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REVISION OF THE ANTILLEAN BATS OF THE GENUS *BRACHYPHYLLA* (MAMMALIA: PHYLLOSTOMATIDAE)

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ABSTRACT

Nongeographic and geographic variation have been analyzed in the genus *Brachyphylla*, which belongs to the Antillean endemic subfamily Phyllonycterinae of the family Phyllostomatidae. Males were found to be generally larger than females; therefore, the sexes were analyzed separately for geographic variation. External measurements except length of forearm were found to display a high degree of individual variation. They were not used in subsequent analyses. Of cranial measurements, greatest length of skull and condylobasal length showed the least individual variation, whereas palatal length, postorbital breadth (in samples from west of the Mona Passage only), and rostral width at canines showed relatively high coefficients of variation. Variation in color was found not to follow any geographic pattern.

Two species—*Brachyphylla cavernarum* and *B. nana*—were recognized in the genus. *B. cavernarum* occurs on Puerto Rico, the Virgin Islands, and the Lesser Antilles as far south as St. Vincent. Three subspecies are recognized. Populations of large bats occur on St. Croix in the Virgin Islands and the Lesser Antilles as far south as St. Vincent. The smallest individuals occur only on the island of Barbados. Populations of bats of intermediate size, described herein as a new subspecies, occur on Puerto Rico and most of the Virgin Islands. *Brachyphylla nana* is a monotypic species occurring on Cuba, Isle of Pines, Grand Cayman, Middle Caicos, and Hispaniola and as a sub-Recent fossil on Jamaica.

INTRODUCTION

Bats of the genus *Brachyphylla* belong to the subfamily Phyllonycterinae. This subfamily, which is endemic to the West Indies, belongs to the family Phyllostomatidae, the New World leaf-nosed bats. Members of the genus *Brachyphylla* occur throughout most of the Greater and Lesser Antilles south to St. Vincent and Barbados, and in the Bahamas on Middle Caicos Island. The genus is known on Jamaica only from fossil material.

The genus *Brachyphylla* was erected by Gray in 1834 to include the new species *B. cavernarum*. Gray (1838) placed the genus in the tribe Phyllostomina of the family Vespertilionidae. Gervais (1855–1856) placed the genus in the tribe Stenodermina, which subsequently was recognized as the subfamily Stenoderminae of the family Phyllostomatidae. In 1866, Gray erected the tribe Brachyphyllina with *Brachyphylla* as the sole genus. Later, Dobson (1878) included *Brachyphylla* in his group Stenodermata but stated that it was the most closely related of all known genera of phyllostomatids to the desmodontines. McDaniel (1976) in his study of the brain anatomy also thought that *Brachyphylla* was most closely allied to the Desmodontinae or possibly the Stenoderminae. H. Allen (1898) placed *Brachyphylla* in the subfamily Glossophaginae, but separated it in a group termed Brachyphyllina along with *Phyllonycteris* and *Erophylla*. Miller (1898) in describing *Reithronycteris* followed this arrangement but clearly allied *Reithronycteris* with *Brachyphylla*, *Phyllonycteris*, and *Erophylla*. Miller later changed his opinion and stated that he (Miller, 1907) could detect no indication that *Brachyphylla* was a phyllonycterine and placed it in the subfamily Stenoderminae. Here it remained until Silva-Taboada and Pine (1969) presented evidence based on osteology, behavioral characteristics, and host-parasite specificity for considering *Brachyphylla* a member of the subfamily Phyllonycterinae. Slaughter (1970) reflected on the similarity between this genus and *Sturnira* and thought it possible that these two genera, in addition to the glossophagines and stenodermines were related to some unknown common ancestor, and concluded that the dentition offers no evidence that *Brachyphylla* is any more closely related to the stenodermines than *Sturnira*. It should be pointed out, however, that *Sturnira* is now included in the Stenoderminae by most authorities.

In erecting the genus *Brachyphylla*, Gray (1834) described *cavernarum* from St. Vincent as the first species. Subsequently three additional species have been described, *nana* by Miller (1902*a*) from Cuba, *minor* by Miller (1913) from Barbados, and *pumila* by Miller (1918) from Haiti. Koopman (1968) presented evidence for considering *minor* a subspecies of *cavernarum*. Varona (1974) without presenting any evidence recognized only one species, *cavernarum*, with all other previously recognized species as subspecies thereof. Jones and Carter (1976) and Silva-Taboada (1976) recognized two species, *cavernarum* and *nana*, with *minor* as a subspecies of the former and *pumila* of the latter. Buden (1977) studying geographic variation in Greater Antillean populations agreed with Varona's (1974) arrangement.

The systematics of *Brachyphylla* remained virtually unstudied except for description of species until Koopman's work in 1968. Since that time, four additional papers have appeared dealing with this subject (Varona, 1974; Jones and Carter, 1976; Silva-Taboada, 1976; Buden, 1977). These authors have

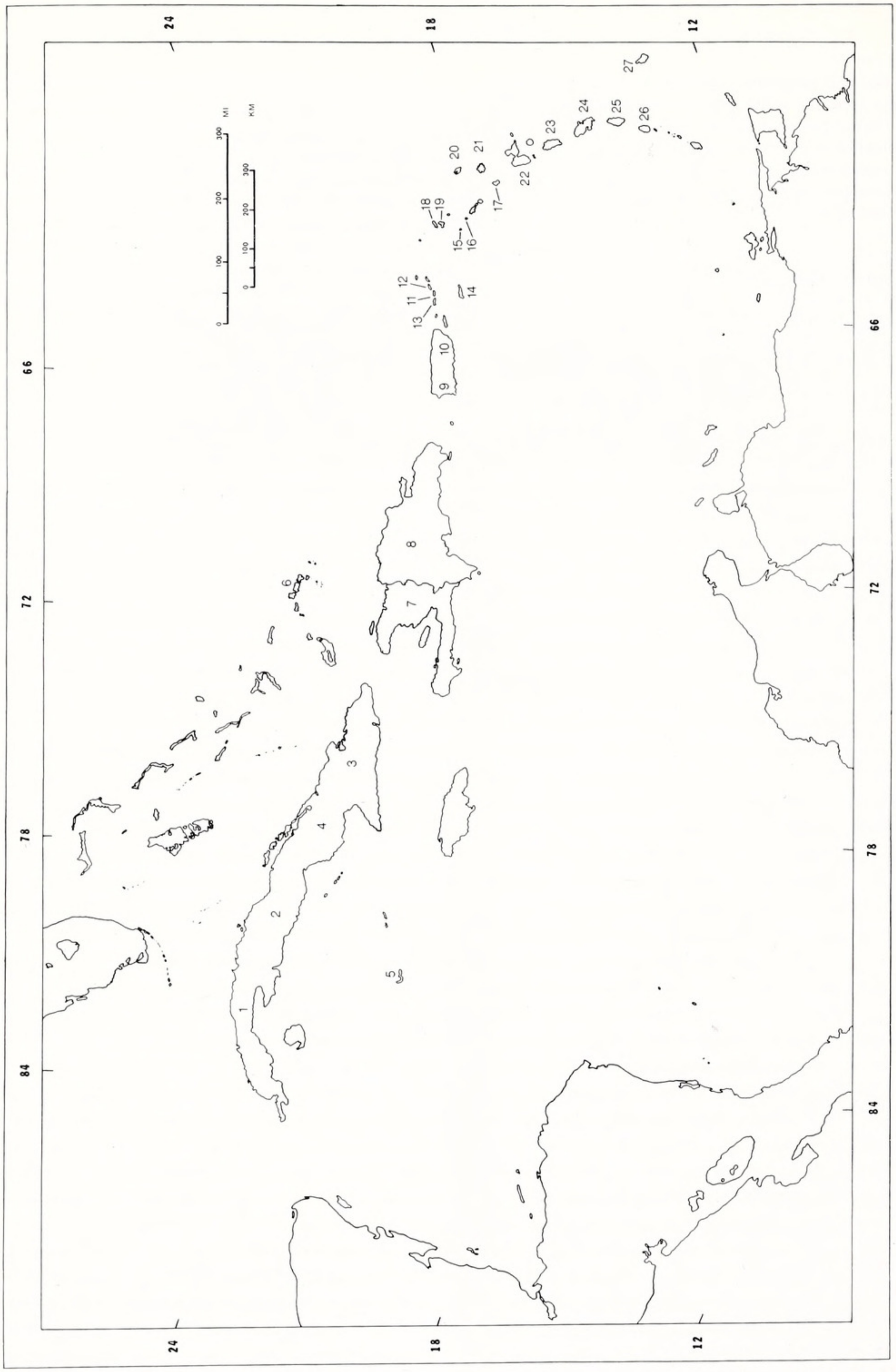

Fig. 1.—Geographic areas included in samples of *Brachyphylla*. See text for localities included in each sample.

not agreed as to how many species to recognize in the genus nor have they examined in detail variation throughout the geographic range of the genus. We have assessed herein inter- and intraspecific relationships in the genus using both univariate and multivariate analyses. We examined samples from throughout the range of the genus including fossil material from Jamaica. The results of these studies are presented below.

MATERIALS AND METHODS

In the course of this study, 648 specimens were examined. Most of these consisted of either standard museum skins and skulls or specimens preserved in fluid with skulls removed. In addition skull only, skin only, or complete fluid-preserved specimens were examined. All holotypes were examined by the authors. Individuals were judged to be adults if the phalangeal epiphyses were completely fused. Specimens consisting of a skull only were considered to be adult if the cranial sutures were well ossified.

External measurements were obtained from labels of specimens prepared as standard museum skins, except for length of forearm, which was taken with dial calipers on the dried skins and fluid-preserved specimens. This measurement was taken from the posteriormost projection of the olecranon process (elbow) to the anteriormost projecting point of the wrist with the wing flexed.

Definitions of cranial measurements are given below. All measurements are given in millimeters.

Greatest length of skull.—Greatest distance from the anteriormost projection of the incisors to the posterior portion of the occipital bone.

Condylobasal length.—Greatest distance from the anterior part of the premaxillae (not including the incisors) to the posteriormost part of the occipital condyles.

Palatal length.—Greatest distance from the posterior edge of the anterior palatal foramen to the anteriormost edge of the palate.

Depth of braincase.—Skull was placed on a microscope slide and the least distance measured from the dorsalmost portion of the skull to the ventralmost part of the slide, thereafter, the thickness of the slide was subtracted from this value.

Zygomatic breadth.—Greatest width across zygomatic arches, measured at right angles to the longitudinal axis of cranium.

Breadth of braincase.—Greatest width across braincase, measured at right angles to the long axis of the cranium.

Mastoid breadth.—Greatest width across mastoid processes, measured at right angles to the long axis of the cranium.

Postorbital breadth.—Least width across postorbital constriction, measured at right angles to the long axis of the cranium.

Length of maxillary toothrow.—Least distance from the lip of the posterior alveolus of M^3 to the anterior lip of the alveolus of the canine.

Rostral width at canines.—Least width across rostrum immediately posterior to the canines.

Breadth across upper molars.—Least distance measured at right angles to long axis of the cranium from labial side of the crowns of one maxillary toothrow to the labial side of the other toothrow.

Mandibular length.—Least distance measured from the mandibular symphysis (not including the incisors) to the midpoint of a line connecting the articular processes of the right and left mandible.

All adult specimens from throughout the geographic range of *Brachyphylla* were grouped into 26 samples for males and 25 for females as follows (see also Fig. 1): *sample 1*—Habana Province, Cuba; *sample 2*—Las Villas Province, Cuba; *sample 3*—Oriente Province, Cuba; *sample 4*—Camagüey Province, Cuba; *sample 5*—Grand Cayman; *sample 6*—Middle Caicos, Bahamas; *sample 7*—Haiti; *sample 8*—Dominican Republic; *sample 9*—western Puerto Rico (Adjuntas, Guanica, Utuado); *sample 10*—eastern Puerto Rico (Comerio, Corozal, San Juan, El Verde, Pueblo Viejo, Trujillo Alto); *sample 11*—St. John, Virgin Islands; *sample 12*—Norman, Virgin Islands; *sample 13*—St. Thomas, Virgin Islands; *sample 14*—St. Croix, Virgin Islands; *sample 15*—Saba; *sample 16*—St. Eustatius; *sample 17*—Montserrat; *sample 18*—Anguilla; *sample 19*—St. Martin; *sample 20*—Barbuda; *sample 21*—Antigua; *sample 22*—Guadeloupe; *sample 23*—Dominica; *sample 24*—Martinique; *sample 25*—St. Lucia; *sample 26*—St. Vincent; *sample 27*—Barbados.

Selected measurements were also taken from fragmented *Brachyphylla* Pleistocene or sub-Recent fossil material from Jamaica. In order to compare these measurements to extant material similar measurements were also taken from adult specimens from the selected localities including both *Brachyphylla cavernarum* and *B. nana*. These were grouped into seven samples as follows: *sample a*—Cuba (five males, five females); *sample b*—Middle Caicos (five males, five females); *sample c*—Dominican Republic (five males, five females); *sample d*—Jamaica (fossils); *sample e*—Puerto Rico (five males, five females); *sample f*—St. John (five males, two females); *sample g*—Norman (five males, five females). The following measurements were taken from this material: *palatal length*—as for extant material; *rostral width at canines*—as for extant material; *length of maxillary toothrow*—as for extant material; *interorbital breadth*—least distance across interorbital region measured at right angles to the long axis of the cranium; *height of coronoid process*—least distance from a line connecting the angular process and ventral surface of the mandible to the dorsalmost point of the coronoid process; *width of articular process*—least width across the articular process; *mandible breadth at M_3*—least breadth of mandible at level of M_3; *length of mandibular toothrow*—least distance from posterior lip of alveolus of M_3 to anterior lip of alveolus of canine.

Dried skins examined in the study were assigned to one of the five color standards. The five specimens used for the color standards and a description of their color as as follows: 1) TTU 22761 (male)—Haiti, Dept. du Sud, 1 km S, 1 km E Lebrun, on the dorsum base of hair white, pattern blackish gray; 2) MCZ 21430 (male)—Martinique, on dorsum base of hair white, pattern blackish brown; 3) AS 5531 (female)—Puerto Rico, 17.7 km NE Utuado, on dorsum base of hair white, pattern grayish brown sometimes with buffish tint; 4) TTU 20975 (female)—Guadeloupe, Grande-Terre, 1 km N, 1 km W St. François, on dorsum base of hair white, pattern dark brown with a very faint reddish tint; 5) AS 5126 (male)—Barbados, St. Thomas Parish, Cole's Cave, on dorsum base of hair white with yellowish tint, pattern dark brown with generally more of a buffy tint than color standard 3.

Statistical analyses were performed on an IBM 370 computer at Texas Tech University. Univariate analyses of individual variation, secondary sexual variation, and geographic variation were performed using the UNIVAR program, developed and introduced by Power (1970). Standard statistics (mean, range, standard deviation, standard error, variance, and coefficient of variation) are generated by this program. In the event of two or more groups being compared, a single-classification analysis of variance (ANOVA) to test for significant differences between or among means is employed. Sums of Squares Simultaneous Test Procedure (SS-STP) (Gabriel, 1964) was used to determine maximally nonsignificant subsets, if means were found to be significantly different. See also Smith (1972) for an overview of these statistical methods.

Some of the multivariate analyses were performed using the Numerical Taxonomy System (NT-SYS) package developed by F. J. Rohlf, R. Bartcher, and J. Kishpaugh at the University of Kansas. The samples (OTUs) were grouped localities discussed above, and the values for each character were means for the measurements. Matrices of Pearson's product-moment correlation and phenetic distance coefficients were derived. Cluster analyses were conducted using UPGMA (unweighted pair group method using arithmetic averages) on the correlation and distance matrices, and phenograms were generated for both. Only distance phenograms were used because they gave higher coefficients of cophenetic correlation than the correlation phenograms. These phenograms give a two-dimensional multivariate view of the data with characters unweighted. The first three principal components were then extracted from a matrix of correlation among characters and three-dimensional projections of the samples onto the first three principal components were made. This provides a three-dimensional view of the data with unweighted characters. For the theory and use of these tests see Sokal and Sneath (1963), Schnell (1970), Atchley (1970), Choate (1970), Genoways and Jones (1971), Smith (1972), Genoways (1973), and Sneath and Sokal (1973).

Other multivariate analyses performed involved use of the Statistical Analysis System (SAS) package developed by Barr and Goodnight (Service, 1972). Individual specimens, and not series of means as in NT-SYS, were used in these analyses. Specimens with missing data could not be used, consequently sample sizes for SAS analyses were substantially reduced in some cases. To determine the degree of divergence among samples, a multivariate analysis of variance (MANOVA) and canonical analysis were performed. Canonical analysis of the data provides weighted combinations of the characters, which maximize the distinction among groups. This analysis extracts characteristic roots and vectors and computes mean canonical variates for each sample. Additional orthogonal axes are constructed, which extract the next best combination of characters, emphasizing those with the least within sample and greatest among-sample variation, hence, providing the next best combination of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate represents an identifiable fraction of the total variation. Sample means and individuals were plotted on those canonical variates, which account for the greatest fraction of total variation. The relative importance of each original variable (character) to a particular canonical variate was computed by multiplying the vector variable coefficient by the mean value of the dependent variable, summing all variable values for a particular vector, and then computing the percent of relative importance of each variable per vector. These techniques have recently been used in the study of mammals by Schmidly and Hendricks (1976), Yates and Schmidly (1977), and Yates et al. (1978).

NON-GEOGRAPHIC VARIATION

Three kinds of nongeographic variation—variation with age, secondary sexual variation, and individual variation—are discussed in the following section.

Variation with Age

One external and 12 cranial measurements of one non-adult male from Oriente Province, Cuba, and one non-adult female from Martinique are respectively, as follows: length of forearm, —, 56.8; greatest length of skull, 26.0, 28.6; condylobasal length, 23.3, 26.0; palatal length, 7.9, 9.9; braincase depth, 11.1, 11.5; zygomatic breadth, 13.5, 15.1; breadth of braincase, 11.8, 11.7; mastoid breadth, 12.8, 13.3; postorbital breadth, 6.3, 5.9; length of maxillary toothrow, 8.9, 9.8; rostral width at canines, 6.5, 6.4; breadth across upper molars, 9.4, 10.2; mandibular length, —, 16.8.

Comparing measurements of the subadult male from Oriente Province, Cuba, with those of adult males (1–4) from Cuba (Table 1) shows that there is overlap in only four measurements (breadth of braincase, mastoid breadth, postorbital breadth, rostral width at canines). A similar comparison between the subadult and adult females from Martinique (24) shows no overlap in measurements tested (Table 1). Only adult specimens (phalangeal epiphyses completely fused) were used in the study of geographic variation.

Secondary Sexual Variation

External and cranial measurements of adult males from each sample were tested against those of adult females utilizing single classification ANOVA. This was done in order to establish if any significant differences in size exist between the sexes. The results are shown in Table 1.

In samples from west of the Mona Passage, males proved to be significantly ($P < 0.05$) larger than females in two measurements (greatest length of skull, zygomatic breadth) in specimens from Habana Province, Cuba (sample 1); in one measurement (length of hind foot) in specimens from Las Villas Province, Cuba (sample 2), and in two measurements (length of hind foot, postorbital breadth) in specimens from the Dominican Republic (sample 8). On the other hand, females were found to be significantly larger than males in one measurement (length of ear) in specimens from Las Villas Province (sample 2).

In samples from east of the Mona Passage, males

Table 1.—*Geographic variation and secondary sexual variation in external and cranial measurements of* B. nana *(seven samples of males, and eight samples of females) and* B. cavernarum *(19 samples of males and 17 samples of females). Statistics given are number, mean, two standard errors, range, coefficient of variation, F_s value. Means for males and females that are significantly different at* $P < 0.05$ *are marked with an asterisk. See text for key to sample numbers.*

Sample no.	Male				Female				F_s
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	
				Brachyphylla nana					
				Total length					
1	2	79.0 ± 2.00	78–80	1.8	1	75.0			
2	2	87.5 ± 9.00	83–92	7.3	4	84.0 ± 4.90	80–90	5.8	4.581
3	1	95.0			2	93.5 ± 7.0	90–97	5.3	
4	2	82.5 ± 5.0	80–85	4.3	1	81.0			
7	1	80.0			1	79.0			
8	26	72.0 ± 1.28	65–78	4.5	25	73.8 ± 1.74	67–84	5.9	2.68
				Length of hind foot					
1	2	16.5 ± 1.0	16–17	4.3	1	16.0			
2	8	19.5 ± 0.38	19–20	2.7	4	18.0 ± 1.16	17–19	6.4	20.0*
3	1	21.0			2	21.5 ± 3.0	20–23	9.9	
4	2	18.0	18		1	19.0			
5					1	17.0			
7	1	19.0			1	19.0			
8	26	16.0 ± 0.43	13–18	6.8	25	15.3 ± 0.53	12–17	8.6	4.043*
				Length of ear					
1	2	20.0	20		1	19.0			
2	9	17.2 ± 1.04	16–21	9.1	4	21.5 ± 1.30	20–23	6.0	33.639*
3	1	21.0			2	23.0 ± 6.00	20–26	18.4	
4	2	21.0	21		1	21.0			
5					1	21.0			
6	7	20.7 ± 0.37	20–21	2.4	12	20.3 ± 0.05	19–21	4.3	1.674
7	1	19.0			1	20.0			
8	25	19.7 ± 0.55	17–22	7.0	25	19.8 ± 0.52	17–22	6.5	0.101
				Length of forearm					
1	13	59.2 ± 1.34	53.0–61.4	4.1	9	58.1 ± 0.81	56.3–59.8	2.1	1.361
2	13	58.8 ± 0.80	56.8–61.3	2.5	7	58.7 ± 1.08	57.0–61.0	2.4	0.030
3	5	59.0 ± 2.02	55.2–61.0	3.8	2	60.3 ± 0.20	60.2–60.4	0.2	0.558
4	2	55.3 ± 1.00	54.8–55.8	1.3	1	57.7			
5					1	60.2			
6	7	56.2 ± 1.81	51.5–58.3	4.3	12	56.7 ± 0.59	54.6–58.5	1.8	0.375
7	1	58.9			4	58.7 ± 0.65	57.9–59.5	1.1	
8	35	56.7 ± 0.50	53.5–59.1	2.6	29	57.2 ± 0.56	54.1–60.3	2.6	1.424
				Greatest length of skull					
1	12	28.7 ± 0.28	27.6–29.4	1.7	9	28.2 ± 0.42	27.1–29.0	2.2	4.547*
2	11	28.4 ± 0.30	27.5–29.2	1.7	7	28.4 ± 0.28	27.7–28.8	1.3	0.039
3	7	28.3 ± 0.29	27.5–28.6	1.3	3	28.5 ± 0.50	28.0–28.8	1.5	0.553
4	2	28.8 ± 0.50	28.5–29.0	1.2	1	27.4			
5					1	28.9			
6	7	28.7 ± 0.43	28.0–29.4	2.0	12	28.9 ± 0.27	28.4–29.8	1.6	0.568
7	1	28.3			4	28.6 ± 0.40	28.2–29.1	1.4	
8	34	28.3 ± 0.18	27.2–29.3	1.8	33	28.2 ± 0.18	27.1–29.0	1.8	0.639
				Condylobasal length					
1	12	25.5 ± 0.29	24.5–26.2	2.0	7	25.3 ± 0.47	24.4–26.3	2.4	0.631
2	13	25.3 ± 0.23	24.7–26.0	1.7	7	25.4 ± 0.35	24.8–25.9	1.8	0.205
3	7	25.0 ± 0.23	24.6–25.5	1.2	3	25.3 ± 0.70	24.6–25.7	2.4	0.829
4	2	25.4 ± 0.20	25.3–25.5	0.6	1	24.4			
5					1	25.6			
6	6	25.4 ± 0.43	24.5–25.9	2.1	12	25.3 ± 0.23	24.7–26.0	1.6	0.280
7	1	24.9			4	25.2 ± 0.46	24.7–25.8	1.8	
8	35	24.9 ± 0.16	23.7–25.7	1.9	32	24.8 ± 0.17	23.7–25.7	2.0	1.220

Table 1.—*Continued.*

Sample no.	Male				Female				F_s
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	
				Palatal length					
1	11	9.3 ± 0.23	8.7–9.9	4.1	8	9.3 ± 0.26	8.7–9.9	4.0	0.005
2	13	9.1 ± 0.12	8.7–9.4	2.3	7	9.1 ± 0.27	8.7–9.6	4.0	0.0
3	7	9.2 ± 0.24	9.0–9.9	3.4	3	9.5 ± 0.24	9.3–9.7	2.2	1.23
4	2	9.3 ± 0.10	9.2–9.3	0.8	1	9.0			
5					1	9.4			
6	7	9.8 ± 0.28	9.0–10.1	3.8	12	9.5 ± 0.19	8.9–10.0	3.5	1.685
7	1	9.4			4	9.6 ± 0.44	9.2–10.1	4.6	
8	36	9.5 ± 0.13	8.7–10.4	4.0	33	9.4 ± 0.18	8.5–10.6	5.4	1.386
				Depth of braincase					
1	12	11.9 ± 0.15	11.5–12.2	2.2	8	11.8 ± 0.20	11.4–12.1	2.5	0.454
2	12	11.9 ± 0.17	11.4–12.3	2.5	7	12.0 ± 0.16	11.7–12.2	1.8	0.226
3	5	11.7 ± 0.35	11.3–12.1	3.3	3	11.7 ± 0.29	11.5–12.0	2.1	0.044
4	2	12.0	12.0		1	11.7			
5					1	11.9			
6	6	12.3 ± 0.29	11.6–12.6	2.9	12	12.2 ± 0.13	11.8–12.5	1.8	0.126
7	1	11.9			4	12.3 ± 0.22	12.1–12.6	1.8	
8	32	11.9 ± 0.12	11.3–12.8	2.9	31	11.9 ± 0.12	11.3–12.6	2.9	0.261
				Zygomatic breadth					
1	10	15.2 ± 0.10	14.9–15.4	1.1	7	14.9 ± 0.11	14.7–15.1	1.0	17.704*
2	13	15.2 ± 0.21	14.5–16.0	2.5	7	15.3 ± 0.25	14.9–15.9	2.2	0.572
3	6	15.1 ± 0.41	14.4–15.7	3.3	4	14.9 ± 0.69	14.0–15.5	4.6	0.390
4	2	15.1 ± 0.10	15.0–15.1	0.5	1	14.8			
5					1	15.1			
6	7	15.1 ± 0.26	14.6–15.6	2.3	12	15.3 ± 0.17	14.7–15.7	2.0	1.094
7	1	14.7			5	15.1 ± 0.37	14.6–15.5	2.7	
8	34	14.8 ± 0.12	14.2–15.5	2.3	30	14.8 ± 0.15	14.0–15.4	2.8	0.000
				Breadth of braincase					
1	13	11.9 ± 0.19	11.0–12.4	2.9	9	11.8 ± 0.21	11.4–12.2	2.6	0.166
2	13	11.8 ± 0.14	11.4–12.4	2.1	7	11.7 ± 0.17	11.3–12.0	1.9	0.000
3	7	11.8 ± 0.25	11.4–12.3	2.9	4	11.8 ± 0.33	11.4–12.2	2.8	0.007
4	2	12.0 ± 0.20	11.9–12.1	1.2	1	11.7			
5					1	11.7			
6	6	11.8 ± 0.13	11.6–12.0	1.4	12	11.9 ± 0.10	11.5–12.1	1.5	0.612
7	1	11.2			5	11.8 ± 0.20	11.5–12.1	2.0	
8	37	11.8 ± 0.09	11.2–12.3	2.2	30	11.7 ± 0.09	11.2–12.2	2.2	0.182
				Mastoid breadth					
1	12	13.5 ± 0.19	12.9–14.0	2.5	7	13.2 ± 0.16	12.8–13.4	1.6	3.492
2	13	13.7 ± 0.16	13.1–14.1	2.1	7	13.4 ± 0.27	12.9–13.9	2.7	3.553
3	7	13.3 ± 0.33	12.7–14.0	3.2	4	13.4 ± 0.30	13.1–13.7	2.2	0.100
4	2	13.8 ± 0.40	13.6–14.0	2.0	1	13.1			
5					1	13.8			
6	5	13.6 ± 0.16	13.4–13.8	1.3	12	13.7 ± 0.14	13.2–14.0	1.8	0.146
7	1	13.7			5	13.1 ± 0.30	12.8–13.5	2.6	
8	34	13.4 ± 0.13	12.9–14.4	2.9	31	13.3 ± 0.12	12.8–13.9	2.5	0.263
				Postorbital breadth					
1	12	6.2 ± 0.18	5.7–6.8	5.1	9	6.1 ± 0.15	5.8–6.5	3.7	0.283
2	13	6.1 ± 0.11	5.9–6.6	3.4	7	6.2 ± 0.11	6.0–6.4	2.4	1.028
3	7	6.0 ± 0.30	5.6–6.6	6.7	4	6.1 ± 0.27	5.7–6.3	4.4	0.251
4	2	6.2 ± 0.10	6.1–6.2	1.4	1	6.2			
5					1	6.0			
6	7	6.2 ± 0.08	6.1–6.4	1.7	12	6.1 ± 0.12	5.7–6.6	3.5	1.510
7	1	6.1			5	6.3 ± 0.11	6.1–6.4	2.1	
8	38	6.4 ± 0.06	6.0–7.0	3.0	33	6.2 ± 0.05	6.0–6.5	2.5	13.688*

Table 1.—*Continued.*

Sample no.	Male N	Male $\overline{X} \pm 2$ SE	Male Range	Male CV	Female N	Female $\overline{X} \pm 2$ SE	Female Range	Female CV	F_s
				Length of maxillary toothrow					
1	13	9.5 ± 0.11	9.1–9.8	2.1	9	9.5 ± 0.14	9.2–9.8	2.2	0.017
2	11	9.4 ± 0.11	9.2–9.8	2.0	7	9.3 ± 0.20	8.8–9.6	2.8	1.828
3	7	9.3 ± 0.15	9.0–9.6	2.1	4	9.4 ± 0.16	9.2–9.6	1.7	1.207
4	2	9.1	9.1		1	9.0			
5					1	9.4			
6	7	9.5 ± 0.16	9.3–9.8	2.2	11	9.5 ± 0.12	9.2–9.9	2.2	0.488
7	1	9.4			5	9.3 ± 0.22	8.9–9.5	2.7	
8	34	9.4 ± 0.06	9.0–9.8	2.0	25	9.4 ± 0.07	9.0–9.7	1.8	0.00
				Rostral width at canines					
1	12	6.6 ± 0.10	6.3–6.9	2.7	9	6.6 ± 0.20	5.9–7.0	4.4	0.031
2	12	6.6 ± 0.10	6.3–6.9	2.7	7	6.7 ± 0.23	6.0–6.9	4.5	0.047
3	7	6.5 ± 0.20	6.1–6.9	4.1	2	6.7 ± 0.10	6.6–6.7	1.1	0.365
4	2	6.7 ± 0.20	6.6–6.8	2.1	1	6.7			
5					1	6.7			
6	7	6.5 ± 0.15	6.2–6.8	3.1	11	6.3 ± 0.16	5.9–6.8	4.2	2.413
7	1	5.9			4	6.2 ± 0.20	5.9–6.3	3.2	
8	37	6.2 ± 0.08	5.6–6.7	3.7	29	6.1 ± 0.08	5.8–6.7	3.5	2.755
				Breadth across upper molars					
1	12	10.5 ± 0.09	10.2–10.6	1.4	9	10.3 ± 0.23	9.8–10.8	3.4	1.087
2	11	10.4 ± 0.11	10.1–10.6	1.7	7	10.4 ± 0.33	9.6–10.8	4.2	0.000
3	7	10.2 ± 0.24	9.8–10.6	3.0	4	10.2 ± 0.33	9.8–10.6	3.2	0.010
4	2	10.3 ± 0.20	10.2–10.4	1.4	1	10.3			
5					1	10.5			
6	7	10.2 ± 0.12	10.0–10.4	1.6	12	10.3 ± 0.08	10.1–10.5	1.3	2.229
7	1	9.4			4	10.1 ± 0.13	9.9–10.2	1.2	
8	36	9.9 ± 0.07	9.5–10.4	2.2	26	10.0 ± 0.10	9.6–10.5	2.6	0.610
				Mandibular length					
1	10	17.4 ± 0.20	16.7–17.8	1.9	6	17.2 ± 0.29	16.8–17.8	2.0	0.602
2	13	17.5 ± 0.22	16.7–17.9	2.2	7	17.5 ± 0.32	16.8–17.9	2.4	0.072
3	6	17.2 ± 0.41	16.7–18.1	2.9	1	17.5			
4	2	17.6 ± 0.90	17.1–18.0	3.6	1	16.9			
5					1	17.4			
6	7	17.3 ± 0.27	16.8–17.8	2.1	12	17.1 ± 0.24	16.4–17.7	2.4	1.054
7	1	17.9			4	17.6 ± 0.46	17.1–18.2	2.6	
8	35	17.3 ± 0.13	16.3–18.2	2.2	28	17.3 ± 0.14	16.5–18.1	2.1	0.030
				Brachyphylla cavernarum					
				Total length					
9	8	86.6 ± 3.33	79–92	5.4	11	88.9 ± 1.9	84–95	3.5	1.614
10	23	92.5 ± 3.4	82–118	8.9	19	96.7 ± 4.4	84–115	9.8	2.377
11	52	94.0 ± 1.21	84–104	4.6	7	89.1 ± 3.8	82–95	5.6	7.298*
12	33	92.3 ± 1.76	88–103	5.5	19	93.3 ± 1.9	86–102	4.5	0.543
13	1	95.0							
14	2	93.5 ± 7.0	90–97	5.3	2	96.5 ± 10.1	91–102	8.1	2.212
18	9	90.2 ± 2.0	85–95	3.3					
19	1	90.0			2	102.0 ± 2.0	101–103	1.4	
22	3	90.3 ± 2.4	88–92	2.3	2	90.5 ± 1.00	90–91	0.8	0.012
23	8	91.1 ± 2.99	87–98	4.6	4	88.3 ± 0.50	88–89	0.6	1.756
24	10	91.6 ± 1.41	89–95	2.4	19	89.6 ± 1.57	86–93	2.6	3.786
25	2	94.5 ± 1.0	94–95	0.7					
26	2	84.5 ± 9.0	80–89	7.5	1	90.0			
27	3	91.0 ± 1.15	90–92	1.1	8	90.6 ± 1.85	86–94	2.9	0.056

Table 1.—*Continued.*

Sample no.	Male N	Male X̄ ± 2 SE	Male Range	Male CV	Female N	Female X̄ ± 2 SE	Female Range	Female CV	F_s
				Length of hind foot					
9	8	20.4 ± 1.60	16–23	11.1	11	21.0 ± 1.24	17–23	9.8	0.396
10	22	21.4 ± 0.41	16–23	6.5	19	21.9 ± 0.30	15–23	6.0	4.165*
11	52	22.4 ± 0.23	19–25	3.8	7	21.6 ± 0.74	20–23	4.5	5.537*
12	33	21.5 ± 0.52	18–24	6.9	19	22.1 ± 0.43	20–23	4.2	2.194
13	1	23.0							
14	2	20.0	20		2	19.5 ± 1.00	19–20	3.6	3.00
18	9	22.6 ± 0.35	22–23	2.3					
19	1	23.0			2	23.0	23		
22	3	21.3 ± 0.67	21–22	2.7	2	21.5 ± 1.00	21–22	3.3	0.086
23	8	22.5 ± 0.53	21–23	3.4	4	22.5 ± 1.0	21–23	4.4	0.000
24	10	20.3 ± 0.85	18–22	6.6	9	19.1 ± 1.39	17–23	10.9	2.232
25	2	21.5 ± 1.00	21–22	3.3					
26	2	21.5 ± 3.0	20–23	9.9					
27	3	20.7 ± 1.33	20–22	5.6	8	21.1 ± 0.7	20–23	4.7	0.431
				Length of ear					
9	8	21.3 ± 0.73	20–23	4.9	11	20.9 ± 0.87	19–23	6.9	0.323
11	43	22.0 ± 0.26	20–26	3.8	5	23.4 ± 0.49	23–24	2.3	3.146
12	33	22.4 ± 0.38	20–24	4.9	19	22.8 ± 0.41	21–24	3.9	2.002
14	2	21.0	21		2	20.5 ± 1.00	20–21	3.4	3.000
21	1	21.0							
22	3	21.0 ± 3.06	18–23	12.6	2	24.0	24		
23	8	23.0 ± 0.53	22–24	3.3	4	22.3 ± 0.5	22–23	2.3	3.158
24	5	20.2 ± 1.47	19–23	8.1	6	19.7 ± 0.67	18–20	4.2	0.492
25	2	21.0	21						
26	2	23.0	23						
27	3	22.7 ± 0.67	22–23	2.6	8	22.4 ± 0.37	22–23	2.3	0.664
				Length of forearm					
9	8	64.0 ± 1.19	60.7–65.4	2.6	11	65.1 ± 1.10	60.4–67.0	2.8	1.734
10	61	65.0 ± 0.47	61.6–69.4	2.8	24	65.0 ± 0.77	60.3–68.2	2.9	0.128
11	38	63.3 ± 0.59	60.0–66.4	2.9	7	63.3 ± 1.41	60.9–65.7	2.9	0.000
12	18	62.5 ± 0.87	60.0–66.1	3.0	8	62.8 ± 1.31	60.0–65.5	3.0	0.127
13	1	64.3							
14	6	64.1 ± 1.61	60.2–65.5	3.1	8	65.6 ± 0.49	64.5–66.8	1.1	4.019
15	6	65.6 ± 2.07	61.6–68.7	3.9	5	65.7 ± 2.28	62.0–68.0	3.9	0.002
16	3	65.3 ± 2.05	63.9–67.3	2.7					
17	1	65.2			2	63.9 ± 0.60	63.6–64.2	0.7	
18	9	65.7 ± 1.18	62.3–67.4	2.7					
19	6	65.4 ± 0.10	65.3–65.6	0.2	5	65.2 ± 0.44	64.5–65.9	0.8	9.940*
20	4	65.4 ± 0.78	64.4–66.3	1.2	3	67.3 ± 2.60	65.9–69.9	3.3	2.578
21	6	66.6 ± 0.90	65.3–67.9	1.6	5	67.6 ± 0.96	65.8–68.4	1.6	2.131
22	19	65.6 ± 0.69	63.0–68.9	2.3	13	65.4 ± 0.85	63.1–68.8	2.3	0.081
23	9	63.9 ± 0.93	62.3–65.7	2.2	7	64.6 ± 2.09	60.4–67.6	4.3	0.495
24	10	65.0 ± 1.88	59.6–68.1	4.6	9	66.8 ± 1.34	64.4–71.1	3.0	2.408
25	10	65.0 ± 0.59	62.9–66.5	1.4	5	65.5 ± 1.41	63.0–66.7	2.4	0.526
26	5	64.6 ± 0.40	61.8–65.5	2.4	6	65.2 ± 0.81	64.3–66.8	1.5	0.555
27	6	61.0 ± 1.06	59.2–63.1	2.1	12	61.1 ± 0.53	59.3–62.4	1.5	0.056
				Greatest length of skull					
9	9	31.4 ± 0.31	30.5–32.0	1.5	11	31.3 ± 0.29	30.6–31.8	1.5	0.000
10	66	31.7 ± 0.15	30.5–33.0	1.9	27	31.4 ± 0.20	30.3–32.1	1.6	4.681*
11	48	31.4 ± 0.17	30.1–32.7	1.8	5	31.5 ± 0.71	30.6–32.7	2.5	0.098
12	26	31.6 ± 0.25	30.2–32.9	2.0	8	31.0 ± 0.49	30.2–32.2	2.3	4.309*
13	1	32.0							

Table 1.—*Continued.*

Sample no.	Male N	Male $\bar{X} \pm 2$ SE	Male Range	Male CV	Female N	Female $\bar{X} \pm 2$ SE	Female Range	Female CV	F_s
14	6	32.2 ± 0.30	31.7–32.6	1.1	8	32.3 ± 0.30	31.6–32.7	1.3	0.192
15	6	32.1 ± 0.54	31.4–33.0	2.1	5	31.6 ± 0.43	31.0–32.3	1.5	2.036
16	3	32.3 ± 0.41	31.9–32.6	1.1					
17	1	32.2			3	31.7 ± 0.81	31.0–32.4	2.2	
18	8	32.1 ± 0.31	31.5–32.8	1.4	1	32.4			
19	8	32.1 ± 0.41	31.3–33.0	1.8	8	31.6 ± 0.29	31.2–32.2	1.3	3.233
20	4	32.4 ± 0.14	32.2–32.5	0.4	7	32.0 ± 0.45	31.1–32.8	1.8	1.976
21	9	31.9 ± 0.26	31.2–32.5	1.2	8	31.9 ± 0.23	31.5–32.5	1.0	0.000
22	18	32.0 ± 0.26	30.9–32.8	1.7	13	31.6 ± 0.38	30.4–32.4	2.2	3.621
23	8	31.9 ± 0.40	31.2–32.8	1.8	8	31.9 ± 0.15	31.6–32.2	0.6	0.129
24	10	32.2 ± 0.19	31.8–32.8	0.9	9	31.7 ± 0.40	30.6–32.3	1.9	6.208*
25	10	31.9 ± 0.32	31.0–32.5	1.6	7	32.1 ± 0.51	30.7–32.7	2.1	0.654
26	5	31.9 ± 0.48	31.3–32.7	1.7	8	32.2 ± 0.36	31.7–33.3	1.6	0.505
27	7	30.5 ± 0.36	30.0–31.2	1.5	11	30.5 ± 0.24	29.6–30.9	1.3	0.043
				Condylobasal length					
9	8	28.0 ± 0.34	27.2–28.5	1.7	11	27.8 ± 0.29	27.2–28.4	1.7	0.580
10	63	28.1 ± 0.13	26.4–29.5	1.9	24	28.0 ± 0.21	27.2–29.0	1.9	0.438
11	49	28.2 ± 0.13	27.2–29.1	1.7	5	27.9 ± 0.65	26.8–28.7	2.6	1.402
12	27	28.2 ± 0.21	27.3–30.0	1.9	8	28.0 ± 0.24	27.3–28.3	1.2	1.280
13	1	28.4							
14	6	28.6 ± 0.39	27.8–29.0	1.7	9	28.5 ± 0.31	28.0–29.4	1.6	0.070
15	6	28.6 ± 0.48	27.9–29.3	2.1	5	28.0 ± 0.39	27.6–28.6	1.6	4.073
16	3	28.8 ± 0.37	28.4–29.0	1.1					
17	1	29.0			3	28.2 ± 0.58	27.7–28.7	1.8	
18	8	28.5 ± 0.30	27.9–29.0	1.5	1	28.8			
19	8	28.7 ± 0.53	27.7–29.8	2.6	7	28.4 ± 0.21	28.1–28.7	1.0	0.929
20	4	29.2 ± 0.26	28.8–29.4	0.9	4	28.2 ± 0.69	27.4–28.9	2.5	6.892*
21	8	28.5 ± 0.14	28.2–28.7	0.7	8	28.3 ± 0.29	27.6–28.9	1.5	1.811
22	19	28.4 ± 0.24	27.1–29.0	1.9	13	28.1 ± 0.34	26.8–29.0	2.2	1.479
23	8	28.6 ± 0.33	27.9–29.4	1.6	7	28.4 ± 0.16	28.1–28.7	0.7	0.941
24	9	28.5 ± 0.24	28.0–29.0	1.3	9	28.2 ± 0.25	27.6–28.6	1.3	4.330
25	9	28.6 ± 0.34	27.9–29.2	1.8	7	28.6 ± 0.48	27.6–29.4	2.2	0.000
26	4	28.6 ± 0.54	28.0–29.3	1.9	8	28.4 ± 0.24	28.0–29.0	1.2	1.032
27	7	27.1 ± 0.40	26.3–27.7	1.9	12	27.0 ± 0.26	26.3–27.6	1.6	0.086
				Palatal length					
9	9	11.7 ± 0.24	11.3–12.2	3.1	11	11.6 ± 0.25	10.8–12.1	3.6	0.808
10	67	11.7 ± 0.10	10.8–12.6	3.4	27	11.5 ± 0.18	10.8–12.6	4.1	1.445
11	51	12.0 ± 0.13	11.0–12.9	3.9	6	11.3 ± 0.52	10.5–12.4	5.6	9.496*
12	31	12.1 ± 0.17	11.2–12.9	4.0	16	12.0 ± 0.24	11.0–12.7	4.0	1.101
13	1	11.8							
14	6	12.6 ± 0.28	12.3–13.1	2.7	8	12.2 ± 0.39	11.3–13.0	4.5	3.033
15	6	12.2 ± 0.53	11.5–12.9	5.3	5	11.8 ± 0.33	11.4–12.4	3.1	1.026
16	3	12.5 ± 0.58	12.0–13.0	4.0					
17	1	11.9			3	11.6 ± 0.35	11.3–11.9	2.6	
18	8	12.4 ± 0.15	12.1–12.8	1.7	1	12.2			
19	8	12.3 ± 0.34	11.5–12.8	4.0	8	12.0 ± 0.39	11.1–13.0	4.5	0.675
20	4	12.4 ± 0.26	12.0–12.6	2.1	7	12.2 ± 0.40	11.6–13.0	4.4	0.499
21	9	12.1 ± 0.30	11.4–12.7	3.7	7	12.0 ± 0.44	11.1–12.6	4.8	0.055
22	19	11.9 ± 0.27	10.6–12.8	5.0	13	11.9 ± 0.26	11.2–12.7	4.0	0.013
23	9	11.9 ± 0.23	11.5–12.5	2.9	8	12.2 ± 0.23	11.8–12.7	2.7	2.163
24	9	12.0 ± 0.25	11.3–12.3	3.1	9	11.8 ± 0.23	11.3–12.4	3.0	1.712
25	10	12.2 ± 0.28	11.6–12.7	3.7	4	12.5 ± 0.45	12.1–13.1	3.6	0.410
26	5	11.9 ± 0.33	11.4–12.3	3.1	8	11.8 ± 0.12	11.5–12.0	1.4	0.958
27	7	11.4 ± 0.39	10.7–12.0	4.5	12	11.6 ± 0.32	10.7–12.3	4.8	0.449

Table 1.—*Continued.*

Sample no.	Male N	Male $\bar{X} \pm 2$ SE	Male Range	Male CV	Female N	Female $\bar{X} \pm 2$ SE	Female Range	Female CV	F_s
				Depth of braincase					
9	8	13.4 ± 0.17	13.1–13.7	1.8	11	13.2 ± 0.20	12.5–13.7	2.6	0.993
10	65	13.4 ± 0.10	12.5–13.9	3.0	25	13.1 ± 0.13	12.4–13.6	2.5	12.368*
11	50	13.3 ± 0.10	12.4–13.9	2.6	5	13.1 ± 0.33	12.5–13.4	2.8	0.796
12	29	13.3 ± 0.13	12.3–13.9	2.6	8	13.2 ± 0.26	12.7–13.6	2.8	1.103
13	1	13.8							
14	6	13.6 ± 0.38	13.0–14.3	3.4	9	13.6 ± 0.20	13.3–14.1	2.2	0.048
15	6	13.5 ± 0.24	13.0–13.8	2.2	5	13.2 ± 0.19	13.0–13.5	1.6	2.072
16	3	13.7 ± 0.18	13.5–13.8	1.1					
17	1	12.9			3	13.1 ± 0.18	12.9–13.2	1.2	
18	8	13.4 ± 0.21	13.0–13.7	2.2	1	13.1			
19	7	13.8 ± 0.37	13.0–14.4	3.6	8	13.4 ± 0.20	13.0–13.7	2.1	2.655
20	4	13.2 ± 0.35	12.8–13.6	2.7	5	13.2 ± 0.38	12.7–13.7	3.2	0.000
21	9	13.2 ± 0.24	12.3–13.5	2.7	8	13.2 ± 0.22	12.9–13.7	2.3	0.179
22	18	13.4 ± 0.19	12.4–13.9	2.9	13	13.2 ± 0.21	12.4–13.7	2.9	3.730
23	8	13.3 ± 0.28	12.6–13.9	3.0	7	13.3 ± 0.13	13.0–13.5	1.3	0.058
24	10	13.5 ± 0.15	13.1–13.9	1.7	9	13.2 ± 0.28	12.7–13.8	3.2	4.673*
25	8	13.4 ± 0.19	13.1–13.9	2.1	7	13.4 ± 0.22	13.0–13.9	2.1	0.028
26	4	13.3 ± 0.30	12.9–13.5	2.3	7	13.1 ± 0.26	12.7–13.6	2.7	0.422
27	6	13.1 ± 0.08	13.0–13.2	0.8	12	12.7 ± 0.18	12.2–13.3	2.4	6.921*
				Zygomatic breadth					
9	7	17.0 ± 0.34	16.4–17.6	2.6	11	17.0 ± 0.21	16.5–17.7	2.0	0.026
10	65	17.2 ± 0.11	15.8–18.1	2.6	26	17.0 ± 0.17	16.0–17.7	2.5	5.041*
11	47	17.2 ± 0.13	16.5–18.0	2.5	6	16.7 ± 0.42	15.9–17.2	3.1	6.857*
12	29	17.2 ± 0.12	16.7–17.8	2.0	12	17.1 ± 0.29	16.2–18.0	2.9	0.104
13	1	17.1							
14	4	17.5 ± 0.19	17.2–17.6	1.1	7	17.5 ± 0.37	16.5–17.9	2.8	0.019
15	6	17.4 ± 0.27	16.8–17.8	1.9	5	17.1 ± 0.28	16.8–17.6	1.8	1.573
16	3	17.7 ± 0.37	17.5–18.1	1.8					
17	1	17.2			3	17.0 ± 0.07	16.9–17.0	0.3	
18	8	17.5 ± 0.24	17.0–18.0	1.9	1	17.5			
19	7	17.5 ± 0.29	17.0–18.2	2.2	7	17.3 ± 0.28	16.8–17.9	2.1	1.136
20	4	17.4 ± 0.35	16.9–17.7	2.0	7	17.1 ± 0.31	16.5–17.6	2.4	1.822
21	9	17.5 ± 0.17	17.0–17.9	1.4	8	17.2 ± 0.22	16.5–17.4	1.8	5.436*
22	18	17.4 ± 0.25	16.0–18.2	3.0	11	17.3 ± 0.30	16.6–18.3	2.9	0.088
23	8	17.4 ± 0.21	17.0–17.9	1.7	7	17.5 ± 0.25	17.0–18.0	1.9	0.548
24	10	17.7 ± 0.20	17.2–18.2	1.8	8	17.0 ± 0.36	16.3–17.5	3.0	13.149*
25	9	17.3 ± 0.18	16.6–17.6	1.6	7	17.5 ± 0.26	17.0–17.8	2.0	1.560
26	3	17.1 ± 0.64	16.5–17.6	3.2	8	17.3 ± 0.29	16.8–17.8	2.3	0.376
27	8	16.5 ± 0.13	16.2–16.7	1.1	10	16.5 ± 0.23	16.0–17.2	2.2	0.262
				Breadth of braincase					
9	9	12.6 ± 0.10	12.4–12.9	1.2	11	12.6 ± 0.16	12.2–13.1	2.1	0.005
10	66	12.8 ± 0.07	12.3–13.6	2.2	28	12.5 ± 0.11	11.9–12.9	2.2	19.992*
11	51	12.8 ± 0.07	12.3–13.2	1.8	7	12.6 ± 0.12	12.4–12.8	1.3	3.242
12	29	12.7 ± 0.08	12.3–13.3	1.7	11	12.6 ± 0.17	12.3–13.1	2.2	1.761
13	1	13.0							
14	6	13.0 ± 0.15	12.8–13.3	1.4	9	13.0 ± 0.23	12.4–13.4	2.7	0.000
15	6	13.0 ± 0.15	12.8–13.3	1.4	5	12.8 ± 0.13	12.6–13.0	1.2	3.924
16	3	13.1 ± 0.13	13.0–13.2	0.9					
17	1	12.6			3	12.7 ± 0.07	12.6–12.7	0.5	
18	8	12.8 ± 0.22	12.4–13.4	2.5	1	13.0			
19	8	12.9 ± 0.18	12.5–13.2	2.0	8	12.8 ± 0.16	12.4–13.1	1.8	0.683
20	4	12.9 ± 0.21	12.6–13.1	1.6	6	12.8 ± 0.15	12.6–13.0	1.5	0.151
21	9	12.8 ± 0.17	12.5–13.3	2.0	8	12.8 ± 0.12	12.5–13.0	1.3	0.562
22	19	12.7 ± 0.13	12.3–13.1	2.2	13	12.7 ± 0.16	12.4–13.3	2.3	0.332
23	9	12.9 ± 0.26	12.2–13.3	3.0	7	12.7 ± 0.19	12.2–12.9	2.0	1.407

Table 1.—*Continued.*

Sample no.	Male				Female				F_s
	N	$\overline{X} \pm 2$ SE	Range	CV	N	$\overline{X} \pm 2$ SE	Range	CV	
24	10	13.1 ± 0.14	12.7–13.4	1.7	10	12.7 ± 0.20	12.1–13.0	2.5	13.807*
25	10	12.9 ± 0.13	12.6–13.2	1.6	7	12.8 ± 0.19	12.4–13.2	2.0	0.647
26	5	12.9 ± 0.23	12.5–13.2	2.0	8	12.8 ± 0.21	12.4–13.2	2.3	0.423
27	8	12.4 ± 0.11	12.2–12.7	1.3	12	12.3 ± 0.15	11.9–12.7	2.2	2.039
					Mastoid breadth				
9	8	14.8 ± 0.26	14.2–15.4	2.5	11	14.6 ± 0.21	14.2–15.4	2.4	0.995
10	65	15.0 ± 0.08	14.1–15.7	2.1	24	14.6 ± 0.11	14.1–15.1	1.8	24.343*
11	46	14.8 ± 0.10	14.0–15.3	2.2	5	14.4 ± 0.27	14.0–14.8	2.1	4.320*
12	27	14.8 ± 0.12	14.2–15.4	2.2	7	14.6 ± 0.32	14.1–15.2	2.9	1.237
13	1	14.6							
14	6	15.1 ± 0.19	14.9–15.5	1.6	9	14.9 ± 0.29	14.3–15.5	2.9	0.465
15	6	15.0 ± 0.33	14.4–15.6	2.7	5	14.5 ± 0.37	14.0–14.9	2.8	3.472
16	3	15.1 ± 0.47	14.7–15.5	2.7					
17	1	14.9			3	14.3 ± 0.41	14.0–14.7	2.5	
18	8	14.9 ± 0.17	14.5–15.3	1.6					
19	8	15.0 ± 0.25	14.5–15.6	2.4	8	14.9 ± 0.17	14.5–15.3	1.6	0.432
20	4	15.0 ± 0.44	14.6–15.6	3.0	5	14.6 ± 0.33	14.1–15.1	2.5	2.105
21	9	14.9 ± 0.11	14.6–15.1	1.1	8	14.7 ± 0.25	14.2–15.3	2.4	2.319
22	18	14.9 ± 0.17	14.1–15.5	2.4	13	14.7 ± 0.22	14.1–15.5	2.7	2.025
23	8	15.0 ± 0.16	14.7–15.4	1.5	6	14.8 ± 0.15	14.5–15.9	1.3	5.846*
24	10	15.0 ± 0.15	14.7–15.5	1.6	9	14.6 ± 0.31	14.0–15.4	3.2	6.294*
25	9	15.0 ± 0.18	14.5–15.4	1.8	7	14.8 ± 0.30	14.1–15.4	2.7	0.448
26	3	14.7 ± 0.12	14.6–14.8	0.7	8	14.7 ± 0.18	14.4–15.0	1.7	0.000
27	7	14.4 ± 0.27	13.7–14.8	2.5	12	14.1 ± 0.17	13.7–14.6	2.0	4.007
					Postorbital breadth				
9	8	6.5 ± 0.11	6.3–6.7	2.3	11	6.4 ± 0.10	6.1–6.6	2.5	0.359
10	67	6.5 ± 0.04	6.0–6.8	2.4	28	6.5 ± 0.08	6.1–6.8	3.2	2.127
11	53	6.4 ± 0.06	5.8–6.9	3.2	7	6.5 ± 0.11	6.2–6.7	2.3	2.254
12	31	6.3 ± 0.07	5.9–6.8	3.0	15	6.3 ± 0.08	6.0–6.6	2.6	0.280
13	1	6.5							
14	6	6.4 ± 0.11	6.2–6.6	2.1	9	6.4 ± 0.10	6.2–6.6	2.4	0.078
15	6	6.4 ± 0.11	6.3–6.6	2.1	5	6.2 ± 0.15	6.0–6.4	2.6	3.330
16	3	6.4 ± 0.18	6.3–6.6	2.4					
17	1	6.2			3	6.2 ± 0.07	6.1–6.2	0.9	
18	9	6.4 ± 0.12	6.2–6.7	2.7	1	6.5			
19	8	6.4 ± 0.17	6.1–6.9	3.8	8	6.3 ± 0.13	6.0–6.5	2.9	0.211
20	4	6.1 ± 0.17	5.9–6.3	2.8	7	6.2 ± 0.11	6.0–6.4	2.4	1.404
21	9	6.3 ± 0.13	6.0–6.6	3.1	8	6.3 ± 0.09	6.0–6.4	2.1	0.111
22	19	6.5 ± 0.08	6.2–6.9	2.6	13	6.3 ± 0.09	6.1–6.6	2.5	5.361*
23	8	6.3 ± 0.08	6.1–6.4	1.9	8	6.3 ± 0.08	6.2–6.5	1.7	1.762
24	10	6.4 ± 0.07	6.2–6.5	1.7	10	6.4 ± 0.11	6.1–6.6	2.8	0.102
25	11	6.3 ± 0.07	6.1–6.5	1.9	6	6.3 ± 0.15	6.1–6.6	2.8	0.133
26	5	6.4 ± 0.09	6.3–6.5	1.6	8	6.4 ± 0.12	6.2–6.7	2.6	0.202
27	8	6.3 ± 0.15	6.1–6.6	3.5	12	6.2 ± 0.10	5.8–6.5	2.8	2.179
					Length of maxillary toothrow				
9	9	10.6 ± 0.13	10.3–10.9	1.9	11	10.7 ± 0.15	10.1–11.0	2.3	0.650
10	62	10.7 ± 0.05	10.1–11.1	1.9	24	10.7 ± 0.08	10.4–11.0	1.8	0.661
11	38	10.8 ± 0.06	10.3–11.2	1.9	7	10.7 ± 0.20	10.4–11.1	2.5	0.347
12	22	10.7 ± 0.10	10.3–11.1	2.2	11	10.7 ± 0.06	10.5–10.8	0.9	0.148
13	1	10.7							
14	6	11.0 ± 0.10	10.8–11.1	1.1	8	10.9 ± 0.21	10.5–11.3	2.8	0.887
15	6	10.9 ± 0.16	10.6–11.1	1.8	5	11.0 ± 0.24	10.6–11.2	2.4	0.479
16	3	11.1 ± 0.18	11.0–11.3	1.4					
17	1	11.0			3	11.0 ± 0.44	10.6–11.3	3.4	
18	9	11.0 ± 0.24	10.6–11.6	3.3	1	11.5			

Table 1.—*Continued.*

Sample no.	Male N	Male $\overline{X} \pm 2$ SE	Male Range	Male CV	Female N	Female $\overline{X} \pm 2$ SE	Female Range	Female CV	F_s
19	6	10.9 ± 0.10	10.7–11.0	1.1	5	10.8 ± 0.15	10.7–11.0	1.5	1.129
20	4	11.3 ± 0.14	11.2–11.5	1.3	7	11.1 ± 0.20	10.6–11.4	2.4	1.900
21	9	11.0 ± 0.11	10.7–11.2	1.5	8	11.0 ± 0.14	10.5–11.1	1.8	0.877
22	19	11.0 ± 0.11	10.6–11.6	2.1	13	10.9 ± 0.13	10.6–11.4	2.1	2.659
23	9	11.0 ± 0.06	10.9–11.2	0.9	8	11.0 ± 0.12	10.8–11.2	1.6	0.000
24	10	11.1 ± 0.12	10.7–11.3	1.7	9	10.9 ± 0.10	10.6–11.1	1.4	7.159*
25	11	11.0 ± 0.12	10.7–11.3	1.8	8	11.1 ± 0.13	10.7–11.2	1.7	0.026
26	4	10.9 ± 0.30	10.5–11.2	2.7	8	11.0 ± 0.15	10.8–11.4	1.9	0.355
27	8	10.6 ± 0.14	10.3–10.9	1.9	12	10.5 ± 0.13	10.0–10.8	2.1	0.173
				Rostral width at canines					
9	9	7.2 ± 0.11	7.1–7.6	2.3	11	7.1 ± 0.08	6.8–7.3	1.9	1.995
10	67	7.2 ± 0.06	6.5–7.6	3.4	28	7.1 ± 0.08	6.5–7.4	3.0	9.096*
11	52	7.3 ± 0.07	6.6–7.7	3.4	7	7.0 ± 0.21	6.6–7.4	3.9	7.397*
12	30	7.3 ± 0.08	6.8–7.8	2.9	14	7.2 ± 0.08	6.9–7.5	2.2	4.375*
13	1	7.4							
14	6	7.3 ± 0.12	7.2–7.6	2.1	8	7.2 ± 0.14	7.0–7.6	2.8	0.962
15	6	7.2 ± 0.26	6.8–7.7	4.4	5	7.2 ± 0.21	6.8–7.4	3.2	0.052
16	3	7.3 ± 0.18	7.1–7.4	2.1					
17	1	6.8			3	7.4 ± 0.57	6.8–7.7	6.7	
18	8	7.3 ± 0.19	7.0–7.8	3.6	1	7.4			
19	8	7.5 ± 0.24	7.0–8.1	4.5	8	7.2 ± 0.16	6.8–7.4	3.0	2.491
20	4	7.6 ± 0.05	7.6–7.7	0.6	7	7.1 ± 0.12	6.9–7.3	2.3	37.664*
21	9	7.3 ± 0.14	7.0–7.6	2.8	8	7.2 ± 0.18	6.8–7.6	3.5	0.448
22	18	7.4 ± 0.13	6.7–7.8	3.8	13	7.2 ± 0.09	6.9–7.4	2.4	3.884
23	9	7.4 ± 0.23	6.8–7.9	4.6	8	7.2 ± 0.13	7.0–7.5	2.4	2.337
24	9	7.4 ± 0.15	7.1–7.8	3.0	9	7.1 ± 0.15	6.7–7.5	3.1	11.422*
25	11	7.4 ± 0.12	7.0–7.5	2.6	7	7.3 ± 0.08	7.2–7.5	1.5	0.233
26	5	7.4 ± 0.20	7.1–7.7	3.1	8	7.2 ± 0.12	7.0–7.4	2.3	2.392
27	8	6.9 ± 0.15	6.6–7.2	3.0	12	6.7 ± 0.14	6.3–7.0	3.6	2.070
				Breadth across upper molars					
9	9	11.5 ± 0.28	10.9–12.2	3.7	11	11.5 ± 0.10	11.2–11.7	1.5	0.244
10	66	11.5 ± 0.07	10.8–12.1	2.6	27	11.5 ± 0.11	10.9–12.1	2.4	0.558
11	50	11.6 ± 0.09	10.9–12.3	2.7	7	11.2 ± 0.22	10.8–11.7	2.6	7.009*
12	26	11.5 ± 0.11	11.0–12.1	2.5	14	11.7 ± 0.15	11.2–12.2	2.4	2.569
13	1	11.7							
14	5	11.7 ± 0.29	11.2–12.0	2.7	8	11.8 ± 0.19	11.4–12.2	2.3	0.046
15	6	11.7 ± 0.27	11.2–12.2	2.8	5	11.7 ± 0.46	11.2–12.4	4.4	0.015
16	3	11.7 ± 0.18	11.6–11.9	1.3					
17	1	11.1			3	11.9 ± 0.27	11.6–12.0	1.9	
18	9	11.8 ± 0.21	11.4–12.3	2.7	1	12.2			
19	6	11.8 ± 0.34	11.4–12.4	3.5	7	11.6 ± 0.25	11.0–12.0	2.8	0.439
20	4	12.0 ± 0.06	11.9–12.0	0.5	7	11.5 ± 0.18	11.2–11.9	2.1	11.128*
21	9	11.8 ± 0.16	11.6–12.2	2.0	8	11.8 ± 0.28	10.9–12.1	3.3	0.130
22	19	11.8 ± 0.15	11.0–12.3	2.8	13	11.7 ± 0.19	11.2–12.2	2.9	0.276
23	9	11.8 ± 0.18	11.3–12.2	2.2	8	11.8 ± 0.20	11.3–12.1	2.3	0.000
24	10	12.0 ± 0.19	11.5–12.4	2.5	10	11.6 ± 0.14	11.2–12.0	1.9	10.770*
25	10	11.7 ± 0.12	11.3–12.0	1.7	7	11.9 ± 0.11	11.8–12.2	1.2	7.171*
26	5	11.7 ± 0.19	11.6–12.1	1.8	8	11.7 ± 0.23	11.2–12.2	2.8	0.006
27	8	11.1 ± 0.15	10.9–11.5	1.9	11	11.2 ± 0.19	10.8–11.9	2.9	0.576
				Mandibular length					
9	8	19.9 ± 0.26	19.3–20.3	1.9	11	19.9 ± 0.24	19.3–20.4	2.0	0.053
10	63	19.9 ± 0.10	19.0–20.9	2.1	26	19.9 ± 0.18	19.1–20.9	2.3	0.105
11	45	20.3 ± 0.10	19.6–21.0	1.7	7	20.1 ± 0.26	19.7–20.5	1.7	2.069
12	26	20.2 ± 0.21	19.4–20.8	2.7	10	20.1 ± 0.26	19.4–20.8	2.1	0.945
13	1	20.1							

Table 1.—*Continued.*

Sample no.	Male				Female				F_s
	N	$\bar{X} \pm 2$ SE	Range	CV	N	$\bar{X} \pm 2$ SE	Range	CV	
14	4	20.6 ± 0.38	20.0–20.8	1.8	9	20.3 ± 0.19	20.0–20.7	1.4	2.328
15	6	20.6 ± 0.31	20.3–21.1	1.8	5	20.0 ± 0.54	19.4–20.6	3.0	3.938
16	3	20.5 ± 0.20	20.4–20.7	0.8					
17	1	20.8			2	20.0 ± 0.60	19.7–20.3	2.1	
18	9	20.6 ± 0.34	20.0–21.5	2.5	1	21.1			
19	7	20.7 ± 0.39	20.0–21.3	2.5	7	20.4 ± 0.26	19.9–21.0	1.7	1.520
20	4	20.7 ± 0.49	20.1–21.3	2.4	7	20.6 ± 0.34	19.8–21.0	2.2	0.184
21	7	20.4 ± 0.29	19.8–20.9	1.9	8	20.4 ± 0.21	19.9–20.8	1.5	0.000
22	19	20.5 ± 0.16	19.7–21.0	1.7	12	20.4 ± 0.28	19.5–21.0	2.4	0.809
23	8	20.5 ± 0.19	20.1–20.9	1.3	7	20.4 ± 0.17	19.9–20.5	1.1	0.875
24	9	20.8 ± 0.13	20.5–21.1	0.9	7	20.3 ± 0.26	19.8–20.8	1.7	14.000*
25	9	20.6 ± 0.27	19.8–21.1	1.9	6	20.5 ± 0.26	20.0–20.9	1.5	0.429
26	4	20.7 ± 0.47	20.2–21.3	2.3	8	20.7 ± 0.34	19.9–21.3	2.3	0.000
27	7	19.5 ± 0.30	18.9–20.0	2.0	11	19.7 ± 0.20	19.1–20.3	1.7	1.781

proved to be significantly larger than females in the following measurements from localities shown in parentheses: total length (St. John, 11); length of hind foot (St. John, 11); length of forearm (St. Martin, 19); greatest length of skull (eastern Puerto Rico, 10; Norman Island, 12; Martinique, 24); condylobasal length (Barbuda, 20); palatal length (St. John, 11); braincase depth (eastern Puerto Rico, 10; Martinique, 24; Barbados, 27); zygomatic breadth (eastern Puerto Rico, 10; St. John, 11; Dominica, 23; Martinique, 24); breadth of braincase (eastern Puerto Rico, 10; Martinique, 24); mastoid breadth (eastern Puerto Rico, 10; St. John, 11; Dominica, 23; Martinique, 24); postorbital breadth (Guadeloupe, 22); length of maxillary toothrow (Martinique, 24); rostral width at canines (eastern Puerto Rico, 10; St. John Island, 11; Norman Island, 12; Barbuda, 20; Martinique, 24); breadth across upper molars (St. John Island, 11; Barbuda, 20; Martinique, 24); mandibular length (Martinique, 24).

Although males exceeded females significantly in size in all 16 measurements except length of ear from one or more localities, females proved to be significantly larger than males in length of hind foot in the sample from eastern Puerto Rico (10), and in breadth across upper molars in specimens from St. Lucia (25).

Samples showing males to be significantly larger than females in more than one character include eastern Puerto Rico, St. John Island, Norman Island, Barbuda, and Martinique. With the exception of the sample from Barbuda, all these correspond to fairly large samples. However, Guadeloupe, also represented by a large (males 19, females 13) sample, showed significant differences in males over females only in postorbital breadth.

Forearm measurements, which because of loading in pregnant females, might be expected to be greater in females than males, average longer in females than males in 11 of 15 samples, but never significantly. In two samples the sexes have the same average length of forearm. In specimens from St. Martin, length of forearm in males was significantly longer than that of females.

Conclusions.—In general, males are larger than females in the genus *Brachyphylla*. Therefore, in all subsequent analyses, where size was involved, males and females were treated separately.

Individual Variation

In samples from west of the Mona Passage, external measurements, excluding length of forearm, were found to vary much more (CV, 1.8 to 18.4) than forearm and cranial measurements (CV, 0.2 to 6.7) (Table 1).

Of forearm and cranial measurements, palatal length (CV, 0.8 to 5.4), rostral width at canines (CV, 1.1 to 4.5), and postorbital breadth (CV, 1.4 to 6.7) showed the highest individual variation, whereas greatest length of skull (CV, 1.2 to 2.2) and condylobasal length (CV, 0.6 to 2.4) showed the least.

In samples from east of the Mona Passage, variation in external measurements (excluding length of forearm) was again found to be higher (CV, 0.6 to 12.6) than in forearm and cranial measurements (CV, 0.2 to 6.7). Of the latter, palatal length showed the most variation (CV, 1.4 to 5.6) and greatest length of skull (CV, 0.4 to 2.5) and condylobasal length (CV, 0.7 to 2.6) the least. Rostral width at canines also showed relatively high coefficients of variation (CV, 0.6 to 6.7).

Conclusions.—From both east and west of the Mona Passage, external measurements taken from the skin tags proved to be highly variable. As pointed out by Sumner (1927), external measurements can be expected to vary more because of the fact that these were usually taken by various collectors under different circumstances. Because of missing data and high individual variation, total length, length of hind foot, and length of ear were excluded from subsequent analyses.

SPECIFIC RELATIONSHIPS

Because of the discordance in the literature (see Introduction) concerning the specific relationships within the genus, both univariate and multivariate analyses were employed to compare the geographic samples. Standard statistics for samples of males and females from geographic samples are given in Table 1.

Univariate Analyses

The SS-STP analyses revealed geographic samples west of the Mona Passage (samples 1 to 8) grouped in one subset, differing significantly from all other samples in the following cranial measurements: greatest length of skull (females); condylobasal length (males and females); palatal length (males); zygomatic width (males and females); length of maxillary toothrow (females); breadth across upper molars (females); mandibular length (males). The results of these analyses for condylobasal length and mastoid breadth are shown in Table 2. This division corresponds to the specific division in the genus as recently suggested by Silva-Taboada (1976) in which he recognized two species, *B. nana* from west of the Mona Passage and *B. cavernarum* from the remainder of the geographic distribution of the genus.

Characters that showed wide overlap of subsets were depth of braincase (males) and postorbital breadth (males and females). The remainder of the characters all tend to show basically a break across the Mona Passage, with varying numbers of overlapping subsets.

Multivariate Analyses

Distance phenograms for both males and females generated with the NT-SYS program package are illustrated in Fig. 2. In addition, a map (Fig. 3), including values for both sexes, presents appropriate distance coefficients between the connected samples; in most cases, distance coefficients have been given only for contiguous samples. The first three principal components extracted from the principal component analyses are shown for males and females (Fig. 4).

The distance phenograms for both male (cophenetic correlation value, 0.975) and female (cophenetic correlation value, 0.965) *Brachyphylla* clearly show two major groups. In both cases the upper cluster corresponds to samples west of the Mona Passage (Cuba, 1 to 4; Grand Cayman, 5; Middle Caicos, 6; and Hispaniola, 7 and 8), whereas the lower cluster corresponds to samples east of the passage (Puerto Rico, 9 and 10; Virgin Islands, 11 to 14; and the Lesser Antilles, 15 to 27). Distance coefficients on the map also clearly show this break across the Mona Passage with values of 1.96 for males and 2.04 for females. On the other hand, these values between contiguous samples west of the passage, and between similar samples to the east of it are less than 1.00, except between St. Lucia and Barbados where it is 1.03 in the females.

The amount of phenetic variation explained by the first three principal components, for males and females, respectively, was 90.6% and 91.3%, 5.1% and 4.6%, and 2.1% and 1.7% (total, males, 97.8%; females, 97.6%). Results of factor analyses showing characters influencing the first three components for both males and females are given in Table 3. The high percentage of variation explained by the first component in both males and females reveals that size is the major factor separating the two groups in the principal component analyses. From the factor analysis it can be seen that on the first component, postorbital width is not weighted heavily (males 0.643 and females 0.677) in separating the groups, whereas all the other characters contribute heavily (above 0.900). Postorbital breadth (Component II) and rostral width at canines (Component III) influence the other components most heavily.

Examination of three-dimensional plots reveals basically the same pattern as the distance phenograms for both sexes. Samples on the left of the plot are the same samples that were found in the upper cluster of the phenograms, which are the samples

Table 2.—*Results of two SS-STP analyses (condylobasal length and mastoid breadth) of geographic variation in* Brachyphylla nana *and* B. cavernarum. *Vertical lines to the right of each set of means connect maximally nonsignificant subsets at the 0.05 level. See text for key to sample numbers.*

Males			Females		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
	Condylobasal length				
20	29.2		25	28.6	
16	28.8		14	28.5	
19	28.7		19	28.4	
26	28.6		23	28.4	
14	28.6		26	28.4	
15	28.6		21	28.3	
25	28.6		17	28.2	
23	28.6		24	28.2	
24	28.5		20	28.2	
21	28.5		22	28.1	
18	28.5		10	28.0	
22	28.4		15	28.0	
11	28.2		12	28.0	
12	28.2		11	27.9	
10	28.1		9	27.8	
9	28.0		27	27.0	
27	27.1		2	25.4	
1	25.5		3	25.3	
4	25.4		6	25.3	
6	25.4		1	25.3	
2	25.3		7	25.2	
3	25.0		8	24.8	
8	24.9				
	Mastoid breadth				
16	15.1		14	14.9	
14	15.1		19	14.9	
24	15.0		25	14.8	
23	15.0		23	14.8	
19	15.0		21	14.7	
15	15.0		26	14.7	
10	15.0		22	14.7	
25	15.0		10	14.6	
20	15.0		24	14.6	
18	14.9		12	14.6	
21	14.9		9	14.6	
22	14.9		20	14.6	
9	14.8		15	14.5	
12	14.8		11	14.4	
11	14.8		17	14.3	
26	14.7		27	14.1	
27	14.4		6	13.7	
4	13.8		2	13.4	
2	13.7		3	13.4	
6	13.6		8	13.3	
1	13.5		1	13.2	
8	13.4		7	13.1	
3	13.3				

from west of the Mona Passage. Samples on the right of the plot correspond to all samples east of the passage. Sample 27 (Barbados) is somewhat separated from the cluster of samples on the right, and corresponds to the presently recognized subspecies *B. c. minor*.

In both male and female *Brachyphylla*, multivariate analysis of variance (MANOVA) showed that there were significant ($P < 0.0001$) morphological differences among samples for all characters in the following statistical tests (Hotelling-Lawley's Trace, Pillai's Trace, Wilks' Criterion, and Roy's Maximum Root Criterion).

Two-dimensional plots of the samples onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial characters are presented for 26 male samples in Fig. 5 and for 24 female samples in Fig. 6. The amount (percentage) of phenetic variation represented in the first three canonical variates for male and female *Brachyphylla*, respectively, was 87.1 and 76.9 for variate I, 4.2 and 7.5 for variate II, and 3.2 and 4.5 for variate III. Combined the first three canonical variates express 94.5% in males and 88.9% in females. In both males and females it took all 13 canonical variates to explain all the variation. The relative contributions of each character to the first three canonical variates in males and females are given in Table 4.

Examination of the two-dimensional plots of the samples of both males and females reveals two distinct groups well separated on the first variate. Samples of the population east of the Mona Passage are grouped in the cluster at the top and those from west of the passage in the cluster at the bottom. In both males and females, length of maxillary toothrow (males 23.5, females 15.7) and mandibular length (males 15.4, females 20.2) contributed the heaviest toward separating the two groups on the first variate. Other characters that contributed more than 10% on the first variate include breadth across upper molars in males, and condylobasal length in females. The following characters in males contributed more than 10% on the second variate, condylobasal length, palatal length, depth of braincase, postorbital breadth, and rostral width at canines, and on the third variate, forearm length, greatest length of skull, postorbital breadth, and mandibular length; and in females on the second variate, greatest length of skull, condylobasal length, and rostral width at canines, and on the third variate, greatest length of skull and mandibular length.

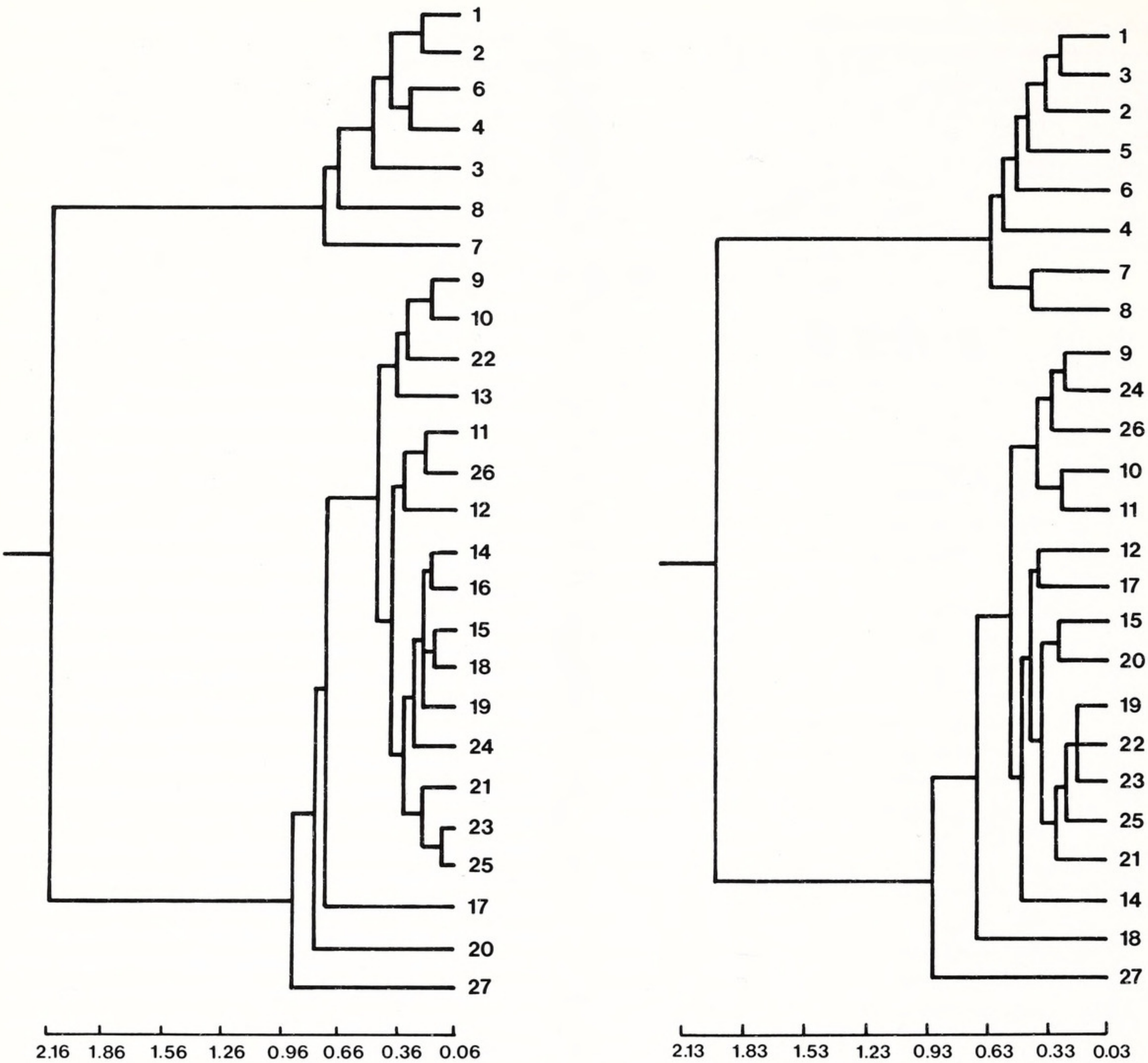

Fig. 2.—Phenograms of numbered samples (see Fig. 1 and text) of *Brachyphylla* (males left, females right) computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for males is 0.975 and for females 0.965.

The SAS canonical variate analyses, therefore, closely correspond to the NT-SYS cluster analysis and the principal component analysis in separating the two groups.

Variation in Color

Color in the genus *Brachyphylla* does not exhibit a great deal of variation. Typically the hair is white to yellowish white at the base with the tips darker in some areas on the dorsum. These darker areas, which vary in size, occur as a distinct patch on top of the head and neck and a V-shaped mantle starting approximately at the shoulders and meeting posteriorly in the middle of the dorsum. The flanks are ususally lighter colored. The darker areas may be blackish gray, blackish brown, grayish brown, or dark brown in color.

In 38 skins from Cuba, 47% correspond to color standard 5, whereas nearly an equal proportion (37%) are comparable to color standard 3 (see Ma-

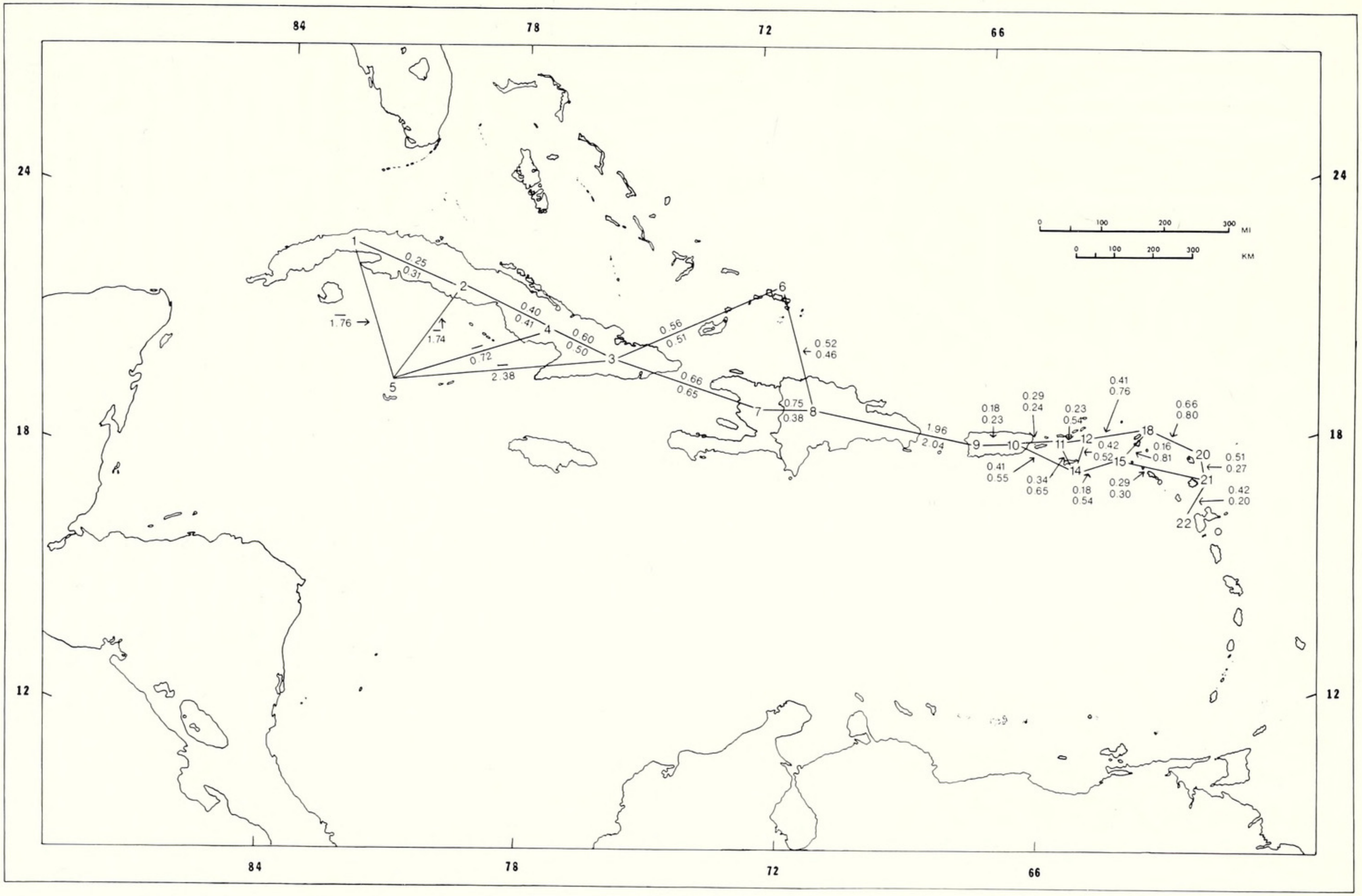

Fig. 3.—Map showing distance coefficients (from distance matrices) between samples of *Brachyphylla* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 1 and text for key to samples.

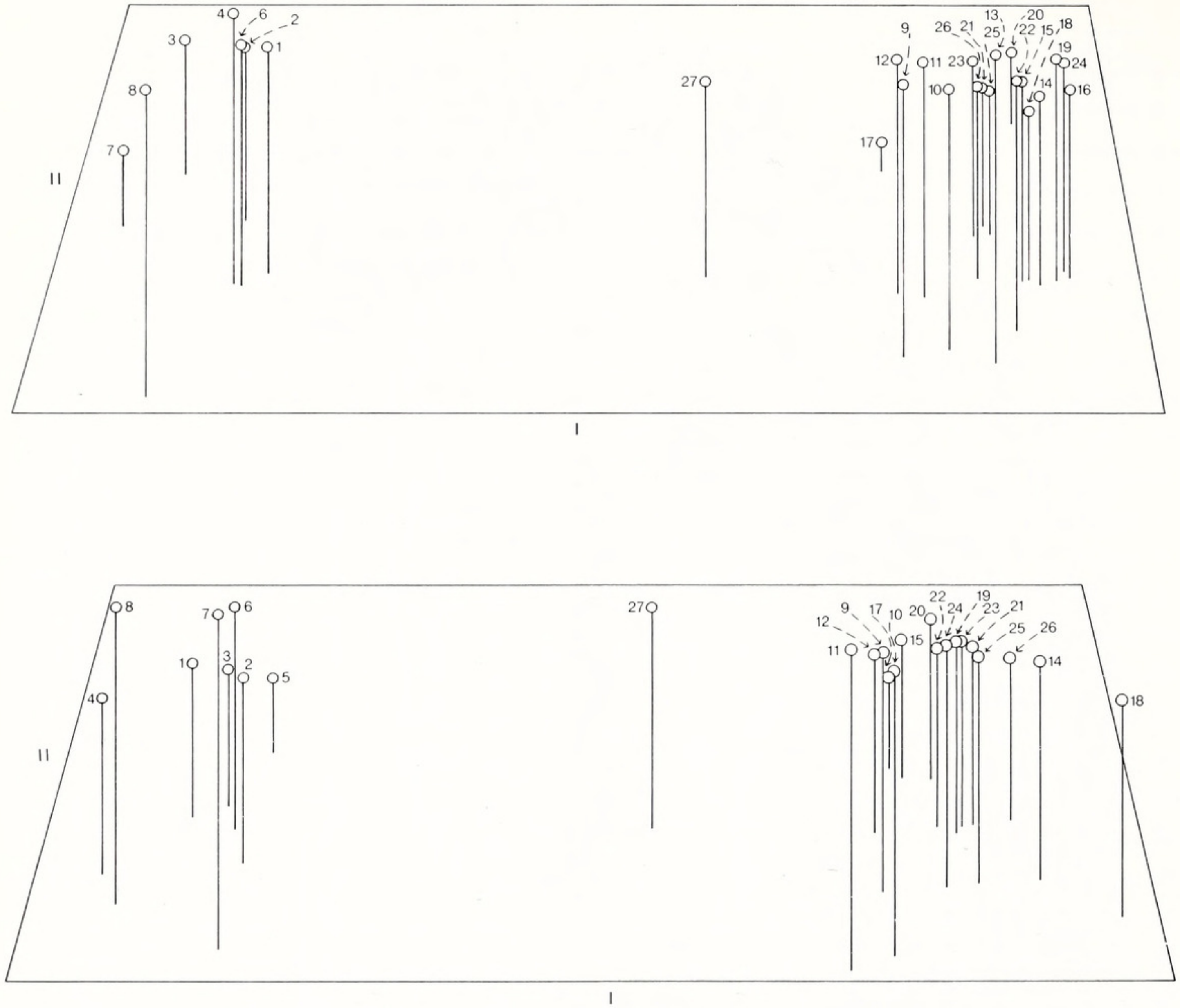

Fig. 4.—Three-dimensional projections of samples of *Brachyphylla* (males above, females below) onto the first three principal components based on matrices of correlation among one external and 12 cranial measurements. Components I and II are indicated in the figure and component III is represented by height. See Fig. 1 and text for key to samples.

terials and Methods). Therefore, the majority have the base of the hair white to yellowish white with the tips of the hair in the dorsal V-pattern varying from grayish brown to dark brown with varying shades of buff. The dark brown specimens having a yellowish tint, all from the Albert Schwartz Collection, have a more washed-out appearance than the color standard 5. Other specimens (16%) from Cuba were blackish brown (color standard 2).

Of 56 skins examined from Hispaniola, 63% have hair white at the base with blackish gray tips (color standard 1). However, there is also a large percentage (35%) that are grayish brown colored, sometimes tinted buffish (color standard 3), which corresponds in color to all specimens examined from Middle Caicos (19) and Grand Cayman (1).

From Puerto Rico, 57 skins were examined. Of these, 42% were blackish brown (color standard 2) in color; however, nearly an equal number (35%) were grayish brown, some with a buffy tint (color standard 3). The remainder consisted of 18% blackish gray specimens (color standard 1), and 5% yellowish dark brown specimens (color standard 5). The latter specimens are mostly from the Albert Schwartz Collection. The majority (54%) of the 41 bats from St. John Island are blackish brown in col-

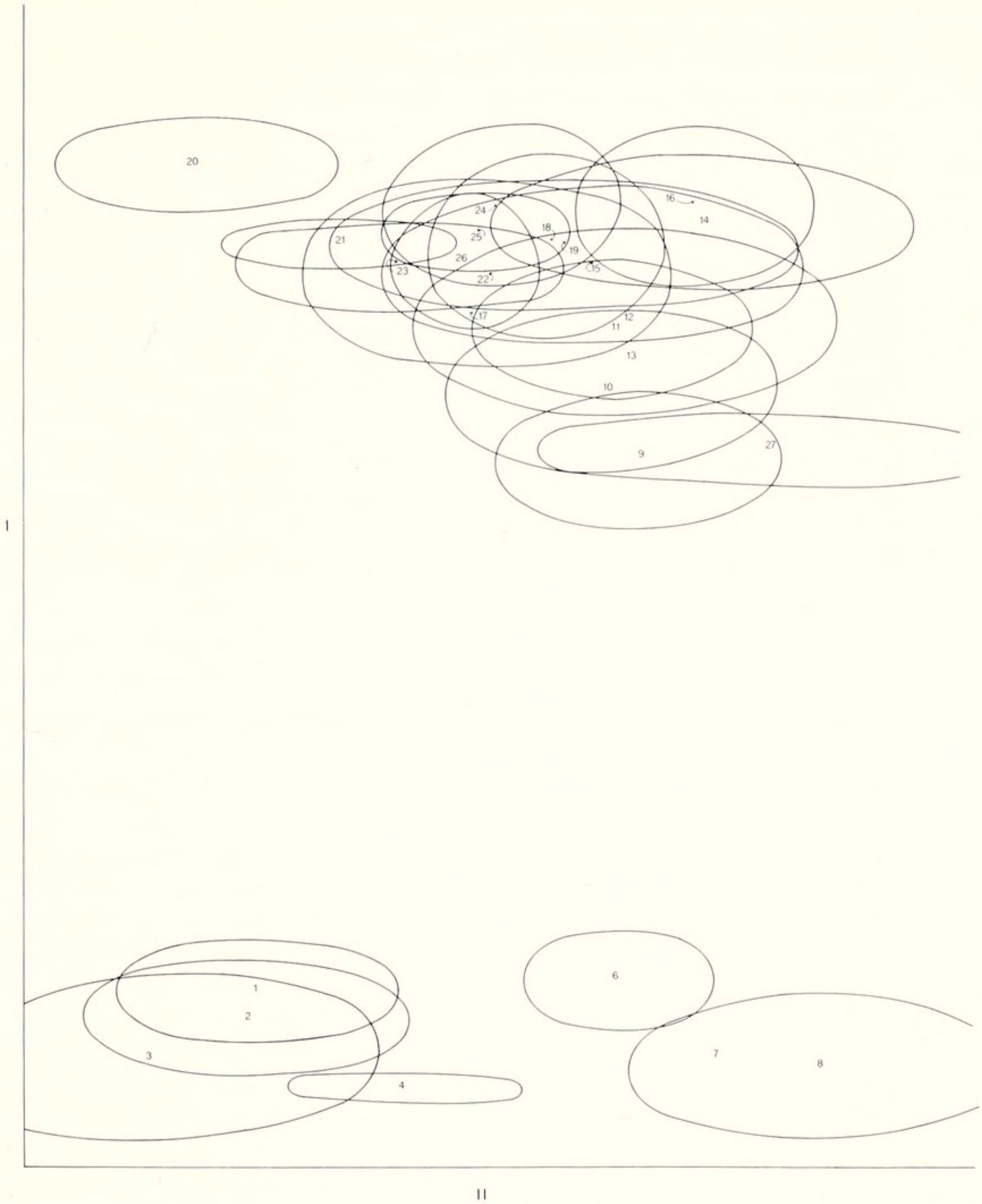

Fig. 5.—Two-dimensional projection of male samples (mean and one standard deviation) of *Brachyphylla* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

or (color standard 2). The remainder varied from grayish brown (34%) (color standard 3) to dark brown (12%), tinted buff or reddish (color standard 4). Over 30 specimens from Norman Island were found to be molting and were excluded from color analysis. Of the 26 remaining skins that were studied, 46% were found to be grayish brown (some with a buffish tint) (color standard 3), 35% blackish brown (color standard 2), 15% dark brown with a reddish tint (color standard 4), and 4% blackish gray (color standard 1). All specimens from St. Thomas (1), St. Croix (4), Anguilla (9), St. Martin (16), and Antigua (1) were blackish brown in color (color standard 2).

Of the seven specimens examined from Guadeloupe, three were blackish gray (color standard 1), two dark brown (color standard 4), one grayish brown (color standard 3), and one dark yellowish brown (color standard 5). Ten of 12 bats from Dominica were blackish brown colored (color standard 2); the remaining two were grayish brown (color standard 3). Of nine specimens from Martinique,

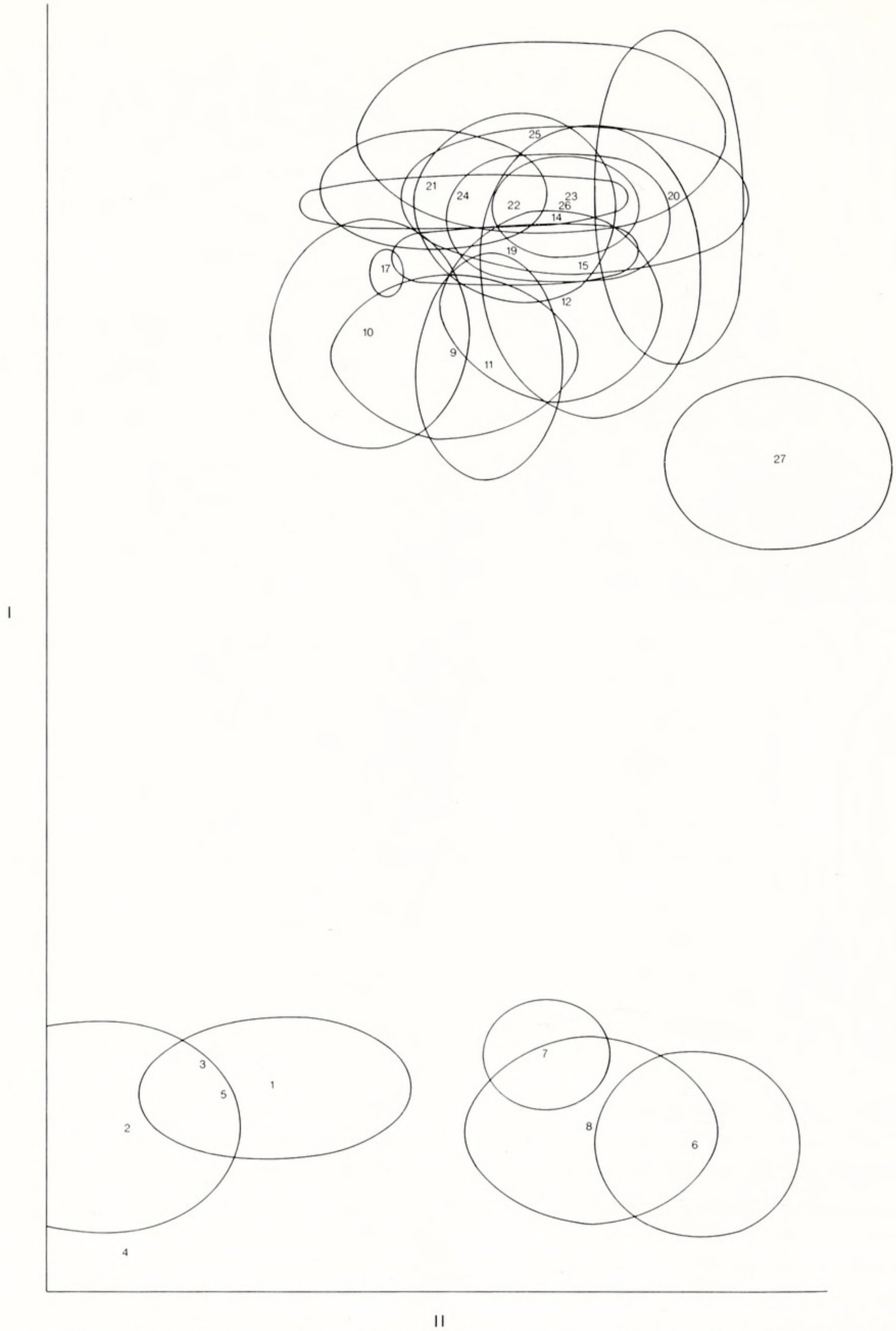

Fig. 6.—Two-dimensional projection of female samples (mean and one standard deviation) of *Brachyphylla* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

six were blackish brown (color standard 2) and three yellowish dark brown (color standard 5). All three specimens from St. Vincent were blackish gray (color standard 1). Coat color in most (nine of 14) specimens from Barbados have the base of the hair yellowish white with the tips of the hair dark brown and tinted buffy (color standard 5). All (nine) of these specimens are from the Albert Schwartz

Table 3.—*Factor matrix from correlation among 13 characters of* Brachyphylla *studied, showing characters influencing the first three components.*

Characters	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Length of forearm	0.940	0.125	−0.163	0.947	0.084	−0.020
Greatest length of skull	0.993	0.058	−0.049	0.991	0.017	0.069
Condylobasal length	0.987	0.108	−0.040	0.996	0.030	0.002
Palatal length	0.983	0.034	−0.089	0.981	0.052	0.129
Depth of braincase	0.967	−0.162	−0.002	0.969	−0.051	0.156
Zygomatic breadth	0.994	0.055	−0.004	0.993	0.019	0.031
Breadth of braincase	0.972	−0.025	0.173	0.988	−0.015	0.037
Mastoid breadth	0.978	0.050	−0.097	0.975	0.041	0.036
Postorbital breadth	0.643	−0.760	−0.063	0.677	−0.728	−0.107
Length of maxillary toothrow	0.979	0.113	−0.100	0.985	0.049	0.046
Rostral width at canines	0.933	0.027	0.343	0.905	0.184	−0.377
Breadth across upper molars	0.972	0.026	0.210	0.979	0.099	−0.108
Mandibular length	0.980	0.092	−0.128	0.990	−0.020	0.042

Collection. Other material from Barbados have the base of the hair white with blackish gray tips (color standard 1) in two specimens, and grayish brown with a buffish tint (color standard 3) in three others.

There is little variation in color in bats of this genus. All have the same basic pattern of color. The variation that is present is in color of the tips, which varies from grayish brown to blackish gray, and in

Table 4.—*Eigenvalues of canonical variates showing the percentage influence among 13 characters of* Brachyphylla. *Eigenvalues shown represent the normalized vector coefficient of each character.*

Characters	Vector I		Vector II		Vector III	
	Eigenvalue	Percent influence	Eigenvalue	Percent influence	Eigenvalue	Percent influence
		Males				
Length of forearm	0.0072	4.8	−0.0088	6.3	−0.0264	15.8
Greatest length of skull	−0.0204	6.8	−0.0032	1.0	−0.0411	12.2
Condylobasal length	−0.0199	6.0	−0.0479	14.5	−0.0307	8.2
Palatal length	0.0408	5.0	0.1000	12.4	0.0613	6.7
Depth of braincase	0.0319	4.6	0.0884	12.6	0.0289	3.7
Zygomatic breadth	0.0095	1.9	−0.0386	7.1	−0.0435	7.1
Breadth of braincase	0.0665	9.1	0.0380	5.3	−0.0050	0.6
Mastoid breadth	−0.0148	2.4	0.0130	2.1	−0.0262	3.7
Postorbital breadth	−0.0995	6.9	0.2331	16.4	−0.2212	13.6
Length of maxillary toothrow	0.2049	23.5	−0.0121	1.4	−0.0051	0.5
Rostral width at canines	−0.0376	3.0	−0.1400	10.9	0.0440	3.0
Breadth across upper molars	0.0883	10.8	−0.0482	5.9	−0.0089	1.0
Mandibular length	0.0716	15.4	0.0192	4.1	0.1275	24.1
		Females				
Length of forearm	0.0151	9.2	−0.0325	8.4	0.0088	2.6
Greatest length of skull	0.0197	6.0	0.1546	19.2	−0.1887	27.0
Condylobasal length	−0.0415	11.1	−0.2381	26.2	−0.0696	8.9
Palatal length	0.0486	5.3	0.0965	4.3	0.0566	3.0
Depth of braincase	−0.0233	2.9	0.0737	3.9	0.1341	7.4
Zygomatic breadth	0.0467	7.6	0.0990	6.6	−0.0830	6.4
Breadth of braincase	−0.0278	3.4	0.0006	0.1	−0.0909	5.3
Mastoid breadth	−0.0361	5.0	0.0257	1.5	−0.0385	2.6
Postorbital breadth	0.0662	4.1	−0.2989	7.7	0.1967	5.8
Length of maxillary toothrow	0.1551	15.7	0.2197	9.3	−0.0719	3.5
Rostral width at canines	−0.0189	1.3	−0.3608	10.1	−0.0120	0.4
Breadth across upper molars	0.0757	8.3	−0.0546	2.5	0.0280	1.5
Mandibular length	0.1067	20.2	0.0051	0.4	0.2836	25.6

the bases of the hair, which vary from whitish to reddish and yellowish white. Some authors (Goodwin, 1933; Sanborn, 1941; Buden, 1977) believed that variation in color in *Brachyphylla* followed a geographic pattern. Basically, they felt that the underfur of specimens from Hispaniola was more distinctly white than in specimens from Cuba, Puerto Rico, and Lesser Antilles. They also stated that the tips of the hair were more conspicuously pale brown with reddish or yellowish tones compared to specimens from the remainder of the geographic range of the genus.

We have not been able to detect these differences in the material that we have studied. Specimens on Cuba were mostly grayish brown to dark brown with a buffy or reddish tint but some specimens lacked this tint. The same was true for the underfur, which had a reddish or buffy tint in most individuals but in some it was white. Most of the specimens from Hispaniola corresponded to color standard 1 but 35% matched with color standard 3 as did 37% from Cuba.

On Puerto Rico, Norman Island, and Guadeloupe, specimens matched four of the five color standards, indicating that color variation on these islands nearly spans that found in the entire genus. Specimens from St. John Island and Barbados, recognized as a distinct subspecies, corresponded to three of the color standards.

We have not been able to detect any geographic trends in this variation in color. There appears to be little variation in color and what variation is present can nearly be spanned by individuals from a single island.

Taxonomic Conclusions

We interpret the univariate and multivariate analyses as revealing that the genus *Brachyphylla* represents two species, *Brachyphylla nana* from Cuba, Grand Cayman, Middle Caicos, and Hispaniola, and *B. cavernarum* from Puerto Rico, Virgin Islands, and the Lesser Antilles as far south as St. Vincent and Barbados. The latter species is clearly the larger of the two; the range of some measurements of *B. cavernarum* not overlapping those of *B. nana* in some characters.

It is also worthy of note that no species of parasites are known to be common to both *B. cavernarum* and *B. nana*. However, within *nana*, Cuba and the Dominican Republic share one species of the genus *Trichobius* and within *cavernarum* Guadeloupe and Martinique share a species of *Ornithodoros* (Webb and Loomis, 1977). *B. cavernarum* and *B. nana* do share the streblid genus *Trichobius*, but host different species.

Buden (1977), considering these two species to be conspecific, argued that the size differences between the two allopatric taxa are nearly matched by those found among Middle American populations of *Artibeus jamaicensis*, which were treated as subspecies by Davis (1970). However, these differences are in fact more comparable to size differences seen between *A. jamaicensis* and *A. lituratus* in Central America.

A further argument presented by Buden (1977) for recognizing only one species is that there are no differences in the standard karyotypes of the two taxa. However, when considering the fact that, for example, species included in *Artibeus*, *Sturnira*, *Vampyrops*, and *Myotis* show no intrageneric variation in chromosomal complements (Baker, 1973; Bickham, 1976), this argument is of little value. It should also be pointed out that *Erophylla bombifrons* and *Phyllonycteris poeyi*, both endemic West Indian phyllonycterines, have identical karyotypes (Baker and Lopez, 1970; Nagorsen and Peterson, 1975) to *Brachyphylla*, but no one has considered even placing them in the same genus.

Throughout the remainder of this study, we have considered the genus *Brachyphylla* to be composed of two species—*B. cavernarum* and *B. nana*.

SYSTEMATIC ACCOUNTS

Genus **Brachyphylla**

1834. *Brachyphylla* Gray, Proc. Zool. Soc. London, pp. 122–123, 12 March.

Type species.—Brachyphylla cavernarum Gray.

Definition

Resembles the other phyllonycterines externally in all respects except for having a more stocky build with a shorter snout; lower lip with median groove ridged by papillae; nodular ridges on chiropatagium; calcar absent; five lumbar vertebrae, fifth lacking neural spine; skull relatively long, narrow; upper incisors markedly different in size and shape, inner one large, higher than long, recurved, outer one rounded, minute, flat-crowned; anterior upper premolar minute; posterior upper premolar high and short; crowns of upper and lower molars heavily wrinkled; first lower molar with distinct posterointernal cusp, differing markedly from last premolar; interpterygoid space not extending forward as a palatal emargination; nasal region without emargination; ears small, separate; nose-leaf rudimentary; tail very short if present and wholly enclosed by interfemoral membrane. Dentition, I,2/2; C,1/1; P,2/2; M,3/3 = 32, karyotype 2N = 32, FN = 60.

Ecology

Brachyphylla occupies most of the islands in the Greater and Lesser Antilles. A notable exception is Jamaica from where it is known only from Pleistocene or sub-Recent fossil material. These bats are primarily cave dwelling but have been recorded from an old sugar factory by Bond and Seaman (1958), from an underground unused sugar house by Koopman (1975), and from a large well by Nellis and Ehle (1977). For the observations on roosting sites of *Brachyphylla,* see Allen (1911), Barbour (1945), Goodwin (1933), Gundlach (1877), Miller (1902*b*, 1913), and Nellis and Ehle (1977). The microclimate in the caves inhabited by this bat varies from relatively hot, humid, and stable on Cuba (Silva-Taboada and Pine, 1969) to relatively cool, not too humid, and less stable on Middle Caicos (Buden, 1977).

The diet of *B. cavernarum* is pollen, fruit, and insects (Bond and Seaman, 1958; Nellis, 1971; Gardner, 1977; Nellis and Ehle, 1977) and that of *B. nana* is fruit, pollen, nectar, and insects (Silva-Taboada and Pine, 1969; Gardner, 1977). Indications are that *B. cavernarum* is a good thermoregulator (McManus and Nellis, 1972). Nellis and Ehle (1977), however, noted that the body temperature of the young, in contrast to adults, seemed to be lowered during sleep.

Only ectoparasites have been reported from the genus *Brachyphylla* (Silva-Taboada and Pine, 1969; Ubelaker et al., 1977; Webb and Loomis, 1977). Webb and Loomis (1977) summarized the ectoparasites known to be found on *Brachyphylla nana* (six species of five genera) and *B. cavernarum* (six species of five genera). No species of parasites are common between *nana* and *cavernarum*. However, two genera, *Ornithodoros* (Argasidae) and *Trichobius* (Steblidae), have been found on both. Two species of *Ornithodoros* have been found on *nana* from Cuba and one on *cavernarum* from Guadeloupe and Martinique. One species of *Trichobius* has been found on each *nana* and *cavernarum*. The same species of *Trichobius* known from Cuba was found also on these bats from the Dominican Republic.

Brachyphylla cavernarum

Distribution

This species occurs on Puerto Rico, the Virgin Islands, and down the Lesser Antillean chain as far as St. Vincent and Barbados.

Diagnosis

Distinguished by large external and cranial size. Various other cranial and dental characteristics suggested in the literature to separate the two species appear to be attributable to individual, age, and secondary sexual variation.

Comparisons

The two species, which occur allopatrically, can be readily distinguished. *Brachyphylla cavernarum* is larger than *Brachyphylla nana,* especially in cranial measurements (Table 1). In length of maxillary toothrow and mandibular length, there is no overlap in measurements between the two species. No overlap in measurements between males of the two species is present in palatal length, breadth across upper molars, greatest length of skull, and condylobasal length. In the latter two characters, overlap of measurements in females occurs only between the sample of *B. cavernarum* from Barbados in the southern Lesser Antilles and samples of *B. nana* in the Greater Antilles.

Geographic Variation

Standard statistics for males and females from geographic samples (9 to 27, Fig. 1) are given in Table 1.

Univariate Analyses

External measurements.—Because of missing data and consequent small or non-existing samples, external measurements, with the exception of forearm length, were not subjected to SS-STP analysis.

Variation in length of forearm for *Brachyphylla cavernarum* shows the population from Barbados

(27) to have the shortest forearm of all samples for both sexes, and those from St. John (11) and Norman (12) islands to be the next smallest-sized. The range of forearm length in males from Barbados does overlap, to a certain extent, with most other populations, except St. Eustatius (16), St. Martin (19), Barbuda (20), and Antigua (21). This was not the case in females where overlap was found only with samples from Puerto Rico (9, 10), St. John (11), Norman (12), Saba (15), and Dominica (23). Males and females from Antigua (21) had on the average the longest forearms for the species. No clinal variation in forearm length was apparent.

Cranial measurements.—The 12 cranial measurements analyzed are discussed below in three groups—1) five measurements dealing with length of the skull (greatest length of skull, condylobasal length, palatal length, length of maxillary toothrow, and mandibular length); 2) six measurements dealing with breadth of the skull (zygomatic breadth, breadth of braincase, mastoid breadth, postorbital breadth, rostral width at canines, breadth across upper molars); 3) one measurement dealing with depth of the skull (depth of braincase).

Geographic variation in greatest length of skull for *Brachyphylla cavernarum* also shows, as for forearm length, the population from Barbados (27) to be the smallest in size. The range of this measurement in the Barbados population was clearly lower than that found in samples from the remainder of the geographic range of the species. The male Barbados sample showed range overlap in greatest length of skull only with samples from St. Lucia (25), Dominica (23), Guadeloupe (22), Antigua (21), Puerto Rico (9, 10), St. John (11), and Norman (12) and females showed overlap only with samples from St. Lucia (25), Martinique (24), Guadeloupe (22), Puerto Rico (9, 10), St. John (11), and Norman (12). In both sexes there was no overlap in this measurement between the Barbados sample and the nearest population, St. Vincent (26). However, in both sexes overlap was found between measurements of specimens from Barbados and the next to the nearest population, St. Lucia (25). In both sexes, the two samples from Puerto Rico (9, 10) are grouped with those from St. John (11) and Norman (12), being the next four smallest-sized samples. These four areas are, however, at the opposite end of the geographic range of the species from Barbados. The one specimen examined from St. Thomas has a greater skull length than the means observed for the four samples discussed above (9 to 12), but it falls within the range of observed measurement in these samples and because of its geographic position, it is thought to be grouped best with the samples from Puerto Rico, St. John, and Norman. The one male specimen examined from Montserrat (17) corresponds in greatest length of skull to surrounding localities. The sample of males from Barbuda (20) has the largest mean for this character. The one female specimen examined from Anguilla (18) was larger in greatest length of skull than the means of all other samples and above the upper range of this measurement in some samples. The population of females from St. Croix (14) had the longest skull. As in forearm length, no geographic cline in this measurement was apparent. In both sexes, samples from Barbados, Puerto Rico, and the Virgin Islands, although overlapping, tend to be grouped in subsets showing a break with the others.

Variation in condylobasal length of *Brachyphylla cavernarum* follows basically the pattern of variation found in greatest length of skull.

Palatal length displays a pattern of variation somewhat different from the two previous measurements of length. In males the sample from Barbados (27) is again the smallest with the next smallest two being the samples from Puerto Rico (9, 10). However, the palate in the samples from St. John (11) and Norman (12) is relatively much longer. In females this is only true for the sample from Norman (12). The one from St. John (11) is in fact the smallest in size of all samples. The only other measurement in which the population from Barbados (27) was not the smallest is in postorbital breadth for males. The mean palatal length for females from Saba (15) falls between those of Puerto Rico and St. John on the one hand and Norman on the other. Fairly broad overlap in palatal length was found between the different samples of the species. This is also evident from the SS-STP analyses where four broadly overlapping subsets in males and three in females are evident.

Variation in length of maxillary toothrow is essentially the same as for greatest length of skull. However, a somewhat broader overlap of subsets occurs.

The pattern of variation displayed in mandibular length is essentially the same as for greatest length of skull. However, the four subsets in which the female sample means fall overlap much more extensively than in greatest length of skull. The means of the female samples from Saba (15) and Montserrat (17) fall among the means of the populations from Puerto Rico (9, 10), St. John (11), and Norman (12).

The pattern of variation displayed in zygomatic breadth of *Brachyphylla cavernarum* is essentially the same as for greatest length of skull. However, in the males the population from St. Vincent (26) falls within the grouping of populations from Puerto Rico (9, 10), St. John (11), and Norman (12), whereas in greatest length of skull it was just slightly longer than the means of these populations. In females, samples from Martinique (24) and Montserrat (17) displayed a relatively narrow zygomatic breadth, falling within the range of means exhibited by the populations from Puerto Rico, St. John, and Norman. Because of broadly overlapping subsets in females, this could be due to random variation. In males, there is less overlap and an indication of a break between the Virgin Islands and the Lesser Antilles is evident as it was for both sexes in greatest length of skull. The samples from Barbados (27) again averaged the smallest in size for the species.

Variation in breadth of braincase is essentially as in greatest length of skull, with somewhat wider overlap of subsets. It also differs in that the male sample from Guadeloupe (22) displays a relatively narrower breadth of braincase.

Variation in mastoid breadth, judged by the broadly overlapping subsets displayed in SS-STP analysis, could perhaps be explained mainly by random variation. However, the population from Barbados (27) still had the narrowest braincase, and the populations from Puerto Rico, St. John, and Norman still tend to group together exhibiting relatively narrow braincases. In males, the one sample from Puerto Rico (10) exhibited a relatively wide braincase.

Variation in postorbital breadth reveals that the populations from Puerto Rico (9, 10), St. John (11), and Norman (12) have a relatively broad postorbital region, falling among the samples with the largest means. The male sample from Barbuda (20) displays the narrowest postorbital breadth of all samples. The female Barbuda (20) sample also averaged relatively narrow for the species but the Barbados (27) population averaged the narrowest. Fairly widely overlapping subsets in both sexes indicate that little variation is present.

The pattern of variation displayed by rostral width at canines shows very much the same pattern observed in most of the characters studied. Specimens from Barbados (27) have the narrowest rostrum with those from Puerto Rico (9, 10), St. John (11), and Norman (12) being relatively narrow as well. The males from Barbuda (20) have the broadest rostrum, whereas in the females from Barbuda (20) it is relatively much narrower, grouping with the smallest-sized samples.

Variation in width across upper molars follows that of rostral width at canines. Four broadly overlapping subsets are exhibited in both sexes.

Variation in depth of braincase shows little geographic variation, exhibiting only two broadly overlapping subsets in both sexes. The samples of both sexes from Barbados (27) still have the shallowest braincase but the Barbuda (20) samples of both males and females also have a relatively shallow braincase in contrast to the situation in most other characters where this sample averaged relatively large-sized.

Multivariate Analyses

Distance phenograms for both males and females generated with the NT-SYS program package are illustrated in Fig. 7. In addition a map (Fig. 8), including values for both sexes, shows the appropriate distance coefficients between the connected samples; in most cases distance coefficients have been given only for contiguous samples. The first three principal components extracted from the principal component analysis are shown for both males and females in Fig. 9. A factor matrix from correlation among one external and 12 cranial measurements for both sexes is given in Table 5. Two-dimensional plots of the first two variates in a canonical variate analysis generated with the Statistical Analysis System (SAS) package are illustrated for males in Fig. 10 and females in Fig. 11. The relative contribution of each original variable to a particular canonical variable is shown in Table 6.

The distance phenogram (cophenetic correlation coefficient, 0.910) for male *Brachyphylla cavernarum* shows the samples falling into five major groups. The first cluster contains samples from Puerto Rico (9, 10), St. John (11), Norman (12), and St. Thomas (13). Specimens from samples in this cluster are of medium size. The second group includes samples from St. Croix (14), Saba (15), St. Eustatius (16), Anguilla (18), St. Martin (19), Antigua (21), Guadeloupe (22), Dominica (23), Martinique (24), St. Lucia (25), and St. Vincent (26). Although this cluster could be divided into two subclusters, the groupings would not be logical on

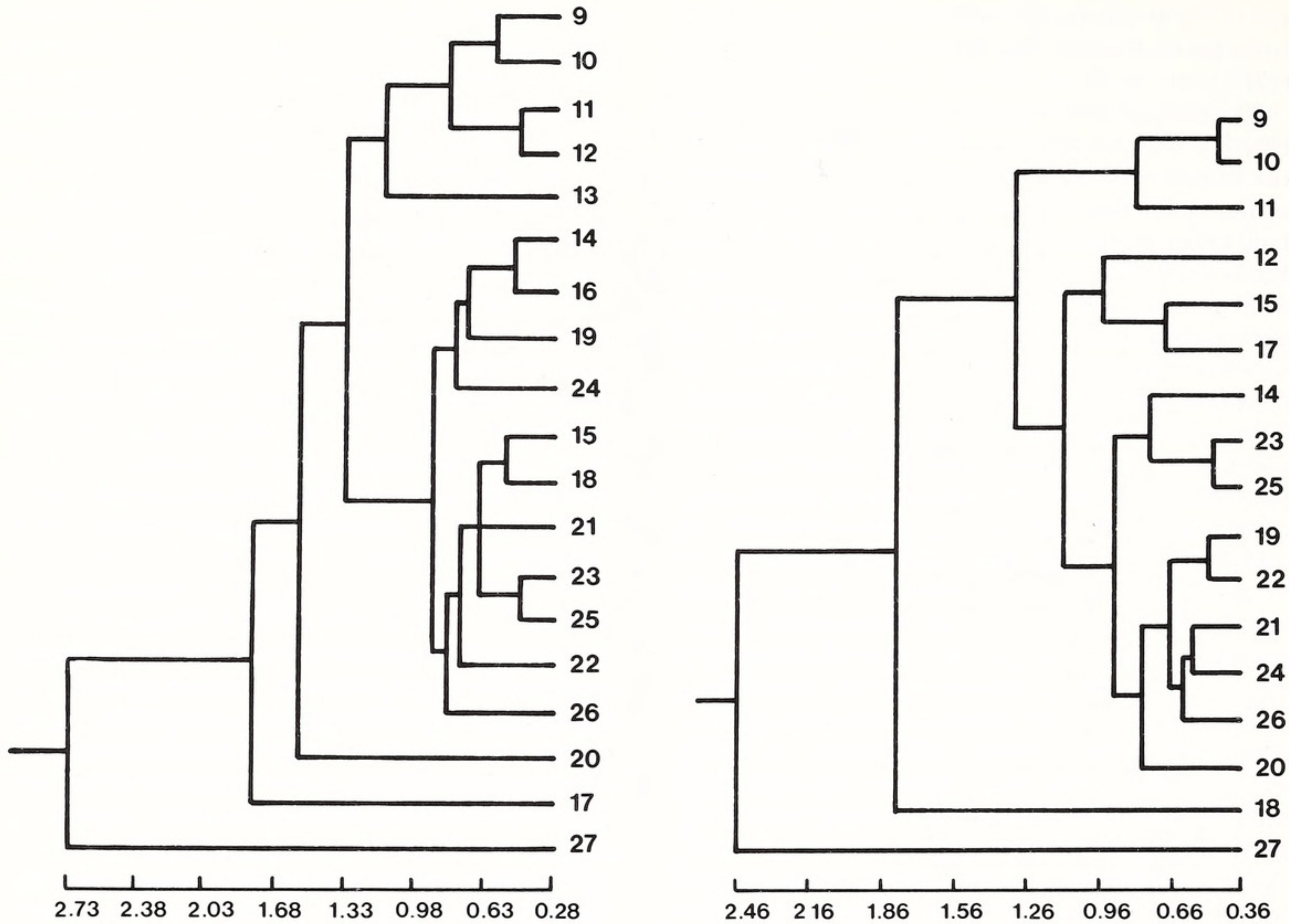

Fig. 7.—Phenograms of numbered samples (see Fig. 1 and text) of *Brachyphylla cavernarum* (males left, females right) computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for males is 0.910 and for females 0.864.

geographical grounds. Groups 3, 4, and 5 include one sample each—Barbuda (20), Montserrat (17), and Barbados (27). The sample of four specimens from Barbuda is large-sized with a relatively narrow postorbital region and shallow braincase. The one specimen from Montserrat (17) is characterized by a long skull that is relatively narrow and shallow. The sample from Barbados consistently averaged among the smallest in size for the species.

The distance phenogram (cophenetic correlation coefficient 0.864) for female *B. cavernarum* reveals the samples falling into five groups. The first cluster consists of samples from Puerto Rico (9, 10) and St. John (11). The second cluster contains samples from Norman (12), Saba (15), and Montserrat (17). The third cluster consists of the following samples: St. Croix (14), St. Martin (19), Barbuda (20), Antigua (21), Guadeloupe (22), Dominica (23), Martinique (24), St. Lucia (25), St. Vincent (26). This cluster could be divided into two subclusters but again this would not be logical on geographic grounds. The fourth and fifth clusters each consist of only one sample each, Anguilla (18) and Barbados (27). The sample from Anguilla consists of only one specimen, which is characterized by a large skull with a relatively shallow braincase. The sample from Barbados, as in the males, is the smallest-sized population within the species.

In both sexes samples from Puerto Rico (9, 10), and St. John (11), group in the one cluster. However, in the case of the males, the sample from Norman (12) is also contained in this cluster, whereas in the females it groups with another cluster, which has no counterpart in the males. This might be indicative of some past gene flow among populations

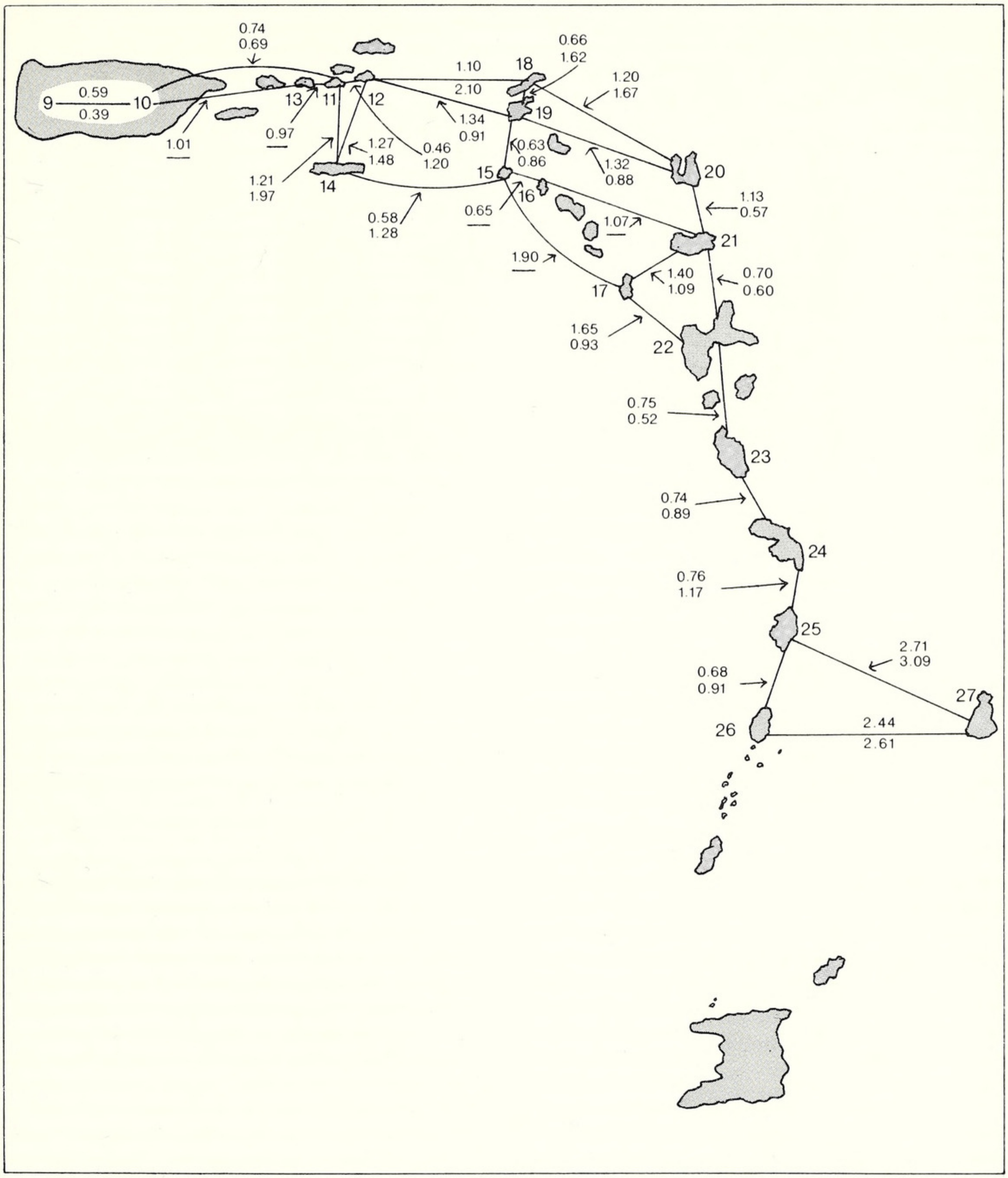

Fig. 8.—Map showing distance coefficients (from distance matrices) between samples of *Brachyphylla cavernarum* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 1 and text for key to samples.

Table 5.—*Factor matrix from correlation among 13 characters of* B. cavernarum *studied, showing characters influencing the first three components.*

Characters	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Length of forearm	0.772	−0.063	−0.341	0.679	−0.069	0.123
Greatest length of skull	0.938	−0.095	−0.178	0.915	−0.136	−0.110
Condylobasal length	0.880	−0.321	−0.064	0.970	−0.116	−0.025
Palatal length	0.826	−0.062	0.005	0.762	0.407	0.247
Depth of braincase	0.409	0.836	−0.068	0.702	−0.078	0.655
Zygomatic breadth	0.930	0.070	−0.150	0.932	0.058	0.186
Breadth of braincase	0.812	0.374	0.049	0.931	−0.009	0.011
Mastoid breadth	0.823	−0.067	−0.276	0.880	−0.248	0.242
Postorbital breadth	−0.121	0.855	−0.405	0.181	−0.949	−0.134
Length of maxillary toothrow	0.839	−0.416	0.156	0.854	0.154	−0.454
Rostral width at canines	0.652	0.414	0.575	0.826	0.106	−0.185
Breadth across upper molars	0.800	0.332	0.398	0.845	0.230	−0.257
Mandibular length	0.854	−0.313	−0.043	0.855	−0.047	−0.258

from Puerto Rico through the Virgin Islands to the remainder of the Lesser Antilles. The population from St. Croix (14), geographically intermediate between the two areas but fairly well isolated from the remainder of the Virgin Islands by a deep channel, do not seem to be instrumental in the relationship. The distinct cluster formed by four male specimens from Barbuda is not matched in the sample of seven females.

The amount of phenetic variation represented in the first three principal components for male and female *Brachyphylla cavernarum*, respectively, was 60.1 and 67.0 for component I, 17.3 and 9.7 for component II, and 7.2 and 7.7 for component III. From the factor analysis it can be seen that in males the first and most important component is heavily influenced by general size; however, depth of braincase showed a relatively low positive value and postorbital breadth a low negative value. This negative influence of postorbital breadth corresponds to what we have seen in the univariate analysis, where this measurement tended to become narrower when others became larger. Component II is influenced by depth of braincase and postorbital breadth. Component III is negatively influenced by length of forearm and postorbital breadth and positively by rostral width at canines and breadth across upper molars. In females, component I is heavily influenced by all characters except postorbital breadth, although not negatively so as in males. Component II is negatively influenced by postorbital breadth. Component III is positively influenced by depth of braincase and negatively by length of maxillary toothrow.

Examination of the three-dimensional plot of the male samples reveals a pattern similar to that of the distance phenogram, whereas in the plot of the female samples the two analyses differ in some ways. The sample of females from Norman (12) clustering in the distance phenogram with samples from Saba (15) and Montserrat (17), appears in the three-dimensional plot to be closer to samples from Puerto Rico (9, 10). Samples from St. Croix (14) and St. Lucia (25) form a distinct cluster in the three-dimensional plot but this is not evident in the distance phenogram. In both the distance phenogram and principal component analysis the samples from Anguilla (18) and Barbados (27) form their own clusters.

In both male and female *Brachyphylla cavernarum*, a MANOVA showed that there were significant ($P < 0.0001$) morphological differences among samples in all four statistical tests (Hotelling-Lawley's Trace, Pillai's Trace, Wilks' Criterion, and Roy's Maximum Root Criterion) utilized. Among individual measurements only depth of braincase in males showed no significant differences among samples. In the univariate analysis of depth of braincase, two broadly overlapping subsets resulted from the SS-STP analysis in both males and females, also suggesting little variation in this measurement between different samples of *Brachyphylla cavernarum*.

The amount (percentage) of phenetic variation represented in the first three canonical variates for male and female *Brachyphylla cavernarum*, respectively, was 53.7 and 33.0 for variate I, 15.1 and 23.1 for variate II, and 8.3 and 15.0 for variate III. Com-

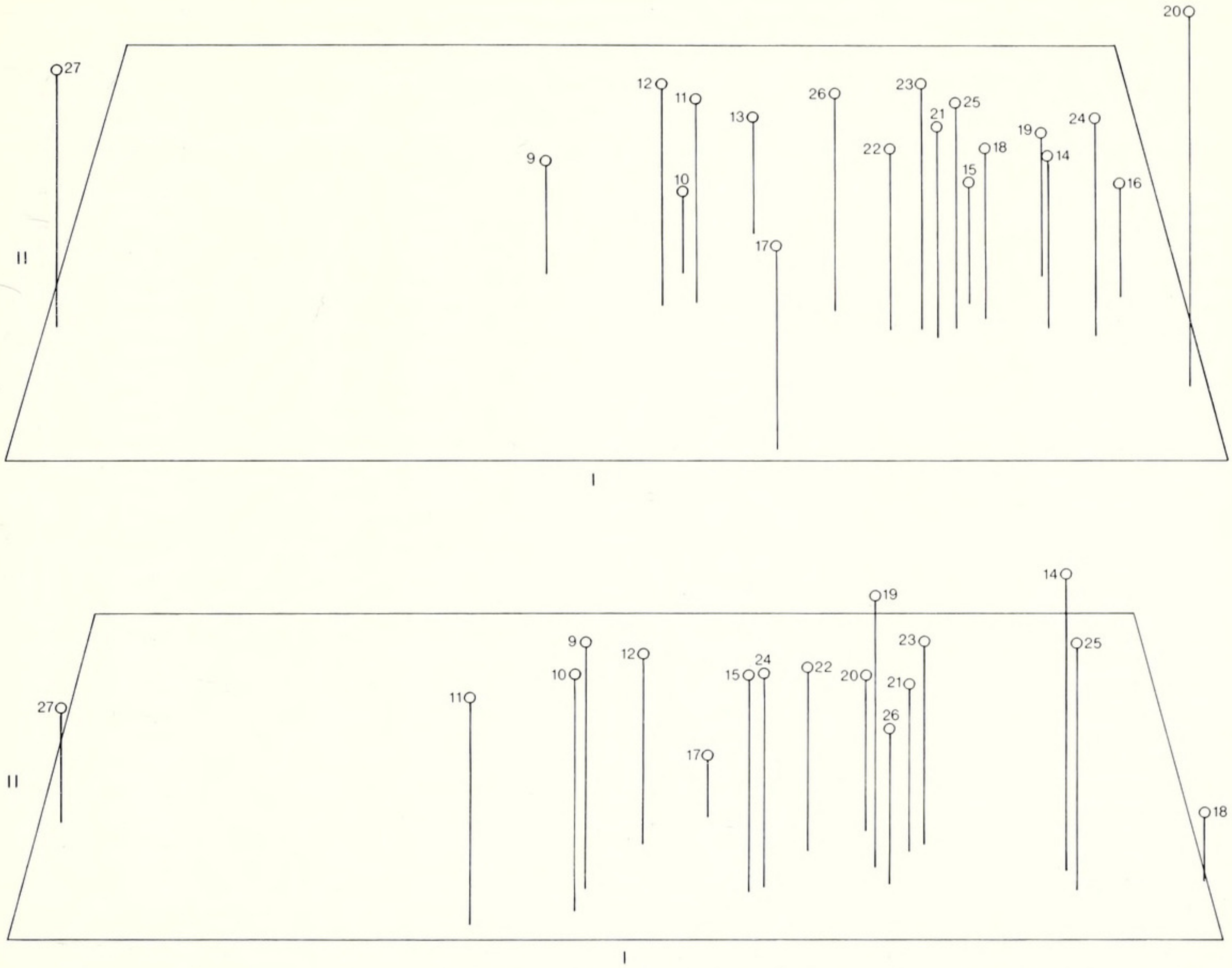

Fig. 9.—Three-dimensional projections of samples of *Brachyphylla cavernarum* (males above, females below) onto the first three principal components based on matrices of correlation among one external and 12 cranial measurements. Components I and II are indicated in the figure and component III is represented by height. See Fig. 1 and text for key to samples.

bined these variates express 77.1% in males and 71.1% in females. In both males and females it took all 13 canonical variates to explain all the variation. The relative contributions of each character to the first three canonical variates in males and females are given in Table 6.

Separation on the first variate in males is heavily (10%) influenced by greatest length of skull, postorbital breadth, length of maxillary toothrow, and mandibular length, and in females by condylobasal length and mandibular length. The second variate in males is heavily (10%) influenced by length of forearm, greatest length of skull, length of maxillary toothrow, and mandibular length, and in females by condylobasal length, length of maxillary toothrow, and rostral width at canines. The third variate in males was most heavily influenced (10%) by condylobasal length, breadth of braincase, and mandibular length. In females length of forearm, condylobasal length, zygomatic breadth, and length of maxillary toothrow contributed more than 10% to the separation of the samples on the third variate.

Examination of the two-dimensional canonical variate plot of the 19 male samples generally reveals a pattern of variation similar to that found in the distance phenogram and principal component analysis. On the first variate, three groups are evident. The one at the top consists of only one sample (Barbuda, 20), one at the bottom consists of the Puerto Rican samples (9, 10), and the main group in the middle includes all other samples, including the one specimen from Montserrat (17), which in both the

Table 6.—*Eigenvalues of canonical variates showing the percentage influence among 13 characters of* B. cavernarum. *Eigenvalues shown represent the normalized vector coefficient of each character.*

Character	Vector I Eigenvalue	Vector I Percent influence	Vector II Eigenvalue	Vector II Percent influence	Vector III Eigenvalue	Vector III Percent influence
Males						
Length of forearm	−0.0066	2.3	0.0285	11.2	0.0136	4.3
Greatest length of skull	−0.0642	10.3	0.0929	17.7	0.0360	5.9
Condylobasal length	−0.0351	5.0	−0.0293	4.9	−0.2016	29.3
Palatal length	0.0117	0.7	−0.0897	6.5	0.0126	0.8
Depth of braincase	0.0303	2.0	−0.1117	9.0	0.0535	3.6
Zygomatic breadth	−0.0218	2.0	0.0594	6.1	0.0151	1.3
Breadth of braincase	0.0926	6.0	0.0140	1.1	−0.1604	10.5
Mastoid breadth	−0.0897	6.9	0.0038	0.4	−0.0586	4.5
Postorbital breadth	−0.4782	15.5	0.1109	4.2	0.1826	6.0
Length of maxillary toothrow	0.3126	29.9	0.2143	24.1	−0.0534	3.1
Rostral width at canines	0.0187	0.7	0.0359	1.6	−0.0762	2.9
Breadth across upper molars	0.0421	2.5	0.0289	2.0	0.1257	7.5
Mandibular length	0.1587	16.3	−0.0933	11.3	0.1751	18.2
Females						
Length of forearm	0.0362	8.6	0.0264	4.8	0.0363	11.5
Greatest length of skull	−0.0152	1.7	0.0998	9.0	0.0348	5.5
Condylobasal length	0.2787	28.9	−0.3084	24.5	−0.1641	22.7
Palatal length	−0.0976	4.3	0.1219	4.1	−0.1068	6.3
Depth of braincase	−0.1637	8.0	0.0329	1.3	−0.0750	4.1
Zygomatic breadth	−0.0618	3.9	0.0987	4.8	−0.1677	14.2
Breadth of braincase	0.1207	5.7	0.2673	9.6	0.0933	5.8
Mastoid breadth	0.0732	4.0	−0.1189	4.9	0.0205	1.5
Postorbital breadth	0.2399	5.7	−0.4875	8.8	0.0208	0.6
Length of maxillary toothrow	−0.0988	4.0	0.3853	11.8	0.3602	19.2
Rostral width at canines	0.3576	9.4	−0.0586	11.9	−0.0147	0.5
Breadth across upper molars	−0.0425	1.8	0.0085	0.3	−0.0165	0.9
Mandibular length	−0.1880	14.0	−0.0728	4.2	−0.0625	6.2

distance phenogram and principal component analysis is clearly separated from the other samples. On the second variate the population from Barbados (27) is well separated, showing one standard deviation overlap only with the samples from St. John (11) and Norman (12). The sample from St. John (11) is somewhat removed on the first variate from the middle cluster and shows some overlap with the western Puerto Rican sample (9) at the bottom. The Norman population (12) falls between the Barbados sample (27), and the main cluster of samples. At the right of the plot, the sample from Antigua (21) shows some separation from the main cluster on the second variate.

Examination of the two-dimensional canonical variate plot of 16 female samples onto the first two variates reveals a pattern of variation generally similar to that found in the distance phenogram and the principal component analyses. Two main groups of samples are evident on the first variate. The one at the bottom consists of only one sample (Barbados, 27) and the group at the top contains the remainder of the samples. The eastern Puerto Rican (10), St. John (11), and Norman (12) populations are clearly separated from the main cluster on the second variate. None of these three sample means are included within a one standard deviation range of any of the other samples nor do their ranges (1 SD) include means of any other samples. The western Puerto Rican sample (9) overlaps extensively with the main cluster, whereas a clear separation from the main cluster and a grouping with eastern Puerto Rico (10), St. John (11), and Norman (12) is illustrated in the distance phenogram and principal component analyses. The sample of two specimens from Montserrat (17) forms a subgroup somewhat removed from the main group on the first variate to the top of the plot and overlaps with the one standard deviation range of the samples from Martinique (24) and St. Lucia (25). At the right of the plot, a sub-

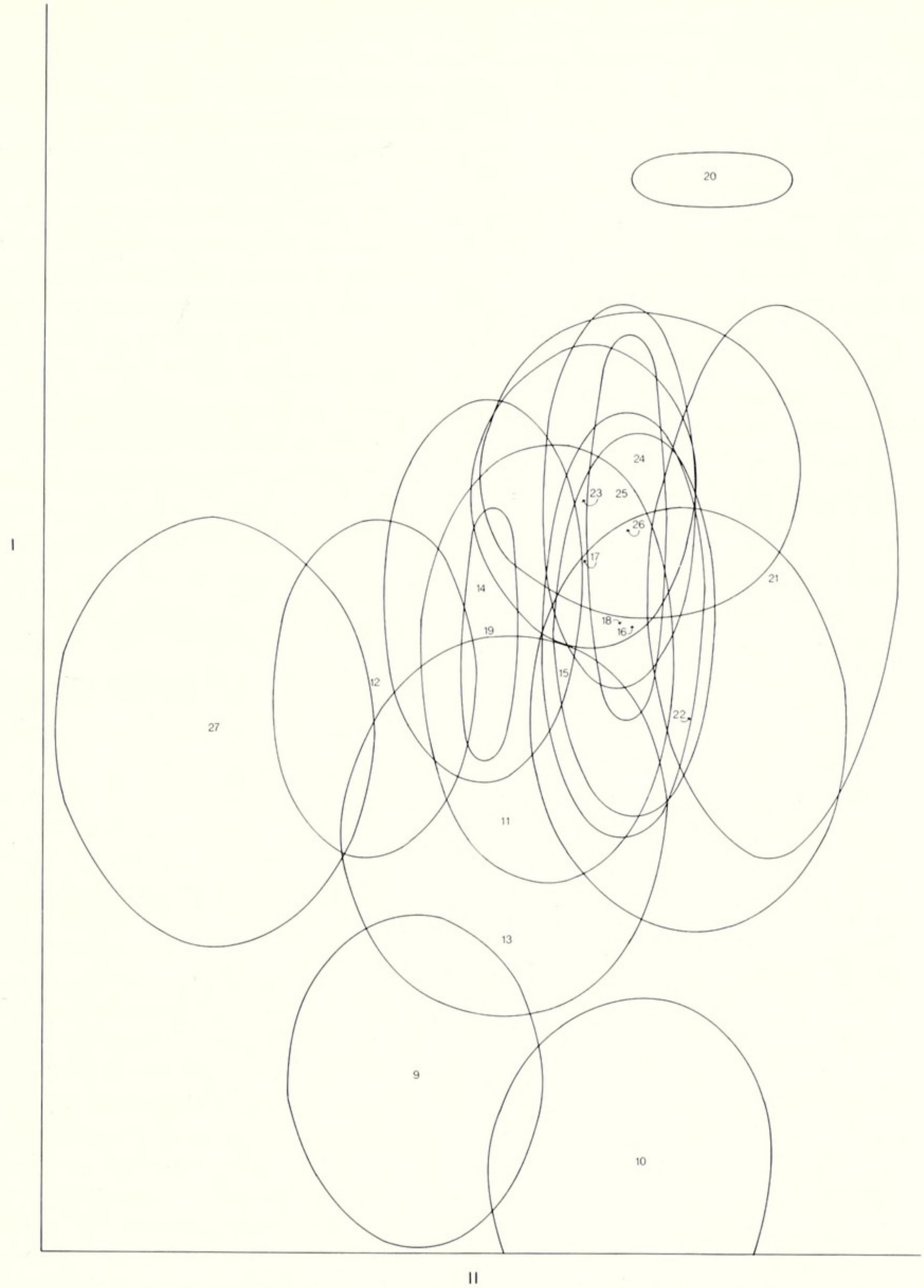

Fig. 10.—Two-dimensional projection of male samples (mean and one standard deviation) of *Brachyphylla cavernarum* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

group separated on the first variate, with no counterpart in the other multivariate analyses, is formed by samples 15 (Saba) and 20 (Barbuda). The means of these two samples fall outside the one standard deviation range of all other samples.

Taxonomic Conclusions

Based upon our assessment of geographic variation in *Brachyphylla cavernarum,* we believe there are three identifiable populations. The smallest individuals in the species, and phenetically the most

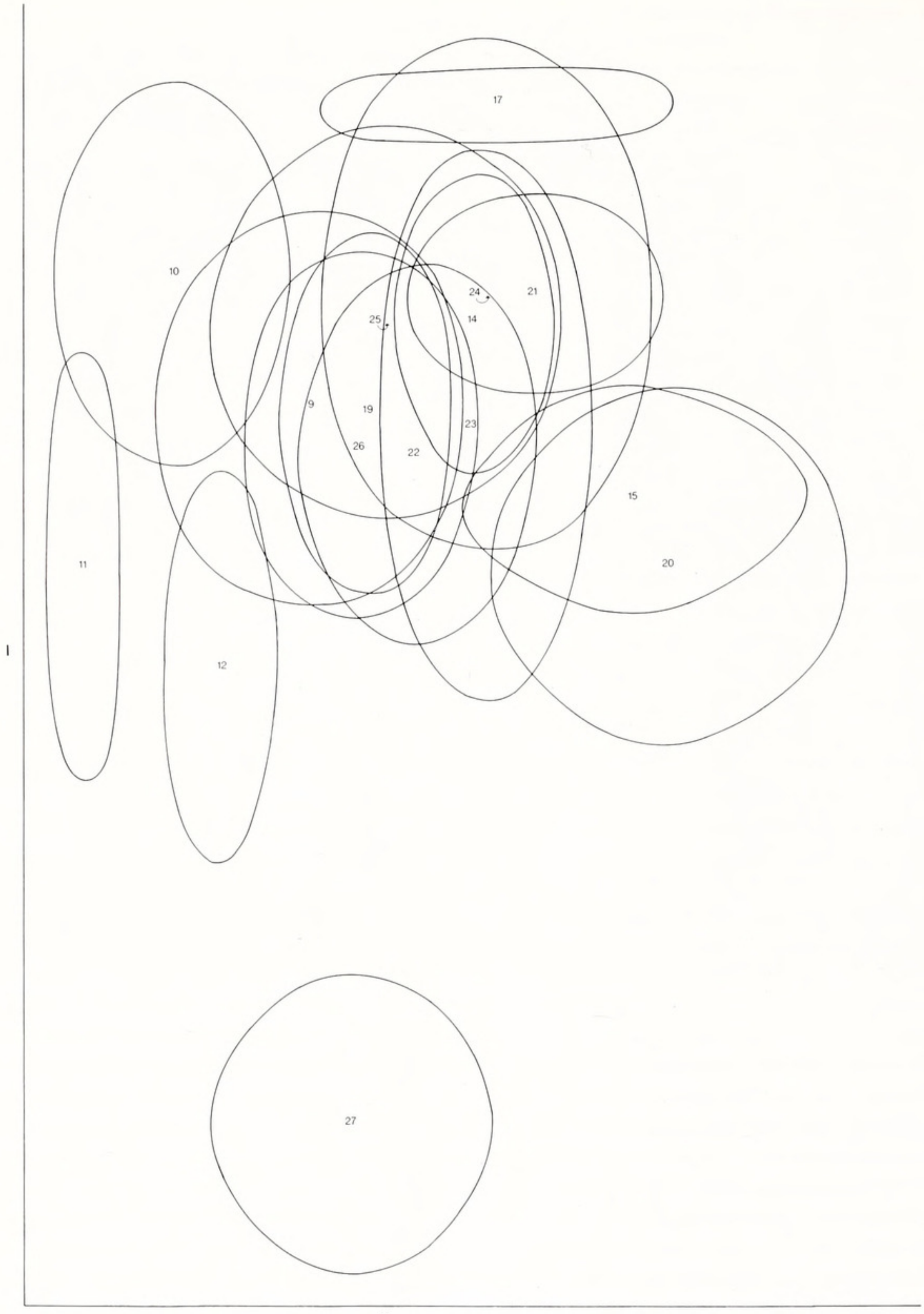

Fig. 11.—Two-dimensional projection of female samples (mean and one standard deviation) of *Brachyphylla cavernarum* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

distinct, occur on Barbados and the name *Brachyphylla cavernarum minor* Miller, 1913, applies to them. The nominate subspecies, *Brachyphylla cavernarum cavernarum*, representing the largest individuals of the species, occurs on St. Croix in the Virgin Islands and Anguilla southward through the Lesser Antilles to St. Vincent. A third subspecies, which is characterized by intermediate size and is described herein as new, occurs on Puerto Rico and most of the Virgin Islands (St. John, Norman, and St. Thomas excluding St. Croix). This subspecies is not distinguished by any one single character but its overall size as measured in multivariate analyses indicates that 80% to 90% of the individuals in this population are distinguishable from Lesser Antillean populations. The population from Barbuda may represent a phenetically identifiable population and, therefore, may represent a separately evolving lineage. However, because our data are inconclusive, we have thought it best not to recognize this population for the time being.

Brachyphylla cavernarum cavernarum Gray, 1834

1834. *Brachyphylla cavernarum* Gray, Proc. Zool. Soc. London, p. 123, 12 March.

Lectotype.—Adult male, in alcohol with skull not removed, BMNH 77.2746, from St. Vincent, Lesser Antilles, obtained by L. Guilding.

Measurements of lectotype.—Length of forearm, 65.5.

Distribution.—Known from St. Croix in the Virgin Islands and Anguilla southward through the Lesser Antilles to St. Vincent.

Comparisons.—The nominate subspecies can be distinguished from *minor* and *intermedia* by its larger overall size (see also Comparisons under *B. c. intermedia*).

Remarks.—*Brachyphylla cavernarum cavernarum* is a large-sized subspecies potentially in contact with the medium-sized *B. c. intermedia* in the north on the Virgin Islands and Puerto Rico, and to the southeast with the small-sized *B. c. minor* from Barbados. The only indication of possible past contact between *cavernarum* and *intermedia* was the grouping of samples of females from Norman Island, Saba, and Montserrat in the female distance phenogram. There is no evidence for intergradation between these two subspecies through the population on St. Croix. This population is clearly related to *B. c. cavernarum*.

If there is intergradation between *cavernarum* and *minor*, it is probably through the population to the northwest of Barbados on St. Lucia rather than the population to the west on St. Vincent. In greatest length of skull (both sexes), condylobasal length (females), breadth across upper molars (males), and mandibular length (males) there was no overlap in the range of measurements between populations on Barbados and St. Vincent; however, there was overlap in both sexes between Barbados and St. Lucia populations.

In the original description Gray listed two cotypes, a male and a female, from St. Vincent. Gray (1838) again stated that this species is known only from St. Vincent. In listing the mammalian specimens present in the collection of the British Museum, Gray (1843) indicated that at that time an additional specimen from Cuba, presented by W. S. MacLeay, was in the collection. From the above it is clear to us that this female specimen from Cuba was not available to Gray when he described *B. cavernarum*. Therefore, Dobson (1878) incorrectly listed this specimen from Cuba as the holotype. Dobson does list a male from St. Vincent and a female from the "West Indies," which may represent the cotypes.

The female paralectotype mentioned by Gray (1834) could not be located in the British Museum (Natural History) collection. The specimen presumably has been destroyed or was exchanged with another institution sometime in the past. However, according to John Edwards Hill (*in litt*., 16 November 1977) "There are in the collections male and female specimens of *B. cavernarum* BM(NH) 7.1.1. 701-702, that came here from the collection of R. F. Tomes. The documentation indicates that Tomes obtained these from the Zoological Society of London and there is every probability that these, too, are from the original series. Both are in good condition: the male is BM(NH) 7.1.1. 701, the female BM(NH) 7.1.1. 702."

Specimens examined (206).—St. Croix: Sion Hill, 11 (AMNH); no specific locality, 6 (4 AMNH, 2 AS). Saba: Bat hole near Land Point, 2 (RMNH); Ladderberg, 6 (RMNH); Windwardside, 1 (AMNH); no specific locality, 2 (RMNH). St. Eustatius: rim of The Quill, 2 (AMNH); no specific locality, 1 (MCZ). Montserrat: no specific locality, 5 (USNM). St. Martin: Lowlands, 16 (AMNH). Barbuda: no specific locality, 12 (USNM). Anguilla: Island Harbor, Fountain Cave, 7 (AMNH); Valley, 3 (AMNH). Antigua: 1 mi E English Harbor, 1 (KU); St. Paul Parish, 2 (FMNH); no specific locality, 17 (3 BMNH, 14 USNM). Guadeloupe: 2 km S, 2 km E Baie-Mahault, Basse-Terre, 1 (TTU); 2 km N Baillif, Basse-Terre, 1 (TTU); 1 km S Basse-Terre, Basse-Terre, 1 (TTU); 1 km S, 4 km W Vernou, Basse-Terre, 1 (TTU); 1 km W Vernou, Basse-Terre, 1 (TTU); 1 km N, 1 km W St. François, Grand-Terre, 27 (TTU); no specific locality, 1 (MCZ). Dominica: Clarke Hall Estate, 100 ft, St. Joseph Parish, 10 (KU); 6 mi NE Roseau, St. Paul Parish, 2 (AS); no specific locality, 6 (1 AS, 5 USNM). Martinique: Bellefontaine, 2 (AMNH); Casé Pilote, 5 (AMNH); 6 km E La Trinité, 4 (AMNH); no specific locality, 9 (1 AMNH, 8 MCZ). St. Lucia: no specific locality, 20 (USNM). St. Vincent: Clifton Hill, 400 ft, St. George Parish, 2 (KU); Kingstown, 150 ft, St. George Parish, 1 (KU), no specific locality, 18 (3 BMNH, 15 USNM).

Brachyphylla cavernarum intermedia,
new subspecies

Holotype.—Adult female, skin, skull, and skeleton, CM 44707; from 1 mi W Corozal, Puerto Rico; obtained by R. J. Baker on 22 July 1969, original no. 1375. Skin, skull, and body skeleton in good condition.

Paratypes.—Two adult males and one adult female, skin, skull, and skeleton, TTU 9819, CM 44708, and TTU 9820; from 1 mi W Corozal, Puerto Rico; obtained by R. J. Baker on 21 July 1969, original nos. S. L. Williams 319, 321, and 320, respectively. Skins, skulls, and body skeletons in good condition.

Measurements.—External and cranial measurements of the holotype and paratypes, respectively, were as follows: total length, 86, 93, 87, 91; length of hind foot, 18, 17, 16, 15; length of ear, 20, 22, 21, 21; length of forearm, 66.5, 66.6, 66.5, 68.0; greatest length of skull, 32.1, 32.1, 32.7, 32.0; condylobasal length, 28.9, 28.4, 28.9, 28.6; palatal length, 12.0, 12.4, 11.8, 11.7; depth of braincase, 13.7, 13.6, 13.8, 13.6; zygomatic breadth, 17.6, 17.5, 17.4, 17.5; breadth of braincase, 12.6, 12.6, 12.9, 12.7; mastoid breadth, 15.0 15.0, 14.9, 14.9; postorbital breadth, 6.5, 6.4, 6.6, 6.6; length of maxillary toothrow, 10.8, 10.8, 10.7, 10.7; rostral width at canines, 7.1, 7.2, 7.5, 7.0; width across upper molars, 12.1, 11.6, 11.8, 11.5; mandibular length, 20.5, 20.5, —, 20.3.

Distribution.—Puerto Rico and Virgin Islands (excluding St. Croix).

Comparisons.—*Brachyphylla cavernarum intermedia* is distinguished from *Brachyphylla cavernarum cavernarum* by its smaller cranial size. From *B. c. minor,* with which it is not potentially in contact, *B. c. intermedia* differs in being larger, both externally and cranially (see Tables 1 and 2). Specimens herein referred to *B. c. intermedia* previously have been reported as *B. c. cavernarum*. No overlap was found in sample means of either sex among *intermedia, cavernarum,* and *minor* in one measurement (range of means in *intermedia, cavernarum,* and *minor,* respectively)—greatest length of skull (males, 31.4–31.7, 31.9–32.4, 30.5; females, 31.0–31.5, 31.6–32.3, 30.5). In length of maxillary toothrow (males, 10.6–10.8, 10.9–11.3, 10.6; females 10.7, 10.8–11.1, 10.5) overlap was observed in sample means of males of *minor* and *intermedia* only. Overlap in sample means of only one of the sexes among the three subspecies is present in condylobasal length (males, 28.0–28.2, 28.4–29.2, 27.1; females, 27.8–28.0, 28.0–28.6, 27.0), breadth of braincase (males, 12.6–12.8, 12.7–13.1, 12.4; females, 12.5–12.6, 12.7–13.0, 12.3), breadth across upper molars (males, 11.5–11.6, 11.7–12.0, 11.1; females, 11.2–11.7, 11.5–11.9, 11.2), and mandibular length (males, 19.9–20.3, 20.4–20.8, 19.5; females, 19.9–20.1, 20.0–20.7, 19.2).

Remarks.—In our opinion, there are populations of three distinct sizes in *Brachyphylla cavernarum*. The populations on Puerto Rico and most of the Virgin Islands are intermediate in size between the large *B. c. cavernarum* of St. Croix and the Lesser Antilles as far south as St. Vincent and the small-sized population of *B. c. minor,* which is restricted to Barbados. This new taxon, *B. c. intermedia,* is potentially in contact with *B. nana* on the west and *B. c. cavernarum* on the east.

Although *B. c. intermedia* is smaller than *B. c. cavernarum,* it is still distinctly larger than *B. nana* (range of greatest length of skull, male, 30.5–33.0, female, 30.3–32.1 in Puerto Rican samples as compared with 27.2–29.3 and 27.1–29.1 in Hispaniolan samples, see also Table 1). We have seen no evidence to indicate intergradation or hybridization between these taxa. See account of *B. c. cavernarum* for possible intergradation with that taxon and the status of the population on St. Croix.

Coloration in *intermedia* is generally blackish brown, or grayish brown tinted buff, whereas *cavernarum* is mostly blackish brown, with a few grayish brown individuals being found.

Choate and Birney (1968) reported on sub-Recent fossil material from Puerto Rico. The only measurements they took that are comparable to ours in the way they were taken are zygomatic breadth, breadth of braincase, and height of coronoid. In both zygomatic breadth and breadth of braincase, ranges of measurements of Recent material encompass those of the sub-Recent material and the means are very close. However, in the sub-Recent material, height of coronoid process ranged lower in addition to averaging smaller. Anthony (1925) after comparing and measuring fossil and Recent *Brachyphylla* from Puerto Rico could find "no differences worthy of mention." We consider the sub-Recent as belonging to the new subspecies.

Specimens examined (233).—PUERTO RICO: 1.5 km N, 13.5 km E Adjuntas, 1 (LSU); Iglesia de la Mora Comerio, 11 (USNM); 1 mi Corozal, 48 (2 CM, 46 TTU); El Verde Field Station, 2 (TTU); 5 km E Guanica, 1 (LSU); 7.5 km E Guanica, 12 (AS); Pueblo Viejo, 13 (9 AMNH, 4 USNM); Cueva de Fari, San Juan, 7 (UMMZ); Trujillo Alto, 4 (AMNH); La Cueva de Mollfulleda, Trujillo Alto, 13 (USNM); 17.7 km NE Utuado, 7

(AS). St. John: Cruz Bay, 4 (AMNH); Lameshur, 14 (AMNH); ½ mi S, ⅗ mi W Lameshur, 42 (40 KU, 2 TCWC). Norman: west end, 53 (15 AMNH, 36 KU, 2 TCWC). St. Thomas: Botany Bay, 1 (AMNH).

Brachyphylla cavernarum minor Miller, 1913

1913. *Brachyphylla minor* Miller, Proc. Biol. Soc. Washington, 26:32, 8 February.

1968. *Brachyphylla cavernarum minor*, Koopman, Amer. Mus. Novit., 2333:5, 19 July.

Holotype.—Adult female in alcohol with skull removed, USNM 101,528, from Cole's Cave, St. Thomas Parish, Barbados, Lesser Antilles, obtained by P. McDonough on 14 June 1899.

Measurements of holotype.—Total length, 78; length of forearm, 61.5; condylobasal length, 26.3; palatal length, 10.8; depth of braincase, 12.6; zygomatic breadth, 15.8; breadth of braincase, 12.0; mastoid breadth, 13.8; postorbital breadth, 6.1; length of maxillary toothrow, 10.3; rostral width at canines, 6.4; width across upper molars, 11.0.

Distribution.—This subspecies is restricted to Barbados, Lesser Antilles.

Comparisons.—Size small for the species cranially; averaging the smallest-sized sample of *B. cavernarum* in all characters except palatal length for females and postorbital breadth in males.

Remarks.—*Brachyphylla cavernarum minor* is well differentiated and is potentially in contact only with *B. c. cavernarum* and can be distinguished from it by its generally shorter forearm and smaller-sized cranium (see also Comparisons under *B. c. intermedia*). *Brachyphylla c. minor* from Barbados shows no overlap in measurements with both its nearest neighbors, St. Vincent (26) and St. Lucia (25) in condylobasal length (males) and forearm length (females), and no overlap with St. Vincent (26) only, in the following characters: greatest length of skull (males and females); condylobasal length (females); breadth across upper molars (males); and mandibular length (males) (see Table 1).

This taxon was considered to be a distinct species until Koopman (1968) reviewed its status. He presented evidence, and our study supports his findings, that this taxon is distinct but only at the subspecific level. The isolation of the island of Barbados to the east of the main chain of the Lesser Antilles undoubtedly has provided the isolation necessary for the genetic differentiation of this population to occur.

Most of the bats from Barbados have hair yellowish white at the base with dark buffy tinted tips. All these specimens are Albert Schwartz Field Series material and as in the case of the Cuban material from this collection might have been exposed to some bleaching. Other material from Barbados have base of hair white with blackish gray tips, or grayish brown with a buffish tint.

Specimens examined (24).—Barbados: Brighton, 250 ft, St. George Parish, 3 (KU); Cole's Cave, St. Thomas Parish, 6 (5 AMNH, 1 USNM); St. Thomas Parish, 1 (USNM); no specific locality, 14 (11 AS, 1 BMNH, 2 FMNH).

Brachyphylla nana

Distribution

This species occurs on Cuba, Isle of Pines (Varona, 1974), Grand Cayman, Hispaniola, Middle Caicos, and as a Pleistocene or sub-Recent fossil on Jamaica.

Diagnosis

See account for *Brachyphylla cavernarum*.

Comparisons

See account for *Brachyphylla cavernarum*.

Geographic Variation

Univariate Analyses

Standard statistics for geographic samples of *Brachyphylla nana* (samples 1–8, Fig. 1) are given in Table 1.

External measurements.—As in *Brachyphylla cavernarum*, because of missing data and consequent small or nonexisting samples, external measurements except length of forearm, were not subjected to ANOVA and SS-STP analyses. However, in spite of small sample sizes, it is apparent that the sample from the Dominican Republic (8) is relatively smaller sized than the others at least in total length.

Length of forearm of the samples from Middle Caicos (6) and the Dominican Republic (8) is relatively short for the species in both males and females. The small sample size available from the Haitian (7) population makes meaningful conclusions difficult concerning the relationship between the Haitian and Dominican Republic populations. In males, the SS-STP analysis shows that the three samples from Cuba (1, 2, 3) fall in one subset, differing significantly from the second subset, which includes samples from the Dominican Republic (8), Middle Caicos (6), and Cuba (Camagüey, 4). Sample 4 consists of only two specimens and their forearm measurements appear to fall within the normal variation of most Cuban samples. Females do not exhibit such a clearcut break in the SS-STP analysis. Although no clinal trend exists in males from Cuba (1–3), there appears to be an increase in size from the small-sized specimens in Habana Province (1) eastward to Oriente Province (3) in females.

Cranial measurements.—The 12 cranial measurements analyzed are discussed below in three groups—1) five measurements dealing with length of the skull (greatest length of skull, condylobasal length, palatal length, length of maxillary toothrow, mandibular length); 2) six measurements dealing with breadth of the skull (zygomatic breadth, breadth of braincase, mastoid breadth, postorbital breadth, rostral width at canines, breadth across upper molars); 3) one measurement dealing with depth of skull (depth of braincase).

Geographic variation in greatest length of skull for *Brachyphylla nana* males shows no significant differences among the seven samples tested, as revealed by an ANOVA. In females the values for greatest length of skull fall into two broadly overlapping subsets. In both sexes the population from the Dominican Republic (8) has a relatively short skull and the one from Middle Caicos (6) a relatively long one. Female samples from Cuba (1–3) show a clinal trend similar to length of forearm, but male samples follow a reverse trend. The two males from Camagüey Province (4) average large for the species. The one female available from this locality is among the smallest for females in the species.

Variation in condylobasal length in *Brachyphylla nana* follows the pattern of variation for greatest length of skull. In this character, however, the females from Cuba (1, 2, 3) do not show any clinal variation, whereas the males do.

Palatal length displays a pattern of variation differing from the previous two cranial measurements. Male samples from the Dominican Republic (8) and Middle Caicos (6) have on the average the longest palate for the species. Although no significant differences were detected among the samples of females with an analysis of variance test, the Dominican Republic (8) and Middle Caicos (6) samples have on the average relatively long palates for the species. The clinal trend among samples from Cuba (1, 2, 3) is not observed in this character.

There is no significant variation in length of maxillary toothrow in both males and females.

No significant variation in mandibular length is displayed. Although differences among samples could be ascribed to random variation, Middle Caicos (6) and Dominican (8) populations tend to have relatively short mandibles.

Variation in zygomatic breadth essentially follows the pattern of variation for greatest length of skull and condylobasal length. However, no clinal variation is present.

No significant differences in breadth of braincase were detected among samples of both males and females of *B. nana* with analysis of variance tests. There were only slight differences (range of 0.2) among samples in both sexes.

No significant differences in mastoid breadth were detected among samples of males, whereas in females two overlapping subsets were present. In both sexes, it was found that the Dominican Republic (8) population clearly averages narrower than did the Middle Caicos population.

Variation in postorbital breadth for males, falling into two overlapping subsets, shows the Dominican Republic (8) population characterized by a relatively broad postorbital region and those from Cuba (1, 2, 3) and Middle Caicos (6) by relatively narrow postorbital regions. No significant differences were detected among the samples of females.

Rostral width at canines displays a pattern of variation in which the population from the Dominican Republic (8) averages the narrowest and those from Cuba (1, 2, 3) relatively wide, whereas the Middle Caicos (6) population is of intermediate size. In males the means fall into two slightly overlapping subsets. The Dominican Republic (8) and Middle Caicos (6) samples are in one subset and all other samples in the second subset. Overlap between the two occurs only in the Caicos sample. Females fall into four overlapping subsets.

The pattern of variation present in breadth across upper molars for males is essentially the same as that found in both sexes for rostral width at canines. The pattern of variation in breadth across upper molars in females differs in that the mean for females from Middle Caicos is closer in size to those of the Cuban samples than to the Dominican Republic one. The clinal variation found in some measurments for Cuban males is also found in breadth across upper molars.

Variation in depth of braincase in both sexes shows the Middle Caicos (6) population characterized by a relatively deep braincase, and the Cuban and Dominican Republic populations by a relatively shallow braincase. The four female specimens from Haiti have relatively deep braincases.

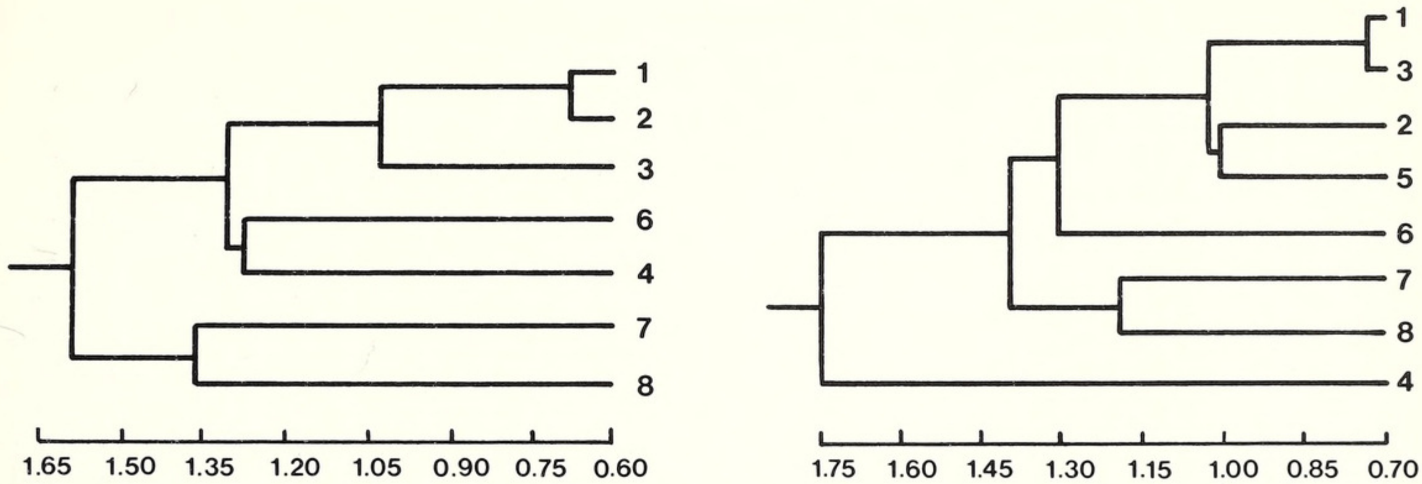

Fig. 12.—Phenograms of numbered samples (see Fig. 1 and text) of *Brachyphylla nana* (males left, females right) computed from distance matrices based on standardized characters and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for males is 0.808 and for females 0.831.

Multivariate Analyses

Distance phenograms for both males and females, generated with the NT-SYS program package, are given in Fig. 12. In addition a map (Fig. 13), including values for both sexes, shows the appropriate distance coefficients between the connected samples; in most cases distance coefficients have been given only for contiguous samples. The first three principal components extracted from the principal component analysis are shown three-dimensionally for both males and females in Fig. 14. A factor matrix from correlation among one external and 12 cranial measurements in both males and females are given in Table 7. Two-dimensional plots of the first two variates in a canonical analysis generated with the Statistical Analysis System (SAS) package are illustrated for males in Fig. 15 and for females in Fig. 16. The relative contribution of each character to the first three canonical variates is shown in Table 8.

The distance phenogram (cophenetic correlation coefficient, 0.808) for male *Brachyphylla nana* shows the samples falling into three major groups. The first cluster contains three samples from Cuba (1, 2, 3). The second cluster contains the samples from Middle Caicos (6), and Camagüey Province, Cuba (4). The two samples in the latter cluster are phenetically quite distinct. The Camagüey sample (4) consists of only two specimens and, as seen in the univariate analysis, they are medium to large sized except in length of forearm and length of maxillary toothrow where they averaged the smallest. The third cluster consists of two phenetically quite

Table 7.—*Factor matrix from correlation among 13 characters of* Brachyphylla nana *studied, showing characters influencing the first three components.*

Characters	Males Component I	Males Component II	Males Component III	Females Component I	Females Component II	Females Component III
Length of forearm	0.316	−0.752	0.047	−0.562	−0.395	0.697
Greatest length of skull	−0.813	0.375	0.277	0.983	0.125	−0.012
Condylobasal length	−0.909	0.160	0.163	0.937	−0.221	0.136
Palatal length	0.073	0.832	−0.426	0.651	0.596	0.156
Depth of braincase	−0.346	0.858	−0.048	0.479	−0.659	−0.168
Zygomatic breadth	−0.889	−0.349	0.093	0.694	−0.058	−0.271
Breadth of braincase	−0.921	−0.113	−0.214	0.485	−0.421	−0.477
Mastoid breadth	−0.181	0.461	0.829	0.730	−0.337	−0.319
Postorbital breadth	0.010	0.617	−0.446	−0.490	0.639	0.268
Length of maxillary toothrow	0.172	0.085	−0.503	0.753	0.215	−0.114
Rostral width at canines	−0.968	−0.209	0.002	−0.013	−0.944	0.107
Breadth across upper molars	−0.930	−0.291	−0.156	0.358	−0.807	−0.251
Mandibular length	0.421	0.237	0.843	0.556	0.200	0.771

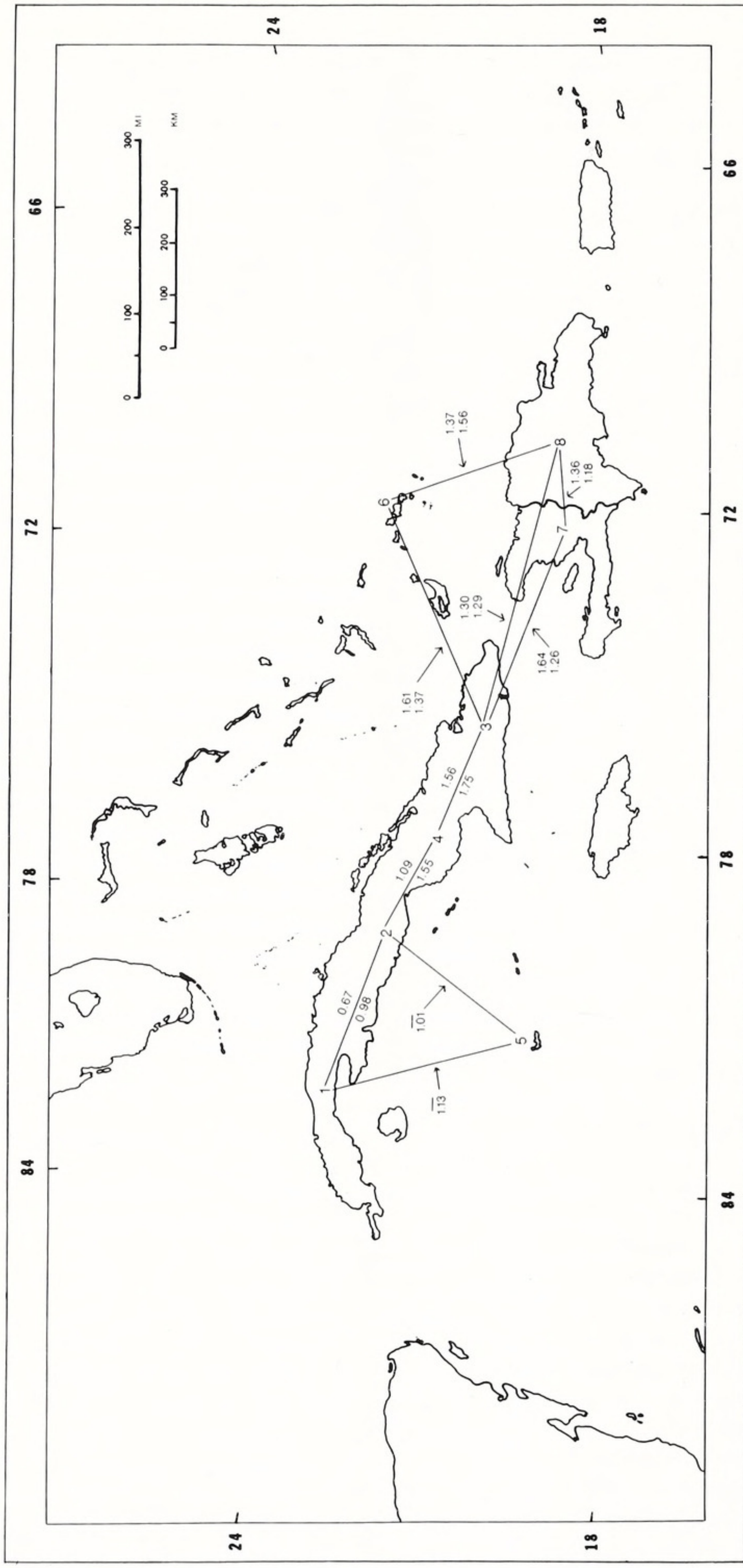

Fig. 13.—Map showing distance coefficients (from distance matrices) between samples of *Brachyphylla nana* that were analyzed in the study of geographic variation. The upper coefficients are for males and the lower for females. See Fig. 1 and text for key to samples.

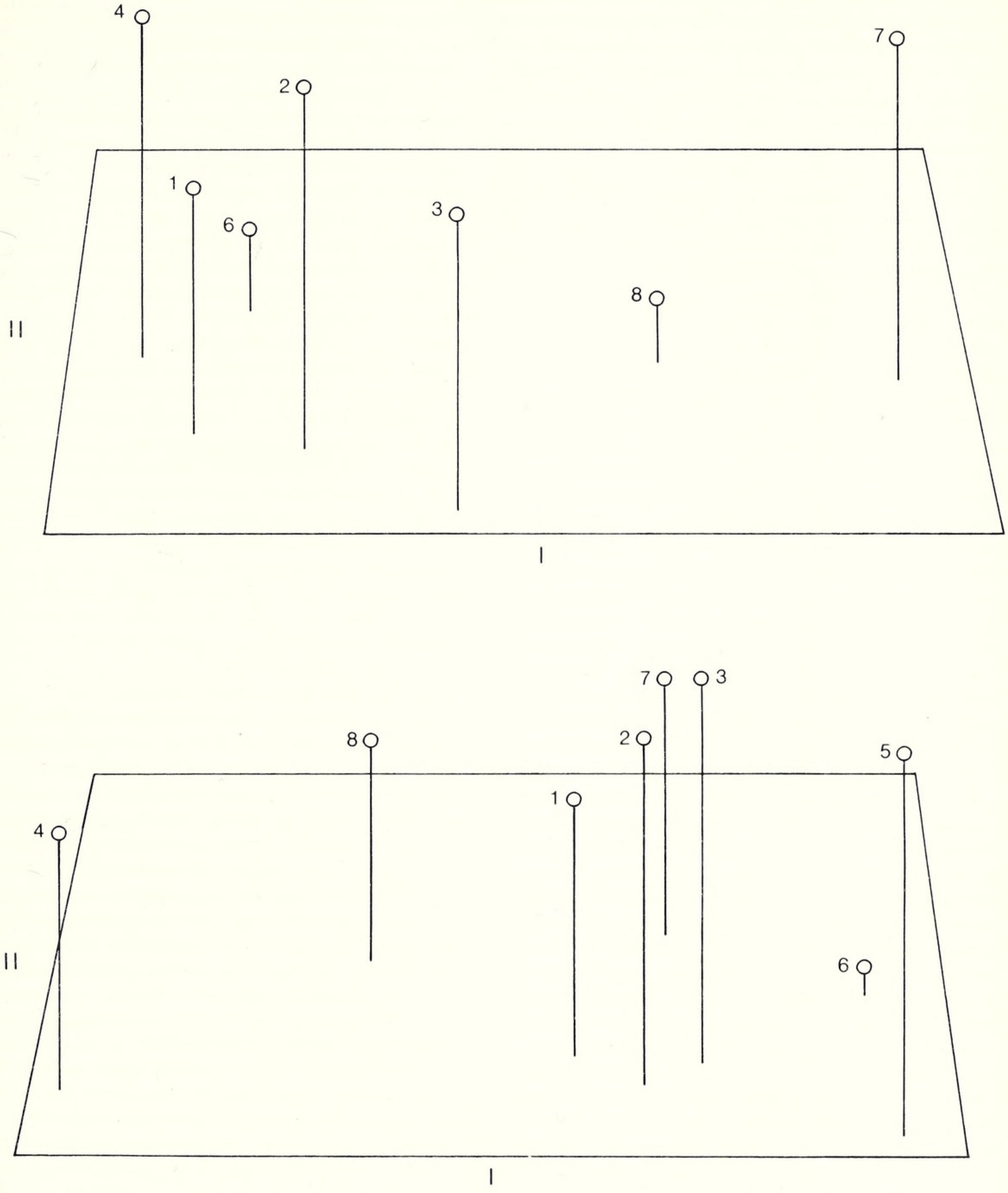

Fig. 14.—Three-dimensional projections of samples of *Brachyphylla nana* (males above, females below) onto the first three principal components based on matrices of correlation among one external and 12 cranial measurements. Components I and II are indicated in the figure and component III is represented by height. See Fig. 1 and text for key to samples.

distinct samples, Haiti (7) and the Dominican Republic (8). The sample from Haiti (7) consists of only one specimen, which varies from relatively small to large in the different measurements taken.

The distance phenogram (cophenetic correlation coefficient, 0.831) for female *Brachyphylla nana* shows the samples falling into four major groups. The first cluster contains samples from Cuba (1, 2, 3) and Grand Cayman (5). The second cluster consists of only one sample, Middle Caicos (6). The third cluster contains the samples from Hispaniola (7, 8). The fourth cluster consists of the sample from Camagüey Province, Cuba (4), and represents a single specimen. This specimen (4) is characterized by a relatively small skull, but its values fall within the range of at least one other Cuban sample.

The distance phenograms of both males and females essentially show the same picture. Samples from Cuba tend to cluster together with the exception of the sample from Camagüey Province (4). Although distantly, the Haitian sample clusters with that from the Dominican Republic. Both male and female distance phenograms show the Middle Caicos samples clustering closer to the Cuban than the Hispaniolan samples, although only distantly so.

The amount (percentage) of phenetic variation represented in the first three principal components for male and female *Brachyphylla nana*, respectively, was 41.5 and 40.8 for component I, 23.7 and 25.7 for component II, and 17.1 and 13.3 for component III. Combined these first three components express 82.3% in males and 79.8% in females. From the factor analysis, it can be seen that characters influencing the different components differ between sexes. In males the first component is heavily negatively influenced by the following characters: greatest length of skull, condylobasal length, zygomatic breadth, breadth of braincase, rostral width at canines, and breadth across upper molars. In females the first component is most heavily influenced positively by greatest length of skull and condylobasal length. In males the second component is heavily positively weighted for palatal length, depth of braincase, and postorbital breadth and negatively for length of forearm. In females a heavy negative weighting was found on component II for rostral width at canines and breadth across upper molars. The third component in males is heavily positively influenced by mastoid breadth and mandibular length. In females the third component is weighted (positive) for length of forearm and mandibular length.

Examination of the three-dimensional plot of the male samples reveals a pattern more or less similar to that of the distance phenogram. The Dominican Republic (8) and the Haitian (7) samples grouped in the lower cluster of the phenogram are shown on the right in the three-dimensional plot, differing from each other on the first and third components. The Middle Caicos (6) and Cuban samples (1, 2, 4) are arranged on the right of the plot with the Oriente Province, Cuba (3) sample falling nearly midway between the samples from the Dominican Republic (8) and Las Villas Province, Cuba (2). This seems to correspond to the conclusion reached in the univariate analysis, where the Cuban samples (1, 2, 3) displayed clinal variation in some measurements, becoming progressively smaller from west to east, with the population from Oriente Province (3) generally approaching the Dominican Republic sample (8) in size.

Examination of the three-dimensional plot of the female samples reveals a pattern with some basic differences from the distance phenogram. The Camagüey Province sample (Cuba, 4) on the left in the three-dimensional plot corresponds to the lower cluster in the distance phenogram. The Dominican Republic sample (8), well removed from sample 4 (Camagüey Province) to the left and the other Cuban (1, 2, 3) and Haitian (7) samples to the right is however, grouped with the Haitian sample (7) in the distance phenogram. The Haitian sample is separated from samples 1, 2, and 3 (Cuba) only on the second component. Therefore, it differs mostly in shape rather than size from the Cuban material. The one specimen from Grand Cayman (5) is grouped with the Cuban (1, 2, 3) populations in the phenogram. It is, however, well separated on the first component in the principal component analysis from these populations. The Grand Cayman specimen is close to the Middle Caicos population on the first component but well separated on the second and third components, suggesting a difference in shape rather than size between the two.

In both male and female *Brachyphylla nana*, multivariate analysis of variance (MANOVA) showed that there were significant ($P < 0.00001$) morphological differences among samples in all four statistical tests (Hotelling-Lawley's Trace, Pillai's Trace, Wilks' Criterion, and Roy's Maximum Root Criterion) utilized. In males the following individual measurements, however, failed to show significant differences among samples: greatest length of skull, breadth of braincase, mastoid breadth, and mandib-

Table 8.—*Eigenvalues of canonical variates showing the percentage influence among 13 characters of* Brachyphylla nana.

	Vector I		Vector II		Vector III	
Character	Eigenvalue	Percent influence	Eigenvalue	Percent influence	Eigenvalue	Percent influence
		Males				
Length of forearm	−0.0354	7.5	0.0767	12.8	−0.0803	14.5
Greatest length of skull	0.0274	2.6	−0.0738	6.1	0.0983	8.4
Condylobasal length	−0.2065	17.7	−0.0125	0.9	0.1004	7.6
Palatal length	0.2340	7.4	−0.1406	3.8	0.0260	0.7
Depth of braincase	−0.0240	1.0	−0.1344	4.6	0.1664	6.0
Zygomatic breadth	−0.0500	2.6	0.2355	10.2	−0.0987	4.5
Breadth of braincase	−0.0825	3.3	0.1709	5.8	−0.2042	7.2
Mastoid breadth	0.0612	2.8	−0.2066	8.1	0.1980	8.1
Postorbital breadth	0.5387	11.5	0.2337	4.2	−0.1181	2.2
Length of maxillary toothrow	0.4703	15.1	0.7122	19.3	0.6221	17.7
Rostral width at canines	−0.2343	5.1	−0.6273	11.6	−0.2832	5.5
Breadth across upper molars	−0.5052	17.5	0.1961	5.7	0.5698	17.5
Mandibular length	−0.0983	6.9	−0.1384	6.9	−0.2081	10.9
		Females				
Length of forearm	−0.1055	11.8	0.0530	6.3	−0.0009	0.2
Greatest length of skull	0.4319	24.0	−0.0344	2.0	0.1146	8.7
Condylobasal length	−0.0382	1.9	−0.5990	30.8	0.0328	2.2
Palatal length	0.0723	1.3	0.1991	3.8	−0.1424	3.6
Depth of braincase	0.1318	3.1	0.1387	3.4	0.4349	13.9
Zygomatic breadth	−0.0100	0.3	−0.4200	13.0	0.3237	13.0
Breadth of braincase	0.2782	6.4	0.1611	3.9	−0.1780	5.6
Mastoid breadth	0.3047	8.0	0.4157	11.4	−0.6531	23.3
Postorbital breadth	−0.9303	11.3	−0.0250	0.3	0.4387	7.2
Length of maxillary toothrow	0.1762	3.2	0.3551	6.8	0.1089	2.7
Rostral width at canines	−0.7437	9.2	0.1798	2.3	−0.3533	5.9
Breadth across upper molars	−0.2416	4.8	−0.2189	4.6	−0.3170	8.5
Mandibular length	−0.4332	14.7	0.3225	11.4	0.1131	5.2

ular length. These measurements as well as length of maxillary toothrow revealed no significant differences among samples in the univariate analysis. In females, condylobasal length, palatal length, breadth of braincase, mastoid breadth, postorbital breadth, length of maxillary toothrow, and mandibular length showed no significant differences among samples in the MANOVA. In the univariate analysis palatal length, breadth of braincase, postorbital breadth, length of maxillary toothrow, and mandibular length also showed no significant difference among samples.

The amount (percentage) of phenetic variation represented in the first three canonical variates for male and female *Brachyphylla nana*, respectively, was 68.5 and 66.4 for variate I, and 12.7 and 20.0 for variate II, and 12.1 and 7.1 for variate III. Combined these three canonical variates express 93.3% in males and 93.7% in females. In males all the variation was explained by the first five canonical variates, whereas in females it was expressed in the first four canonical variates.

In males the following characters contribute more than 10% to variate I in distinguishing among samples: condylobasal length, postorbital breadth, length of maxillary toothrow, and breadth across upper molars; more than 10% to variate II: length of forearm, zygomatic breadth, length of maxillary toothrow, and rostral width at canines; and more than 10% to variate III: length of forearm, length of maxillary toothrow, width across upper molars, and mandibular length. In females, characters contributing more than 10% to variate I are length of forearm, greatest length of skull, postorbital breadth, mandibular length, in variate II, condylobasal length, zygomatic breadth, mastoid breadth, and mandibular length, and in variate III, depth of braincase, zygomatic breadth, and mastoid breadth.

Examination of the two-dimensional canonical variate plot of the male samples reveals the following pattern of variation. Samples from Middle Caicos (6) and Hispaniola (7, 8) are grouped together and are clearly separated from the Cuban samples (1, 2, 3, 4) on the first variate. These two major

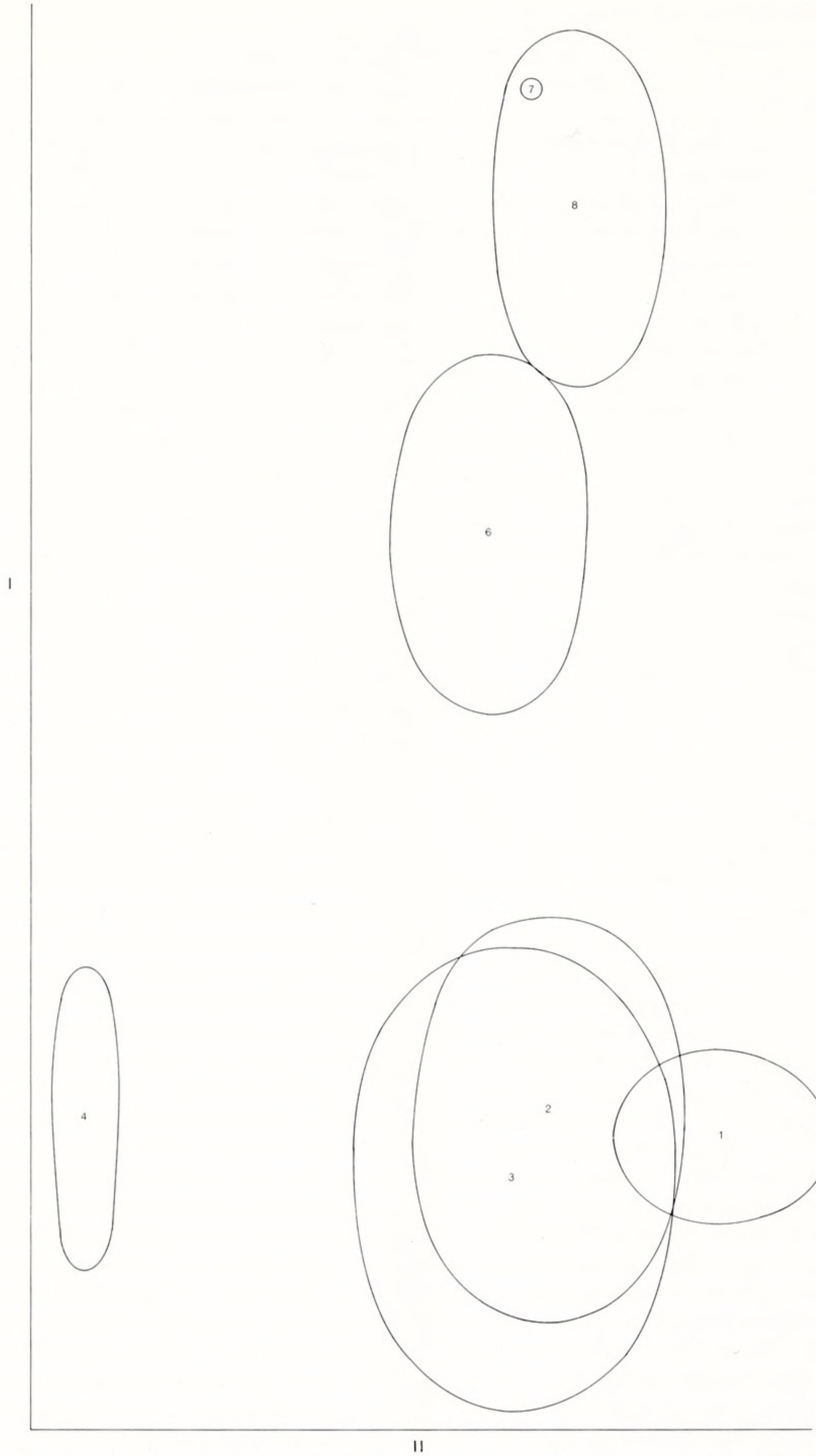

Fig. 15.—Two-dimensional projection of male samples (mean and one standard deviation) of *Brachyphylla nana* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

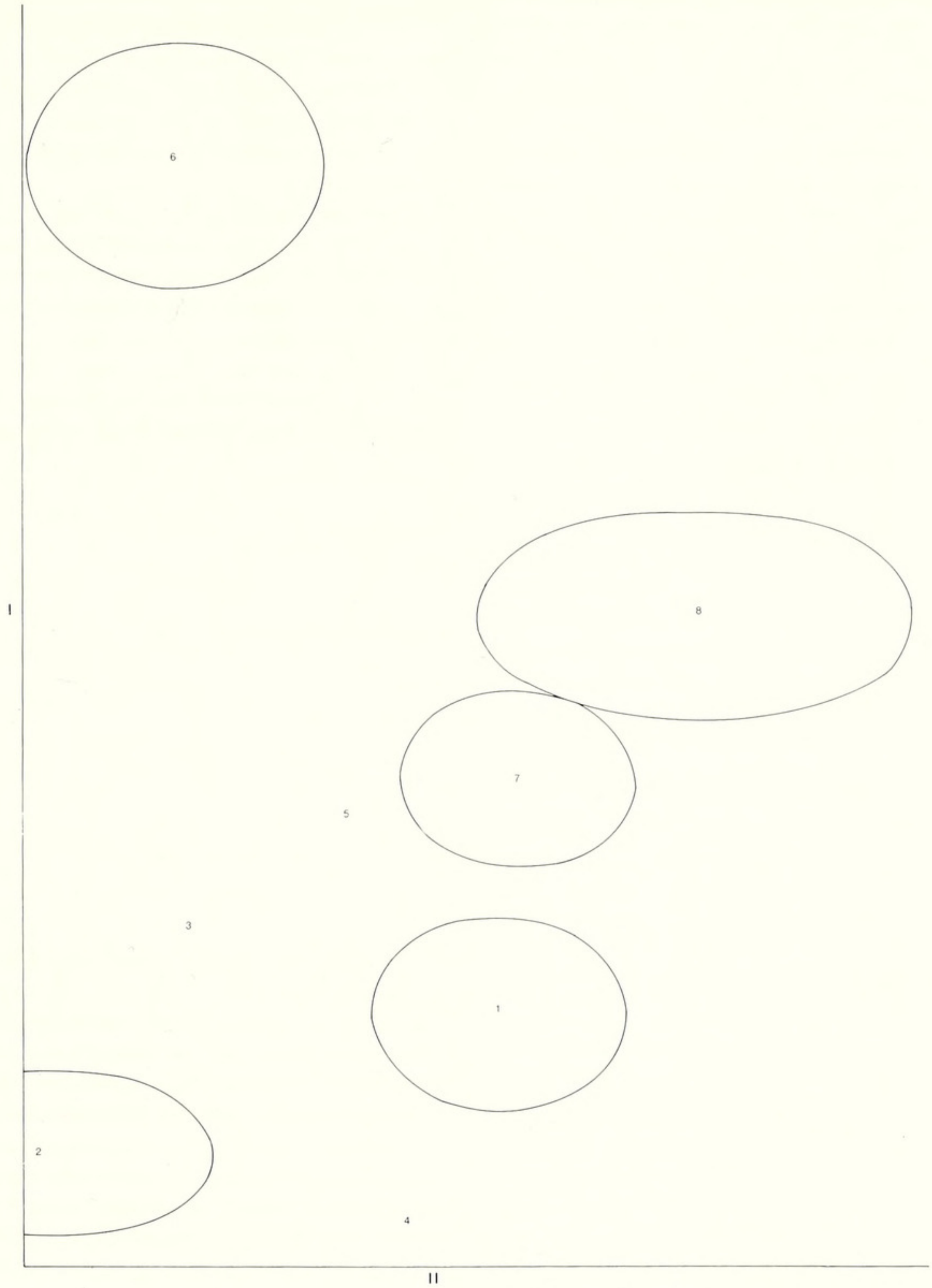

Fig. 16.—Two-dimensional projection of female samples (mean and one standard deviation) of *Brachyphylla nana* onto the first two canonical variates based on a matrix of variance-covariance among one external and 12 cranial measurements. See Fig. 1 and text for key to samples.

groups show no one standard deviation overlap on the first variate. The Cuban group, however, shows overlap between samples 1, 2, and 3, but these are clearly separated from sample 4 on the second variate. The canonical variate analysis shows some basic differences when compared to the principal component analysis. In the principal component analysis the Hispaniolan (7, 8) samples are also separated from the Cuban samples on the first component. However, the Middle Caicos (6) sample is grouped with Cuban material, although differing from these samples on the second and third component. Therefore, in the case of the distance phenogram and principal component analysis the sam-

Table 9.—*Geographic variation in eight cranial measurements of six samples of Recent, and one of Pleistocene or sub-Recent fossil material of* Brachyphylla. *See text for key to samples.*

Sample	N	Mean ± 2 SE	Range	CV
		Palatal length		
a	10	9.3 ± 0.23	8.9–9.9	3.8
b	10	9.5 ± 0.25	8.9–10.0	4.2
c	10	9.5 ± 0.26	9.0–10.2	4.4
d	1	10.1		
e	10	11.8 ± 0.24	10.9–12.2	3.3
f	7	11.8 ± 0.42	11.1–12.8	4.7
g	10	11.9 ± 0.36	11.0–12.8	4.8
		Rostral width at canines		
a	10	6.6 ± 0.11	6.3–6.8	2.6
b	10	6.4 ± 0.17	5.9–6.8	4.3
c	10	6.2 ± 0.15	5.8–6.5	3.8
d	1	6.6		
e	10	7.2 ± 0.13	6.8–7.6	2.9
f	7	7.2 ± 0.21	6.8–7.5	3.9
g	10	7.2 ± 0.09	7.1–7.5	2.0
		Length of maxillary toothrow		
a	10	9.4 ± 0.16	9.0–9.8	2.7
b	10	9.5 ± 0.15	9.2–9.9	2.6
c	10	9.5 ± 0.07	9.3–9.6	1.1
d	1	9.6		
e	10	10.7 ± 0.18	10.1–11.0	2.7
f	7	10.7 ± 0.12	10.4–10.9	1.5
g	10	10.7 ± 0.10	10.5–11.0	1.5
		Interorbital breadth		
a	10	7.8 ± 0.15	7.4–8.1	3.0
b	10	8.4 ± 0.11	8.2–8.7	2.0
c	10	8.1 ± 0.15	7.7–8.6	2.9
d	3	7.7 ± 2.0	7.4–7.8	2.2
e	10	9.0 ± 0.10	8.9–9.4	1.7
f	7	8.6 ± 0.13	8.4–8.9	2.0
g	10	8.5 ± 0.11	8.3–8.9	2.1
		Height of coronoid process		
a	10	7.3 ± 0.14	7.0–7.8	3.1
b	10	7.4 ± 0.12	7.1–7.7	2.5
c	10	7.3 ± 0.13	7.0–7.7	2.9
d	3	7.6 ± 0.14	7.5–7.7	1.5
e	10	9.0 ± 0.15	8.5–9.4	2.6
f	7	9.1 ± 0.18	8.8–9.5	2.6
g	10	9.0 ± 0.18	8.5–9.5	3.1
		Width of articular process		
a	10	2.6 ± 0.12	2.3–2.9	7.5
b	10	2.9 ± 0.06	2.7–3.0	3.3
c	10	2.5 ± 0.10	2.3–2.8	5.9
d	4	2.4 ± 0.18	2.3–2.7	7.9
e	10	3.3 ± 0.12	2.9–3.5	5.6
f	7	3.2 ± 0.12	3.0–3.5	5.0
g	10	3.2 ± 0.10	2.8–3.3	5.2
		Breadth of mandible at M_3		
a	10	1.2 ± 0.05	1.1–1.3	6.7
b	10	1.2 ± 0.03	1.2–1.3	3.9
c	10	1.1 ± 0.04	1.0–1.2	5.6
d	7	1.3 ± 0.06	1.2–1.4	6.9
e	10	1.4 ± 0.04	1.3–1.5	4.9
f	7	1.5 ± 0.04	1.4–1.6	3.8
g	10	1.5 ± 0.04	1.4–1.6	4.8
		Length of mandibular toothrow		
a	10	9.8 ± 0.10	9.5–9.9	1.7
b	10	10.0 ± 0.16	9.6–10.4	2.5
c	10	10.0 ± 0.09	9.7–10.1	1.4
d	2	10.2 ± 0.30	10.0–10.3	2.1
e	10	11.0 ± 0.17	10.5–11.4	2.5
f	7	10.9 ± 0.13	10.7–11.2	1.6
g	10	10.9 ± 0.08	10.7–11.1	1.2

ple from Middle Caicos is placed closer to the Cuban populations, whereas in the canonical analysis it is grouped with the Hispaniolan populations.

In females the two-dimensional canonical variate plot of the samples onto the first two variates shows the Middle Caicos (6) population to be well separated on the first variate and to some extent on the second, from both the Cuban and Hispaniolan populations. Cuban and Hispaniolan samples are closer to each other than either is to the Middle Caicos sample. Therefore, all multivariate analyses of female samples show the Middle Caicos sample to be well separated from the others. In the canonical analysis the Hispaniolan material is grouped with the Cuban material, whereas in both the cluster and principal component analyses they are separated.

Taxonomic Conclusions

Based upon our study of geographic variation in *Brachyphylla nana*, we have chosen to consider it a monotypic species. In five measurements for males and seven measurements for females, either the ANOVA or MANOVA was non-significant. In four of the 13 measurements for the samples of *B. nana* either the ANOVA or MANOVA was non-significant for both sexes, whereas a total of eight were non-significant for at least one sex. The results of the multivariate analyses were inconsistent.

There appears to be very little morphometric variation among our samples of *B. nana*. The range of this variation is, in many cases, encompassed by the four samples from Cuba. Other cranial features used to distinguish *B. nana* and *B. pumila* prove to be inconsistent when large samples are examined. Therefore, we believe the best course of action to follow is to consider *Brachyphylla nana* as being a monotypic species.

Status of Fossil Specimens

The genus *Brachyphylla* is known only as a Pleistocene or sub-Recent fossil from the island of Jamaica. This material was assigned to *B. pumila* by Koopman and Williams (1951). We have taken the opportunity to re-examine this material and to compare it with the two species that we have recognized. Standard statistics from geographic samples listed in Materials and Methods are given in Table 9.

All characters of Pleistocene or sub-Recent fossil material studied with the exception of interorbital breadth showed basically the same pattern of geographic variation. In all cases the fossils grouped with populations that we consider to be *B. nana*. The populations of *Brachyphylla* from Puerto Rico (sample e), St. John (f), and Norman (g) were usually grouped into a subset or subsets significantly different from those populations from Cuba (a), Middle Caicos (b), and Dominican Republic (c). Of the eight measurements, four (rostral width at canines, interorbital breadth, width of articular process, and width of mandible at M_3) showed overlap between the two main areas. The Pleistocene or sub-Recent fossil material generally averaged larger than the Recent material from Cuba, Middle Caicos, and Dominican Republic, but falls within the range of variation displayed by the Recent material. In only two measurements (width of articular process and interorbital breadth) did the Jamaican material average less than the Recent material from Cuba, Middle Caicos, and Dominican Republic. Only in breadth of mandible at M_3 did the Jamaican material show any overlap with the ranges of measurements obtained from specimens from Puerto Rico, St. John, and Norman. Interorbital width in *Brachyphylla* displayed a great deal of geographic variation. Individual variation as indicated by coefficients of variation show width of articular process and breadth of mandible at M_3 to be the most variable.

The cluster, principal components, and canonical variate analyses of these samples reveal the same basic picture. We have illustrated the principal components analysis as being typical.

The first two principal components extracted from the principal component analysis for three *B. nana*, one fossil, and three *B. cavernarum* samples are shown two-dimensionally in Fig. 17. The amount of phenetic variation represented in the first three components was 90.2 for component I, 0.08 for component II, and 0.02 for component III. From the factor analysis (not tabled) it was obvious that the first component is heavily influenced by all characters. Both the second and third components are not notably influenced by any character.

Examination of the two-dimensional plot of the first two principal components reveals two groups of samples. The cluster on the right consists of samples from Puerto Rico, St. John, and Norman; the one on the left contains samples from Cuba, Middle Caicos, Dominican Republic, and Jamaica. The latter group contains the smaller specimens as clearly revealed by the univariate analysis.

Although the Jamaican fossil material tends to be somewhat larger than the Recent material from Cuba, Middle Caicos, and Dominican Republic, it clearly has its relationship to these populations. Decision on whether the bats in the sub-Recent population were actually somewhat larger than in the Recent population or not, must await the discovery of further fossil material. However, we do not believe that the differences noted in the current material warrant taxonomic recognition. Therefore, we assign the Jamaican Pleistocene or sub-Recent fossils to *Brachyphylla nana*.

Brachyphylla nana Miller, 1902

1902. *Brachyphylla nana* Miller, Proc. Acad. Nat. Sci. Philadelphia, 54:509, 12 September.
1918. *Brachyphylla pumila* Miller, Proc. Biol. Soc. Washington, 31:39, 16 May; holotype from Pont de Baisc, Haiti.
1974. *Brachyphylla cavernarum nana*, Varona, Acad. Cien. Cuba, p. 27.
1974. *Brachyphylla cavernarum pumila*, Varona, Acad. Cien. Cuba, p. 27.
1976. *Brachyphylla nana nana*, Jones and Carter, Spec. Publ. Mus., Texas Tech Univ., 10:30, 25 June.
1976. *Brachyphylla nana pumila*, Jones and Carter, Spec. Publ. Mus., Texas Tech Univ., 10:30, 25 June.

Holotype.—Skull of an unsexed adult recovered from owl pellets, USNM 103,828 from El Guama, Cuba, obtained by William Palmer and J. H. Riley on 10 March 1900; original no. 108.

Measurements of holotype.—Condylobasal length, 24.9; palatal length, 8.7; zygomatic breadth, 14.6; braincase breadth, 11.3; postorbital breadth, 5.9; rostral width at canines, 6.4.

Distribution.—This species is known from Cuba, Isle of Pines (Varona, 1974), Grand Cayman, Middle Caicos, Hispaniola, and as a Pleistocene or sub-Recent fossil from Jamaica.

Comparisons.—See Specific Relationships.

Remarks.—Populations described as *pumila* and *nana* were long considered distinct species and most recent authors have considered them to be

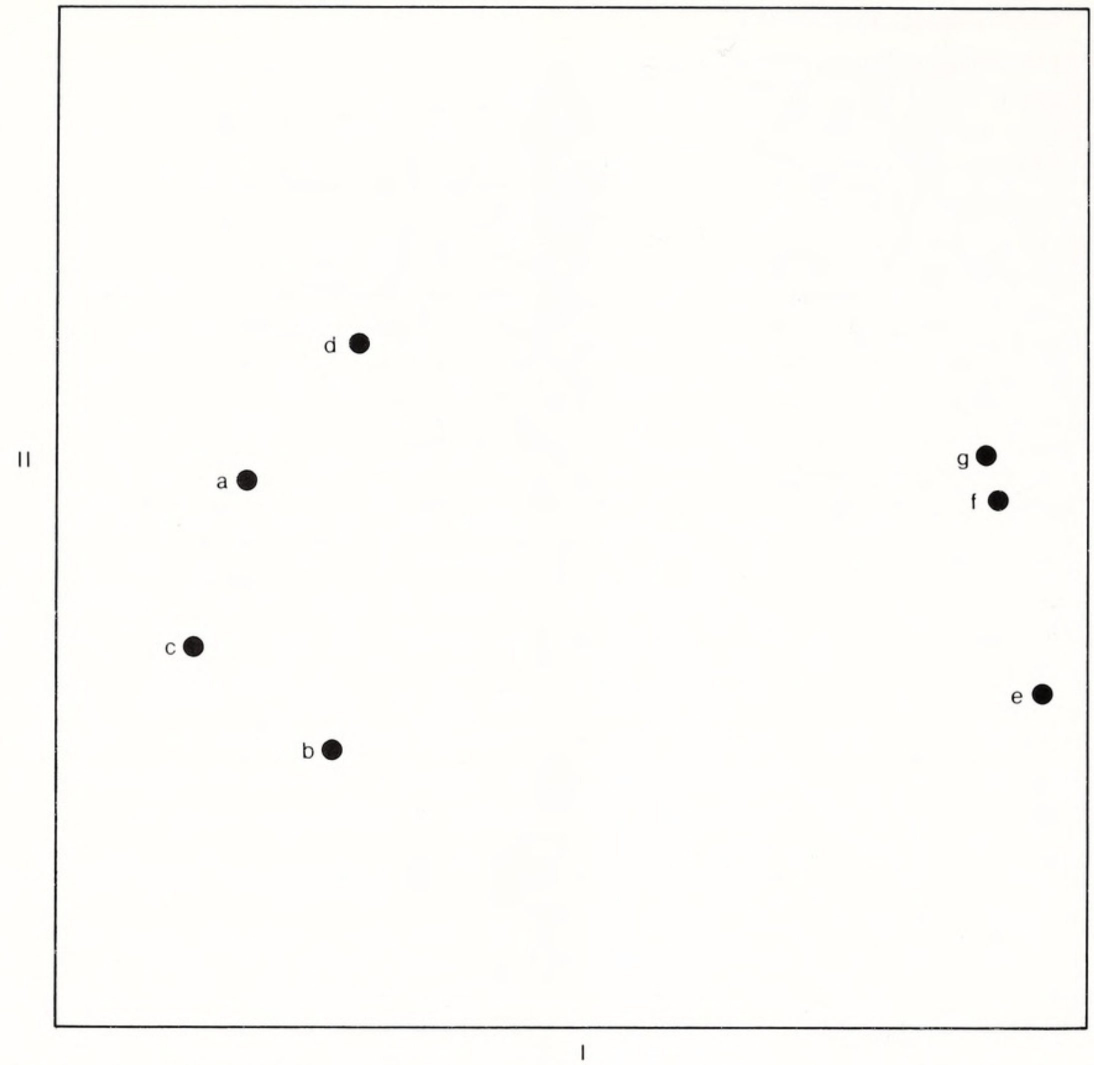

Fig. 17.—Two-dimensional projection of seven samples (six Recent and one Pleistocene or sub-Recent) of *Brachyphylla* onto the first two principal components. See text for key to samples.

distinct at least at the subspecific level (see Silva-Taboada, 1976; Jones and Carter, 1976). However, based upon our analyses and studies, we cannot support this distinction. The populations do not differ much in size and Cuban populations encompass most of the range of variation observed. Various dental and cranial characters, such as difference in size and morphology of M^1 (Miller, 1918), a broader rostrum and palate and larger molars in *B. pumila* (Miller, 1929), shape of interpterygoid fossa (Goodwin, 1933), and depth of pit between orbit and antorbital foramen (Koopman and Williams, 1951), have been used to distinguish these taxa. We have examined these characters in the large series available to us. These characters were found to be individually variable or nonexistent. Buden (1977) found *nana* to have a deeper and more robust zygomatic arch than *pumila*; however, we are unable to appreciate this character in our material.

Dorsal pelage coloration does not appear to separate taxa either. Individuals corresponding to color standard 3 were found in relatively high numbers on all islands—Cuba, 37%; Hispaniola, 35%; Middle Caicos, 100%; Grand Cayman, 100%. The majority of the specimens (63%) from Hispaniola are slightly darker than the majority of material (47%) from Cuba being a blackish gray (standard 1) as compared to dark brown (standard 5). However, in view of the only slight differences in color found throughout this genus and fairly broad overlap between all island populations of *B. nana,* we see no reason based upon color to consider this taxon to be polytypic.

Two recent authors, Varona (1974) and Buden (1977), have recognized *nana* and *pumila* as distinct subspecies but placed them in *B. cavernarum* and considered the genus to be monotypic. Buden (1977) claimed that "differences in size among these allopatric populations is nearly matched by those found among Middle American populations of *Artibeus jamaicensis* that are treated as subspecies by Davis (1970)." We disagree with this conclusion based upon our studies. *Brachyphylla cavernarum* and *B. nana* differ considerably in size; there is no overlap between these two species in six of 12 cranial measurements taken. In our opinion, these differences more nearly resemble those found between sympatric populations of the Middle American species *Artibeus jamaicensis* and *A. lituratus*. We, therefore, believe that the differences observed between these allopatric populations of *Brachyphylla* are best represented by considering them to be distinct species.

Brachyphylla nana is known on the island of Jamaica only as a Pleistocene or sub-Recent fossil (Koopman and Williams, 1951). Based upon the reconstruction of the fossil bat faunas by Williams (1952), *B. nana* occurred in about the middle of the known record for bats on the island but no time frame is possible. It was contemporary with members of the genera *Ariteus, Mormoops, Phyllonycteris, Erophylla, Monophyllus,* and *Macrotus,* but had disappeared before *Artibeus* appeared in the fossil record. Although it is tempting to theorize some sort of competition to account for the extinction of *Brachyphylla* on Jamaica, the reasons must be far more complex because almost identical faunas occur today on Cuba and Hispaniola, but *Brachyphylla* has survived there (Baker and Genoways, 1978).

Specimens examined (185).—CUBA: 12 mi E Moron, Camagüey Province, 3 (AS); Cueva de los Indios, Habana Province, 6 (1 AS, 5 MCZ); Cueva del Indio, 3 mi E Tapaste, Habana Province, 12 (AMNH); Cueva de Costilla San Jose de las Lajas, Habana Province, 3 (TCWC); 4 mi S San Jose de las Lajas, Habana Province, 2 (AMNH); 9 km SW San Jose de las Lajas, Habana Province, 8 (AS); Cantabria Cave, Hormiguero, Las Villas Province, 11 (1 KU, 10 UMMZ); Cantabria Cave, 14 km NE Cienfuegos, Las Villas Province, 4 (ROM); Finca de Morales, 8 mi NW Trinidad, Las Villas Province, 5 (AS); Guatanama, Oriente Province, 3 (USNM); Los Angeles, Oriente Province, 1 (MCZ); Santiago, Oriente Province, 3 (FMNH); Santiago de Cuba, Oriente Province, 7 (3 AMNH, 4 FMNH); Cueva de la Cantera, Siboney, 14 km SE Santiago de Cuba, Oriente Province, 2 (ROM); El Guama, Pinar del Rio Province, 1 (USNM). GRAND CAYMAN: Old Man Bay, 1 (LSU). DOMINICAN REPUBLIC: Cueva no. 2 Los Patos, Barahona Province, 47 (1 AMNH, 1 FMNH, 43 PSNH, 1 TCWC, 1 USNM); Upper Los Patos Cave, Barahona Province, 8 (4 AMNH, 4 PSNH); Los Patos, Barahona Province, 1 (ROM); Cueva Wunker, 19.3 km W La Romana, La Romana Province, 6 (PSNH); Sosúa, Puerta Plata Province, 7 (AS); Cueva el Limón, Samana, Samana Province, 3 (PSNH); Cueva de Sierra de Agua San Cristobal, Samana Province, 2 (ROM). CAICOS ISLANDS: Conch Bar, Middle Caicos, 19 (LSU). HAITI: Daiquini [=Diquini], 3 (2 BMNH, 1 FMNH); 1 km S, 1 km E Lebrun, Department du Sud, 4 (TTU); Port de Paix, 1 (USNM). JAMAICA: Dairy Cave, Dry Harbor [=Discovery Bay], St. Ann Parish, 12 (AMNH).

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