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SYSTEMATICS OF THE GENUS *RHOGEESSA*  
(CHIROPTERA: VESPERTILIONIDAE)

By

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The several species of Neotropical bats of the vespertilionid genera *Rhogeessa* and *Baeodon* include some of the smallest of living mammals, although one species approaches in size the common big brown bat, *Eptesicus fuscus*, of North America. Most of the species occur at low elevations, in habitats ranging from desert scrub to rain forest, and appear to be insectivorous. They range from the lowlands of northern México to southern Brasil, but are poorly represented in collections from South America south of Venezuela and Colombia.

Allen (1866) described the genus *Rhogeessa* including two species, *R. parvula* and *R. tumida*. He implied close relationships of *Rhogeessa* with *Nycticejus* [= *Nycticeius*], *Nyctinomus* [= *Tadarida*], and with the Noctilionidae. Dobson (1878) referred *Rhogeessa* to a subgenus of the genus *Vesperugo* [= *Vespertilio*]. However, Thomas (1892) retained *Rhogeessa* as a full genus, and stated that it was most closely related to *Nycticejus* [= *Nycticeius*]. Subsequently, Miller (1897) and others have followed Thomas. Miller (1906) erected a new genus, *Baeodon*, for *Rhogeessa alleni* Thomas. Although Simpson (1945) included *Baeodon* in *Rhogeessa*, other recent authors, including Tate (1942), Hall and Kelson (1959), and Koopman and Cockrum (1967) have retained them as separate genera.

The eight nominal species of *Rhogeessa* were described in the following sequence: *R. parvula* (Tres Mariás Islands, Nayarit) and

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*R. tumida* (Veracruz) by H. Allen in 1866; *R. alleni* (Jalisco) by Thomas in 1892; *R. minutilla* (Margarita Island) and *R. gracilis* (Puebla) by Miller in 1897; *R. io* (Venezuela) and *R. velilla* (Ecuador) by Thomas in 1903, and *R. bombyx* (Colombia) by Thomas in 1913. Hall (1952) reduced *R. tumida* to a subspecies of *R. parvula*, an arrangement followed by Hall and Kelson (1959) and several authors prior to 1959. No new taxa were described in the genus *Rhogeessa* until Goodwin's (1958) revision, in which he named three subspecies, *R. tumida major* (Oaxaca), *R. tumida riparia* (Venezuela), and *R. parvula aeneus* (Yucatán). At the same time he included *R. bombyx* as a subspecies of *R. tumida*, and reduced *R. minutilla*, *R. io*, and *R. velilla* to subspecies of *R. parvula*.

The distributional ranges Goodwin gave for the seven subspecies he recognized suggest a montage of isolated subspecies, some separated by gaps of over 1500 miles. On the basis of my preliminary examination of specimens in the Museum of Natural History at the University of Kansas, I concluded that his taxonomic arrangement failed to elucidate the actual intra- and interspecific relationships within the genus. Comments made by Alvarez and Aviña (1965) and by Jones, *et al.* (1971) also suggest the need for a revision of the genus *Rhogeessa*. Therefore, with the 650 specimens now available, I have undertaken a new revision, employing multivariate statistical analyses.

## MATERIALS AND METHODS

A total of 653 specimens of *Rhogeessa* was examined. Included were 8 *alleni* (2 bacula), 350 *R. tumida* (43 bacula), 160 *R. parvula* (28 bacula), 112 *R. minutilla* (11 bacula), 9 *R. gracilis* (4 bacula) and 14 (1 baculum) of an unnamed species. Although a substantial number of juvenal specimens was encountered, no more than one per locality was included in the total number of specimens examined. Because many important specimens are preserved in alcohol, skulls from these specimens were removed and cleaned.

I examined the following holotypes: *R. gracilis*; *R. tumida*; *R. tumida major*; *R. tumida riparia*; *R. parvula*; *R. parvula aeneus*; *R. minutilla*. Holotypes of *R. alleni*, *R. bombyx*, *R. io*, and *R. velilla* were examined for me by J. E. Hill of the British Museum of Natural History. C. O. Handley of the National Museum of Natural History generously made available to me his notes on the holotypes of *R. io*, as compared with various specimens in the NMNH. Topotypes of *R. velilla* and *R. parvula* were examined by me.

I recorded all available label and field note information, plus three external measurements, length of fur, nine cranial measurements, three bacular measurements, color of dorsum and of venter, presence or absence of sagittal crest, age (adults: phalangeal



epiphyses ossified; juveniles: epiphyses not ossified) and toothwear (1—none; 2—present but scarcely noticeable; 3—easily noticeable on canines and molars, but little cusp detail obscured; 4—heavy, much cusp detail obscured). Measurements were taken following in general the methods outlined by Handley (1959), with exceptions or additions as noted below: forearm (FA); third metacarpal (3MC); tibia (from center of knee joint to point of attachment of calcar to ankle); fur (greatest length in center of dorsum); greatest length of skull (GLS—including incisors); depth of braincase (DB); postorbital width (POW); mastoid width (MW); width across second upper molars (M2-M2); width of second upper molar (M2—as measured with ocular micrometer); maxillary toothrow (MAX); mandibular toothrow (MAND); measurements of bacular length, depth, and width follow LaVal (1973, Fig. 1).

A set of nine specimens (Table 1) was chosen as color standards and matched to named colors from Ridgway (1912). Unfortunately certain specimens, notably those from northwestern Venezuela, fell outside the limits of variation delimited by the color standards; these were compared directly with Ridgway (1912).

TABLE 1. Colors from Ridgway (1912) applied to specimens used as color standards (tip color only).

Specimen no.	Color no.	Dorsum	Venter
TCWC 19756	1	Fuscous-Black	Buffy Brown
KU 102619	2	Hair Brown	Cartridge Buff
KU 29886	3	Tawny-Olive	Light Ochraceous-Buff
KU 107494	4	Buffy Brown	Cartridge Buff
KU 105565	5	Buckthorn Brown	Light Ochraceous-Buff
KU 90754	6	Pinkish Cinnamon	Cinnamon Buff
UNM 27545	7	Warm Buff	Light Ochraceous-Buff
KU 97050	8	ca. Light Ochraceous-Buff	Pinkish Buff
KU 61171	9	Dresden Brown	Light Ochraceous-Buff

Karyotypes were not examined by me, but I have seen partial results of a study of karyotypic variation in the genus now being conducted by R. J. Baker (pers. com.) and his students. Baker and Patton (1967) documented the differences in karyotypes between *R. tumida* from Chiapas and *R. parvula* from Sonora and Nayarit. Specimens identified by Baker and Patton as *R. gracilis* are not of that species (Baker, pers. com.) and are almost certainly *R. parvula*, collected at the opposite end of the long cline beginning in Sonora.

Scanning electron micrographs were made of hairs from the mid-dorsal region of specimens of each species. Because the appearance of *Rhogeessa* hairs varies substantially depending on the angle of view and the portion of the hair photographed, all photographs were made of the mid-section of each hair; the hair was oriented

so that the side of the scales bearing the V-shaped depression in the rim would face the film. Polaroid negatives ( $4 \times 5$  in) were exposed for 70 seconds on a ETEC Autoscan scanning electron microscope, made available to me by the Department of Entomology, Kansas State University, Manhattan.

Penes were removed from 89 of the males examined, and cleared and stained to reveal the bacula, using Anderson's (1960) method. Bacula were measured with an ocular micrometer.

All data recorded were punched on IBM cards, and statistical analyses performed on the GE 635 computer at the University of Kansas Computation Center. Although *t*-tests performed between the sexes indicated a significant level of sexual dimorphism for some measurements at some localities, the small sample sizes prevalent in this genus made separation of the sexes impractical. Samples usually contained a fairly well-balanced proportion of the two sexes, which would tend to offset any possible bias due to sexual dimorphism.

Gabriel's Sum of Squares Simultaneous Testing Procedure (SS-STP) was performed, first with all species in the same analysis, and then each species was analyzed separately. An SS-STP program available at the University of Kansas Museum of Natural History (as modified by Gary Powers) gives 13 standard statistics, calculates and lists non-significant subsets, and prints these in graphic form, with means in descending sequence (Figs. 10, 11, 13). The SS-STP procedure, as related to systematics, is discussed by Smith (1972), who lists some of the more important literature references.

The University of Kansas Numerical Taxonomy Program (NT-SYS) developed by E. J. Rohlf, J. Kishpaugh, and R. Barteher was utilized to give the following statistical information: 1) standardized data correlations between localities and a two-dimensional phenogram based on these; 2) cophenetic correlation, in which cophenetic values are plotted on scatter diagrams against the correlation coefficients used in the phenogram; 3) standardized data distances between localities, and a two-dimensional phenogram based on these; 4) a second cophenetic correlation, plotting cophenetic values against distance coefficients; 5) a principal component analysis in which the first five principal components are calculated; 6) a Varimax Factor Rotation by the Kaiser Method; and 7) the variance-covariance matrices projected onto the principal components (both rotated and non-rotated), and two-dimensional scattergrams plotting each of the principal components against each of the others.

A stepwise discriminant analysis was also carried out, using the University of California BMD07M program; this program identifies each individual specimen based on the criteria derived from the analysis. It computes canonical correlations and coefficients

for canonical variables, and plots the first two canonical variables on a two-dimensional scattergram.

All of the multivariate analyses were computed using the same nine characters, all of which are skin and skull measurements made by myself. These were chosen for several reasons, one of which dealt with problems resulting from missing data. Discriminant function analysis indicated that all contributed significantly to variation observed among the samples analyzed. Other characters examined either did not contribute to variation among samples, or contributed so strongly to singling out one or more species or samples that I felt they would tend to obscure the close relationships which are typical of species within this genus. Further, I wanted to see if a multivariate analysis based on a few measurements made of morphological characters, which I would expect to be highly correlated, would support suspected relationships based on other kinds of characters (such as distribution of hair on uropatagium, size of  $i3$ , presence of cingual cusps, bacula, hair, etc.). Blackith and Reyment (1971) stated that "Where the organisms are fairly closely related, and all the measurements are quantitative, . . . Satisfactory analyses have been made with as few as three to six characters, although ten might be regarded as more optimal. . . ."

In the analyses performed by the NT-SYS program, only sample means were utilized. To help assure that means used would be representative of the geographic area which they represented, several small samples often were pooled (for example, several samples of one or two specimens each from various localities on the Caribbean slope of Honduras were combined). In other cases, large samples from a single locality were utilized. The areas from which each of the samples was taken, along with the abbreviations used in this paper, are as follow: Tamaulipas, coast (Tamp 1); Tamaulipas, interior (Tamp 2); San Louis Potosí (SLP); Veracruz, northern (VC-N); Veracruz, central (VC-C); Veracruz, southern (VC-S); Campeche (Camp); Yucatán and northern Quintana Roo (Yuc); Chiapas, Pacific Coast (Chiapas); Oaxaca, Pacific slope (Oax); Guerrero (Guer); Michoacán (Mich); Colima (Colima); Jalisco (Jal); Nayarit (Nay); Sinaloa, southern (Sin-S); Sinaloa, central (Sin-C); Sonora (Son); Guatemala, Pacific Coast (Guat); El Salvador (El Salv); Honduras, Caribbean slope (Hond); Nicaragua, Caribbean slope (Nic); Costa Rica, Interior (CR); Panamá, Pacific slope (Pan); Colombia, north (Colomb); Venezuela, north-west (Venez-NW, 1-5); Venezuela, coast (Venez-C, 1-2); Venezuela, interior (Venez-int); Venezuela, northeast (Venez-NE); Trinidad (Trin); Guyana (Guyana). All specimens of *R. gracilis*, *R. alleni*, and the unnamed species are pooled into single samples.

Fewer samples, each representing more individual samples combined into larger pooled samples, were used in the stepwise dis-

criminant analysis, because the kind of output generated by that program would be unintelligible if a very large number of individual samples were chosen. These samples, along with their abbreviations, are as follows: Southwestern México—Oaxaca and Guerrero (SWMEX); Michoacán (MICH); West-central México—Jalisco, Colima, Nayarit, southern Sinaloa (WCMEX); Northwestern México—northern Sinaloa and Sonora (NWMEX); Eastern México—Tamaulipas, San Luis Potosí, and Veracruz (EMEX); Northern Yucatan Peninsula (YUC); Central America—Tabasco through Panamá, excluding Caribbean slope from Nicaragua to Panamá (CENTAM); Caribbean slope from Nicaragua to Panamá (NICPAN); Northern Colombia (COLOMB); Northern Venezuela (VENEZ); Arid northwestern Venezuela and extreme northeastern Colombia (DRYVEN); Guyana (GUYANA); Trinidad (TRIN); all *R. gracilis* (GRACIL); all *R. alleni* (ALLEN); all specimens of the unnamed species (MIRA).

Although sexual dimorphism in size was detected within some samples, *t*-tests did not show it to be consistently significant. On the average, females are as much as 4% larger than males. However, in *R. minutilla* from Venezuela, males are slightly larger on the average.

#### ACKNOWLEDGMENTS

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### ANALYSIS OF CHARACTERS

Goodwin (1958), in his revision of the genus *Rhogeessa*, stated that the genus (exclusive of *Baeodon*) could be separated into three species: "a big eared species with thin flying membranes [*gracilis*], a large species with short ears and thick membranes [*tumida*], and a small species [*parvula*]." He further stated that "The proportionate length of the forearm and color of the pelage cannot be relied on as determining factors except in a very general way. Cranial measurements can also be confusing unless accompanied by comparative material." As might be anticipated from these introductory remarks, Goodwin did not state clearly how to distinguish among *parvula*, *tumida*, and the various subspecies into which he divided them.

As suggested by Goodwin, skin and skull measurements are inadequate for distinguishing among species, except in the case of *R. alleni*, which is larger in most cranial variates than any other species examined, and the new species, *R. mira*, which is smaller than any specimens of *R. parvula* from Michoacán or adjoining states. However, in the multivariate analyses, notably the principal component analysis, the canonical variate analysis, and the discriminant function analysis, the measurements taken were adequate to discriminate many of the samples from each other (see table 4, and Figs. 4, 7, 8, 12). The discriminant function analysis indicated that greatest length of skull and forearm were the best and second best discriminators, respectively. Thus, I chose these two variables to demonstrate geographic variation by means of univariate analyses.

*Color of fur*.—Variation in relative positions of light and dark bands seems to separate *alleni* and *gracilis* from all other species. Individual variation in contrast between bases and tips renders pelage coloration of limited usefulness in identification of individual specimens of the other four species, but differences are evident when series are compared. Molting individuals take on a grayish

cast because dark gray hairs grow up throughout the old pelage before it is shed. Thus, newly molted individuals are much darker in color than individuals in old pelage. In the species which have pale bases and darker tips, individual color variation is accounted for primarily by differences in tip color, whereas color differences among samples and species typically result from variation in basal color.

*Length of fur.*—Although some individual variation in fur length occurs, this character is sufficiently constant within a population to separate certain species, and to illustrate geographic variation among populations in a single species.

*Distribution of fur on uropatagium.*—This character evidences so little individual variation that it is a fairly reliable means of separating one of the species from the other five species.

*Degree of toothwear.*—Toothwear was negligible in about 90 percent of specimens examined, except in the case of *R. minutilla*, in which more than 35 percent of the specimens had moderate to heavy toothwear.

*Lingual cingulum of C1.*—In all species except *gracilis* and *mira* two (rarely one) cusps are present on the lingual cingulum of the C1. These cusps are variable in development, from higher and sharper than the example shown in figure 1A, to lower and more rounded. They tend to be obscured in individuals with heavy toothwear. In the species lacking cusps, the cingulum is perfectly smooth and straight, lacking even the slightest swelling (Fig. 1B).

*Bacula.*—With the exception of *R. alleni*, bacula of the various species are not sharply differentiated from each other. Although

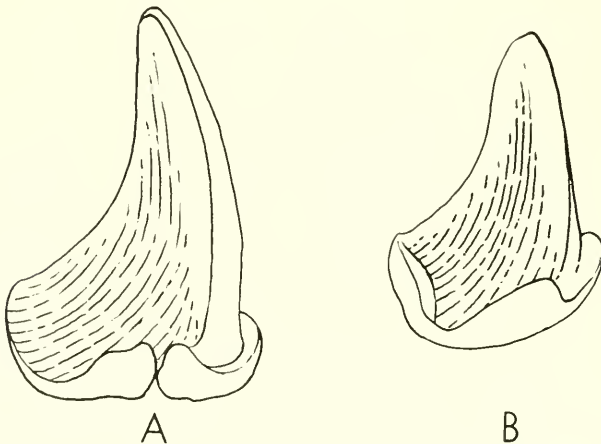


FIG. 1. Upper right canine of two species of *Rhogocessa*, lingual view. A. *R. parvula*, UA 10319, Jalisco; B. *R. mira*, UNAM 8594, Michoacán.  $\times 25$ .

bacular shape shows substantial geographic and individual variation within species, it also seems to differ among species in areas of sympatry and near sympatry (Fig. 2). Single bacula of *parvula*, *tumida*, *gracilis*, and *alleni* were illustrated and described by Brown, et al. (1971), but these authors did not examine bacular variation.

*Microstructure of hair*.—Benedict (1957) examined hairs from

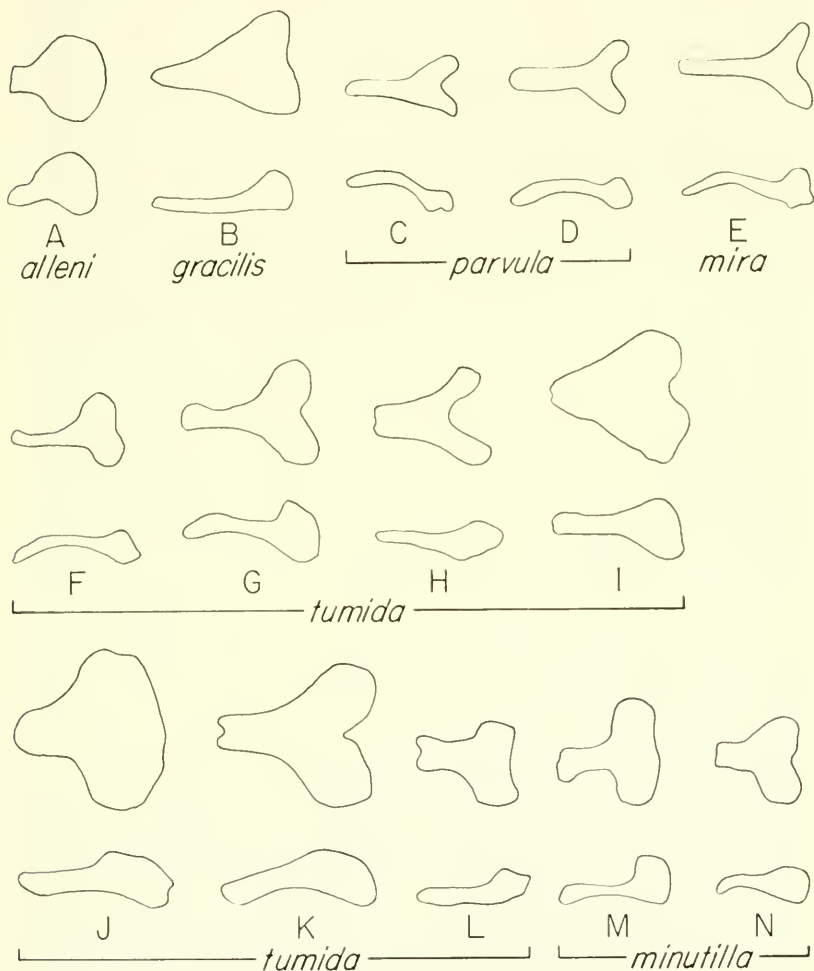


FIG. 2. Top and lateral outline views of bacula of 14 specimens of *Rhogessa*. A. *R. alleni*, KU 97307, Michoacán; B. *R. gracilis*, KU 92951, Jalisco; C. *R. parvula*, KU 97080, Sinaloa; D. *R. parvula*, UNAM 8865, Guerrero; E. *R. mira*, UNAM 8953, Michoacán; F-L, all *R. tumida*: F. KU 55172, Tamaulipas; G. KU 82923, Veraacruz; H. LACM 18683, Chiapas; I. TCWC 24127, Nicaragua; J. MVZ 113936, Colombia; K. KU 119073, Venezuela; L. AMNH 66824, Ecuador; M. *R. minutilla*, NMNH 441783, Venezuela; N. *R. minutilla*, NMNH 441805, Venezuela.  $\times 25$ .

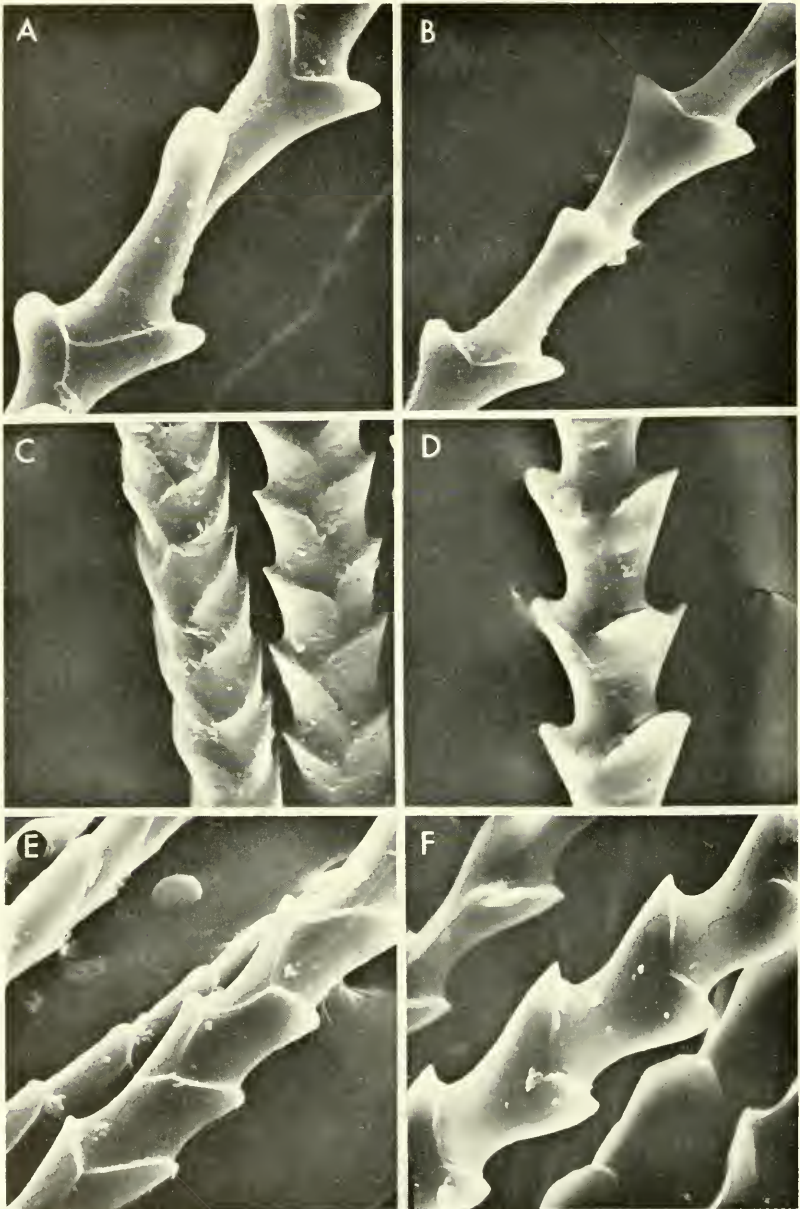


FIG. 3. Scanning electron micrographs of hairs of six species of *Rhogeessa*. A. *R. mira*, UNAM 8593, Michoacán; B. *R. parvula*, KU 107494, Jalisco; C. *R. minutilla*, AMNH 130673, Venezuela; D. *R. alleni*, KU 61171, Oaxaca; E. *R. tumida*, KU 119073, Venezuela; F. *R. gracilis*, KU 97050, Jalisco.  $\times 1400$ .



most of the known genera of bats, including hairs from a specimen of *R. parvula*. Unfortunately, she neither illustrated a hair from *Rhogeessa* nor stated where the specimen was captured, and she had only a light microscope at her disposal. Benedict (1957) and Quay (1970) implied that hair structure was most useful as a taxonomic tool at the generic and suprageneric levels. Although the relationship (if any) of geographic, sexual, age, and individual variation to hair structure cannot be evaluated here because of small sample sizes, it is evident (Fig. 3) that there are differences in hair structure among species of *Rhogeessa*.

The two similar lowland species of western México, *R. mira* and *R. parvula*, differ from all other species in that each scale is rotated 90° along its linear axis, in relation to adjoining scales; in the other species scales are in alignment with each other. Based on hair structure, two other groupings seem to be evident. In *R. alleni* and *R. gracilis* the scales appear to be cone-shaped rings which are bilaterally symmetrical, subtending a full 360° (the coronal scales of Benedict). In *R. tumida* and *R. minutilla* the scales are alternate and overlapping (imbricate scales of Benedict) with the visible portion subtending an angle of 180° or perhaps slightly greater.

## SYSTEMATIC ACCOUNTS

### *Rhogeessa* H. Allen, 1866

*Rhogeessa* H. Allen, 1866:285 [Type species.—*Rhogeessa parvula* H. Allen, 1866, designated by G. S. Miller, 1897 in accordance with page priority].  
*Bacodon* G. S. Miller, 1906:85 [Type species.—*Rhogeessa alleni* Thomas, 1892, by original designation]. Valid as a subgenus.

*Description*.—As given by H. Allen (1866) and G. S. Miller (1897) except as noted below. Skull drawings appear in Hall and Kelson (1959; *R. parvula*) and G. S. Miller (1897; *R. tumida*); skull photographs are included by Goodwin and Greenhall (1961; *R. tumida* and *R. minutilla*). The i3 varies in size from minute (visible only under magnification) to only slightly smaller than i2; i1 and i2 tricuspid, with outer cusp much lower than other two cusps; i3 bicuspid or unicuspid; lingual cingulum of C1 well developed, usually with accessory cusps; parastyle, paracone, protocone, and first and second commissures are only structures present on M3; width of posterior half of m3 substantially less than width of anterior half; maxillary cheek teeth converging anteriorly; basisphenoid pits absent; rostrum narrower than braincase; membranes relatively thin; baculum saddle-shaped at proximal end, with well-developed proximal lateral knobs, poorly-developed proximal median knob, and long, usually narrow shaft, circular or elliptical in cross section near distal end; length 0.50 to 0.80 mm; penis short, 3-4; baculum extends to within 0.5 of distal end of penis.

TABLE 2. Measurements of individual and pooled samples from selected localities, arranged to demonstrate geographic variation. Mean $\pm$ 2 standard errors of the mean.

	FA	3MC	GLS	DB	POW	MW	M2M2	CICI	MAX
W. Mexico	33.0 $\pm$ .78	31.9 $\pm$ .82	15.0 $\pm$ .16	<i>R. alleni</i> 5.4 $\pm$ .11	3.2 $\pm$ .05	7.8 $\pm$ .12	6.0 $\pm$ .14	4.3 $\pm$ .13	5.4 $\pm$ .08
W. Mexico	32.1 $\pm$ .88	30.4 $\pm$ .78	13.5 $\pm$ .29	<i>R. gracilis</i> 4.8 $\pm$ .17	3.1 $\pm$ .13	6.7 $\pm$ .22	4.9 $\pm$ .15	3.4 $\pm$ .14	4.6 $\pm$ .09
Oaxaca	31.2 $\pm$ .78	30.0 $\pm$ .66	13.5 $\pm$ .20	<i>R. parvula</i> 4.8 $\pm$ .16	3.2 $\pm$ .07	7.1 $\pm$ .14	5.4 $\pm$ .07	3.7 $\pm$ .17	4.8 $\pm$ .08
Guerrero	30.5 $\pm$ .43	29.4 $\pm$ .48	13.3 $\pm$ .14	4.8 $\pm$ .12	3.1 $\pm$ .07	6.9 $\pm$ .12	5.3 $\pm$ .10	3.6 $\pm$ .09	4.7 $\pm$ .06
Michoacán	29.9 $\pm$ .84	28.6 $\pm$ .64	13.0 $\pm$ .09	4.7 $\pm$ .08	2.9 $\pm$ .15	7.1 $\pm$ .10	5.3 $\pm$ .07	3.8 $\pm$ .07	4.7 $\pm$ .04
Colima	28.9 $\pm$ .43	28.0 $\pm$ .39	12.6 $\pm$ .15	4.6 $\pm$ .10	3.1 $\pm$ .06	6.8 $\pm$ .11	5.2 $\pm$ .07	3.6 $\pm$ .05	4.4 $\pm$ .07
Jalisco	28.6 $\pm$ .67	27.3 $\pm$ .53	12.7 $\pm$ .17	4.6 $\pm$ .10	3.1 $\pm$ .07	6.8 $\pm$ .12	5.0 $\pm$ .09	3.6 $\pm$ .06	4.4 $\pm$ .07
Nayarit	27.5 $\pm$ .34	26.6 $\pm$ .35	12.2 $\pm$ .11	4.5 $\pm$ .08	3.1 $\pm$ .07	6.6 $\pm$ .08	4.9 $\pm$ .06	3.4 $\pm$ .04	4.2 $\pm$ .06
Sinaloa-S	28.1 $\pm$ 1.01	26.7 $\pm$ .82	12.2 $\pm$ .12	4.4 $\pm$ .06	2.9 $\pm$ .04	6.6 $\pm$ .11	4.9 $\pm$ .16	3.4 $\pm$ .17	4.3 $\pm$ .17
Sinaloa-C	27.9 $\pm$ .33	26.8 $\pm$ .33	12.3 $\pm$ .18	4.4 $\pm$ .10	3.0 $\pm$ .05	6.5 $\pm$ .08	4.9 $\pm$ .06	3.4 $\pm$ .05	4.2 $\pm$ .07
Sonora	28.3 $\pm$ .53	26.8 $\pm$ .58	11.9 $\pm$ .21	4.3 $\pm$ .12	2.9 $\pm$ .04	6.3 $\pm$ .08	4.8 $\pm$ .11	3.3 $\pm$ .07	4.2 $\pm$ .06
Michoacán	26.0 $\pm$ .40	25.4 $\pm$ .42	11.4 $\pm$ .11	<i>R. mitra</i> 4.4 $\pm$ .10	2.8 $\pm$ .08	6.2 $\pm$ .10	4.6 $\pm$ .08	3.2 $\pm$ .06	3.9 $\pm$ .05
Tamp. 1	31.5 $\pm$ .47	30.9 $\pm$ .36	13.4 $\pm$ .11	<i>R. tumida</i> 5.0 $\pm$ .06	3.3 $\pm$ .07	7.0 $\pm$ .06	5.5 $\pm$ .06	3.8 $\pm$ .05	4.6 $\pm$ .06
Tamp. 2	31.6 $\pm$ .22	31.1 $\pm$ .28	13.4 $\pm$ .08	4.9 $\pm$ .05	3.3 $\pm$ .04	7.0 $\pm$ .06	5.4 $\pm$ .05	3.8 $\pm$ .04	4.7 $\pm$ .03
SL Potosí	30.2 $\pm$ .36	29.5 $\pm$ .37	13.1 $\pm$ .11	4.9 $\pm$ .07	3.3 $\pm$ .05	6.9 $\pm$ .07	5.4 $\pm$ .07	3.8 $\pm$ .06	4.6 $\pm$ .06
Veracruz-N	31.2 $\pm$ .76	30.5 $\pm$ .63	13.5 $\pm$ .18	5.0 $\pm$ .14	3.3 $\pm$ .06	7.0 $\pm$ .13	5.6 $\pm$ .12	3.9 $\pm$ .06	4.8 $\pm$ .06
Veracruz-C	30.1 $\pm$ .59	29.0 $\pm$ .63	13.2 $\pm$ .15	4.8 $\pm$ .11	3.4 $\pm$ .08	6.8 $\pm$ .10	5.5 $\pm$ .14	3.9 $\pm$ .08	4.7 $\pm$ .07
Veracruz-S	29.9 $\pm$ .51	29.1 $\pm$ .40	13.1 $\pm$ .13	4.8 $\pm$ .08	3.3 $\pm$ .06	7.0 $\pm$ .09	5.5 $\pm$ .07	3.9 $\pm$ .08	4.7 $\pm$ .05
Campeche	29.0 $\pm$ .65	28.2 $\pm$ .53	12.8 $\pm$ .19	4.7 $\pm$ .14	3.1 $\pm$ .11	6.7 $\pm$ .18	5.1 $\pm$ .12	3.6 $\pm$ .12	4.4 $\pm$ .06

TABLE 2. *Concluded.*

	FA	3MC	GLS	DB	POW	MW	M2M2	CICI	MAX
Yucatán	27.1±.81	26.1±.67	12.4±.24	4.5±.10	3.0±.09	6.4±.08	5.0±.14	3.6±.16	4.3±.12
Chiapas	29.4±.72	28.5±.66	13.5±.21	5.0±.09	3.4±.08	7.0±.13	5.7±.10	3.8±.08	4.8±.04
Guatemala	29.2±.95	28.1±.66	12.8±.23	4.7±.12	3.3±.09	6.9±.17	5.4±.17	3.7±.13	4.5±.09
El Salvador	29.0±.52	28.0±.43	12.6±.19	4.6±.09	3.2±.08	6.8±.09	5.2±.09	3.6±.08	4.4±.08
Honduras	29.7±.69	28.8±.55	13.0±.15	4.7±.09	3.3±.09	6.8±.13	5.3±.06	3.7±.07	4.5±.05
Nic. (Carib.)	30.0±1.62	28.8±1.14	13.3±.45	4.9±.21	3.3±.11	7.1±.23	5.4±.20	3.8±.10	4.6±.13
Costa Rica	30.2±1.33	29.3±1.06	13.1±.12	4.9±.07	3.3±.06	7.0±.08	5.3±.05	3.7±.06	4.5±.06
Panamá	29.6±.50	28.3±.44	12.7±.18	4.6±.09	3.2±.05	6.8±.12	5.2±.07	3.6±.10	4.3±.06
Colombia	28.7±1.30	27.8±1.11	12.4±.22	4.5±.16	3.2±.06	6.7±.18	5.1±.12	3.5±.06	4.3±.18
Venez.NW	27.7±.47	26.9±.23	12.5±.07	4.5±.14	3.2±.07	6.6±.11	5.2±.10	3.6±.06	4.2±.10
Venez.-C	28.7±.85	27.8±.72	12.5±.23	4.5±.08	3.2±.10	6.9±.10	5.1±.16	3.6±.10	4.3±.04
Venez.-NE	28.0±.38	27.0±.50	12.7±.14	4.5±.10	3.2±.10	6.9±.19	5.2±.14	3.7±.12	4.4±.11
Venez.-Int.	28.2±.72	27.3±.69	12.6±.33	4.6±.13	3.1±.05	6.7±.10	5.1±.10	3.6±.08	4.3±.08
Trinidad	29.5±.63	27.7±.37	12.7±.42	4.6±.21	3.2±.11	6.7±.35	5.1±.17	3.6±.14	4.4±.10
Guyana	28.5±.50	27.4±.54	12.6±.13	4.6±.14	3.3±.07	6.7±.10	5.3±.05	3.6±.07	4.4±.07
<i>R. minutilla</i>									
Venezuela 1	26.8±.58	26.4±.66	12.5±.13	4.4±.08	3.0±.04	6.6±.10	5.0±.08	3.6±.05	4.4±.07
Venezuela 2	27.8±.49	27.0±.55	12.8±.17	4.6±.11	3.0±.06	6.8±.09	5.1±.10	3.8±.06	4.6±.09
Venezuela 3	27.0±.41	26.5±.35	12.5±.10	4.5±.06	2.9±.05	6.5±.06	5.0±.07	3.6±.05	4.4±.05
Venezuela 4	26.9±.42	26.3±.44	12.4±.12	4.4±.07	2.9±.05	6.5±.10	5.1±.09	3.6±.07	4.3±.08
Venezuela 5	27.3±.25	27.1±.20	12.9±.11	4.6±.08	3.0±.04	6.8±.06	5.1±.05	3.7±.06	4.6±.05

*Comparisons.*—Although *Rhogeessa* shares its dental formula with several other genera of bats, only *Nycticeius* has been suggested to be a close relative. The only diagnostic differences noted by any authors relate to the lower incisors, which are well spaced, of uniform size, and have three cusps of equal size in *Nycticeius*. In my comparison of *N. humeralis*, type species of its genus, with *Rhogeessa*, the following additional differences were observed in *Nycticeius*: mesostyle of M3 present, but low; third commissure of M3 present; width of posterior half of m3 only slightly less than width of anterior half; maxillary toothrows parallel; basisphenoid pits present; rostrum nearly as wide as braincase; membranes relatively thick; baculum with enlarged distal knob, relatively small proximal lateral knobs, and poorly developed proximal median knob (see Plate I in Hamilton, 1949); length about 2.25 to 2.6 in four specimens; penis long, about 7-8; baculum extends from midpoint of penis to a point about 1.5 short of distal end of penis. The karyotype of *N. humeralis* differs in numerous ways from those of *R. tumida* and *R. parvula* (Baker and Patton, 1967). Karl Koopman (pers. com.) checked the list of characters listed above in seven additional species of *Nycticeius* (*schlieffeni*, *pallidus*, *greyi*, *balstoni*, *rueppelli*, *hirundo*, and *albofuscus*). Information on bacula and karyotypes was not available. Most of the other characters seemed to be consistent among the specimens of the species examined by Dr. Koopman, except penes were seen only for *greyi*, *balstoni*, and *hirundo*; the mesostyle and third commissure of M3 and the relative widths of anterior and posterior halves of m3 in *rueppelli* were more like *Rhogeessa* than in other species of *Nycticeius*; basisphenoid pits were rather weakly developed in some species.

#### Subgenus *Baeodon* G. S. Miller, 1906

*Baeodon* G. S. Miller, 1906:85 [Type species.—*Rhogeessa alleni* Thomas, 1892, by original designation].

*Description.*—As in account of genus, except as follows: i3 unicuspid, peglike, one sixth to one eighth cross-sectional area of i2; postorbital width narrow relative to overall skull size; skull large relative to body; first phalanx of third digit long relative to third metacarpal.

#### *Rhogeessa* (*Baeodon*) *alleni* Thomas

*Rhogeessa alleni* Thomas, 1892:477 [Holotype.—BMNH 93.2.5.25 from Santa Rosalia, near Autlán, Jalisco, México; A. C. Buller, collector].

*Baeodon alleni*—G. S. Miller, 1906:85.

*Holotype.*—British Museum of Natural History 93.2.5.25, adult female, preserved in alcohol, faded, skull removed. Measurements in table 3.



TABLE 3. Measurements of holotypes.

	FA	3MC	TIB	FUR	GLS	DOB	POW	MW	M2M2	CICI	MAX	MAND	M2
<i>tumida</i>	30.5	29.5	11.0	—	13.0	5.0	3.2	6.5	5.1	3.6	4.6	—	—
<i>io</i> <sup>a</sup>	27.9	27.2	10.9	3-4	12.0	—	3.1	—	4.9	3.3	4.3	5.3	1.3
<i>vetilla</i> <sup>b</sup>	27.9	27.3	10.8	3-4	11.8	4.3	3.2	6.5	5.1	3.3	4.2	5.2	1.2
<i>bombyx</i> <sup>b</sup>	31.5	30.4	12.4	3-4	14.3	5.4	3.6	7.4	6.0	4.2	5.0	6.3	1.5
<i>aeneus</i>	27.9	26.7	—	4	12.4	4.6	3.0	6.6	5.0	3.4	4.2	5.3	—
<i>riparia</i>	28.4	28.0	10.0	4	12.7	4.4	3.3	7.2	5.4	3.8	4.4	5.4	—
<i>parvula</i>	28.0	26.9	—	—	—	—	2.8	—	4.6	3.3	4.0	—	—
<i>major</i>	31.7	29.5	12.5	6	13.4	4.9	3.0	7.1	5.5	3.9	4.8	6.0	—
<i>mira</i>	26.2	26.1	10.4	4	11.1	4.3	2.6	6.0	4.5	3.1	3.8	—	1.0
<i>minutilla</i>	25.8	25.0	10.1	5	12.2	—	3.0	—	5.1	3.6	4.5	5.3	—
<i>alleui</i> <sup>b</sup>	34.8	33.6	14.9	4-5	15.6	5.5	3.3	8.0	6.3	4.5	5.5	6.8	2.0
<i>gracilis</i>	33.4	30.0	13.0	6	13.6	—	3.1	—	5.0	3.3	4.7	—	—

<sup>a</sup> Measurements taken by J. E. Hill and C. O. Handley.<sup>b</sup> Measurements taken by J. E. Hill.

*Description.*—A very large species of *Rhogeessa*, with tribanded dorsal fur and minute i3. Distal one fourth of dorsal hairs close to Dresden Brown, center one half buffy, and basal one fourth gray; ventrally, tips close to Light Ochraceous-Buff, bases gray; fur 4-6; dorsum of uropatagium almost bare; average ratio of third metacarpal to first phalanx of third digit 2.20:1; sagittal crest present in 8 of 9 skulls; sagittal and occipital crests form “helmet” above occiput; i3 average diameter 0.1, with little variation; cusps on lingual cingulum of C1 small, one or two in number; skull large in all dimensions except postorbital width.

*Bacula.*—The two *R. alleni* bacula examined are 0.44, 0.50 in length, 0.20, 0.22 in depth, and 0.44, 0.28 in width. In addition to their short lengths, these two bacula are notable for their short shaft and widely flaring proximal lateral knobs, with convex proximal margins (Fig. 2A). Although these bacula are quite distinct

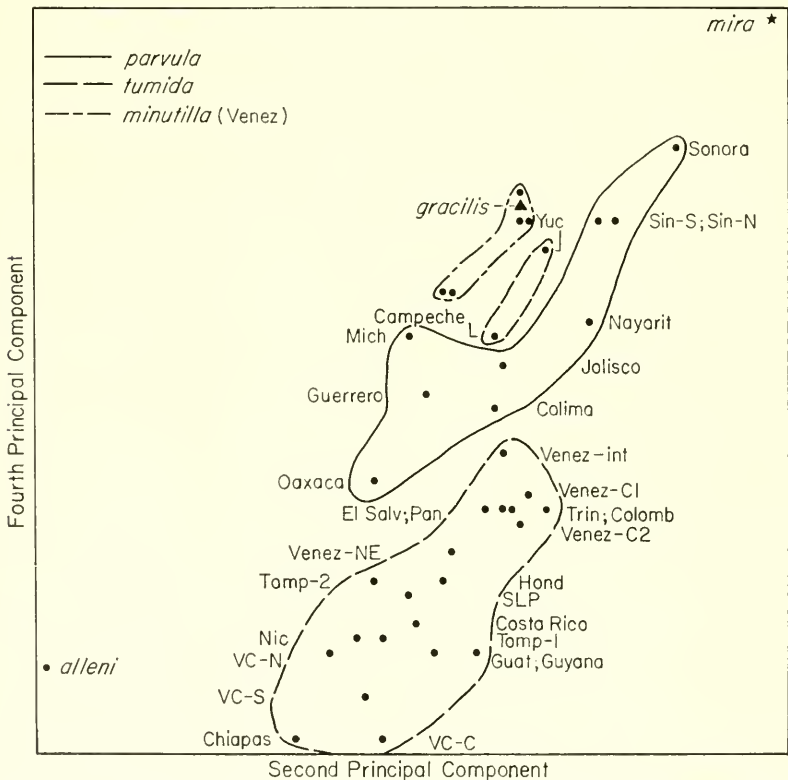


FIG. 4. Scatter diagram of second and fourth principal components of six species of *Rhogeessa*. Each symbol represents a sample mean. The symbols for *gracilis* (triangle), *alleni* (square), and *mira* (star) represent single pooled samples of all available specimens of those species.

from those of any other North American species of *Rhogeessa*, a few South American specimens of *R. tumida* possess bacula with similar development of the lateral knobs; however, the bacula have a longer shaft and greater length than those of *alleni*.

*Comparison.*—*Rhogeessa* (*Baeodon*) *alleni* is larger in cranial measurements (except postorbital width) than any specimens of the three species with which it occurs sympatrically in southwestern México (Table 2). Among the samples of specimens from southwestern México compared in table 2, *t*-tests showed that mean ratios of third metacarpal to first phalanx were significant between *parvula* and *alleni*, and between *gracilis* and *alleni*, at  $P = < .001$ , with no overlap. *Rhogeessa alleni* is separated from both by the characters given in the subgeneric description of *Baeodon*. It is easily separated from *gracilis* by the shorter ears and relatively narrow basal band of the dorsal fur; it can be easily distinguished from *parvula* by the three-banded dorsal fur (two-banded in *parvula*). In the multivariate analyses presented graphically here, Figs. 4, 6, 7, 8, 12, 14), *alleni* is distinctly separated from the other species of *Rhogeessa*, supporting assignment of that species to a monotypic subgenus. No specimens were misidentified by the discriminant function analysis (Table 4).

*Distribution.*—Mountains of western México, from central Oaxaca north to central Jalisco (Fig. 5). Altitudinal range from 125 m to 2000 m. Vegetation at the seven known localities seems to be either desert scrub or thorn forest. Although *R. alleni* may be more widespread than these few records indicate, it is probably restricted to western México northwest of the Isthmus of Tehuantepec.

*Reproduction.*—An individual caught on 6 August was not pregnant, and another female taken on 29 November was not lactating. An adult male captured on 28 March had testes 3 mm long. No juveniles were found.

*Remarks.*—In removing *alleni* from the genus *Rhogeessa* and erecting the genus *Baeodon* for it, Miller (1906) only mentioned a single diagnostic character, the minute i3. Relative size of teeth and even number of teeth vary within other vespertilionid genera. In *R. parvula* size of i3 is variable, and in some specimens approaches the condition observed in *R. alleni*. In most other characters, *alleni* is clearly similar to other species of *Rhogeessa*, although it has by far the largest skull of any species in the genus. For these reasons there seems to be no justification for assignment of *R. alleni* to a genus separate from *Rhogeessa*.

It should also be mentioned that the nominal species *Baeodon meyeri* Pine is not a *Rhogeessa* (see Pine, *et al.* 1971) and will not be treated in this revision.

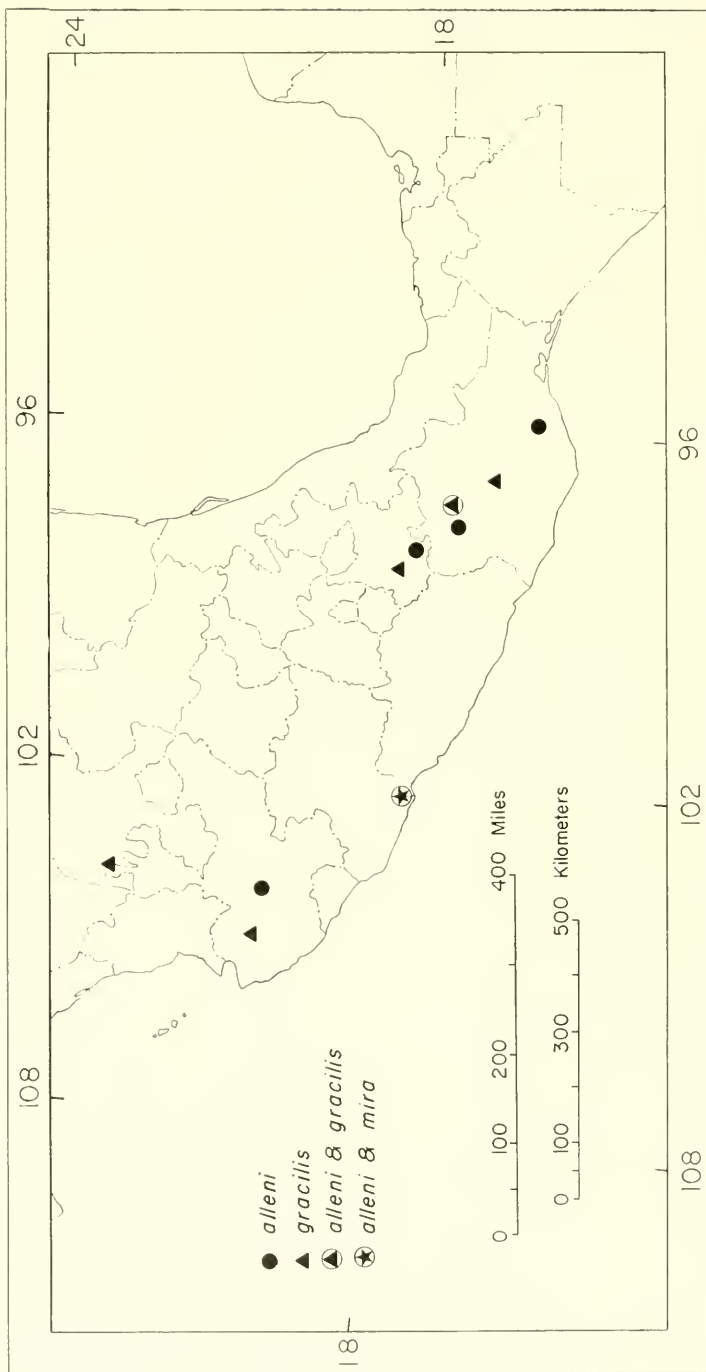


FIG. 5. Map showing localities from which were examined specimens of one or more of three species of *Rhogassa*.



Subgenus *Rhogeessa* H. Allen, 1866

(see citation under account of genus)

*Description*.—As in account of genus, except that cross-sectional area of  $i_3$  always greater than one sixth cross-sectional area of  $i_2$ ; postorbital width wide relative to overall skull size; skull small relative to body; first phalanx of third digit usually short relative to third metacarpal.

*Rhogeessa (Rhogeessa) gracilis* G. S. Miller

*Rhogeessa gracilis* G. S. Miller, 1897:126 [Holotype.—NMNH 70694 from Piaxtla, Puebla, México, elevation 1100 m; E. W. Nelson and E. A. Goldman, collectors].

*Holotype*.—National Museum of Natural History 70694, adult male, preserved in alcohol with skin peeled back from skull; penis and baculum removed, cleared, and stained; baculum 0.72 in length, 0.20 in depth, 0.44 in width. Compared with KU 97050. Other measurements in table 3.

*Description*.—A large species of *Rhogeessa* with very long ears (average length 18, based on collectors' measurements), long, three-banded dorsal fur, and relatively narrow skull. Distal one fourth of dorsal hairs close to Light Ochraceous-Buff; center one fourth a paler buff, and basal one half dark grayish brown; ventrally, tips close to Pinkish Buff, bases dark grayish brown; fur 6-7; dorsum of uropatagium with sparse fur extending almost to knees; mean of ratios of third metacarpal to first phalanx of third digit 2.56 to 1; sagittal crest present in 7 of 8 skulls, but poorly developed, as are occipital crests;  $i_3$ , 0.2 or greater in width, nearly as large as  $i_2$ ; lingual cingulum of C1 low, smooth, lacking cusps; skull moderate in size, but relatively narrow; slope of forehead steep; braincase inflated.

*Bacula*.—Measurements of four *R. gracilis* bacula: 0.72-0.80 in length, 0.16-0.28 in depth, and 0.40-0.54 in width. As viewed from above (Fig. 2B) the triangular outline of the baculum of *gracilis* differentiates it from the other three species with which it occurs sympatrically. In lateral profile the relatively straight shaft contrasts with the normally curved shaft of the other species.

*Comparisons*.—The large ears and unique color banding pattern allow *gracilis* to be separated easily from all other species. Likewise, the skull differs from those of other *Rhogeessa* in the relatively steeply sloping forehead, inflated braincase, and narrow lateral dimensions. In superficial appearance, the skull could be mistaken for that of a *Myotis*. In other species of the genus, the skulls are similar to those of *Eptesicus*, with respect to their widths and the slightly sloping foreheads, and their tendency to form a supra-occipital "helmet."

The distance phenogram (Fig. 6) separates *gracilis* rather well from the other samples of similarly-sized individuals of other species. The discriminant function analysis correctly identified all specimens (Table 4), and the plot of the first and second principal components (not figured) placed *gracilis* well outside the main cluster of sam-

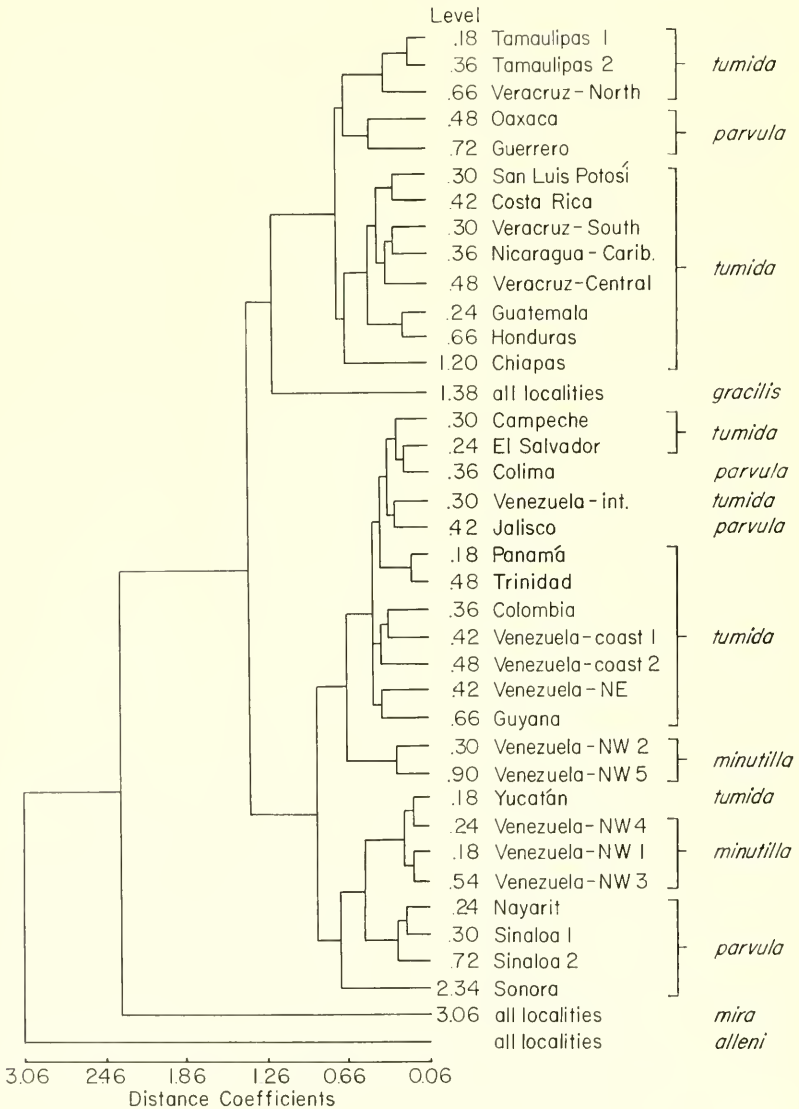


FIG. 6. Distance phenogram of species and pooled samples of *Rhogessa*, based on multivariate analysis of 9 mensural characters. Computed from the distance matrix. The cophenetic correlation is 0.860.

ples. Although other multivariate methods were of little value, they suggested that *gracilis* is more closely related to the other species of the subgenus *Rhogeessa* than it is to *Baeodon*.

*Distribution*.—Mountains of western México, from Jalisco, Oaxaca, and Puebla (Fig. 5). Altitudinal range from 600 m to 2000 m. The three specimens in the University of Kansas collection were taken at three localities described as follows by the collector: "pine-oak forest"; "oak forest"; "deciduous forest along stream, pine-oak forest on hills." However, it is not safe to assume that *gracilis* is restricted to this kind of vegetation, because one of the other specimens was taken at 600 m, where the predominating vegetational association in western México is thorn forest and desert scrub.

*Reproduction*.—A female captured on 15 May contained two 17 mm embryos. Two subadults taken on 27 July were nearly adult in size. No other information concerning reproduction in the species is available.

#### *Rhogeessa (Rhogeessa) parvula* H. Allen

*Rhogeessa parvula* H. Allen, 1866:285 [Holotype.—ANSP 1832 from Tres Marias Islands, Nayarit, México; Col. Grayson, collector].

*Rhogeessa tumida major* Goodwin, 1958:4 [Holotype.—AMNH 175263 from San Bartolo Yautepec, Oaxaca, México, 800 m; Thomas MacDougall, collector].

*Holotype*.—Academy of Natural Sciences of Philadelphia 1832, adult, sex indeterminant (male, according to Allen, 1866); skin disintegrated; skull intact but damaged, i3 notably smaller than i1 or i2; compared with KU 105565 and KU 107494 from Jalisco, and KU 90754 from Sinaloa. Measurements in table 3.

*Description*.—A small to moderate-sized *Rhogeessa* with short ears and relatively hairy uropatagium. Distal one third of dorsal hairs, Hair Brown to Warm Buff; basal two thirds, which may or may not contrast with tips, pale grayish to buff to pale yellow; ventrally, tips from Cartridge Buff to Light Ochraceous-Buff, bases concolor to slightly contrasting with tips; fur 3-7; sparse to moderately thick fur on dorsum of uropatagium usually extends halfway from knees to feet; ratio of third metacarpal to first phalanx of third digit averaging 2.66 to 1 in area of sympatry with *alleni* and *gracilis*; sagittal crest absent in 115 of 131 skulls; i3 varies in size from nearly equal to i2, to minute, but never as small as in *alleni*; lingual cingulum of C1 well-developed, bearing two cusps of variable size; in some, cusps much higher than in example of figure 1A; skull small to moderate in size; forehead slope slight; postorbital width narrow in relation to length of skull.

*Bacula*.—The average dimensions of 28 bacula are: length, 0.63 (0.48-0.76); depth, 0.13 (0.08-0.20); and width, 0.34 (0.22-0.42). Bacula of *parvula* are characterized by a long, slender, curved





shaft, roughly elliptical in cross-section, and by short proximal knobs, extending at a 45° angle to the sagittal plane of the baculum, separated proximally by an indentation, and curving ventrally around urethra (Figs. 2C and 2D); width approximately one half length of baculum. They differ from most *tumida* bacula in being more slender, from both the dorsal and lateral aspects. Juveniles and some adults (sexually immature individuals?) with shorter shaft and knobs.

*Comparisons.*—*Rhogeessa* (*Rhogeessa*) *parvula* are easily distinguished from *alleni* and *gracilis*, as outlined under the accounts of those species. This species differs from *R. mira* in its greater size and the presence of cusps on cingulum of C1. In the Isthmus of Tehuantepec *parvula* and *tumida* are known from localities only 50 miles distant, and are probably sympatric. Here the two species cannot be distinguished on the basis of size. (Table 2). Chiapan specimens of *tumida*, as compared to Oaxacan specimens of *parvula*, are differentiated by darker tips of dorsal fur, which contrast more sharply with bases. The uropatagium is virtually bare, and the i3 is nearly as large as the i2.

The two most consistent characters for separating *parvula* and *tumida*, fur coverage on uropatagium and relative size of i3 and i2, seem to be exaggerated in the Isthmus of Tehuantepec, where sympatry may occur. No specimens from that area exhibit intermediacy in these characters. For these reasons it seems advisable to regard *parvula* and *tumida* as species.

The discriminant function analysis (Table 4) correctly identified 76 of 115 specimens; of the 39 incorrectly identified, all but 8 were identified as being *R. tumida*. The plot of the second and fourth principal components (Fig. 4) reveals a close relationship between *parvula* and the two samples of *tumida* from the Yucatan Peninsula, but shows good separation between *parvula* and the other species, including most samples of *tumida*. The canonical scattergrams (Figs. 7 and 8) indicate a wide overlap with *tumida*.

*Distribution and geographic variation.*—Western México, from central Sonora south and east to the Isthmus of Tehuantepec (Fig. 9). Altitudinal range from sea level to 1600 m; however, the highest elevation recorded from Nayarit and states to the north is 600 m. Vegetational associations from which *R. parvula* is known include scrub desert, thorn forest, tropical deciduous forest, and pine-oak forest. Broad-leaved and evergreen forests (mostly cloud forest) of various compositions occur locally in portions of the range of *parvula*, but I am unable to establish definitely that any specimens were taken in those kinds of vegetation.

Variation in *R. parvula* is essentially clinal. Size measurements indicate increasing size from north to south (Table 2), with topotypes from the Tres Mariás Islands close to specimens from Sonora.

The north-south cline and widely overlapping non-significant subsets are well illustrated by the measurements of forearm (Fig. 10) and greatest length of skull (Fig. 11). Distance coefficients suggest that the cline is steeper south of Jalisco (Fig. 15), but there is no logical point at which a line separating two subspecies might be drawn. There is a tendency for specimens from more southerly localities to have fur extending farther out the uropatagium, to be brighter in color, to have longer fur, to have relatively smaller  $i3$ , and to have a more well developed sagittal crest; all of these trends appear to be clinal, with perhaps the most rapid changes occurring in Michoacán (one known locality) and the western half of Guerrero (no known localities). Were it not for the intermediacy of the series from Michoacán, it could easily be maintained that the northern and southern populations represented two subspecies (or two species, *vide* Goodwin, 1958).

*Reproduction and molt.*—Pregnant females were recorded from the months of February (27th), March, April, May, and early June.

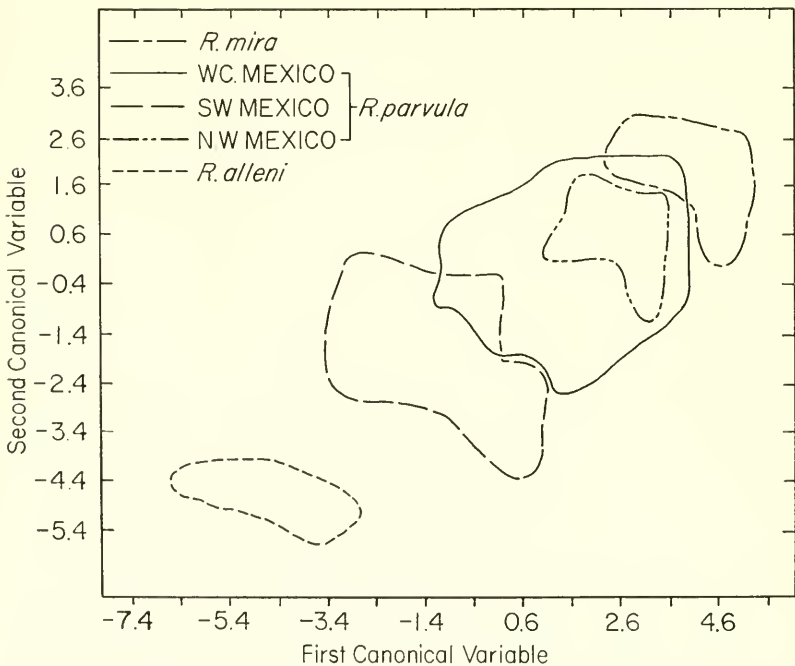


FIG. 7. Scatter diagram from first two canonical variables for three species of *Rhogeessa* from western México. The lines were formed by connecting the outlying dots within each of the 5 pooled samples. The spaces enclosed by the lines originally contained the following number of dots, each representing an individual specimen: *R. mira*, 13; WCMEX, 75; SWMEX, 28; NWMEX, 12; *R. alleni*, 7. Specimens of unknown identity may be plotted on canonical scattergrams for purposes of identification. See Appendix 1.

Lactating females were taken during April (27th), May, June, and July (3rd). Because few embryo measurements are available, there is no indication of any definite growth trends or patterns. The only juveniles (flying young) recorded were taken on 14 June, 18 July, 9 September, and 18 September. The presence of flying young and embryos in Guerrero in June and February-March, respectively, suggests that parturition occurs earlier in the southern portion of the range of *R. parvula*. At least eight females from Sinaloa and Sonora contained two embryos, but two bats from Guerrero and one from Sonora contained only one embryo each. One female was molting on 4 July, which would be anticipated, if she had just weaned her young. The new pelage was dark gray, contrasting sharply with the pale, old pelage. Two males from July and several females from August and September exhibited very dark-colored tips, suggestive of recent molt. Negative data showed that some females collected on various dates during March, April, May, June, July, and September were not pregnant. Weights for 30 non-pregnant individuals varied from 3 to 8. No seasonal trends in weight could be detected.

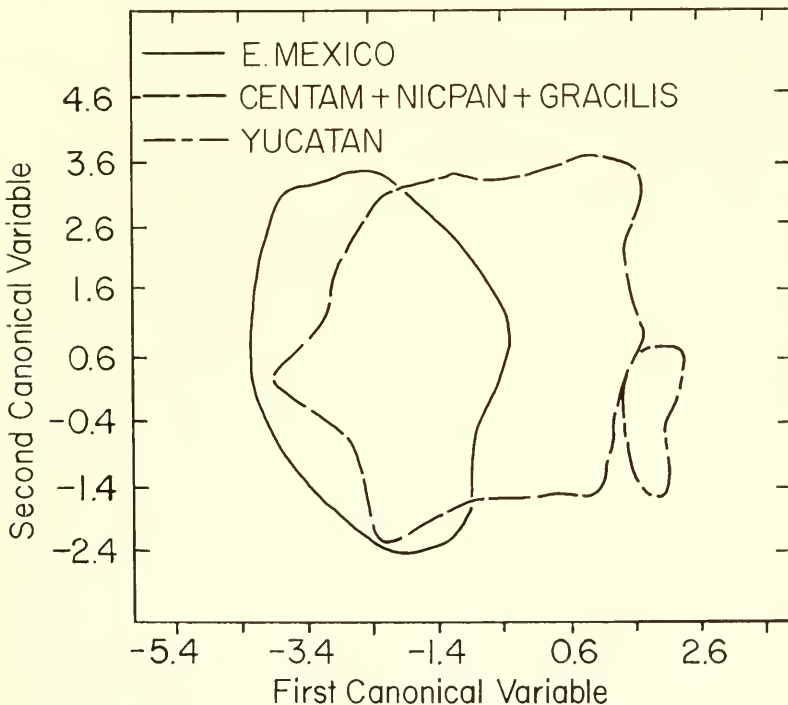


FIG. 8. Scatter diagram from first two canonical variables for three pooled samples of *Rhogeessa tumida*. The following numbers of dots are enclosed by the lines: EMEX, 85; CENTAM + NICPAN + GRACIL, 90; Yucatán, 5.

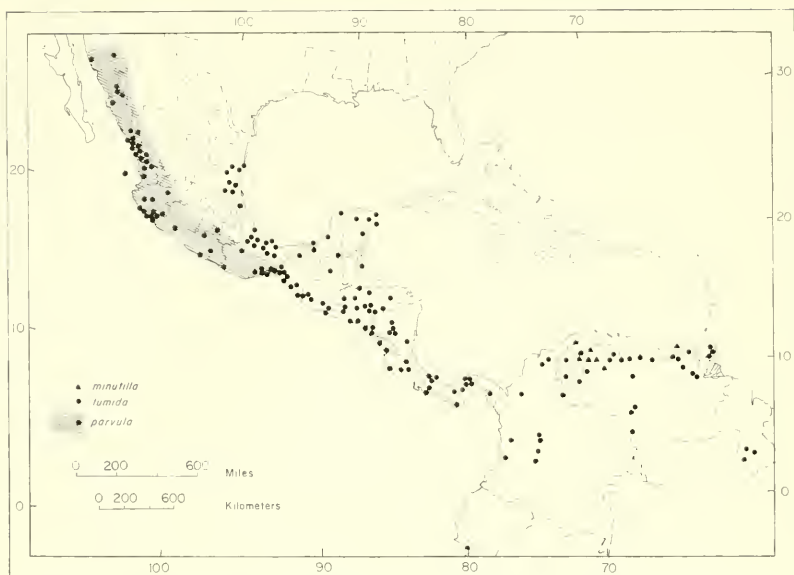


FIG. 9. Map showing localities from which were examined specimens of one of three species of *Rhogeessa*. The shaded area represents the distribution of *R. parvula*, the unshaded area, *R. tumida*. The triangles representing *minutilla* are all in northwestern Venezuela and adjacent Colombia, plus the island of Margarita.

*Remarks.*—Goodwin (1958) used size as the major criterion for separating *parvula* and *tumida*. He lacked specimens from Jalisco, Nayarit, and Sinaloa where a clinal change occurs; therefore, it is not surprising that he identified the larger specimens from southwestern México as *tumida*. Specimens of *tumida* from adjoining Chiapas and Veracruz are much like Oaxacan *parvula* in size. Goodwin also assigned populations of small individuals from the Yucatan Peninsula and parts of South America to *parvula*. In addition to the nominate subspecies, he assigned four other subspecies to *parvula*. One of these, *minutilla*, is here regarded as a species; the other three are relegated to the synonymy of *tumida*.

#### *Rhogeessa (Rhogeessa) mira*, new species

*Holotype.*—Universidad Nacional Autónoma de México 8594, adult male, skin, skull, and baculum, from 20 km N El Infiernillo, Michoacán, México, elevation 125 m; collected by Ticul Alvarez, 29 November 1964. Collector's measurements, overall length, 70; tail, 33; foot, 6; ear, 12; length of testis, 9; external and cranial measurements in Table 3.

*Etymology.*—The specific epithet *mira* is feminine for the Latin *mirus*, meaning wonderful, astonishing, or extraordinary. These

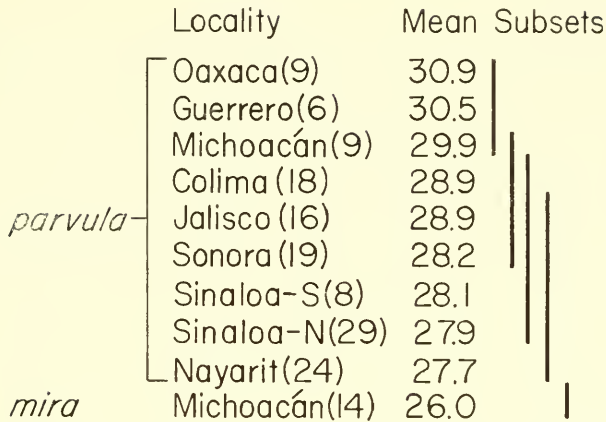


FIG. 10. SS-STP analysis showing geographic variation in forearm length in *Rhogessa parvula*. The vertical bars connect samples within each non-significant subset (at the 0.05 level). For example, the mean of Sinaloa-S is not significantly different from the mean of Sonora, but is significantly different from the mean of *mira*.

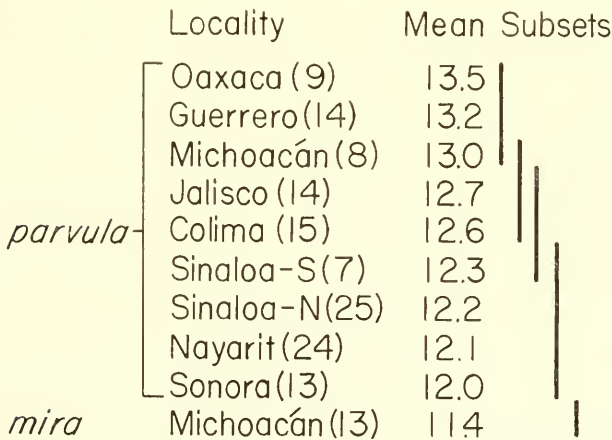


FIG. 11. SS-STP analysis showing geographic variation in greatest length of skull of *Rhogessa parvula*.

were my initial reactions upon examining a specimen of *R. mira* and comparing it with the much larger species taken at the same locality, *R. alleni* and *R. parvula*.

*Description*.—An extremely small *Rhogessa* with smooth-edged lingual cingulum of C1 and external characteristics much as in *R. parvula*. Distal one third of dorsal hairs Buckthorn Brown to Buffy Brown; basal two thirds more buffy than tips, not contrasting strongly with tips; ventrally, overall color like that of bases of dorsal



hairs, tips not contrasting; fur 4; sparse fur on dorsum of uropatagium extends to or past knees; sagittal crest absent; i3 only slightly smaller than i2; lingual cingulum of C1 smooth, lacking the slightest suggestion of cusps; skull very small; forehead slope moderate.

*Baculum*.—Measurements of the single baculum examined (Fig. 2E) are: length 0.66, depth 0.12, and width 0.34. It could not be distinguished from bacula of some *R. parvula*.

*Comparisons*.—*R. mira* is easily distinguished from the other three species in western México on the basis of size. It resembles *gracilis* in its smooth lingual cingulum of C1. Otherwise it could not possibly be confused with *gracilis* or *alleni*. The lack of cingual cusps, small overall size, and relatively large size of i3 separate it from sympatric *parvula*. Nine specimens of *parvula* from the type locality of *mira* are all redder and yellower than any specimens of *mira* caught at the same time, or at any other time. Furthermore, there is no size overlap among specimens of the two species caught at the type locality. Certain specimens of *parvula* from Sonora and the Tres Mariás Islands are almost as small as *mira*, but tend to have a less steeply sloping forehead, wider and longer rostrum, cingual cusps on C1, smaller, more crowded i3, and less fur on uropatagium. Small individuals of *tumida* and *minutilla* from Yucatán, Venezuela, and Ecuador differ in color, skull outline, cingual cusps, nearly bare uropatagium, and shape of baculum.

Generally, the multivariate analyses placed *mira* well away from most samples of all other species. Based on these analyses alone, *mira* would seem almost as distinct from other *Rhogeessa* as in *R. alleni*. However, in external and cranial characters not included in the multivariate analyses, *mira* is more similar to the others, especially to *parvula*. In the univariate analysis *mira*, which had the lowest means among all samples for most of the variates measured, usually formed a nonsignificant subset with Sinaloa and Sonora, with Sonora, or alone (as in Figs. 10 and 11).

*Remarks*.—All the specimens from 7 km N El Infiernillo were caught in nets over a small cement water trough, in an area of cactus-mesquite vegetation (Alvarez and Aviña, 1965). Collected at the same time were *R. alleni*, *R. parvula*, *Balantiopteryx plicata*, *Macrotus waterhouseii*, and *Micronycteris megalotis*. The *Rhogeessa* were taken on five nights, 25 and 27 March, and 26, 28, and 29 November, all in 1964. The capture of three species of *Rhogeessa* during one night, in one net, is of interest, because each of the three is in a non-overlapping size range. This suggests successful partition of the feeding niche, possibly based on prey size. The failure to achieve this kind of diversity within the genus *Rhogeessa* outside of western México could be accounted for by the presence of additional Neotropical species of the genus *Myotis* in those areas, although this suggestion is highly speculative at this time. It is also

noteworthy that *R. mira* is among the smallest of all species of bats, although it exceeds in size specimens of the species *Tylonycteris pachypus* of Southeast Asia, and possibly specimens of certain species of *Pipistrellus*, notably *P. minimus*.

### *Rhogeessa* (*Rhogeessa*) *tumida* H. Allen

*Rhogeessa tumida* H. Allen, 1866:286 [Holotype.—ANSP 1831 (skin), NMNH 37329 (cranium), and NMNH 84021 (lower jaw) from Mirador, Veracruz, México, ca. sea level; Dr. Sartorius, collector].

*Rhogeessa io* Thomas, 1903:382 [Holotype.—BMNH 94.9.25.1 from Valencia, Carabobo, Venezuela; A. Mocquerys, collector].

*Rhogeessa velilla* Thomas, 1903:383 [Holotype.—BMNH 99.8.1.5 from Puná, Isla Puná, Gulf of Guayaquil, Ecuador, elev. 10 m; P. O. Simons, collector].

*Rhogeessa bombyx* Thomas, 1913:569 [Holotype.—BMNH 13.10.29.1 from Condoto, Chocó, Colombia, elev. 300 ft; Dr. H. G. F. Spurrell, collector].

*Rhogeessa tumida riparia* Goodwin, 1958:5 [Holotype.—AMNH 69968 from Cumanacoa, Sucre, Venezuela, elev. 700 ft; G. H. H. Tate, collector].

*Rhogeessa parvula aeneus* Goodwin, 1958:6 [Holotype.—AMNH 91234 from Chichén-Itzá, Yucatán, México, elev. ca. 10 m; R. T. Hatt, collector].

*Holotype*.—"Museum of Smithsonian Institution" S195, male, is the number listed by H. Allen (1866) as the holotype of *tumida*. Part of the confusion regarding the location, status, and numbers of the various parts of the holotype was discussed by Hall (1952). The skin, in alcohol and appearing to be a female, is in the Academy of Natural Sciences of Philadelphia, no. 1831. Two labels are with the specimen; one reads "1831 Harr. Allen *Rhogeessa tumida* Mirador, Mex. TYPE H. Allen." The other bears only the number S195. The cranium, NMNH 37329, is now in a vial bearing that number. The accompanying lower jaw, numbered NMNH 84021, seems to match the cranium perfectly. In another vial, labelled NMNH 84021, is a cranium bearing that number and a lower jaw numbered NMNH 37329. These also seem to match perfectly, which is significant, because the two skulls in question differ in size. The vial holding NMNH 84021 is also labelled "formerly 7842" which would make it the paratype of *R. parvula*. It appears that the lower jaws were switched before the skulls were numbered. In any case NMNH 37329 (cranium) is obviously of the species now occurring in eastern México, and should be regarded as the holotype. The holotypes of *R. tumida* and *R. t. riparia* were compared with KU 29886 from Veracruz, TCWC 19756 from Nicaragua, UNM 27545 from Oaxaca, and AMNH 91234 from Yucatán (holotype of *R. p. aeneus*), among others. Handley (*in litt.*) compared the holotype of *R. io* with NMNH 374017, *R. tumida* from Urama, Venezuela, and J. E. Hill (*in litt.*) compared the holotypes of *R. io* and *R. velilla* with each other. Handley also compared the holotype of *R. velilla* with NMNH 312113, *R. tumida* from Ft. Kobbe, Panamá. Measurements are in table 3.

*Description.*—A small to moderate-sized *Rhogeessa* with short ears and nearly bare uropatagium; otherwise highly variable. Distal one third of dorsal hairs Fuscous-Black to Pinkish Cinnamon, except in Venezuela and Guyana, where darkest specimens Brussels Brown, and palest specimens somewhat darker than those from other parts of the species' range; bases usually buffy gray to buffy yellow, and may or may not contrast sharply with tips; ventrally, tips Buffy Brown to Light Ochraceous-Buff, concolor to somewhat paler at bases; fur 3-4 (rarely 5); sparse hairs on dorsum of uropatagium rarely extend as far as knees; sagittal crest present in approximately half of all specimens examined, but present in only one fourth of specimens from Colombia, Venezuela, Trinidad, and Guyana;  $i_3$  usually smaller than  $i_2$ , but may equal  $i_2$ ; even when  $i_3$  equals  $i_2$ ,  $i_3$  has less well-developed cusps; lingual cingulum of C1 with two small cusps, sometimes only a suggestion of cusps present; skull small to moderate in size; forehead slope slight; "helmet" often present in North American specimens, rarely in South America.

*Bacula.*—Twenty-nine bacula of North American specimens have dimensions as follows: length, 0.65 (0.50-0.80); depth, 0.19 (0.12-0.28); and width, 0.52 (0.36-0.84). In fourteen specimens from South America, means are: length, 0.66 (0.48-0.80); depth, 0.19 (0.14-0.24); width, 0.60 (0.44-0.74). The only apparent difference between the two groups is in width, and this is not statistically significant.

In shape, both individual and geographic variation are apparent (Fig. 2F-L). Generally, as compared to bacula of *parvula*, the bacula of *tumida* possess wider shafts, wider spreading (laterally), and wider (distal-proximal) proximal knobs; their width exceeds one half their length. In Central America the bacula of *tumida* tend to be Y-shaped, due to deeper indentation between ends of proximal knobs. The distal free portion of shaft is shorter than that portion from which knobs extend. In some, additional widening of shaft results in a roughly triangular shape. In Colombia, Y-shaped, triangular, and intermediate specimens appear; whereas in Venezuela, Guyana, and Trinidad, the Y-shape is rare, and in some the proximal knobs extend laterally at an angle of  $90^\circ$  to the shaft.

*Comparisons.*—In the Isthmus of Tehuantepec *R. tumida* differs from *R. parvula* as outlined under the account of that species. In general, the bare uropatagium and relatively large  $i_3$  of *tumida* distinguish all *tumida* from all *parvula*. Other characters tend to be geographically variable and thus will not separate consistently the two species. In northwestern Venezuela and adjacent Colombia, where *tumida* apparently occurs sympatrically with *minutilla*, *tumida* is larger on the average, and has proportionately greater post-orbital width (Table 2). *Rhogeessa tumida* is always darker in color (both fur and membranes). It has a greater difference in

length between forearm and third metacarpal, and the tibia is shorter. Toothwear is rarely heavy. In most of the extensive range of *tumida* there is no other species of *Rhogeessa* present.

The discriminant function analysis correctly identified 194 of 212 specimens as *tumida* (Table 4). Two were misidentified as *minutilla*, one as *gracilis*, and 15 as *parvula*. In the pooled sample of 75 from Central America, a region where a bewildering amount and kind of geographic variation occurs, only 15 were correctly identified as being from Central America. The value of the other multivariate analyses is discussed under *parvula*. It is noteworthy that the canonical scattergram (Fig. 12) seems to separate *tumida* in South America surprisingly well from *minutilla*.

*Distribution and geographic variation.*—Tamaulipas, south in Caribbean lowlands, including the Yucatan Peninsula, to Pacific versant in Chiapas, throughout Central America, and South America, locally south to southern Brazil, Bolivia, and Ecuador (Fig. 9). Sea level to 1500 m in North America, with the higher elevations from Chiapas through Costa Rica; sea level to 1200 m in South America. A large majority of all specimens were collected from below 500 m. *Rhogeessa tumida* seems to be known from virtually every major vegetational association in tropical North America and northern South America, within the limits imposed by elevational restrictions. It is difficult to generalize in terms of geographic variation in size, since clines are poorly developed and skin and skull measurements do not indicate the same kinds of trends. Mexican specimens (excluding Yucatán) tend to be the largest, followed by specimens from Central America (excluding Caribbean coast) and then specimens from South America (including Yucatán, but excluding Pacific coast of Colombia).

The SS-STP analyses for forearm and greatest length of skull (Fig. 13) illustrate geographic changes in size. Note that specimens from Costa Rica (interior), from Nicaragua (Caribbean lowlands), and from eastern México have the largest forearms, with the intermediate sized bats being from the Pacific versant of Central America (including Chiapas) and southern Campeche. Most of the smallest specimens are from South America, but those from the northern Yucatan Peninsula are the most diminutive of all. Based on greatest length of skull, the same group of samples (with the addition of Chiapas) is largest in size, but they are arranged in a different sequence. The middle-sized group is similar except for sequence and the loss of the El Salvador-Nicaragua (Pacific versant) sample which drops to a position among the South American samples. The Colombian sample also drops significantly in the standings. However, two specimens from the Pacific coast of Colombia are as large as specimens from Nicaragua (Caribbean) and are not included in the sample from Colombia.

The distance coefficients (Fig. 14) differ substantially in value



in various parts of the range and support my contention that variation is essentially non-clinal. The largest values in the conterminous portion of the range are those between southern Campeche and Veracruz, and between Campeche and Pacific coastal Chiapas. Values between Campeche and Guatemala, El Salvador, and Honduras are much lower, however. Few specimens are available from the Yucatan Peninsula, but it appears that a South-North cline of decreasing size is operative, resulting in specimens from Yucatán and Quintana Roo which are more like South American specimens in size than like those from adjacent areas. From Honduras south and east through western Panamá, it appears that clines from small to large and pale to dark operate along a Pacific-Caribbean axis. Two specimens from the Pacific coast of Colombia are also large and dark. It seems probable that the large, dark population of Caribbean Central America extends across Panamá in the far east to join the large, dark bats of Colombia, but no specimens are available

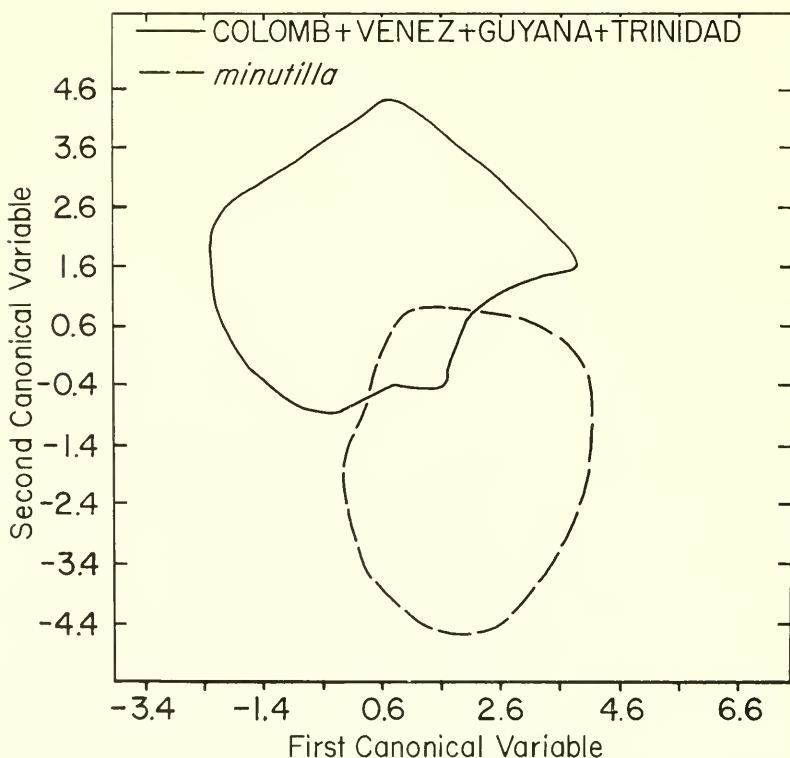


FIG. 12. Scatter diagram from first two canonical variables for *Rhogessa tumida* (4 pooled samples) and *R. minutilla* in South America. The following numbers of dots are enclosed by the lines: COLOMB + VENEZ + GUYANA + TRINIDAD, 49; *minutilla*, 62.



to support that hypothesis. If true, it will pose some rather interesting systematic problems.

Farther south along the Pacific Coast of South America, two specimens known from Puna Island, Ecuador, are both very small in size, and are similar to specimens from the Caribbean coast of Colombia and Venezuela. Two specimens from Brazil are very much like specimens from Chiapas and Guatemala, in size and color. I was not able to examine the single specimen from Bolivia in the Field Museum of Natural History. South of Venezuela and central Colombia, *R. tumida* is represented by so few specimens that it is not possible to speculate on geographic variation or even on the limits of geographic distribution. Because of the absence of specimens among large collections of bats from some parts of Brazil, Perú, Bolivia, Paraguay, and Uruguay, I believe that *R. tumida* is truly a rare species in much of South America, and may be only locally distributed.

Color is both individually variable, based on age of pelage, and geographically variable. Eastern Mexican specimens tend to be closer to the red and yellow end of the spectrum, with little contrast

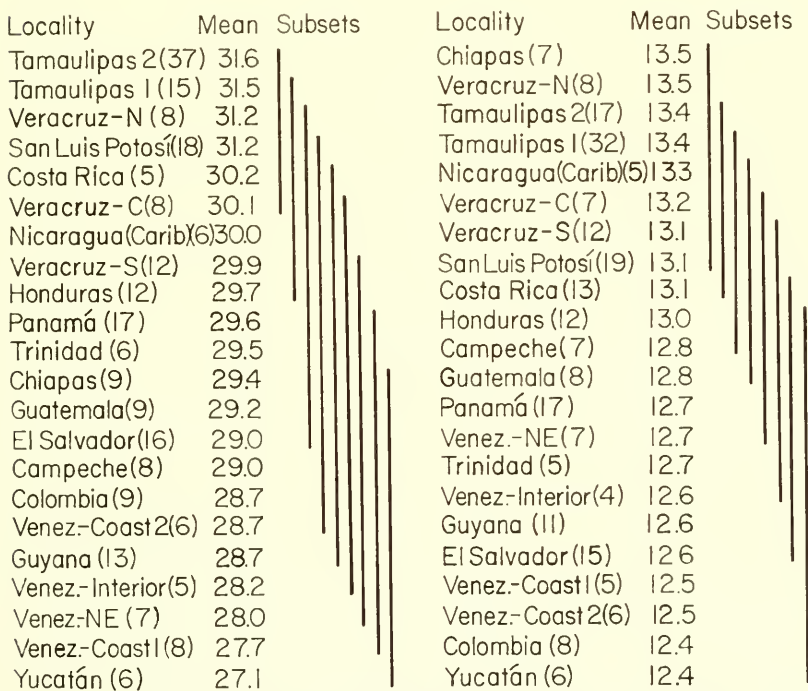


FIG. 13. SS-STP analysis showing geographic variation in forearm (left) and in greatest length of skull (right) of *Rhogeessa tumida*.

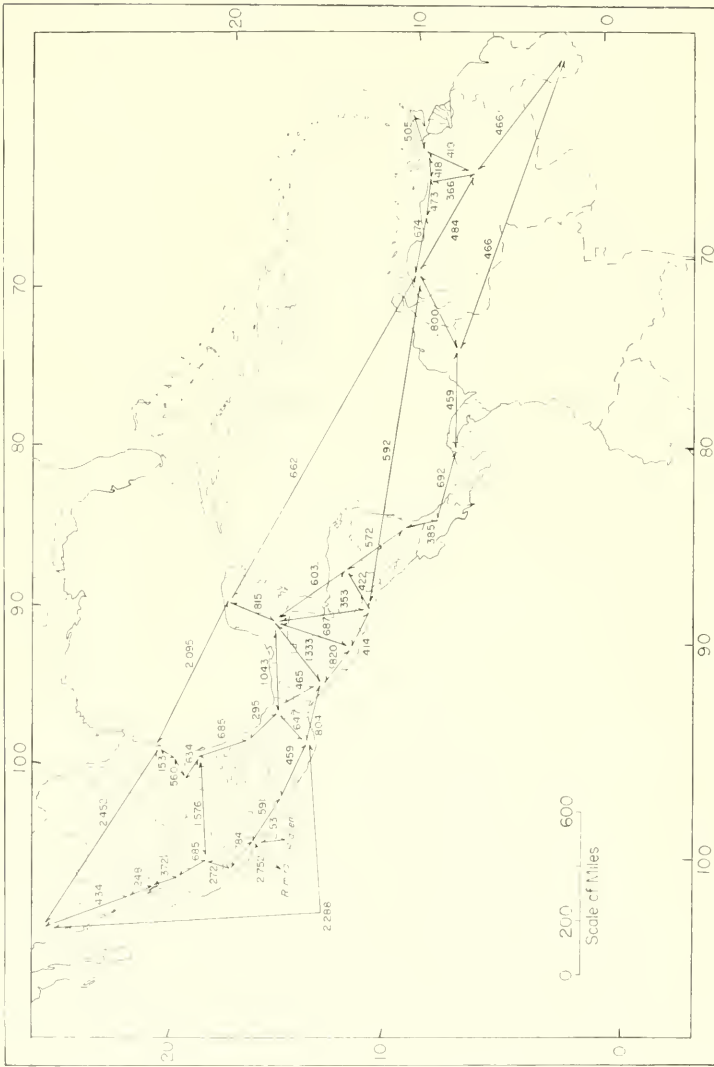


FIG. 14. Map showing selected distance coefficients from the distance matrix between localities and pooled samples of five species of *Rhiogessa*. The lines diverging from northwestern Venezuela all show distance coefficients between *R. minutilla* and *R. tumida*. *Rhiogessa gracilis* is not represented on the map.

between bases and tips. Specimens from the Yucatan Peninsula, Chiapas, Caribbean coast of Nicaragua and Panamá, and Pacific coast of Colombia tend to have buffier bases and darker brown or black tips, which contrast strongly with bases. Specimens from the Pacific coast of Central America tend to resemble eastern Mexican specimens in color. In South America, most of the color combinations known from North America occur, but many redder and yellower specimens also occur, with differing combinations of base and tip color. Throughout the range, males tend to be darker than females; however, this observation may represent an artifact, because many series of specimens have been collected during early summer, when males have probably recently molted and females have not.

Based on the data obtained in this study, I have been unable to divide the wide-ranging *R. tumida* into sympatric species, allopatric species, or into subspecies, although one or more of these actions ultimately may be necessary. The preliminary karyotypic studies of R. J. Baker (pers. com.) indicate that animals having at least four different karyotypes exist within the geographic range of *R. tumida*. Two different karyotypes are represented among animals from southern Chiapas, and individuals from the Caribbean lowlands of Nicaragua, and from Trinidad, differ karyotypically from specimens collected in Pacific coastal Central America. At this point it is not possible to evaluate these karyotypic trends in terms of the systematics of *R. tumida*.

*Reproduction and molt.*—Relatively few preparators of *Rhogeessa* specimens have recorded data on reproductive condition. More information is available on *tumida* than the other species, even though much of it is negative. Pregnant females were taken in May in Tabasco. Nine bats caught in Guatemala, El Salvador, Honduras, and Nicaragua were pregnant in the period from 14 February through 28 April. Gravid females were taken in Costa Rica on 9 March, and in Panamá on 25 February. A pregnant individual from Venezuela was captured on 23 March, and another, possibly pregnant, on 12 October. Lactating females were collected on various dates from 24 May to 20 June in Tamaulipas and 30 April to 12 June in Veracruz. Others were taken on 12 June in Oaxaca, May in Tabasco, 18 July in Nicaragua, and 29 March and 7 May in Costa Rica. Bats recorded as not pregnant, or as not lactating, were caught in most months of the year, but few of these were from the spring or early summer months.

Based on these data, it appears that gestation, parturition, and lactation extend from mid-February through mid-July. Obviously, there is variation in dates for reproductive events among females. To what extent this is geographically correlated cannot be determined, however. Of ten specimens for which the number of embryos was recorded, three had but one embryo, and the remainder

two. Juveniles were taken on 23 dates scattered during the period 21 May through 27 August. One Venezuelan juvenile was caught on 4 October. Because this individual was captured at a locality within 5°N of the equator, it seems possible that a somewhat different breeding cycle prevails at that latitude.

Males with enlarged testes (6-7) were taken during September, November, December, and January. Bats from other months had testes ranging in size from 2 to 5, suggesting that maximum production of spermatozoa may occur during the autumn and early winter, as in Temperate Zone vespertilionid bats. Five males were molting in late May and June, and three females in July, suggesting coordination with reproductive cycles.

*Remarks.*—Included in the synonymy are five names applied to subspecies of either *tumida* or *parvula* by Goodwin (1958). *Rhogeessa io* Thomas and *R. t. riparia* Goodwin are names applied to Venezuelan specimens. There is little geographic variation in this area, and, although the holotype of *riparia* is a larger individual than the holotype of *io*, it would be pointless to apply these names to subspecies. There is no sharp break in Panamá or Colombia which would tend to validate the recognition of a distinct South American subspecies.

*Rhogeessa velilla* Thomas, based on a specimen from Ecuador, may be applicable to a subspecies, but the specimens which might show a pattern of geographic variation deserving of nomenclatural recognition have not yet been collected. The holotype of *velilla* does not differ in size from the holotype of *io*, and J. E. Hill (*in litt.*) noted that they were almost identical. The holotype of *R. bombyx*, from the Pacific coastal lowlands of Colombia, is typical of the large individuals which seem to occur along the Caribbean versant of Central America (from Nicaragua southward) and the west coast of Colombia. At present I choose not to recognize *bombyx* as a species or subspecies because of the apparent clinal transition from small pale individuals on the Pacific coast of Central America to large, dark individuals on the Caribbean coast. The substantial gaps in eastern Panamá and Colombia suggest that subsequent collecting may reveal a more accurate rendition of variation in this region.

*Rhogeessa parvula aeneus* Goodwin is a name applied to small individuals from Yucatán and northern Quintana Roo. According to my notes "This skull [holotype of *tumida*] is almost identical to AMNH 91234, holotype of *aeneus* . . . (although latter is smaller)." The size of specimens from various localities in Campeche, southern Quintana Roo, and Belice suggests a clinal change. I prefer not to give nomenclatural recognition to various segments of a cline, especially when the dividing line would be of necessity arbitrary.

***Rhogeessa (Rhogeessa) minutilla* G. S. Miller**

*Rhogeessa minutilla* G. S. Miller, 1897:139 [Holotype.—NMNH 63216 from Margarita Island, Venezuela; Lt. Wirt Robinson, collector].

*Rhogeessa parvula minutilla*—Goodwin 1958:7.

*Holotype*.—National Museum of Natural History 63216, adult male, skin and skull. This specimen was compared with 98 other specimens of *minutilla* from Venezuela and Margarita in the NMNH, as well as with 51 specimens of *tumida* from Venezuela and Trinidad. Measurements of holotype appear in table 3.

*Description*.—Essentially as in description of Venezuelan *tumida*. Major differences will be noted under "Comparisons." Distal one third of dorsal hairs Cinnamon Buff to near Sudan Brown; basal two-thirds contrasting with tips, Light Buff in most specimens; ventrally, Warm Buff to Light Ochraceous-Buff to Cinnamon Buff; fur 4-5; sagittal crest present in 26 of 76 skulls.

*Bacula*.—Mean dimensions of eleven bacula from specimens of *minutilla* (all from northwestern Venezuela) are: length, 0.50 (0.40-0.60); depth, 0.17 (0.12-0.22); width, 0.50 (0.40-0.62). As compared to bacula of South America *tumida*, the bacula of *minutilla* are shorter and narrower; lateral knobs extend at a higher angle from shaft, and approach a right angle in some specimens (Figs. 2M and 2N). Some *minutilla* bacula resemble closely those of some *tumida*.

*Comparisons*.—Despite their great similarity, there are some consistent differences between *tumida* and *minutilla*. The two species are compared in tables 2 and 5.

Univariate analyses give poor separation of *tumida* and *minutilla* in South America, but the multivariate analyses allow a somewhat different perspective. The plot of the second and fourth principal components (Fig. 4) and of the first and second canonical variables (Fig. 12) show remarkably good separation between these two species. The discriminant function table (Table 4) indicates that 42 of 62 specimens of *minutilla* were correctly identified. Ten specimens of the 12 misidentified as *tumida* were identified as *tumida*

TABLE 5. A comparison of major characters which distinguish *Rhogeessa tumida* and *R. minutilla* in northwestern Venezuela.

<i>R. tumida</i>	<i>R. minutilla</i>
Fur and membranes darker	fur and membranes paler
"helmet" rarely present	"helmet" usually present
POW greater	POW less
tibia shorter	tibia longer
heavy toothwear rare	heavy toothwear common
tragus shorter	tragus longer
third metacarpal at least 1 mm shorter than forearm	third metacarpal about 0.5 mm shorter than forearm



from Yucatán, and eight as *parvula*. Only two were misidentified as *tumida* from South America.

*Distribution.*—Arid lowlands of Margarita Island, northwestern Venezuela, and adjoining portion of the Guajira Peninsula of Colombia (Fig. 9) *Rhogeessa minutilla* occurs from sea level to 500 m. Virtually all of this region is vegetated by desert scrub and thorn forest. Although there appear to be minor differences in size and color among the samples examined, there are no obvious trends that might suggest geographic variation.

*Reproduction and molt.*—No pregnant females have been recorded; however, numerous specimens collected in June and July were recorded as being not pregnant. Juveniles were taken from late June through mid-July. Five males from June and July had small testes, measuring 2-3. Molting females were taken on 30 June, 17 July, and 18 July; a single molting male was recorded from 16 July.

*Remarks.*—The type locality (Margarita Island) is approximately 500 km east of the main range of *minutilla*; its separation by an area where only *tumida* seems to occur is a strangely anomalous situation. Yet the three specimens from Margarita can be easily matched by bats from northwestern Venezuela. It seems probable that during a more arid (interglacial?) period the range of *minutilla* was continuous along the northern coast of South America, and reached at least one of the offshore islands. On the other hand, the lowered sea levels characteristic of periods of glaciation may have facilitated a crossing from the mainland to Margarita, or vice versa. Arid habitat in the areas occupied by *minutilla* today is separated by areas of more mesic vegetation. No specimens of *minutilla* seem to have been taken in areas where *tumida* is common, but a few specimens of *tumida* have come from within or very near the main range of *minutilla*.

## DISCUSSION

The multivariate statistical analyses (utilizing only mensural characters) were undertaken with the intent of illustrating the degree to which dots representing sample means or individual specimens would cluster in multidimensional space. I hoped these analyses would give some clue to evolutionary (and thus systematic) relationships, as well as demonstrate geographic variation.

The results of the multivariate analyses (Figs. 4, 6, 7, 8, 12 and 14) were helpful, but hardly conclusive; in some cases results were confusing or even contradictory. In general, they seem to indicate that *R. alleni* is phenetically distant from the other species of *Rhogeessa*, thus supporting my subgeneric separation of that species. Although *Rhogeessa gracilis* and *R. mira* are closer phenetically to the other species than is *alleni*, the degree of phenetic separation

varies among the different analyses. *Rhogeessa gracilis* seems to be closer to the others than *R. mira*. However, when one examines characters not included in the statistical analyses, the reverse seems to be true; i.e., *mira* is closely related to *parvula*, and *gracilis* seems very distinct from all other species.

*Rhogeessa parvula*, *R. tumida*, and *R. minutilla*, on the other hand, are shown to be closely related by both the multivariate statistics and the other characters discussed in the species accounts. Thus it appears that there are four closely related species, which probably evolved by isolation from a common ancestor, plus two peripheral species (*alleni* and *gracilis*) which were separated from the common ancestor of the other four at a much earlier point in time. It is also possible that the genus is polyphyletic and that *alleni*, and even more likely, *gracilis* are similar to *Rhogeessa* only by convergence. When *gracilis* is karyotyped, some light may be shed on this question.

Because four species occur sympatrically in western México, it seems safe to assume that *Rhogeessa* evolved there from a primitive vespertilionine bat, which perhaps also gave rise to *Eptesicus* and *Pipistrellus*. These latter two genera, however, are almost cosmopolitan, and encompass many species. If we therefore postulate a much longer evolutionary history for them, then *Rhogeessa* is either much younger as a genus, or has been blocked in its efforts to expand its distributional range and diversify into additional species by such factors as competitive exclusion by other insectivorous species, or by other evolutionary and zoogeographic problems.

Periodic climatic changes before and during the Pleistocene probably led to periods of isolation between lowland populations on the western and eastern coasts of México, making possible the occurrence of separate but similar species (*tumida* and *parvula*) on the coasts. The eastern population spread southward throughout Central America and northern South America, finding climates much like those in eastern México. In order for speciation to have occurred in northwestern Venezuela, producing *R. minutilla*, ancestral *R. tumida* must have reached South America before or during the Pleistocene, so that the climatic changes necessary to isolate a population there could have taken place. Presently, *R. tumida* may be in the process of invading central and southern South America, where it seems to be rare and local in distribution.

In western México the lowland population must have been broken into two segments at one point in time, to allow speciation of *R. mira* from *R. parvula*. How and when this might have occurred is not clear. Because *alleni* and *gracilis* normally are found at higher elevations than *parvula* or *mira*, it can be speculated that geographic isolation of different mountain masses and associated contrasts in climate and vegetation led to their speciation at an

early date, and that these same factors have maintained the present restricted distributional ranges of these two species.

Figures 4, 5, and 14 tell us something about multidimensional geographic variation. Because the dots are not in a straight line, figure 4 demonstrates that the rate of clinal change differs among variables, and figure 14 shows that the rate of clinal change differs among samples in different portions of the species' geographic ranges. Figure 4 shows increasing size from upper right to lower left, and figure 5 groups samples of similar size.

#### KEY TO THE SPECIES OF *RHOGEESSA*

1. Greatest length of skull more than 14.5; i3 unicuspid, 1/6 to 1/8 cross-sectional area of i2; ratio of third metacarpal to first phalanx of third digit averaging 2.20 to 1 ..... Subgenus *Baeodon*; *R. alleni*  
 Greatest length of skull less than 14.5; i3 often bicuspid, having cross-sectional area greater than 1/6 that of i2; average ratio of third metacarpal to first phalanx of third digit more than 2.20 to 1 ..... Subgenus *Rhogeessa*, 2
2. Ears averaging 18; dorsal fur obviously 3-banded, darker at bases ..... *R. gracilis*  
 Ears averaging 15 or less; dorsal fur 2-banded, paler at bases ..... 3
3. Greatest length of skull averaging 11.4; lingual cingulum of C1 smooth, lacking cusps ..... *R. mira*  
 Greatest length of skull averaging 11.9 to 13.5; lingual cingulum of C1 not smooth, usually with cusps ..... 4
4. Uropatagium sparsely to heavily furred from base to point halfway from knees to foot; i3 usually much smaller than i2 ..... *R. parvula*  
 Uropatagium furred only at base; i3 usually only slightly smaller than i2 ..... 5
5. Color pale; helmet usually present; POW averaging 2.9 or 3.0; third metacarpal averaging 0.5 mm shorter than forearm ..... *R. minutilla*  
 Color dark; helmet usually absent; POW averaging 3.1 or 3.2; third metacarpal at least 1 mm shorter than forearm ..... *R. tumida*

#### SUMMARY

More than 650 specimens of bats of the Neotropical genera *Rhogeessa* and *Baeodon* were examined to determine the number of genera and species that should be recognized, as well as to evalu-

ate geographic variation within each species. In addition to the usual morphological characters, large numbers of bacula were measured and compared, and hairs were examined by scanning electron microscopy. The preliminary results of a study of karyotypic variation in *Rhogeessa* by R. J. Baker and associates were taken into account. Both multivariate and univariate statistical methods were utilized.

One species, *Rhogeessa alleni*, is assigned to the subgenus *Baeodon*, and is a large-skulled form restricted to western México. The remaining five species are assigned to the subgenus *Rhogeessa*. *Rhogeessa parvula*, restricted to western México, is characterized by a hairy uropatagium. *Rhogeessa gracilis*, also restricted to western México, possesses much larger ears than do the other species. A new species, *R. mira*, is presently known only from two localities in Michoacán, and is substantially smaller than the other three species inhabiting western México. *Rhogeessa tumida*, an extremely variable (and perhaps composite) species, ranges from Tamaulipas to Brazil and Bolivia. *Rhogeessa minutilla*, a pale desert species, is restricted to Margarita Island, northwestern Venezuela, and the adjoining Guajira Peninsula of Colombia.

#### RESUMEN

Con el fin de determinar el número de géneros y especies que deben ser reconocidos y también analizar la variación dentro de cada especie, se examinaron mas de 650 especímenes de murciélagos neotropicales de los géneros *Rhogeessa* y *Baeodon*. Además de los caracteres morfológicos usualmente empleados, se midieron y compararon los báculos, y se examinaron los pelos por medio de un microscopio electrónico de "scanning." Fueron tomados además en consideración, el estudio hecho por R. J. Baker y compañeros, sobre la variación en los kariotipos de *Rhogeessa*; y finalmente para el análisis estadístico se usó los métodos de univarianza y multivarianza.

Una de las especies, *Rhogeessa alleni*, una forma de cráneo grande, restringida a el Occidente de México, es asignada al subgénero *Baeodon*. Las otras cinco especies son asignadas a el subgénero *Rhogeessa*. *Rhogeessa parvula*, restringida a México occidental, está caracterizada por tener un uropatagio cubierto de pelo. *Rhogeessa gracilis*, también restringida a México occidental, tiene orejas que son mas grandes que las de las otras especies. Una especie nueva, *R. mira*, conocida solamente de dos localidades de Michoacán, es la mas pequeña de las cuatro especies en México occidental. *Rhogeessa tumida*, una especie extremadamente variable y posiblemente un "composite species" (compuesta de mas de una especie), se extiende desde Tamaulipas hasta Brasil y Bolivia. *Rhogeessa minutilla*, una especie de color pálido, encon-



trada en áreas desérticas, es restringida a la Isla Margarita, el Noroeste de Venezuela, y la península de la Guajira de Colombia y Venezuela.

### SPECIMENS EXAMINED

For each species, countries are listed from north to south, and from west to east. States, departments and provinces are given in the same sequence following each country, and individual localities are listed in the same manner following each state, department or province. Localities which have not been precisely located on a map are placed in quotation marks. Abbreviations for museums given with specimen numbers are those listed in the Acknowledgments section of this paper. Localities from which specimens were examined are represented on the distribution maps only insofar as space permits. Many map spots cover several (as many as five) localities.

#### *Rhogeessa alleni*

MÉXICO: *Jalisco*: Piedra Gorda, ca. 8 km NW Soyatlán del Oro, 1600 m, UA 10292. *Michoacán*: 20 km N El Infiernillo, UNAM 8597; 7 km N El Infiernillo, ca. 125 m, KU 97307. *Puebla*: 10 mi W Acatlán, 6000 ft, TCWC 8480. *Oaxaca*: 2 mi NNW Tamazulapan [=Tamazulapám], 1990 m, KU 61170-1; Cuicatlán, 590 m, KU 29439; 2 mi N, 6 mi W Nejapa, KU 68773.

#### *Rhogeessa gracilis*

MÉXICO: *Jalisco*: 5 mi NE Huejuquilla, 6200 ft, KU 108976; 10 mi SE Talpa de Allende, 5350 ft, KU 97050; 17 km SE Talpa de Allende, 5200 ft, KU 92951. *Puebla*: Piaxtla, about 1100 m, NMNH 70691, 70694. *Oaxaca*: Valero Tanjano, 2 mi W Tomallim [=Tomellin?], MVZ 78315-6; Cerro San Felipe, San Felipe del Agua, about 1700 m, AMNH 186901; "Isthmus of Tehautepec," NMNH 38294.

#### *Rhogeessa parvula*

MÉXICO: *Sonora*: Estero Tastiota, sea level, MVZ 85290; 28 mi E Mazatlán, 500 m, UNM 18587; W Side Alamos, KU 24853-4; near Alamos, UA 2717; Casa Las Delicias, Alamos, UA 2969; La Aduana, LACM 13247; 8 mi (by road) S Río Alamos, Alamos, about 200 m, UA 16956, 16981-3; 11.3 mi SSE Alamos, Río Cuchijaga, UA 14270; "Rancho Guirocoba," LACM 9700. *Sinaloa*: 1 mi S El Cajón, 1800 ft, KU 100401; 16 km NNE Choix, 1700 ft, KU 90752, 90754; 1 mi S, 6 mi E El Carrizo, KU 105563; 7 mi ESE Sanalona, 600 ft, KU 100402; La Cruz, 30 ft, KU 90755, 90757; Elota, sea level, UA 6358, LACM 19011; ½ mi E Piaxtla, sea level, KU 61163-8; km marker 1289 on Mex. hwy. 15, 9 km W Río Piaxtla, sea level, UA 15991-3, 17189-90; 14 mi N Mazatlán, sea level, UA 13477, 13978, LSU 10431-3; Punta de Cauca, 11 mi N, 2.5 mi E Mazatlán, LACM 12498-500; Mazatlán, LACM 16531; Chupaderos, on Río Panuco, about 26 mi NE Villa Unión, 800 ft, UA 9725, LACM 19080-1; 2 mi E Palmito, KU 97078-81; 5 mi NE Concordia on Mex. hwy. 40, 100 m, UA 11059; 12 km N Villa Unión, 400 ft, KU 95878; Escuinapa, 100 ft, TCWC 14471; 5 mi WSW Plomosas, 800 ft, KU 97082, 97084. *Durango*: Santa Ana, 12 km E Cosalá, Sinaloa, 1300 ft, KU 90759. *Nayarit*: Huajicori, Río del Bajar, 120 m, UA 9724, LACM 19079; 4 km S Playa Novilleros, sea level, UA 11037; about 40 mi E Acaponeta,



La Cuchara, LACM 13821; Tres Mariás Islands, San Juanito Island, AMNH 180543-4; Tres Mariás Islands, María Madre Island, AMNH 180522, NMNH 92413; "Tres Mariás Islands," NMNH 84021, ANSP 1832; 5 mi NE San Blas,  $\frac{1}{4}$  mi N Singaita, sea level, UA 18552-3; 8 mi E San Blas, about 200 m, UA 8278-9; LACM 12503-5, 12507, 13244-6, 13436-41;  $\frac{1}{2}$  mi E San Blas, 10 ft, KU 39723-5; 4 mi S, 5 mi E San Blas, UNM 16858. *Jalisco*: 9 mi N Guadalajara, 4000 ft, KU 107493-4; 2 mi S La Cuesta, 1500 ft, KU 111613-5; Piedra Gorda, about 8 km NW Soyatlán del Oro, about 1600 m, UA 10294; El Salitre, about 4 km N Soyatlán del Oro, about 1600 m, UA 10590, 10602; Río de Aguacate, about 4 km E Soyatlán del Oro, about 1300 m, UA 10307; about 4 km S Soyatlán del Oro, about 1500 m, UA 10319-20; Cuitzamala, 25 ft, KU 105564; 2 mi N Tenacatita, 25 ft, KU 105565-6; 10 mi NNE Pihuamo, 3500 ft, KU 108974-5. *Colima*: Rancho Tavernillas, about 35 km NW Pueblo Juárez, 350 m, UA 8838, LACM 19082; Tabarnillas, 6 km N Agua Zarca, UNAM 6321-3; Pueblo Juárez, 330 m, UNAM 5643; 2 km N Tlapeixtes, near Manzanillo, sea level, UA 10676; 1 km N Tlapeixtes, near Manzanillo, sea level, UA 10686; Colima, about 500 m, NMNH 52065-6, 52102; "4 mi S Cerro de Ortega," UA 3299; 2 mi E Cuyutlan, LACM 11271-7; 5 mi SE Armeria, LACM 11729-30. *Michoacán*: 20 km N El Infiernillo, UNAM 8592; 7 km N El Infiernillo, ENCB 990-7. *Guerrero*: "Guerrero," NMNH 187713; 4.3 km N Teloloapan, 1480 m, UNAM 8864-7; Ojo de Agua, 3.4 km N Mexicapán, 1480 m, UNAM 9984-5, 10684-5; El Ojo de Agua de Chapa [7 km SSE Teloloapan], UNAM 1990-2; 8 km SW Teloloapan, 1300 m, UNAM 11869; Agua del Obispo, 3300 ft, TCWC 6351; Naltianguis, about 500 m, NMNH 269315-6. *Morelos*: Río Oaxtepec, 1 km S Oaxtepec, 890 m, UNAM 9706. *Oaxaca*: Santo Domingo, NMNH 73269; San Carlos Yau-tepec, San Bartolo Yau-tepec, 800 m, AMNH 167467, 175263; 9 mi NW Tehautepec, near sea level, UNM 27545; Tehautepec, sea level, AMNH 178744; 8 km NW Salina Cruz, ENCB 3487-8; 20 mi W Tapanatepec, sea level, UA 13440-2; Río Ostuta, 4 mi W Zanatepec, sea level, AMNH 186406.

*Rhogeessa mira*

MÉXICO: *Michoacán*: 20 km N El Infiernillo, UNAM 8593-6; 7 km N El Infiernillo, ENCB 998-1007.

*Rhogeessa tumida*

MÉXICO: *Tamaulipas*: Santa María, 870 m, AMNH 148196; 4 mi N La Pesca, sea level, KU 55192; 3 mi N La Pesca, sea level, KU 55191, 55193, 55208; 2 mi N La Pesca, sea level, KU 55198-208; 1 mi N La Pesca, KU 55194-7; 2 mi S, 10 mi W Piedra, Sierra de Tamaulipas, 1200 ft, KU 55152-63; 55165-89; 3 mi S, 16 mi W Piedra, Sierra de Tamaulipas, 1400 ft, KU 55190; 30 mi N El Mante, Río Cielito, TCWC 25679. *San Luis Potosí*: 10 mi WSW Ebano, LSU 4047; 19 km SW Ebano, LSU 4942-53; 3 km N Taninul, 650 ft, LSU 4936-41. *Veracruz*: 25 mi W Tampico, KU 82922; El Higo, 6 km NNW Ejido El Chote, about 75 m, UNAM 11063; 12.5 mi N Tihuatlán, 300 ft, KU 88427-34; Boca del Río, 10 ft, KU 29886; Río Blanco, 20 km W Piedras Negras, 400 ft, KU 19231; 24 mi S Veracruz, near sea level, AMNH 203917; San Andrés Tuxtla, 360 m, UNAM 9485; 9 mi ENE Catemaco, ca. 200 m, UNAM 7751-2; 24 mi S Santiago Tuxtla, Los Tuxtlas, TCWC 9488; Mirador, sea level, NMNH 37329 (skull) + ANSP 1831 (skin of NMNH 37329); Achotal, FMNH I-1419; 2.3 km W, 3 km SSW, 2.5 km SW, and 4.1 km S Tenochtitlán, 50 m, UM 116286-91, 116293-98. *Oaxaca*: 3 km W Estación Vicente, Municipio de Acatlán, 60 m, UNAM 11492-3. *Tabasco*: Rancho El Tumbo, 4 km E F.F.C.C. El Zapote, Macuspana, UNAM 1717, 1959-60. *Chiapas*: Rancho San Fernando, 42 km W Cintalapa, 500 m, UA 15711; 32 mi SW Cintalapa, Rancho San Miguel, TTU 11274-5; 2 mi SW

Las Cruces, about 600 m, KU 61169; Finca San Salvador, 15 km SE San Clemente, 1000 m, KU 102619; 11.9 mi SE Tres Picos, Puente El Mosquito, TTU 11354-5; Pijijiapan, 10 m, UM 96523-4; 5 km SE Pijijiapan, 100 ft, TCWC 14466-9; Prusia, 1000 m, UM 88196-8; Huehuetán, 35 m, NMNH 78600; 7 mi ENE Tapachula, about 300 m, KU 68772; 3.8 mi SW Tapachula, TTU 11133; 14 km SW Tapachula, 50 m, KU 120535. *Yucatán*: 10 mi W Progreso, LACM 18167; Piste, 10 m, KU 92000; Chichén-Itzá, AMNH 91234, UNAM 1808, MCZ 10807, 32868, UM 79938. *Campeche*: 5 km S Champotón, 10 m, KU 92007-9; La Tuxpeña, NMNH 170858; Isla del Carmen, 1 km S Puerto Real, 3 m, KU 92010; Balchacaj [=Balchacah?], Laguna de Terminos, FMNH 47394; 65 km S, 128 km E Escárcega, KU 93536. *Quintana Roo*: 4 km WSW Puerto Juárez, 5 m, KU 92001; Pueblo Nuevo X-Can, 10 m, KU 92002-3; Isla Cozumel, 4 km N San Miguel, KU 92004-5; 4 km NNE Felipe Carrillo Puerto, 30 m, KU 92006.

GUATEMALA: "Moca Guatalon," MCZ 28144. *El Petén*: La Libertad, 170 m, AMNH 144697. *San Marcos*: Finca [E] Porvenir, FMNH 50063. *Quetzaltenango*: Finca Los Pirineos, near Santa María de Jesús, ca. 1500 m, FMNH 50062. *Suchitepequez*: Mocá, about 1000 m, FMNH 41649, 41828-30, 41856-7. *Santa Rosa*: Finca Santa Isabel, about 200 m, FMNH 74012; Astillero, 25 ft, KU 64992-3.

BELICE: *Belize*: Turneffe Island, Calabash Cay, LSU 7148.

HONDURAS: "Patuca River," NMNH 36062. *Cortez*: 23 mi by road N San Pedro Sula, ca. sea level, TTU 13297. *Yoro*: Portillo Grande, 4100 ft, MCZ 33869. *Copán*: Copán, 660 m, TCWC 19752. *Santa Bárbara*: 12 km N Santa Bárbara, TTU 13295-6; 7 mi N Santa Bárbara, 120 m, TCWC 19753-5. *Olancho*: 10.3 mi by road SSW Dulci Nombre de Culmí, TTU 13298, 13300-1. *Comayagua*: 3 km W Comayagua, 580 m, TCWC 21106-7. *Distrito Central*: La Flor Archaga, ca. 800 m, MCZ 28976; Comayagua, 1000 m, MCZ 28975. *La Paz*: El Pedrero, 3000 ft, AMNH 126901-4. *Francisco Morazán*: 2 mi S El Zamorana, ca. 1200 m, TCWC 11017; Escuela Agrícola Panamericana, MCZ 45401. *El Paraíso*: Chichicaste, 480 m, TCWC 22108.

EL SALVADOR: *Chalatenango*: San José del Sacare, 3600 ft, MVZ 130998; 20 km W Chalatenango, 250 m, TCWC 19751. *Cuscatlán*: Colima, MVZ 130990-1. *Usulután*: Puerto del Triunfo, sea level, MVZ 130994-5. *San Miguel*: Río San Miguel, 13° 25' N, 225 ft, MVZ 130991-3.

NICARAGUA: *Matagalpa*: 6 km N Tuma, 550 m, TCWC 24126-7; Uluce [=Uluse?], AMNH 29863; 1 km NE Esquipulas, 420 m, KU 115148. *Chinandega*: 6.5 km N, 1 km E Cosiguina, 10 m, KU 115145-7; Hda. Bellavista, 720 m, Volcán Casita, KU 106284; Chinandega, about 20 m, AMNH 28996. *Boaco*: Santa Rosa, 17 km N, 15 km E Boaco, 300 m, KU 111233-4. *Carazo*: 3 km N, 4 km W Diriamba, 600 m, KU 111235-6. *Zelaya*: 10 km W Rama, 40 m, TCWC 19756; 4.5 km NW Rama, TTU 13313; 3 km NW Rama, TTU 13317-8. *Rivas*: 6.9 mi E San Juan del Sur, TTU 13320.

COSTA RICA: "Pacific Coast," AMNH 4966. "Finca San Miguel," FMNH 67305-6. *Alajuela*: San Torte, between San Carlos and Altamira, ROM 60464. *Guanacaste*: Sánara [=Samari?], LACM 26669. *Puntarenas*: Boca del Barranca, LACM 23767, 25258. *San José*: Río Corrogres, about 2 km NW Santa Ana, 820 m, LSU 12989-93; Finca Lornessa, about 2 km NW Santa Ana, 850 m, LSU 14750-7.

PANAMÁ: "Panamá," MCZ 33525. *Bocas del Toro*: 7 km SSW Changuinola, sea level, NMNH 315776; Almirante, sea level, NMNH 315774-5; Isla Bastimentos, sea level, NMNH 335419. *Chiriquí*: Bugaba, about 200 m, MCZ 10446; 8 mi SE Progreso, sea level, NMNH 363107. *Coclé*: 3 mi W Churubé, 300 ft, NMNH 331910; Santa Clara, sea level, NMNH 296265. *Los Santos*: Guanico Arriba, about 200 m, NMNH 323605. *Canal Zone*: Ft. Sherman, sea level, NMNH 396406; Summit Gardens, about 100 m,

NMNH 304930; San Pablo, NMNH 171212-3, 223330; Curundu, NMNH 309219; Ft. Kobbe, sea level, NMNH 309220; Ft. Kobbe Beach, sea level, NMNH 312108-13, 313777-82; Ancon, MCZ 28100; Tapia, AMNH 140472. *Darién*: La Palma de Darién, sea level, MVZ 113936.

COLOMBIA: *Magdalena*: "San Alberto," LACM 16781; Río Guaimaral, Valledupar, 168 m, NMNH 281310; Colonia Agrícola Caracolico, Santa Marta, about 200 m, NMNH 281921. *Bolívar*: Catiral Upper Río San Jorge, FMNH 69526. *Norte de Santander*: 10 mi N Cueta [=Cúcuta], FMNH 18725-6. *Tolima*: Honda, Las Margaritas, ROM 49045, 49048; Guamo, about 300 m, UAB 426. *Cundinamarca*: Mesitas de Colegio, 1200 m, AMNH 207922, LACM 19064-5. *Valle*: Río Raposo, about 100 m, NMNH 334744. *Huila*: 16 km NE Villavieja, 1600 ft, MVZ 113936.

VENEZUELA: *Zulia*: 30 mi E Maracaibo, sea level, NMNH 260191; Perija, Río Cogollo, sea level, FMNH 21984; 48 km WNW Encontrados, 54 m, NMNH 441790; 38 km WNW Encontrados, 37 m, NMNH 441791. *Trujillo*: 23 km NW Valera (nr. Agua Santa), 90 m, NMNH 372488. *Mérida*: Sta. Elena, Río Guachi, FMNH 21985. *Yacujay*: 8 km N, 18 km W San Felipe, near Minas de Aroa, 400 m, NMNH 441773-5; 19 km NW Urama, km 40, 100 m, NMNH 372487, 372489, 374016-8. *Aragua*: nr. Rancho Grande, sea level, NMNH COH7876-7. *Miranda*: 5 km S, 5 km E Caracas, Encantados, 570 m, NMNH 441776; 1 km E Río Chico, sea level, NMNH 387738; 5 km E Río Chico, nr. Puerto Tuy, sea level, NMNH 387736-7. *Sucure*: Takal, 11 km SSW Cumaná, about 200 m, KU 119074; 2.5 km W Cumaná, 5 m, KU 119072; Cuchivano, 700 ft, AMNH 69968; 4 km S, 25 km E Carúpano (nr. Manacal), 170 m, NMNH 409487. *Guárico*: Calabozo, Est. Biol., NMNH UCV4871. *Mouqas*: Jusepin, about 100 m, KU 119073; 54 km SE Maturín, Mata de Bejuco, 18 m, NMNH 441792-4; 60 km SE Maturín, LACM 14355. *Apure*: 60 km NE Pto. Paéz, Hato Cariben, La Villa, 76 m, NMNH 374019-20; 8 km NW Pto. Paéz, Cerro de los Murciélagos, 76 m, NMNH 374021. *Amazonas*: 65 km SSW Puerto Ayacucho, Morocoy, 161 m, NMNH 409488.

TRINIDAD: "Trinidad," NMNH 141885. *St. George*: Maracas Valley, TTU 5409, 5457; Maracas, 500 ft, AMNH 183163; Maracas Valley, Waterfalls Rd., about 1100 ft, AMNH 176379, ROM 31438-9, 31453; Port of Spain, sea level, FMNH 51157-8. *St. Patrick*: San Rafael Rancho Estate, Santa Maria [=St. Mary's?], TTU 5257; Siparia, about sea level, AMNH 179965-6, 182924, 183861.

GUYANA: *Rupununi*: Dadanawa House, ROM 32348; Cotanrib, Isl., 5 mi above Dadanawa, left bank Rupununi River, ROM 59709-10; nr. Shea v. Kuitaro, ROM 43093; Tacatu R. area, 40 mi SW Dadanawa, ROM 58843; (remaining localities not precisely located, but near four previously listed localities) Ikoni Tau, ROM 40764, 40766-7; Kuitaro River, ROM 32783, 46211; Raa Wau, ROM 40798; Tamtoon, ROM 36842; Weri More, ROM 44527.

ECUADOR: *Puná*: Puna Island, San Ramón, sea level, AMNH 66824.

BRASIL (not mapped): *Maranhao*: Alto Parnaíhyha? [Alto Parnaíba, 9° 06' S, 45° 57' W?], FMNH 26465. *Mato Grosso*: 264 km (by road) N Xavatina, Serra do Roncador, 12° 51' S, 51° 46' W, 1750 ft, NMNH 393759.

*Rhogeessa minutilla*

COLOMBIA: *Guajira*: 119 km N, 32 km W Maracaibo, Venezuela, 15 m, NMNH 441781-2.

VENEZUELA: *Zulia*: 114 km N, 32 km W Maracaibo, 12 m, NMNH 441777; 114 km N, 28 km W Maracaibo, 15 m, NMNH 441778-80, 441783-9; Río Aurare, sea level, FMNH 18711; Empeladi Savanna, FMNH 18742-5. *Falcon*: Capatárida, 55 m, NMNH 441795-9, 441801, 441819-36; 6 km SSW Capatárida, Santa Rosa, NMNH 441771-2, 441800, 441802-13, 441815-18.

*Lara*: Río Tocuyo, 500 m, AMNH 130671-2, 130674-6, 130711-4, 131192; 10 km N El Tocuyo, Caserío Boro, 528 m, NMNH 443183, 443186, 455992, 455994, 455997-9, 456000-1, 456009-15, 456020-24, 456028-9, 456031-2, 456035-7, 456039. *Margarita Island*: "Margarita Island," NMNH 63216, 113497; Nueva Esparta, 2 km N, 30 km W Porlamar (nr. Teatas de María Guevara), 10 m, NMNH 405828.

## APPENDIX 1

To plot unknown specimens on any of the three canonical scattergrams (Figs. 7, 8, and 12), first make the nine standard measurements outlined in the section on materials and methods, and substitute into the following formulae:

$$X_{\text{axis}} \text{ (First canonical variable)} = (-0.46)(\text{FA}-29.04) - 0.16(3\text{MC}-28.28) \\ + 0.47(\text{CLS}-12.90) - 0.94(\text{DB}-4.66) - 2.09(\text{POW}-3.14) + \\ 0.05(\text{MW}-6.78) - 1.44(\text{M2M2}-5.20) - 0.21(\text{C1C1}-3.66) - \\ 1.64(\text{MAX}-4.48).$$

$$Y_{\text{axis}} \text{ (Second canonical variable)} = 0.08(\text{FA}-29.04) + 0.42(3\text{MC}-28.28) \\ + 0.58(\text{CLS}-12.90) - 0.11(\text{DB}-4.66) + 5.59(\text{POW}-3.14) - \\ 1.47(\text{MW}-6.78) + 0.95(\text{M2M2}-5.20) - 0.42(\text{C1C1}-3.66) - \\ 5.12(\text{MAX}-4.48).$$

The two coordinates thereby obtained can then be plotted on the appropriate scattergram in the usual manner.

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