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MORPHOLOGICAL DIFFERENTIATION BETWEEN *RHOGEESSA MINUTILLA* AND *R. TUMIDA* (MAMMALIA: CHIROPTERA: VESPERTILIONIDAE)

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Abstract.—Two nominal species of *Rhogeessa, R. minutilla* and *R. tumida,* co-occur in tropical South America. The distinction between these two species is based on somewhat ambiguous morphological characters (LaVal 1973). To better distinguish the two species, univariate and multivariate analyses were performed on 19 cranial and osteological characters. Ten were found to differ significantly between the two species based on univariate analyses. All but two of these were significant in the multivariate analyses. Thus, the two species are morphologically well differentiated. A key based on the morphometric analyses is presented to facilitate the identification of the two *Rhogeessa* species.

The genus *Rhogeessa,* exclusively Neotropical in distribution, contains five or six species (Goodwin 1958, LaVal 1973, Ramirez Pulido 1982, Nowak & Paradiso 1983), of which two, *R. minutilla* and *R. tumida,* occur in South America. *Rhogeessa minutilla* was described by Miller (1897; Type: USNM 63216, male) from Margarita Island, off the coast of Venezuela. The species ranges as far north on the mainland as Panama and is broadly distributed throughout mainland Venezuela and Colombia. *Rhogeessa tumida,* described from Veracruz, Mexico, by Allen (1866; Type: USMN 84012, male), overlaps the distribution of *R. minutilla* from Panama to Venezuela. Because the two species are so difficult to distinguish morphologically (LaVal 1973), Smith & Genoways (1974) suggested that *R. minutilla* probably is a geographic race of *R. tumida.* The purpose of this report is to evaluate the morphological differentiation of these taxa and the validity of *R. minutilla* as a distinct species.

Methods

Characters examined.—Ten individuals of each species were measured for 19 cranial and wing-bone characters (Fig. 1). Cranial characters (abbreviations in parentheses) included: Breadth of braincase (BB); Condylobasal length (CBL); depth of braincase (DB); greatest length of skull (GLS); mastoid breadth (MB); length of mandibular toothrow (MTL); length of maxillary toothrow (MXT); postorbital breadth (POB); postpalatal length (PPL); width across upper canines (WUC); and width across upper molars (WUM). Wing-bone measurements (taken from dried skins) are length of forearm (FA); metacarpal of digit 3 (IIIm); first (proximal) phalanx of digit 3 (IIIp1); second phalanx of digit 3 (IIIp2); metacarpal and first phalanx of digit 4 (IVm and IVp); and metacarpal and first phalanx of digit 5 (Vm and Vp). Zygomatic breadth, a character commonly employed in morphometric analyses, was not used because most of the specimens examined had damaged zygomatic arches.

Measurements were taken to the nearest 0.01 mm with digital calipers. Statistical analyses were performed on AT&T 6386 WGS or Compaq Deskpro 386/33 microcomputers using the Statistical Analysis System software, version 6.03 (SAS Institute Inc., 1988a, 1989b). Tests of normality were performed invoking the normal option

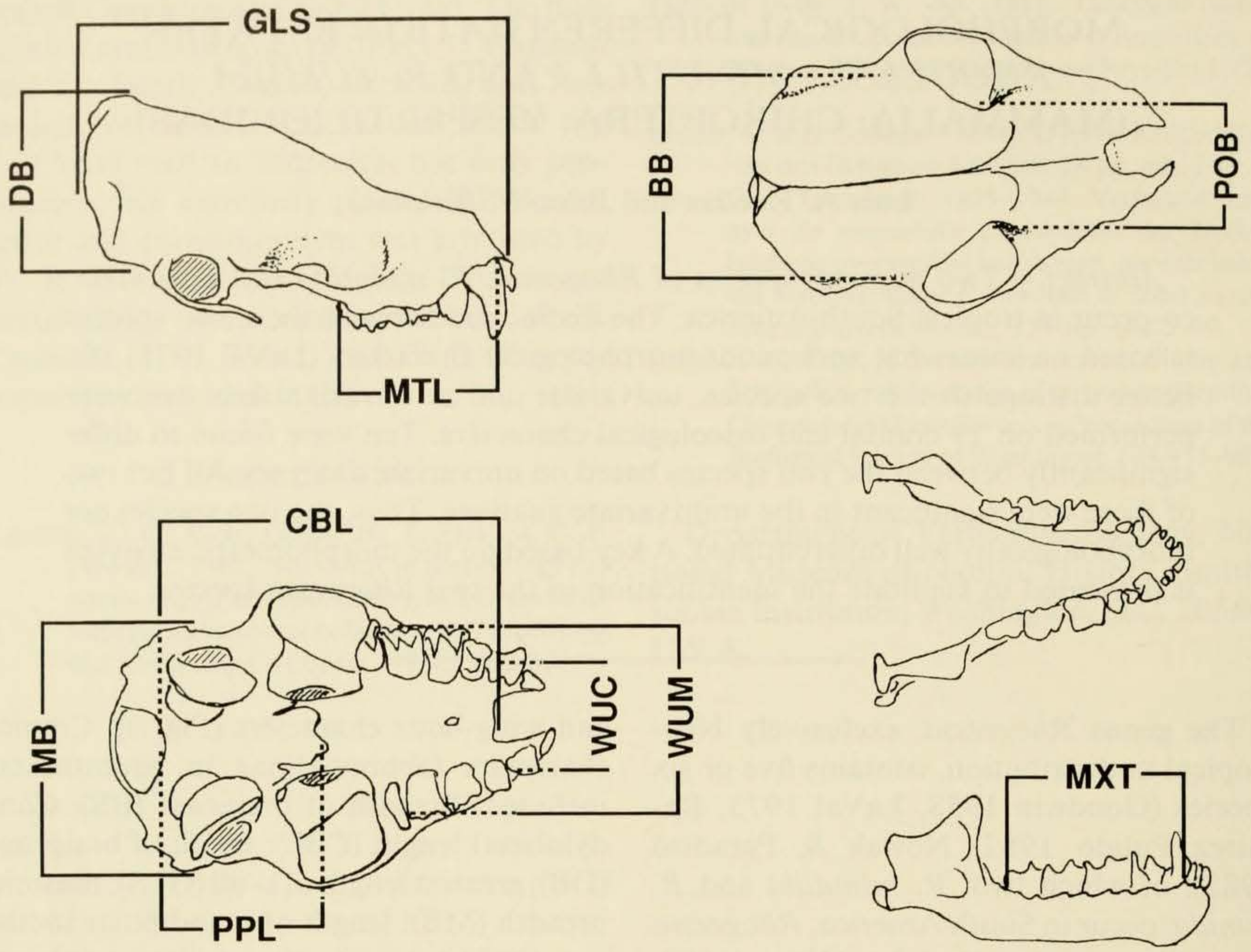

Fig. 1. Cranial measurements taken for the morphological analysis of *Rhogeessa minutilla* and *R. tumida* carried out herein. Abbreviations are explained in the methods section. Skull drawing based on Texas Cooperative Wildlife Collection specimen 9488, *R. tumida,* female, Veracruz, Mexico.

of the UNIVARIATE procedure, which tests for normality using the Shapiro-Wilk statistic, W, and provides the associated probability value. Sexual dimorphism in each character was evaluated using a *t*-test (PROC TTEST). Sexes were grouped for characters where no sexual dimorphism was found, and a *t*-test carried out to determine which characters were significantly different between species, given that the intent of the exercise was to distinguish between the two nominal taxa. Characters found to differ significantly between the two species then were used in multivariate analyses grouping the taxa both a priori (canonical discriminant analysis, PROC CANDISC) and a posteriori (principal component analysis, PROC PRINCOMP). A discriminant function analysis (PROC DISCRIM) was used to develop discriminant criteria to classify each individual. Classification error rates were obtained using posterior probability estimates based on crossvalidation, said to reduce both the bias and variance of the estimator (Hora & Wilcox 1982).

Materials Examined

Rhogeessa minutilla.—Venezuela: Lara; Caserio Boro, 10 km N El Tocuyo, 9°53′N, 69°47′W, 6 males (USNM 455998, 456000, 456002, 456005–456007), 4 females (USNM 456003, 456004, 456009, 456028).

Rhogeessa tumida.—Venezuela: Trujillo, 25 km NW Valera, near Agua Santa, 9°32′N, 70°40′W, 1 female (USNM 372488); Falcon, 19 km NW Urama, km 40, 10°37′N, 68°24′W, 1 female (USNM 374018), Apure,

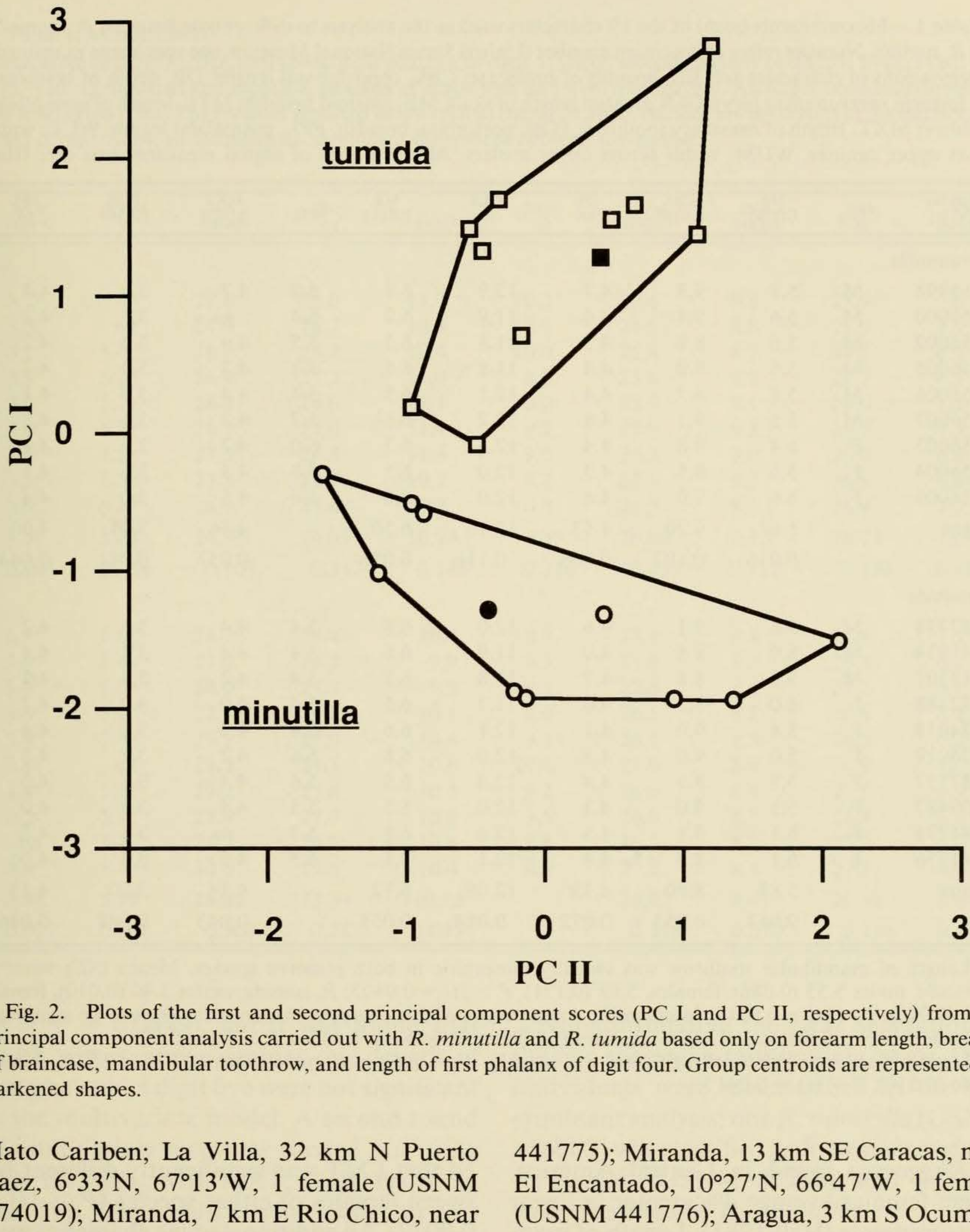

Fig. 2. Plots of the first and second principal component scores (PC I and PC II, respectively) from the principal component analysis carried out with *R. minutilla* and *R. tumida* based only on forearm length, breadth of braincase, mandibular toothrow, and length of first phalanx of digit four. Group centroids are represented by darkened shapes.

Hato Cariben; La Villa, 32 km N Puerto Paez, 6°33′N, 67°13′W, 1 female (USNM 374019); Miranda, 7 km E Rio Chico, near Puerto Tuy, 10°20′N, 65°54′W, 1 female (USNM 387737); Miranda, 1 km E Rio Chico, 10°19′N, 65°58′W, 1 male (USNM 387738); Sucre, 26 km ESE Carupano (Manacal), 10°37′N, 63°01′W, 1 female (USNM 409487); Yaracuy, 20 km NW San Felipe (Minas de Aroa), 10°25′N, 68°54′W, 1 male (USNM 441774), 1 female (USNM 441775); Miranda, 13 km SE Caracas, near El Encantado, 10°27′N, 66°47′W, 1 female (USNM 441776); Aragua, 3 km S Ocumare de la Costa, 10°24′N, 67°46′W, 1 male (USNM 517507).

Results

Of the 19 mensural characters examined (Table 1) sexual dimorphism was encountered only in two, in contrast with species

Table 1.—Measurements (mm) of the 19 characters used in the analysis to differentiate between *R. minutilla* and *R. tumida*. Number refers to specimen number (United States National Museum, see specimens examined). Abbreviations of characters are: BB, breadth of braincase; CBL, condylobasal length; DB, depth of braincase; FA, forearm measurement (dry); GLS, greatest length of skull; MB, mastoid breadth; MTL, length of mandibular toothrow; MXT, length of maxillary toothrow; POB, postorbital breadth; PPL, postpalatal length; WUC; width across upper canines; WUM, width across upper molars. Abbreviations of digital measurements are: IIIm,

Number $P > \|t\|$	Sex	BB 0.0030	CBL 0.0195	DB ns	GLS ns	MB 0.0132	MTL[1]	MXT 0.0059	POB 0.0340	PPL ns
R. minutilla										
455998	M	5.7	9.3	4.7	12.9	6.7	5.9	4.7	3.0	4.4
456000	M	5.6	9.4	4.4	11.9	6.2	5.4	na	3.3	4.2
456002	M	5.6	8.9	4.3	11.8	6.3	5.5	4.4	3.2	4.2
456005	M	5.6	9.0	4.4	11.8	6.6	5.3	4.3	3.0	4.3
456006	M	5.6	8.7	4.4	12.1	6.5	5.4	4.4	3.0	4.1
456007	M	5.5	9.1	4.8	12.2	6.6	5.7	4.7	3.1	4.3
456003	F	5.4	9.8	4.4	12.3	6.3	6.0	4.7	2.9	4.4
456004	F	5.6	9.5	4.3	12.0	6.5	5.8	4.5	3.1	4.1
456009	F	5.6	9.0	4.6	12.0	6.6	5.6	4.5	3.0	4.4
Means		5.62	9.20	4.53	12.16	6.50		4.56	3.05	4.30
SE		0.036	0.107	0.066	0.116	0.056		0.057	0.041	0.044
R. tumida										
387738	M	5.8	9.1	4.6	12.0	6.8	5.4	4.4	3.1	4.2
441774	M	6.0	8.8	4.0	11.9	6.6	5.4	4.4	3.4	4.4
517507	M	5.6	8.8	4.7	11.8	6.7	5.4	4.2	3.3	4.1
372488	F	6.0	8.5	4.0	11.7	6.5	5.4	4.0	3.0	4.2
374018	F	5.8	9.0	4.1	12.1	6.6	5.4	4.4	3.0	4.4
374019	F	5.0	9.0	4.5	12.0	6.8	5.6	4.2	3.2	4.3
387737	F	5.9	8.9	4.4	12.4	6.9	5.6	4.4	3.3	4.0
409487	F	5.5	9.0	4.3	12.0	5.5	5.5	4.4	3.3	4.0
441775	F	6.1	9.1	4.5	12.6	6.8	5.7	na	3.1	4.3
441776	F	6.1	8.9	4.4	12.1	7.1	5.5	4.5	3.3	4.0
Means		5.87	8.90	4.35	12.08	6.72		4.34	3.20	4.19
SE		0.063	0.053	0.072	0.084	0.055		0.043	0.048	0.046

[1] Length of mandibular toothrow was sexually dimorphic in both putative species. Means (*SE*) were: *R. minutilla,* males 5.53 (0.086), females, 5.88 (0.121), $P > |t| = 0.0403$; *R. tumida,* males 5.40 (0.010), females 5.52 (0.045), $P > |t| = 0.0417$. Interspecific comparisons of this character within sexes showed no significant differences between males, but highly significant differences between females, $P > |t| = 0.0077$.

[2] Length of second phalanx of digit three was sexually dimorphic in *R. tumida*: males 10.05 (0.321), females 10.46 (0.210), $P > |t| = 0.0417$.

of *Rhogeessa* found in Central America, where females average 4% greater in linear measurements (Hall 1981). Length of mandibular toothrow (LMT) was significantly different between sexes in both *R. minutilla* ($P > |t| = 0.0403$) and *R. tumida* ($P > |t| = 0.0417$). The proximal phalanx of digit three was sexually dimorphic in *R. tumida* only ($P > |t| = 0.0417$). These characters therefore were not used in subsequent multivariate analyses, although it should be noted that LMT was significantly different between females of either species ($P > |t| = 0.0077$). An additional seven characters were not significantly different between the species, and were omitted from subsequent analyses; these were DB, GLS, PPL, WUM, IIIm, IIIp2, and Vm.

The remaining characters were included in the first round of multivariate analyses. The model including all variables that were significant in the *t*-test was itself significant

Table 1.—Continued.
metacarpal of digit 3; IIIpl, first (proximal) phalanx of digit 3; IIIp2, second phalanx of digit 3; IVm, IVp1, and Vm, Vp1, metacarpal and proximal phalanx of digits four and five, respectively. All finger bone measurements are from dried skins. The *P* values reported below cranial character abbreviations are the results of the interspecific *t*-test comparisons; ns indicates no significant differences between the species.

WUC	WUM	FA	IIIm	IIIp1[2]	IIIp2	IVm	IVp	VM	Vp
0.0450	ns	0.0004	ns		ns	0.0287	0.0001	ns	0.0143
3.7	5.4	27.6	28.0	11.7	10.2	27.6	9.8	27.9	7.6
3.5	na	27.0	26.2	10.8	8.8	25.6	8.8	27.0	7.0
3.5	5.0	26.7	26.2	10.4	10.0	25.4	8.7	26.7	6.8
3.3	5.0	26.9	27.3	11.0	8.2	25.8	8.6	26.7	6.5
3.5	5.2	26.8	26.6	11.1	10.0	25.7	9.1	26.0	7.1
3.6	5.3	26.7	27.0	11.4	9.2	25.9	9.3	26.7	7.3
3.6	5.5	27.3	26.8	11.4	9.0	26.3	9.0	26.3	6.8
3.5	5.3	27.3	25.7	10.2	8.7	25.1	9.2	26.8	6.8
3.6	5.4	26.6	27.4	10.7	10.0	26.3	9.6	26.4	7.2
3.57	5.28	26.98	26.85	10.99	9.39	26.06	9.15	26.74	7.04
0.041	0.054	0.104	0.217	0.149	0.216	0.233	0.123	0.158	0.106
3.4	5.0	28.7	28.4	10.4	10.0	27.4	8.8	27.8	7.1
3.6	5.4	27.6	26.2	9.9	9.3	25.9	8.3	26.4	6.7
3.4	5.0	28.0	27.7	9.8	9.7	27.6	8.6	27.3	6.6
3.4	5.2	27.1	26.8	10.1	8.9	26.5	8.1	26.8	6.2
3.4	5.4	29.1	27.0	10.4	9.3	26.2	8.3	26.3	6.2
3.4	na	29.3	28.1	10.6	10.0	27.9	8.4	26.9	7.0
3.4	5.2	29.2	27.8	10.5	9.2	26.8	8.4	27.6	6.9
3.5	5.1	28.4	27.0	10.8	9.5	26.0	8.7	26.4	6.6
na	5.1	28.2	26.9	10.4	8.8	26.7	8.2	27.2	6.7
3.6	5.4	30.6	27.5	10.4	8.9	27.2	8.4	27.1	6.4
3.46	5.19	28.62	27.34	10.33		26.82	8.41	26.98	6.64
0.027	0.058	0.308	0.212	0.095		0.218	0.070	0.166	0.100

($P > F = 0.0449$), but it was found that width across upper canines and length of first phalanx of digit five were not significant in the multivariate model. A second round of multivariate tests was carried out using only BB, CBL, MB, MXT, POB, FA, IVm and IVp. The multivariate model in this case was highly significant ($P > F = 0.0077$). Using these eight measurements, the two South American species distinctly segregate into groups composed of individuals of either species using both a priori (canonical discriminant analysis, CANDISC) and a posteriori (principal component analysis, PRINCOMP) multivariate tests (Table 2, Fig. 2).

Notwithstanding the clear separation of the two species in multivariate space, three individuals were misclassified in the discriminant analysis: one *R. minutilla* (USNM 456002) was classified as *R. tumida* and two *R. tumida* (USNM 372488 and 441774) were classified as *R. minutilla*.

Discussion

Morphological approaches to questions of species identity are compounded in *Rhogeessa* where the presence of chromosomally distinct populations indicates several potentially cryptic species (Bickham & Baker 1977, Baker 1984, Baker & Bickham

Table 2.—First and second raw canonical coefficients (Can1 and Can2) from the canonical discriminant analysis, and first and second eigenvectors (Prin1 and Prin2) from the principal component analysis carried out on the 10 individuals of each species of *Rhogeessa* discussed in the text. The first canonical vector accounted for all the interspecific variation in the canonical discriminant analysis. In the principal component analysis, all variation was accounted for by the first four principal components (52.1%, 26.5%, 14.0%, and 7.4%, respectively); the first component principally accounts for interspecific differences. The results of the principal component analysis are graphically summarized in Fig. 2.

Character	Can1	Can2	Prin1	Prin2
FA	1.0463	−0.2826	−0.5300	0.2503
PIV	−1.9812	−0.6352	−0.4335	0.5962
BBCS	1.3335	3.0157	0.3884	0.7447
MTR	−1.2991	3.3186	0.6167	0.1651

1986, Baker et al. 1985). In this study, we found ten characters that differed significantly at $\alpha = 0.05$. Thus, from a morphometric standpoint, there appears to be little evidence to support the contention of Smith & Genoways (1974) that *R. minutilla* probably will result in being no more than a geographic race of *R. tumida*. However, populations of *Rhogeessa* are extremely interesting and complex from an evolutionary perspective. Although it is improbable that morphology alone will clarify the phylogenetic relationships among *Rhogeessa* species (LaVal 1973), morphological studies combined with chromosomal and biochemical work may prove useful (Bickham & Baker 1977, Baker et al. 1985). Indeed, as currently known (LaVal 1973, Bickham & Baker 1977, Honeycutt et al. 1980), the South American populations identified herein as the species *R. tumida* represent at least two species. Specimens from Venezuela and Trinidad have karyotypes with a diploid number (2N) of 30, whereas a specimen from Suriname had 2N = 52 (Honeycutt et al. 1980, Baker et al. 1985). Clearly, additional studies of this species, and of *R. minutilla,* are needed and should include chromosomal and biochemical analyses as well as morphological assessment to help clarify relationships within this taxon.

Although there is great overlap in the mensural characters examined, a key to South American species of *Rhogeessa* was constructed based on the above morphometric analyses; additional characters not included in the key may be used as necessary:

1. Color paler; forearm usually shorter than 27.60 mm; first phalanx of digit IV usually longer than 8.62 mm ..... *Rhogeessa minutilla*
– Color darker; forearm usually longer than 27.13 mm; first phalanx of digit IV usually shorter than 8.84 mm ..... *Rhogeessa tumida*

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