therefore, our set of craniodental measurements is rich in nonredundant shape information. The shape comparisons involved in each of these components are straightforward (Table 1): for example, PC2 is mostly a contrast of upper canine height, upper PM4 height, and to a lesser degree interorbital breadth and mandibular condylocanine length (highest positive loadings), with ectotympanic bulla length, M3 breadth, and intercondylar breadth

(lowest negative loadings). The picture that emerges by considering simultaneously all significant loadings is clear: dental and mandibular variables predominate in all shape components. The communalities of the variables summarize the situation: the major determinants (underlined values) of overall shape differences include 4 dental variables, 3 mandibular variables, and 2 cranial variables.

The segregation of *Phyllodia* taxa according to appendicular shape (Fig. 5B) follows a clear pattern (Table 2): 2 variables, the lengths of bones of digit III and tibia, predominate in all shape components. The communalities of the variables indicate that the major determinant of shape differences is the 2nd phalanx of digit III, with the metacarpal and the 1st phalanx of the same digit and the tibia making more moderate contributions.

DISCUSSION

Phyllodia in mainland Venezuela.—Based on the molecular data, Dávalos (2006) assigned 3 smaller Greater Antillean subspecies (*parnellii*, *pusillus*, and *portoricensis*) to *Pteronotus parnellii*, and 3 larger mainland subspecies (*rubiginosus*, *mesoamericanus*, and *mexicanus*) to *P. rubiginosus*. Dávalos (2006) also showed that large *Phyllodia* from Suriname and French Guiana probably represent a separate species more closely related to Greater Antillean forms than to other mainland forms. According to this taxonomic scheme, the correct name for Venezuelan *Phyllodia* occurring south of the Río Orinoco should be *P. rubiginosus rubiginosus* (Dávalos 2006). However, in the present paper we have maintained the traditional name *P. parnellii rubiginosus* because absence of molecular data for *P. p. fuscus* and *P. p. paraguayensis* impedes defining the position of all 3 Venezuelan taxa in the updated nomenclature. Molecular comparisons with other North, Central, and South American *Phyllodia*, and with Greater Antillean *P. parnellii*, are needed to elucidate the phylogenetic relationships of *P. p. fuscus* and *P. p. paraguayensis*.

In most of Venezuela, *Pteronotus parnellii fuscus* and *P. p. rubiginosus* show disjunct distributions, with no records from the Llanos savanna corridor (Fig. 2; Appendix I). Absence in the Llanos cannot be an artifact attributable to poor sampling because *Phyllodia* is easy to collect with mist nets, and because the Venezuelan Llanos have been sufficiently sampled (see Handley 1976; Ibáñez 1981). The 2 taxa are potentially parapatric or sympatric only in the sylvatic northeast of the country, especially considering that *Pteronotus parnellii fuscus* occurs in the eastern portion of the Cordillera de la Costa, and in the Península de Paria (localities 64, 65, and 70–74, Appendix I), and that *P. p. rubiginosus* occurs in the Orinoco delta (Linares and Rivas 2004) and in Trinidad (Smith 1972).

Specimens of *Phyllodia* collected just north of the Río Orinoco (Estado Apure; localities 11 and 12, Appendix I) are considerably smaller than typical *P. p. rubiginosus* from Estados Amazonas and Bolívar (Appendix II). This has at least 2 alternative explanations: *Phyllodia* from Estado Apure could be an isolated population of the smaller *P. p. fuscus*, or could be an undescribed subspecies related to *P. p. rubiginosus*. In

the absence of genetic data, we provisionally assign Apurean *Phyllodia* to *P. p. rubiginosus* (Appendices I and II).

Phyllodia uses an echolocation pattern consisting of 4 or 5 harmonics, each composed of a long constant-frequency component flanked by brief frequency modulations (Vater et al. 2003). This pattern is optimal for detecting flying insect prey amid clutter-producing background, namely dense vegetation (Fenton et al. 1995; Kalko et al. 1998; Kössl et al. 1999; Neuweiler 1990; Roverud et al. 1991; Schnitzler and Kalko 1998; Vater et al. 2003). Therefore, dependence on forests may be responsible for the separation of *Pteronotus parnellii fuscus* and *P. p. rubiginosus* by the savanna corridor of the Venezuelan Llanos and Apurean *Phyllodia* from typical *P. p. rubiginosus* by savannas and the Río Orinoco.

Phyllodia in the *Península de Paraguaná*.—Linares and Ojasti (1974) did not describe the *Phyllodia* endemic to Paraguaná at the species level because they based their diagnosis on differences in size and coloration, and because at the time all members of this subgenus were thought to belong to a single species, *Pteronotus parnellii*, subdivided into numerous subspecies, including *P. parnellii mexicanus* (now *P. rubiginosus mexicanus*—Dávalos 2006), which is only slightly larger than *P. paraguayensis*, and Greater Antillean *P. parnellii* (now the only true *P. parnellii*—Dávalos 2006), which are even smaller than *P. p. paraguayensis*. Although we used a larger sample and different specimens, and more measurements, our results confirm those of Linares and Ojasti (1974) regarding the substantial size difference between *P. p. paraguayensis* and *P. p. fuscus* (Figs. 1 and 4). All the specimens of *P. p. paraguayensis* were smaller than the smallest specimen of *P. p. fuscus* in overall size, and only 1 specimen was similar to the smallest specimen of *P. p. fuscus* in appendicular size (Fig. 4). Our results also show that *P. p. paraguayensis* is considerably different from both *P. p. fuscus* and *P. rubiginosus* in its craniodental shape (no overlap detected with the other 2 taxa; Fig. 5A) and appendicular shape (little overlap with the other 2 taxa; Fig. 5B). The marked differentiation in size and shape involving multiple characters that we now know to exist between *P. p. paraguayensis* and *P. p. fuscus* most likely is the result of little or no recent gene flow between them, in spite of the 2 forms being geographical neighbors (the Istmo de Médanos, which separates them, is only 30 km in length). Therefore, in accordance with the recommendation of assigning distinct species rank to sharply differentiated taxa occurring in close proximity (Helbig et al. 2002), we propose the elevation of *P. p. paraguayensis* to full species status.

Qualitatively, *Pteronotus paraguayensis* can be distinguished from *P. parnellii fuscus* and *P. p. rubiginosus* by a proportionally higher braincase; broader skull, rostrum, palate, and postpalatal extension; less-crowded upper incisors; mandible with a thinner corpus; and a pale yellowish brown, as opposed to dark brown, dorsal and ventral fur. Additionally, there is a substantial difference between the frequency of echolocation signals of *P. paraguayensis* and that of *P. p. fuscus*. The constant component of the echolocation signals of *P. paraguayensis* from Cueva de Piedra Honda (locality 86, Appendix I) has a frequency of approximately 68 kHz (J.

Ochoa-G., in litt.). In contrast, in the geographically close Cueva de Chipare, near Istmo de Médanos (locality 50, Appendix I), and in other localities of Venezuela, the constant component of the echolocation signals of *P. p. fuscus* has a frequency of approximately 62 kHz (J. Ochoa-G., in litt.). The difference (6 kHz) between these 2 taxa is larger than the intraspecific differences known for currently recognized species of *Phyllodia* (E. Kalko, in litt.; J. Ochoa-G., in litt.).

Examination of our data regarding the morphometric variability of the Venezuelan mormoopid bats (see Gutiérrez 2004) indicates that populations of other mormoopids occurring on the *Península de Paraguaná*, *Pteronotus davyi* and *Mormoops megalophylla*, do not differ taxonomically with respect to mainland populations. Because *P. paraguayensis* represents a notable case of endemism, it is interesting to ask why the other 2 species of mormoopids present in Paraguaná have not differentiated from mainland populations, whereas *P. paraguayensis* is so highly differentiated. The answer may have an ecological basis. All mormoopids but those of the subgenus *Phyllodia* typically fly in open areas, such as savannas or over the forest canopy (E. Gutiérrez and J. Molinari, in litt.; see Bateman and Vaughan 1974; Handley 1976), making it difficult to collect them with mist nets. In contrast, bats of the subgenus *Phyllodia* forage mostly inside forests and their flights across areas with little arboreal vegetation might correspond to movements between roosts and foraging sites (E. Gutiérrez and J. Molinari, in litt.; see Bateman and Vaughan 1974). This situation suggests that *P. paraguayensis* may limit its movements to flight within the major forested areas of the peninsula (Cerro Santa Ana, Fila de Monte Cano, and Cerro Colorado), and between such forests and the caves where this species roosts. Bateman and Vaughan (1974) observed *Phyllodia* flying at least 3.5 km from roosts to foraging sites, but no data exist regarding the movements of *P. paraguayensis*. However, because the vegetation of the Istmo de Médanos consists mostly of grasses and very widely scattered shrubs, we consider it unlikely that *P. paraguayensis* or *P. p. fuscus* would fly over the xeric Istmo de Médanos to reach each other's distributional range, a situation that may have promoted the differentiation of *P. paraguayensis*.

Pteronotus paraguayensis is not the only taxon endemic to the *Península de Paraguaná*. A spiny pocket mouse (*Heteromys oasicus*), a subspecies of yellow warbler (*Dendroica petechia paraguanae*), a lizard (*Lepidoblepharis montecanoensis*), a mygalomorph spider (*Chromatopelma cyaneopubescens*), and a palm (*Geonoma paraguayensis*) also have been reported as endemic to the peninsula (Anderson 2003; Bisbal-E. 1990; Klein and Brown 1994; Markezich and Taphorn 1994; Raven 1985; Romero 1989; Tamayo 1971). Furthermore, the snake *Leptodeira bakeri* is found only in Paraguaná and on the nearby island of Aruba (Mijares-Urrutia et al. 1995), and a subspecies of whiptail lizard (*Cnemidophorus lemniscatus splendidus*) is currently known only from Paraguaná (Markezich et al. 1997).

Conservation.—Colonies of *Pteronotus paraguayensis* are known from only 3 caves on the *Península de Paraguaná* (Cueva del Guano, Cueva de Piedra Honda, and Cueva del

Balneario El Pico—Linares and Ojasti 1974; Martino et al. 1997; Matson and Brown 1974; J. Ochoa-G., in litt.; E. Gutiérrez and J. Molinari, in litt.). Other species of bats also roost at these caves, including *P. davyi*, *Mormoops megalophylla*, *Natalus tumidirostris*, and *Leptoncycteris curasoae* (Martino et al. 1997, 1998; Molinari et al. 2005). These caves are located near towns and are easily accessible to local inhabitants (SVE 1972, 1973a, 1973b). In spite of the fact that vampire bats do not occur in Península de Paraguaná, locals often assume that all bat species are sanguivorous, which leads to a general tendency to exterminate them near towns or farms. In August 1997, we found thousands of dead bats, including young of the 4 species aforementioned and *P. paraguayensis*, as a result of car tires that were set aflame at the entrance of the Cueva del Guano. Similar situations could occur in Cueva del Pico, where burned car tires have been found (J. Ochoa-G., in litt.). However, since 2002, a campaign for the conservation of cave-dwelling bats has been carried out at Paraguaná by the Asociación Venezolana para la Conservación de las Areas Naturales (ACOANA), Bat Conservation International (BCI), and local communities (J. Ochoa-G., in litt.). One of the efforts of this campaign was the installation of a gate at the entrance to Cueva de Piedra Honda in 2003. This gate has prevented unauthorized persons from entering the cave. Reduced vandalism has apparently led to a substantial increase in the number of bats roosting in this cave (J. Ochoa-G., in litt.).

Pteronotus paraguayensis has been collected in only 4 localities. Its distributional range is less than 5,000 km². Therefore, in application of the World Conservation Union criteria (IUCN 2001), the species should be considered endangered, and merits special conservation measures. These measures should include an effective protection of caves used by the species as roosts, and of the major areas with dense thorn forest in which the species forages, namely Cerro de Santa Ana, at present considered a "Monumento Natural," and Fila de Monte Cano (Gutiérrez and Molinari, in press).

RESUMEN

En Venezuela, los murciélagos del subgénero *Phyllodia* del género *Pteronotus* (Mormoopidae) están divididos en 3 taxa, *Pteronotus parnellii fuscus*, *P. p. paraguayensis*, y *P. p. rubiginosus*. Comparamos estos taxa con respecto a tamaño y forma corporales mediante análisis de componentes principales y análisis de agrupamiento aplicados a 26 medidas craneodentarias y 7 medidas apendiculares (extremidades anteriores y posteriores) de 267 ejemplares venezolanos. Los análisis indican que la subespecie endémica de la Península de Paraguaná, *P. p. paraguayensis*, difiere de los otros 2 taxa en ser considerablemente más pequeña y en tener formas craneodentaria y apendicular marcadamente distintas; y aunque en menor grado, *P. p. fuscus* y *P. p. rubiginosus* también difieren notablemente uno del otro en estos aspectos morfométricos. Nuestros resultados justifican elevar a *P. p. paraguayensis* al rango de especie. La fuerte dependencia que los miembros de *Phyllodia* muestran con respecto al bosque podría

explicar los elevados niveles de variabilidad morfológica (este artículo) y molecular (estudios previos) del subgénero. La reducida distribución geográfica, población pequeña, y estatus de especie plena de los *Phyllodia* de la Península de Paraguaná justifican medidas de conservación especiales.

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APPENDIX I

Specimens examined are housed in the following institutions: Colección de Vertebrados de la Universidad de Los Andes (CVULA), Mérida; Museo de Biología de la Universidad Central de Venezuela (MBUCV), Caracas; Museo de Ciencias Naturales de Guanare (MCNG), Guanare; Museo de la Estación Biológica de Rancho Grande (EBRG), Maracay; and Museo de Historia Natural La Salle (MHNLS), Caracas. For each taxon, specimens are listed according to secondary political division, locality, coordinates, elevation, and museum catalog number. Asterisks indicate specimens whose current catalog numbers are different from those reported by Gutiérrez (2004). We provide coordinates only for those localities that we found on maps [in brackets] or for which we have global positioning system data.

Pteronotus parnellii rubiginosus.—AMAZONAS: (1) Vía a Nueva Jerusalem, 8 km E carretera Puerto Ayacucho–El Burro, 30 km N de Puerto Ayacucho, 05°51'N, 67°24'W (CVULA 8155*); (2) San Pedro de Cataniapo, Río Cataniapo, [05°35'N, 67°16'W], 105 m (MHNLS 6249); (3) “Raya,” 32 km SSE de Puerto Ayacucho, [05°25'N, 67°36'W], 135 m (EBRG 4894, 4895); (4) Belén, Río Cunucunuma, 56 km NNW de la Esmeralda, [03°39'N, 65°46'W], 150 m (EBRG 4926, 4927); (5) Tamatama (Río Orinoco), 2 km arriba de la boca del Brazo Casiquiare, [03°10'N, 65°49'W], 135 m (EBRG 4873); (6) Río Orinoco, 19 km W La Esmeralda, [03°09'N, 65°41'W], 120 m (MHNLS 9082); (7) Base Cerro Sarisariñama, comunidad indígena Canaracuni, [02°27'N, 64°11'W], 400 m (EBRG 23285, 23286); (8) Mirakapiwei, Río Mavaca, campamento base de la expedición Tapirapeco, [02°02'N, 65°07'W], 270 m, (MBUCV 5249); (9) Alto Río Siapa, [01°26'N, 65°22'W], 525 m (EBRG 18338); (10) Campamento base Cerro La Neblina, Río Mawarinuma, 1.5 km S Neblina, [00°50'N, 66°10'W], 140 m (MBUCV 3264–3266, 3717, 3720–3729). APURE: (11) Hato Cariben, Río Cinaruco, 32 km NE Puerto Páez, [07°37'N, 67°07'W], 76 m (EBRG 4914); (12) Cerro de Los Murciélagos, 8 km NW Puerto Páez, [06°17'N, 67°30'W], 76 m (EBRG 4915–4917). BOLÍVAR: (13) Bajo Caroní, 200 m al Sur del Paso Cachuachi, [08°07'N, 62°52'W], 210 m (MHNLS 10143); (14) Hato El Chaguaramal, 10 km NW El Palmar, 08°06'N, 61°59'W, 360 m (CVULA 8156*); (15) Río Retumbo, a 10 km E Paso Carhuachi, Cuenca Baja del Río Carona, [08°05'N, 62°46'W] (MHNLS 10160); (16) Reserva Forestal Imataca, unidad V, campamento El Buey, CVG, [07°46'N, 61°11'W], 400 m (EBRG 19042, 19043, 22193, 22278, 22279); (17) Reserva Forestal Imataca, unidad V, compartimiento C1, [07°36'N, 61°11'W], 180 m (EBRG 19026–19032, 19053); (18) Reserva Forestal Imataca, compartimiento P2, [07°30'N, 61°12'W], 180 m (EBRG 19025, 19033–19037, 19039); (19) Hato La Florida, 11.4 km S and 45 E Caicara, [07°31'N, 65°42'W], 50 m (EBRG 4869, 4870); (20) Hato La Florida, 14 km S and 45 E Caicara, [07°30'N, 65°42'W], 50 m (EBRG 4933); (21) Hato La Florida, 15 km S and 45 E Caicara, [07°30'N, 65°42'W], 50 m (EBRG 4934); (22) 20 km NW Maripa, entre Ríos Caura y Sipao, [07°30'N, 65°17'W], 40 m (EBRG 17401, 17393); (23) Tumeremo, [07°18'N, 61°29'W], 250 m (CVULA 3920–3923); (24) Represa Guri, San Luis, [07°14'N,

62°45'W] (EBRG 11593–11595, 11597–11601, 11603, 11604, 11606–11609, 11611, 11614–11619, 11628, 11630); (25) Los Patos, 28 km SE El Manteco, [07°11'N, 62°22'W], 350 m (EBRG 4852, 4921); (26) Reserva Forestal Caura, Boca del Río Nichare, [07°00'N, 64°10'W], 100 m (EBRG 22907, 22908, 22928); (27) Río Parapapay, [06°36'N, 62°39'W], 430 m (EBRG 18017); (28) Los Pijiguaos, 160 km SW Caicara, [06°25'N, 66°46'W], 700 m (MHNLS 8285, 8393–8395); (29) Piedra Pintada, [06°19'N, 63°28'W], 265 m (EBRG 17980); (30) Maraba, [06°19'N, 63°32'W], 290 m (EBRG 17978, 17979, 17981); (31) El Manaco, 59 km SE El Dorado, km 74, [06°19'N, 61°19'W], 150 m (EBRG 4854, 4904); (32) 85 km SSE El Dorado, km 125, [06°09'N, 61°22'W] (EBRG 4853); (33) Parque Nacional Canaima, Río Cucurital, confluencia con el Río Purumay, [06°00'N, 62°43'W] (MHNLS 11043, 11059, 11060, 11078); (34) Carretera El Dorado–Santa Elena, km 125, [05°36'N, 61°18'W], 1,050 m (MBUCV 3852, 3853, 3855, 3857, 3858, 3860); (35) El Paují, carretera Santa Elena–Icabarú, [04°29'N, 61°35'W], 900 m (MBUCV 3854, 3856, 3859); (36) Cumbre del Abismo, Fundo Cantarrana, cercano a Icabarú, [04°26'N, 61°43'W], 960 m (MHNLS 6957). DELTA AMACURO: (37) Desembocadura del Caño Acoima al Río Grande, frente al poblado “El Toro,” a 5 km S “El Toro,” [08°29'N, 61°29'W], 5 m (MHNLS 9966, 9967).

Pteronotus parnellii fuscus.—ARAGUA: (38) Ocumare de la Costa, [10°26'N, 67°46'W] (EBRG 1819); (39) Parque Nacional Henri Pittier, Rancho Grande, 12 km NW Maracay, [10°21'N, 67°41'W], 1,100 m (MBUCV 979, 980); (40) Base Cerro Paso del Medio, aproximadamente a 10 km W San Sebastián, 09°56'N, 67°16'W, 460 m (CVULA 8102*); (41) Cueva Los Murciélagos, carretera San Juan de Los Morros–San Sebastián, 7 km W San Sebastián, [09°56'N, 67°19'W], 515 m (EBRG 2517, MBUCV 2212, 2213). BARINAS: (42) Cerro Alto, 2 km de La Soledad, [08°52'N, 70°33'W], 1,400 m (CVULA 6126); (43) Río Barragán, Barinitas, [08°47'N, 70°25'W], 440 m (CVULA 726). CARABOBO: (44) La Copa, 4 km NW Montalbán, [10°30'N, 68°42'W], 1,537 m (EBRG 4896); (45) Ensenada de Patanemo, [10°27'N, 67°55'W], 20 m (MHNLS 3952, 4039); (46) Embalse Río Morón, Campamento Palmichal, [10°19'N, 68°14'W] (EBRG 17085). DISTRITO CAPITAL: (47) Las Aguaitas, Hacienda El Limón, al Norte de la Colonia Tovar, [10°26'N, 67°18'W], 2,000 m (MHNLS 1710); (48) El Trapiche, cerca de El Limón, [10°26'N, 67°07'W], 1,280 m (MBUCV 1502). FALCÓN: (49) Campechano, cerca boca Río Hueque, municipio Píritu, [11°27'N, 68°57'W], 0 m (EBRG 22557); (50) Cueva de Chipare, cerca de Guaibacoa, 11°25'N, 69°28'W, 380 m (CVULA 8103*–8127*); (51) 16 km ENE Mirimire, cerca de La Pastora, [11°13'N, 68°34'W], 70 m (EBRG 4938, 4939); (52) Mirimire, cerca de La Pastora, [11°12'N, 68°37'W] (EBRG 4937); (53) 10 km SSW Urumaco, 11°07'N, 70°19'W, 50 m (CVULA 8101*); (54) Cuare, 10 km W Chichiriviche, [10°56'N, 68°22'W], 3 m (CVULA 3651); (55) Cerro La Danta, al Norte de La Soledad de Uria, Sierra de San Luis, Distrito Miranda, Parque Nacional Juan C. Falcón, [11°14'N, 69°36'W], 1,350 m (MHNLS 9469). GUÁRICO: (56) La

Vira, 57 km S and 49 km E Caracas, [09°57'N, 66°24'W], 620 m (EBRG 4922). LARA: (57) 10 km N El Tocuyo, caserío Boro, [09°55'N, 69°43'W], 528 m (EBRG 4906); (58) Parque Nacional Yacambú, Estación El Blanquito, 9 km [by road] SE Sanare, [09°42'N, 69°35'W], 1,600 m (CVULA 2692, 2694, 2698–2700, 2702, 2703; MBUCV 4869); (59) Parque Nacional Yacambú, La Blanquita, 17.5 km de Sanare, [09°39'N, 69°32'W] (EBRG 4249). MIRANDA: (60) Cueva Cajigal, SE Birongo, [10°31'N, 66°15'W], 250 m (MBUCV 68); (61) Cueva Walter Dupouy, 4 km SW Birongo, [10°29'N, 66°16'W], 195 m (EBRG 2516); (62) Turgua, [10°23'N, 66°45'W], 1,020 m (MBUCV 1503); (63) Agua Blanca, Parque Nacional Guatopo, [10°04'N, 66°28'W], 500 m (MBUCV 2945–2950). MONAGAS: (64) Caripe, cercanías de la Cueva del Guácharo, [10°10'N, 63°31'W], 1,050 m (EBRG 2515; MHNLS 1735, 1736, 2192, 2193; MBUCV 67); (65) Caripe, [10°07'N, 63°29'W], 860 m (MBUCV 432, 434–436, 438, 439, 441, 442, 444, 445, 447–449, 451, 452); (66) Hacienda El 53, carretera San Antonio–Mundo Nuevo, [09°59'N, 63°55'W], 650 m (MHNLS 1623, 1624). NUEVA ESPARTA: (67) Cueva Atagua, Cerro Atagua, Isla de Margarita, [11°06'N, 63°57'W] (MHNLS 592–595, 2345, 2347, 2348); (68) El Valle del Espíritu Santo, Isla de Margarita, [11°00'N, 63°55'W] (CVULA 2062); (69) 3 km S de La Asunción, cerca de La Aguada, Isla de Margarita, [11°01'N, 63°51'W], 50 m (EBRG 4859, 4860, 4928). SUCRE: (70) Uquire, Parque Nacional Península de Paria, [10°42'N, 62°00'W] (EBRG 20606); (71) Parque Nacional Península de Paria, NW Las Melenas, [10°41'N, 62°37'W], 680 m (EBRG 20604); (72) Los Mangos, Parque Nacional Península de Paria, 682 m (EBRG 20605); (73) Ensenada Cauranta, 10 km NE Güiría, [10°38'N, 62°15'W], 90 m (EBRG 11174, 11175); (74) 12 km NE de Güiría, Hacienda La Rosa, [10°38'N, 62°15'W] (EBRG 4881); (75) Península de Araya, carretera Cariaco–Chacopata, [10°37'N, 63°34'W], 5 m (MHNLS 6530); (76) Río Clavellinos, abajo de Embalse Clavellinos, municipio Ribero, [10°22'N, 63°54'W], 300 m (EBRG 23190); (77) Río Grande, Cueva de San Juan Antonio, [10°20'N, 63°18'W], 10 m (MHNLS 1499). TRUJILLO: (78) Embalse Agua Viva, [09°37'N, 70°33'W] (MCNG 2368); (79) 23 km N Valera, cerca de Agua Viva, [09°32'N, 70°40'W], 164 m (EBRG 4848). YARACUY: (80) Minas de Aroa, Aroa, [10°25'N, 68°52'W], 450 m (MHNLS 778); (81) Hacienda “El Ring” (MCNG 821). ZULIA: (82) Quebrada Santa Rosa, afluente Río Güasare, municipio Páez, [11°06'N, 72°15'W], 70 m (EBRG 21823); (83) Río Guasare, Estación El Carbón, municipio Mara, [11°04'N, 72°16'W], 50 m (EBRG 21773, 21799); (84) Hacienda San Benito, 7 km campamento Socuy–Carbozulia, municipio Mara, [approximately 11°04'N, 72°16'W] (EBRG 21538); (85) Campamento Canchano, 30 km W Carrasqueño, [11°02'N, 72°00'W], 50 m (CVULA 2674).

Pteronotus parnellii paraguayensis.—FALCÓN: (86) Cueva de Piedra Honda, Península de Paraguaná, 11°55'N, 70°01'W, 120 m (CVULA 8128*–8140*); (87) Cueva del Guano, cercanías de Pueblo Nuevo, Península de Paraguaná, 11°54'N, 69°56'W, 130 m (CVULA 8141*–8154*).

APPENDIX II

Measurements (in mm) of specimens examined of Venezuelan *Phyllodia* (see Appendix I for localities and museum catalog numbers). Descriptive statistics are: mean (minimum–maximum) standard deviation [sample size].

		<i>Pteronotus parnellii rubiginosus</i> (Amazonas, Bolívar, Delta Amacuro)		<i>Pteronotus parnellii rubiginosus</i> (Apure)	<i>Pteronotus parnellii fuscus</i>	<i>Pteronotus parnellii paraguaniensis</i>
	Sex					
Occipitonasal length	♂♂	22.5 (21.9–23.2) 0.3 [58]	21.7 (21.5–21.9) 0.3 [2]	21.5 (20.7–22.3) 0.3 [61]	19.9 (19.3–20.2) 0.2 [18]	
	♀♀	22.1 (21.1–22.9) 0.4 [54]	21.3 (21.4–21.5) 0.1 [2]	21.3 (20.7–21.8) 0.3 [44]	19.7 (19.0–20.3) 0.4 [7]	
Condylbasal length	♂♂	21.7 (21.1–22.6) 0.4 [59]	20.9 (20.8–21.1) 0.2 [2]	20.7 (19.9–21.8) 0.3 [61]	19.0 (18.3–19.4) 0.3 [18]	
	♀♀	21.4 (20.3–22.2) 0.4 [54]	20.5 (20.5–20.6) 0.0 [2]	20.5 (19.9–21.2) 0.3 [44]	18.9 (18.6–19.5) 0.3 [7]	
Zygorostr length	♂♂	16.1 (15.2–16.8) 0.4 [59]	15.6 (15.5–15.7) 0.1 [2]	15.3 (14.4–16.1) 0.3 [62]	14.1 (13.6–14.4) 0.2 [18]	
	♀♀	15.9 (14.9–16.6) 0.4 [55]	15.2 (15.3–15.4) 0.1 [2]	15.2 (14.4–15.8) 0.3 [44]	14.0 (13.6–14.6) 0.4 [7]	
Braincase depth	♂♂	10.0 (8.9–10.6) 0.4 [59]	9.7 (9.7–9.8) 0.1 [2]	9.3 (8.4–10.0) 0.4 [62]	8.5 (8.1–9.3) 0.3 [18]	
	♀♀	9.7 (8.7–10.4) 0.4 [52]	9.2 (9.5–9.8) 0.5 [2]	9.1 (8.4–10.1) 0.5 [44]	8.3 (8.1–8.5) 0.2 [7]	
Premaxillae–infraorbital foramen length	♂♂	5.3 (4.3–5.9) 0.3 [59]	5.2 (5.1–5.4) 0.2 [2]	5.2 (4.6–5.9) 0.3 [59]	4.9 (4.4–5.5) 0.3 [18]	
	♀♀	5.3 (4.7–5.9) 0.3 [54]	5.1 (5.1–5.2) 0.1 [2]	5.2 (4.4–5.6) 0.2 [43]	4.7 (4.4–4.9) 0.2 [7]	
Maxillary tooththrow length	♂♂	9.8 (9.3–10.9) 0.3 [58]	9.4 [1]	9.3 (8.8–9.7) 0.2 [62]	8.5 (8.1–8.7) 0.2 [18]	
	♀♀	9.6 (9.1–10.2) 0.3 [55]	9.5 (9.4–9.5) 0.1 [2]	9.2 (8.5–9.5) 0.2 [44]	8.5 (8.2–8.7) 0.2 [7]	
Upper canine height	♂♂	3.0 (2.6–3.3) 0.2 [52]	2.8 [1]	2.9 (2.2–3.1) 0.2 [59]	2.8 (2.5–2.9) 0.1 [18]	
	♀♀	2.7 (2.5–3.0) 0.1 [39]	2.5 [1]	2.7 (2.5–3.0) 0.1 [39]	2.7 (2.5–2.8) 0.1 [7]	
Upper PM3 length	♂♂	1.4 (1.3–1.5) 0.1 [58]	1.4 [1]	1.4 (1.2–1.5) 0.1 [58]	1.3 (1.1–1.9) 0.2 [18]	
	♀♀	1.4 (1.1–1.5) 0.1 [54]	1.4 (1.4–1.4) 0.0 [2]	1.3 (1.2–1.5) 0.1 [44]	1.2 (1.1–1.3) 0.1 [7]	
Upper PM4 height	♂♂	1.5 (1.1–1.7) 0.1 [58]	1.4 (1.3–1.5) 0.1 [2]	1.4 (1.1–1.6) 0.1 [58]	1.4 (1.2–1.5) 0.1 [18]	
	♀♀	1.4 (1.1–1.6) 0.1 [45]	1.3 (1.9–1.4) 0.1 [2]	1.4 (1.0–1.6) 0.1 [41]	1.3 (1.2–1.5) 0.1 [7]	
Rostral breadth	♂♂	8.7 (8.1–9.3) 0.3 [59]	8.5 (8.4–8.7) 0.2 [2]	8.2 (7.8–8.6) 0.2 [57]	7.6 (7.4–7.9) 0.1 [18]	
	♀♀	8.5 (7.8–9.3) 0.4 [55]	8.3 (8.3–8.3) 0.0 [2]	8.1 (7.8–8.5) 0.2 [39]	7.5 (7.4–7.6) 0.1 [7]	
Interorbital breadth	♂♂	4.6 (4.1–5.4) 0.2 [58]	4.7 (4.6–4.7) 0.1 [2]	4.4 (4.0–4.8) 0.2 [62]	4.3 (4.1–4.4) 0.1 [18]	
	♀♀	4.5 (4.2–4.8) 0.1 [54]	4.3 (4.4–4.5) 0.1 [2]	4.4 (4.0–4.9) 0.2 [43]	4.3 (4.3–4.4) 0.0 [7]	
Anterior braincase breadth	♂♂	11.1 (10.4–11.6) 0.2 [56]	11.1 (11.1–11.1) 0.00 [2]	10.7 (10.3–11.3) 0.2 [61]	10.3 (10.0–10.5) 0.1 [18]	
	♀♀	10.9 (10.4–11.4) 0.2 [54]	10.6 (10.6–10.6) 0.0 [2]	10.6 (10.1–10.9) 0.2 [44]	10.1 (10.0–10.3) 0.1 [7]	
Posterior braincase breadth	♂♂	10.3 (9.7–10.9) 0.3 [57]	10.1 (10.0–10.1) 0.1 [2]	9.9 (9.4–10.4) 0.2 [61]	9.4 (9.2–9.9) 0.1 [18]	
	♀♀	10.1 (9.5–10.6) 0.3 [55]	9.7 (9.7–9.7) 0.0 [2]	9.8 (9.3–10.3) 0.2 [44]	9.4 (9.1–9.5) 0.1 [7]	
Zygomatic breadth	♂♂	13.2 (12.5–13.9) 0.3 [57]	12.7 (12.4–13.1) 0.6 [2]	12.3 (11.1–12.9) 0.3 [61]	11.6 (11.2–11.9) 0.2 [18]	
	♀♀	12.9 (12.3–13.5) 0.3 [52]	12.3 (12.4–12.5) 0.2 [2]	12.3 (11.7–12.9) 0.3 [42]	11.4 (11.2–11.8) 0.2 [7]	
Upper 1st incisor breadth	♂♂	1.0 (0.9–1.0) 0.0 [59]	0.9 (0.9) 0.0 [2]	0.9 (0.9–1.0) 0.0 [62]	0.9 (0.8–0.9) 0.0 [18]	
	♀♀	1.0 (0.9–1.0) 0.0 [54]	0.9 (0.9–1.0) 0.1 [2]	0.9 (0.9–1.0) 0.0 [44]	0.8 (0.7–0.9) 0.1 [7]	
Palatal length	♂♂	10.4 (9.9–11.1) 0.3 [57]	10.1 (10.0–10.1) 0.1 [2]	9.9 (9.2–10.8) 0.3 [62]	8.9 (8.6–9.2) 0.2 [18]	
	♀♀	10.2 (9.7–10.9) 0.3 [54]	9.7 (9.9–10.0) 0.2 [2]	9.7 (9.2–10.2) 0.2 [44]	8.9 (8.7–9.0) 0.1 [7]	
Ectotympanic bulla length	♂♂	3.6 (3.2–3.9) 0.1 [55]	3.4 [1]	3.4 (3.1–3.6) 0.1 [54]	3.2 (3.0–3.4) 0.1 [18]	
	♀♀	3.5 (3.3–3.9) 0.2 [52]	3.4 (3.4–3.5) 0.0 [2]	3.4 (3.1–3.7) 0.1 [41]	3.2 (3.0–3.2) 0.1 [7]	
Basioccipital breadth	♂♂	1.2 (1.0–1.6) 0.1 [57]	1.1 (1.0–1.1) 0.1 [2]	1.0 (0.8–1.2) 0.1 [56]	0.8 (0.8–0.9) 0.0 [18]	
	♀♀	1.2 (0.9–1.5) 0.1 [53]	0.9 (1.0–1.1) 0.1 [2]	1.0 (1.0–1.2) 0.1 [42]	0.8 (0.8–0.9) 0.1 [7]	
M3 breadth	♂♂	2.3 (2.1–2.6) 0.1 [58]	2.2 (2.2–2.2) 0.0 [2]	2.3 (2.1–2.4) 0.1 [62]	2.0 (1.6–2.1) 0.1 [18]	
	♀♀	2.3 (2.0–2.5) 0.1 [55]	2.2 (2.2) 0.0 [2]	2.2 (2.0–2.4) 0.1 [44]	2.0 (1.9–2.3) 0.1 [7]	
Mandibular tooththrow length	♂♂	10.9 (10.5–11.4) 0.2 [58]	10.5 (10.5–10.5) 0.0 [2]	10.3 (9.9–10.9) 0.2 [56]	9.5 (9.3–9.9) 0.2 [18]	
	♀♀	10.7 (10.1–11.0) 0.2 [55]	10.3 [1]	10.3 (10.0–10.6) 0.2 [38]	9.5 (9.1–9.8) 0.2 [7]	
Mandibular condylocanine length	♂♂	16.1 (15.5–16.8) 0.3 [59]	15.5 (15.5) 0.0 [1]	15.1 (14.4–16.0) 0.3 [61]	13.9 (13.5–14.2) 0.2 [18]	
	♀♀	15.8 (14.9–16.6) 0.4 [55]	15.0 (14.9–15.2) 0.2 [2]	15.0 (14.6–15.5) 0.2 [44]	13.8 (13.1–14.2) 0.3 [7]	
Mandibular depth	♂♂	2.3 (2.1–2.5) 0.1 [59]	2.2 (2.1–2.3) 0.1 [2]	2.2 (1.9–2.5) 0.1 [61]	2.0 (1.7–2.2) 0.1 [18]	
	♀♀	2.3 (2.1–2.6) 0.1 [55]	2.4 (2.3–2.5) 0.1 [2]	2.2 (1.9–2.4) 0.1 [44]	1.9 (1.7–2.1) 0.1 [7]	
m2 breadth	♂♂	1.4 (1.3–1.5) 0.1 [58]	1.4 (1.4–1.4) 0.0 [2]	1.4 (1.2–1.5) 0.1 [59]	1.3 (1.2–1.3) 0.0 [18]	
	♀♀	1.4 (1.3–1.5) 0.0 [55]	1.4 (1.4–1.4) 0.1 [2]	1.3 (1.3–1.4) 0.0 [43]	1.2 (1.1–1.3) 0.1 [7]	
m2 length	♂♂	2.3 (2.1–2.5) 0.1 [56]	2.2 (2.2–2.2) 0.0 [2]	2.2 (2.1–2.3) 0.1 [57]	2.0 (1.8–2.1) 0.1 [17]	
	♀♀	2.2 (2.1–2.4) 0.1 [55]	2.1 [1]	2.2 (1.9–2.3) 0.1 [43]	2.0 (1.9–2.1) 0.1 [7]	
Intercondylar breadth	♂♂	10.9 (10.3–11.5) 0.3 [48]	11.3 (11.3) 0.0 [1]	10.2 (9.3–10.8) 0.3 [56]	9.6 (9.2–9.9) 0.2 [18]	
	♀♀	10.6 (9.7–11.5) 0.4 [51]	—	10.1 (9.7–10.6) 0.2 [38]	9.4 (8.9–9.7) 0.3 [7]	
Mandibular condyle breadth	♂♂	2.3 (1.6–2.6) 0.1 [54]	2.4 (2.4) 0.0 [1]	2.1 (1.9–2.4) 0.1 [59]	2.0 (1.7–2.1) 0.1 [18]	
	♀♀	2.3 (2.0–2.5) 0.1 [52]	2.1 [1]	2.1 (1.9–2.4) 0.1 [43]	2.0 (1.8–2.1) 0.1 [7]	
Forearm length	♂♂	62.4 (57.9–65.5) 1.7 [60]	60.5 (60.4–60.7) 0.23 [2]	59.3 (55.0–62.6) 1.6 [65]	54.4 (53.1–55.8) 0.8 [19]	
	♀♀	62.4 (58.1–67.3) 2.1 [57]	61.5 (61.3–61.7) 0.3 [2]	60.0 (57.7–63.2) 1.5 [45]	54.3 (52.6–55.1) 0.9 [8]	
Third metacarpal length	♂♂	54.2 (50.8–57.4) 1.7 [56]	52.4 (51.6–53.2) 1.2 [2]	51.2 (48.3–54.6) 1.4 [64]	46.6 (44.9–48.6) 0.9 [19]	
	♀♀	54.2 (50.1–58.9) 1.9 [56]	52.1 (51.9–52.3) 0.3 [2]	52.0 (49.0–61.9) 2.0 [43]	46.7 (45.2–47.8) 0.8 [8]	

APPENDIX II.—Continued.

		<i>Pteronotus parnellii rubiginosus</i> (Amazonas, Bolívar, Delta Amacuro)		<i>Pteronotus parnellii rubiginosus</i> (Apure)	<i>Pteronotus</i> <i>parnellii fuscus</i>	<i>Pteronotus parnellii</i> <i>paraguanensis</i>
	Sex					
First phalanx of digit III length	♂♂	11.2 (9.8–12.6) 0.6 [58]	9.9 (9.3–10.6) 0.9 [2]	10.5 (9.4–11.4) 0.4 [65]	9.6 (8.6–10.5) 0.5 [19]	
	♀♀	11.3 (10.2–12.9) 0.6 [58]	10.8 (10.7–10.8) 0.1 [2]	10.7 (9.4–11.6) 0.5 [45]	9.6 (8.8–10.1) 0.5 [8]	
Second phalanx of digit III length	♂♂	18.2 (15.6–20.3) 1.1 [58]	17.9 (17.8–17.9) 0.1 [2]	18.0 (16.2–19.4) 0.7 [65]	16.4 (15.6–17.7) 0.6 [19]	
	♀♀	18.4 (16.4–20.2) 0.9 [58]	18.4 (18.2–18.6) 0.3 [2]	18.3 (16.7–19.6) 0.7 [45]	16.3 (15.9–16.9) 0.4 [8]	
Fourth metacarpal length	♂♂	53.0 (49.4–56.0) 1.5 [58]	51.5 (50.6–52.3) 1.2 [2]	50.2 (46.7–53.8) 1.4 [63]	45.4 (43.9–47.5) 0.9 [19]	
	♀♀	52.7 (49.5–57.4) 1.7 [56]	50.8 (50.8–50.8) 0.0 [2]	50.6 (47.4–53.2) 1.5 [42]	45.4 (44.0–46.4) 0.9 [8]	
Fifth metacarpal length	♂♂	51.5 (47.9–54.4) 1.4 [55]	50.4 (49.3–51.5) 1.5 [2]	48.6 (45.4–51.5) 1.3 [64]	44.1 (42.6–46.5) 1.0 [19]	
	♀♀	51.3 (48.8–55.0) 1.5 [55]	49.7 (49.3–50.0) 0.5 [2]	49.2 (43.4–51.7) 1.6 [42]	43.8 (42.9–44.8) 0.7 [8]	
Tibia length	♂♂	22.4 (20.1–24.7) 1.2 [59]	20.3 (19.8–20.8) 0.8 [2]	20.7 (18.1–22.8) 0.9 [63]	18.8 (17.9–19.8) 0.4 [19]	
	♀♀	22.1 (19.4–24.7) 1.2 [57]	21.5 (21.4–21.6) 0.1 [2]	20.7 (18.5–22.6) 0.8 [45]	18.4 (17.8–19.0) 0.4 [8]	
Total length	♂♂	95.8 (86.0–106.0) 4.1 [45]	94.0 (88.0–100.0) 8.5 [2]	90.9 (76.0–104.0) 4.7 [55]	84.1 (79.0–90.0) 3.5 [19]	
	♀♀	97.0 (70.0–125.0) 9.3 [41]	99.0 (98.0–100.0) 1.4 [2]	90.1 (82.0–98.0) 4.3 [42]	81.6 (79.0–85.0) 1.8 [8]	
Tail length	♂♂	14.3 (10.0–17.0) 1.4 [58]	16 (15.0–16.0) 0.7 [2]	13.4 (11.0–19.0) 1.5 [63]	12.1 (10.0–15.0) 1.5 [19]	
	♀♀	14.5 (12.0–22.0) 1.5 [57]	15.5 (15.0–16.0) 0.7 [2]	13.2 (10.0–16.0) 1.3 [44]	12.3 (11.0–14.0) 1.2 [8]	
Hind-foot length	♂♂	24.3 (18.0–28.0) 2.3 [60]	23 (20.0–25.0) 3.5 [2]	22.2 (18.0–31.0) 2.1 [60]	20.4 (19.0–23.0) 1.1 [19]	
	♀♀	24.0 (17.5–28.0) 2.4 [55]	20.5 (20.0–21.0) 0.7 [2]	22.6 (18.0–26.0) 1.8 [44]	20.4 (19.0–22.0) 0.9 [8]	
Ear length	♂♂	24.8 (7.0–30.0) 3.7 [54]	22.5 (22.0–23.0) 0.7 [2]	23.6 (16.0–30.0) 2.7 [61]	23.6 (18.0–25.0) 1.6 [19]	
	♀♀	24.5 (13.0–28.0) 2.7 [53]	22.0 (22.0–22.0) 0.0 [2]	23.2 (19.0–27.0) 2.3 [43]	22.9 (22.0–25.0) 1.1 [8]	
Mass	♂♂	23.7 (12.3–30.0) 3.6 [22]	—	19.0 (15.0–22.5) 1.8 [33]	14.4 (12.0–17.0) 1.3 [19]	
	♀♀	23.5 (19.0–29.0) 2.6 [24]	—	17.9 (13.2–22.0) 1.9 [30]	13.3 (12.0–16.0) 1.5 [8]	