Morphologic Variation in the Spotted Bat Euderma maculatum

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ABSTRACT: Variation was evaluated in 67 specimens of the spotted bat *Euderma maculatum* from throughout its range. There was significant secondary sexual dimorphism in size for one of 16 characters (females were larger than males in length of forearm). Because of small samples, specimens were grouped into four regional populations. There was significant interpopulation heterogeneity in 10 of 16 characters; the southern population (from Texas to Queretaro, Mexico) was significantly larger than the others in length of ear, and the western population (from California to Utah) was significantly smaller than the others in length of forearm. Populations were widely separated in multivariate analyses.

INTRODUCTION

The spotted bat (*Euderma maculatum*) is among the rarest of North American chiropterans (Barbour and Davis, 1969). Since the first collection of this species in 1890, only 35 specimens were reported in the literature to 1965 (Watkins, 1977). Populations of *E. maculatum* appear to be concentrated in a few areas (*e.g.*, southern British Columbia, southwestern Utah, western and northern New Mexico, and the Big Bend area of Texas). Collecting localities throughout most of the range of this species are represented by one specimen (often these were found dead or dying). Though the distribution of *E. maculatum* extends from British Columbia (Woodsworth *et al.*, 1981) to central Mexico (Hall, 1981), no attempt has been made to assess morphologic variation across the range of this species. Because spotted bats have such an unusual distribution pattern, little is known about many aspects of their biology, and because they are rare, they present an interesting opportunity to examine morphologic variation in a potentially endangered species. The purposes of this study were to investigate the degree of sexual dimorphism, amount and pattern of interlocality variation within each character, and phenetic relationships among populations of spotted bats.

METHODS AND MATERIALS

Questionnaires sent to 506 individuals and institutions revealed that 73 specimens of *Euderma maculatum* existed in 1985 (based upon 317 responses). Morphologic data were obtained from 67 specimens of *E. maculatum*; 46 were examined by me (all were adults) and data from specimen tags of 21 others were provided by museum curators and assistants. Measurements of 36 males, 25 females and six bats of undetermined sex were analyzed. Five external characters were recorded to the nearest millimeter from specimen tags, and length of body was calculated by subtracting length of tail from total length. Length of forearm and nine cranial measurements (Fig. 1) were determined to the nearest 0.1 mm using dial calipers.

Bats were grouped into four regional populations based upon proximity of collecting locality. Including specimens from diverse habitats over a relatively large geographic area in each regional population was assumed to increase variation within each population; this would increase the variance for each population, which would yield a more conservative estimate of differences among populations (museum acronyms are listed in Acknowledgments).

POPULATION 1—NORTHERN (3 males, 4 females, 1 of undetermined sex)—*British Columbia, Canada*: Oliver (0, 1 BCPM). *Colorado*: Moffat Co., Browns Park NWR, Old Headquarters, T10N, R103W, Sec 25, 5350 ft (0, 1 DWRC). *Idaho*: Canyon Co., 15 miles SW Caldwell (1 of undetermined sex, OJS). *Montana*: Yellowstone Co., Billings (1, 0 MSU). *Oregon*: Harney Co., 5.1 miles N Alvord Ranch on Alvord Road E on small road 6.6 miles to Mickey Springs (0, 1 SOSC); Wheeler Co., 0.3 km SSE Clarno (1, 0 PSU). *Utah*: Salt Lake Co., Eaves of Plymouth School, Salt Lake City, 4305 ft (0, 1 UU); Utah Co., Provo (1, 0 BYU). POPULATION 2—WESTERN (13 males, 8 females, 5 of undetermined sex)—*Arizona*: Maricopa Co., Tempe (1, 0 LACM); Mohave Co., 8 miles S St. George, Utah (1, 0 UC); Mohave Co., Beaver Dam Creek at Beaver Dam Resort, 1 mile N Littlefield (1, 1 MNA); Yuma Co., 4 miles S Yuma (1 of undetermined sex, MCZ); Yuma Co., 9 miles E Roll (35 miles E Yuma) (1 of undetermined sex, USNM). *California*: Fresno Co., Friant (1, 0 CSUF); Los Angeles Co., San Fernando Valley (1 of undetermined sex, AMNH); Mariposa Co., 100 yards N Yosemite Museum, Yosemite Nat'l Park (1, 0 MVZ); Mariposa Co., Camp 15, Yosemite Valley, Yosemite N. P. (1, 0 MVZ); Riverside Co., RR tank at Mecca (1 of undetermined sex, MVZ); San Bernardino Co., China Lake (1, 0 LACM). *Nevada*: Clark Co., Las Vegas (0, 1 MVZ); Clark Co., NSU Campus, Las Vegas (1, 0 NSMLV); Lincoln Co., Cathedral Gorge, S of Pioche (0, 1 LACM); Washoe Co., MGM Hotel (0, 1 NSMCC); Washoe Co., Zool. Lab., Univ. Nevada, Reno (1 of undetermined sex, MVZ). *Utah*: Garfield Co., N 40.44, W 112.11 (0, 1 ROM); Washington Co., Fort Pierce below Old Fort Pierce (ruins), ca. 800 m (1, 0 KU); Washington Co., Ft. Pierce Wash (1, 1 MVZ); Washington Co., Ft. Pierce Wash, 8 miles SE St. George (2, 1 CMNH, MVZ,

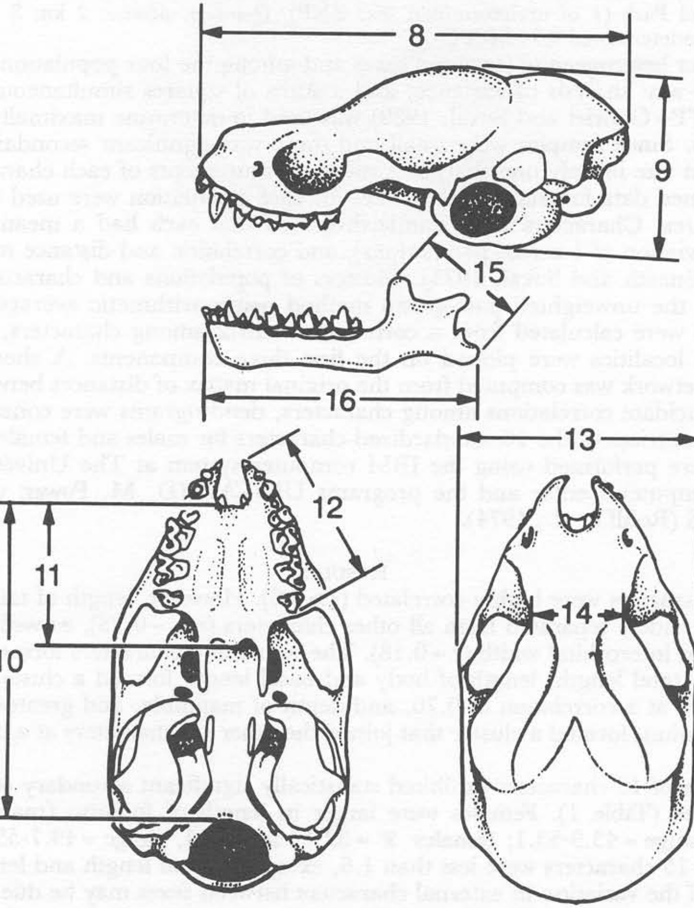

Fig. 1.—Cranium and mandible of *Euderma maculatum* illustrating the nine cranial and mandibular measurements used in this analysis (modified from Hall, 1981). Numbers correspond to the characters listed in Table 1

UC); Washington Co., Fort Pearce Wash, St. George (0, 1 MNA); Washington Co., Pearce Wash, 8 miles SE St. George, ca. 3000 ft (1, 0 UC). POPULATION 3—CENTRAL (12 males, 9 females)—*New Mexico*: Catron Co., 9 miles E Mogollon, Mogollon Mts. (2, 2 MSB); Catron Co., Willow Creek, 10 miles E Mogollon (0, 1 MSB); Catron Co., Woodland Park, T11S, R15W, Sec 35, 7300 ft (0, 1 WNMU); Cibola Co., 5.8 miles N, 13.4 miles E Grants, Mt. Taylor Summit, 11,000 ft (1, 0 MSB); Dona Ana Co., Mesilla Park (1, 0 USNM); Grant Co., Lake Roberts, T14S, R13W, Sec 35 (0, 1 WNMU); Rio Arriba Co., Ghost Ranch (2, 0 MSB, UNAM); San Juan Co., 2 miles N Aztec (1, 0 UC); Sandoval Co., East Fork Jemez River, T18N, R3E (1, 0 NSMLV); Sandoval Co., East Fork Jemez River, T18N, R3E, NE 1/4 Sec 2 (3, 2 MSB); Socorro Co., Weir Tank, 1.5 miles E Springtime Campground, 7200 ft (1, 1 MSB); Socorro Co., Weir Tank, Nogal Canyon, San Mateo Mts., 1.5 miles E Springtime Cmpgd., 2440 m, T9S, R5W, Sec 6 (0, 1 NMSU). POPULATION 4—SOUTHERN (8 males, 4 females)—*Chihuahua, Mexico*: Navarro, 72 km by road W Hidalgo de Parral (2, 0 LACM). *Queretaro, Mexico*: 1 mile NE Pena Blanco, 4450 ft (1, 0 TCWC). *Texas*: Brewster Co., Big Bend Natl. Park (5, 4 FMNH, ISU, KU, LSU, REM, TTU, UM, USNM).

Specimens located, but not used in analyses—*California*: Kern Co., Red Rock Canyon (1 of undetermined sex, MVZ); San Bernardino Co., Twentynine Palms (1, 0 MVZ). *Chihuahua, Mexico*: Navarro, 72 km by road W Hidalgo de Parral (1 of undetermined sex, UNAM). *Utah*: San Juan Co., 5 miles NW Monticello, 6800 ft (1, 0 MVZ); Washington Co., Zion Canyon, Zion National Park (1 of undetermined sex, ZNP). *Queretaro, Mexico*: 2 km S Vizarron (by road) (1 of undetermined sex, MZFC).

Character heterogeneity (between sexes and among the four populations) was tested using a one-way analysis of variance, and a sums of squares simultaneous test procedure (SS-STP—Gabriel and Sokal, 1969) was used to determine maximally nonsignificant subsets. Since samples were small and there was significant secondary sexual dimorphism in size in only one character, mean measurements of each character derived from combined data for males and females for each population were used in multivariate procedures. Characters were standardized (so that each had a mean of 0 and a standard deviation of 1 across populations), and correlation and distance matrices were calculated (Sneath and Sokal, 1973). Clusters of populations and characters were obtained with the unweighted pair-group method using arithmetic averages. Principal components were calculated from a correlation matrix among characters, and projections of the localities were plotted on the first three components. A shortest simply-connected network was computed from the original matrix of distances between populations. To elucidate correlations among characters, dendrograms were constructed from correlation matrices of the 16 standardized characters for males and females combined. Analyses were performed using the IBM computer system at The University of New Mexico Computer Center and the programs UNIVAR (D. M. Power, unpublished) and NT-SYS (Rohlf et al., 1974).

RESULTS

Most characters were highly correlated ($r > 0.8$). However, length of tail and palatal length were widely separated from all other characters ($r = -0.23$), as well as length of toothrow and interorbital width ($r = 0.18$). The remaining characters formed three clusters, that is, total length, length of body and basal length formed a cluster that joined the other two at a correlation of 0.70, and depth of mandible, and greatest length and depth of cranium formed a cluster that joined the other six characters at a correlation of 0.81.

Only one of 16 characters exhibited statistically significant secondary sexual dimorphism in size (Table 1). Females were larger in length of forearm (males $\bar{x} = 50.1$, SD = 1.92, range = 43.9-53.1; females $\bar{x} = 52.1$, SD = 1.44, range = 49.7-55.0). *F*-ratios of the other 15 characters were less than 1.6, except for total length and length of body. A portion of the variation in external characters between sexes may be due to the number of persons recording these data. However, characters that I measured (cranial and mandibular measurements) also exhibited considerable overlap between sexes. Because of small samples and overlap of the only character exhibiting significant sexual dimorphism in size between sexes, sexes were grouped for subsequent analyses.

Significant interpopulation character variation was found among 10 of 16 characters (Table 2). As evidenced by the *F*-ratios, total length, length of body, length of ear and length of forearm exhibited the greatest interlocality variation (*F*-ratios > 8), whereas length of tail, weight, greatest length of cranium and zygomatic width exhibited the least (*F*-ratios < 5).

Populations 3 (Central) and 4 (Southern) had the largest means for all characters except interorbital width, where Population 2 (Western) was largest (Table 2). Population 2 (Western) had the smallest means for 13 of 16 characters (Table 2), and was significantly smaller than the other three populations in length of forearm (Pop. 1, SD = 1.50, range = 49.0-53.4; Pop. 2, SD = 1.92, range = 43.9-51.7; Pop. 3, SD = 1.67, range = 47.6-53.9; Pop. 4, SD = 1.33, range = 50.0-55.0). Population 2 (Western) was significantly larger than the other three in length of ear (Pop. 1, SD = 3.01, range = 39-47; Pop. 2, SD = 3.26, range = 34-47; Pop. 3, SD = 1.93, range = 39-46; Pop. 4, SD = 1.30, range = 45-49).

The populations were not highly correlated (Fig. 2A). Correlation analyses placed Populations 1 and 3 closest, and Populations 2 and 4 together and well apart from the other two ($r = -0.18$). Phenetic distance analysis placed Populations 1 and 3 closest (Fig. 2B). Population 2 joined them at a distance of 1.33, then Population 4 joined at a distance of 1.58. Like the correlation dendrogram, the distance dendrogram did not show a close relationship between any two populations.

Character loadings on principal component I were greater than 0.80 for 10 characters (Table 3). Following the reasoning of Johnston and Selander (1971) and Niles (1973), this component may be taken to represent overall size in both sexes because it accounted for most of the covariation among characters. Population 4 had the highest

TABLE 1.—Secondary sexual dimorphism in size in 16 characters of *Euderma maculatum*. Means (mm) of each character are listed with the degrees of freedom and *F*-ratios derived from one-way analysis of variance. Minimally significant sexual dimorphism assumed where $P \leq 0.05$ (one asterisk)

Character	Char. No.	Character-state means: Males ($n = 36$)	Character-state means: Females ($n = 25$)	Analysis of variance: *df*	Analysis of variance: *F*-ratio
External					
Total length	1	115.9	119.9	1,53	3.51
Length of body	2	66.9	70.1	1,53	2.32
Length of tail	3	49.0	49.8	1,53	0.76
Length of hind foot	4	10.6	10.9	1,53	0.93
Length of ear	5	42.8	42.5	1,52	0.06
Weight (in g)	6	15.3	15.3	1,32	0.00
Length of forearm	7	50.1	52.1	1,52	16.45*
Cranium					
Greatest length	8	19.1	19.3	1,24	1.54
Greatest depth	9	7.9	8.0	1,23	0.47
Basal length	10	14.3	14.2	1,25	1.31
Palatal length	11	6.5	6.6	1,25	0.51
Length of toothrow	12	7.2	7.1	1,26	0.07
Zygomatic width	13	10.4	10.5	1,25	0.72
Interorbital width	14	4.2	4.3	1,25	1.39
Mandible					
Depth of mandible	15	5.2	5.1	1,26	0.90
Length of mandible	16	12.7	12.6	1,26	0.27

TABLE 2.—Morphologic variation in means of 16 characters of *Euderma maculatum*. Statistically homogeneous subsets derived from SS-STP analysis are shown by lines below the population numbers and ranked means (mm). Degrees of freedom and *F*-ratios derived from one-way analysis of variance are listed; minimally significant interpopulation variation assumed where $P \leq 0.05$ (one asterisk), $P \leq 0.01$ (two asterisks) and $P \leq 0.001$ (three asterisks)

		Analysis of variance					
Character	No.	*df*	*F*-ratio	Results of SS-STP analysis			
External							
Total length	1	3,52	9.275***	3	4	1	2
				122.11	120.92	117.00	111.50
Length of body	2	3,52	9.733***	4	3	1	2
				73.75	71.06	67.50	62.55
Length of tail	3	3,52	3.492*	3	1	2	4
				51.06	49.50	49.00	47.17
Length of hind foot	4	3,51	5.009**	4	1	3	2
				11.75	10.83	10.44	10.21
Length of ear	5	3,51	13.103***	4	3	1	2
				46.91	42.22	41.33	41.25
Weight (in g)	6	3,30	4.000*	4	3	1	2
				17.90	14.95	14.75	13.41
Length of forearm	7	3,55	8.970***	4	1	3	2
				52.61	51.04	51.04	49.39
Cranium							
Greatest length	8	3,22	3.769*	4	1	3	2
				19.47	19.45	19.27	18.78
Greatest depth	9	3,22	1.363	4	1	3	2
				8.08	8.05	7.92	7.83
Basal length	10	3,24	1.002	3	1	4	2
				14.34	14.30	14.30	14.04
Palatal length	11	3,24	5.494**	3	1	4	2
				6.75	6.65	6.35	6.26
Length of toothrow	12	3,25	0.257	4	2	1	3
				7.18	7.15	7.15	7.11
Zygomatic width	13	3,24	4.036*	4	1	3	2
				10.83	10.55	10.32	10.29
Interorbital width	14	3,24	0.610	2	4	1	3
				4.27	4.27	4.25	4.20
Mandible							
Depth of mandible	15	3,25	2.658	4	1	3	2
				5.28	5.20	5.12	5.01
Length of mandible	16	3,25	2.933	4	3	1	2
				13.00	12.62	12.60	12.41

loading along component I, and Population 2 had the lowest (Fig. 2C). This component accounted for ca. 65% of the phenetic variation (Table 3). Population 4 was largest for most characters (Table 2); thus, the larger bats are to the right side of Figure 2C.

On principal component II, length of tail, basal length, palatal length, length of toothrow, and interorbital width had higher loadings than on component I (Table 3). Other characters had only weak associations. This component, which represented 29% of the variance of the data (Table 3), separated Populations 2 and 4 toward the front of the plot and Population 3 toward the back (Fig. 2C). Populations 2 and 4 had the lowest mean values for length of tail, basal length and palatal length, and largest mean values for length of toothrow and interorbital width (Table 2).

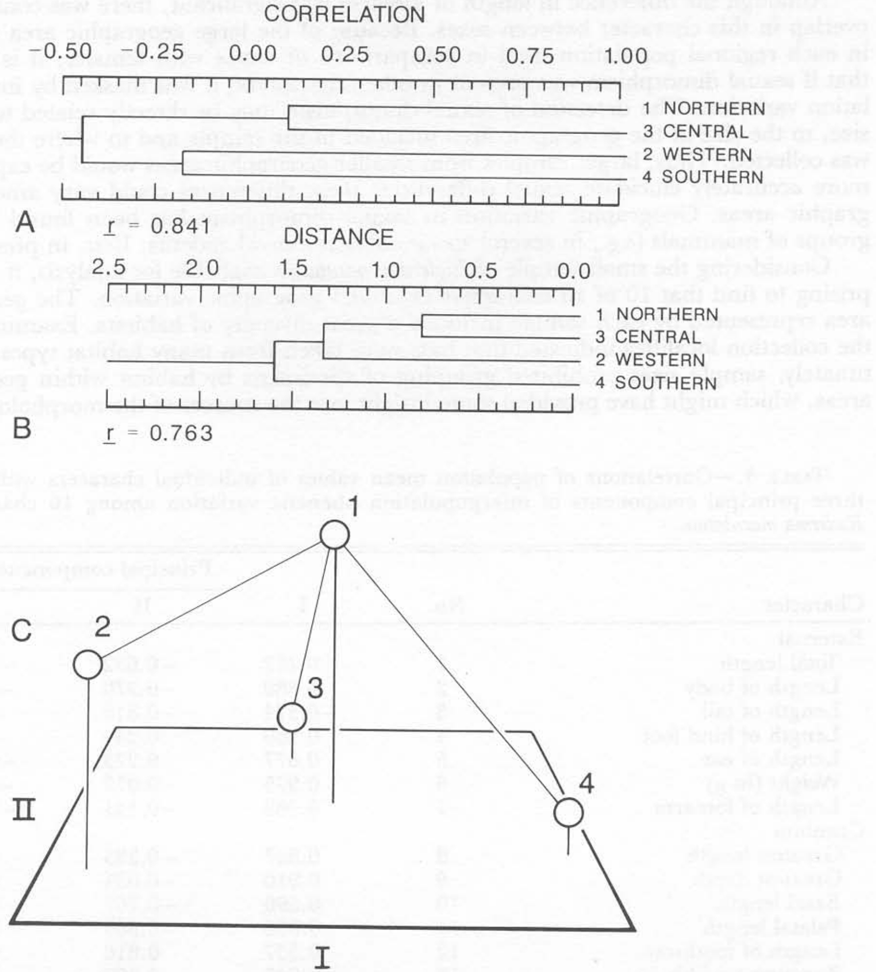

Fig. 2.—Phenograms constructed from correlation (A) and distance (B) matrices and three-dimensional projection (C) of populations onto the first three principal component axes of variation in the matrix of correlations of 16 morphologic characters for *Euderma maculatum*. Accuracy of the phenograms in depicting interpopulation relationships increases from left to right. The cophenetic correlation coefficients (*r*) are provided. The shortest simply-connected network is superimposed on the three-dimensional plot (C)

The third principal component had highest loadings for length of ear and greatest length and depth of cranium (Table 3). Only about 6% of the phenetic variance was explained by this component; no particular trends could be detected along this third component (Fig. 2C).

The three components explained 100% of the character variation (Table 3). Thus, distortion of the phenetic distances between populations was minimal when the character space was reduced to three dimensions. The shortest simply connected network, which connects populations in Figure 2C, also indicated little distortion. Each of the populations was closer to Population 1 than to any other population.

DISCUSSION

Although the difference in length of forearm was significant, there was considerable overlap in this character between sexes. Because of the large geographic area included in each regional population used in comparisons of males with females, it is possible that if sexual dimorphism was present in other characters, it was masked by interpopulation variation. The detection of sexual dimorphism may be directly related to sample size, to the size of the geographic area included in the sample and to where the sample was collected. Thus, larger samples from smaller geographic areas would be expected to more accurately elucidate sexual differences; these differences could vary among geographic areas. Geographic variation in sexual dimorphism has been found in other groups of mammals (*e.g.*, in several species of heteromyid rodents; Best, in press).

Considering the small sample of *Euderma maculatum* available for analysis, it was surprising to find that 10 of 16 characters exhibited geographic variation. The geographic area represented by each sample included a great diversity of habitats. Examination of the collection localities indicated that bats were taken from many habitat types. Unfortunately, sample sizes prohibited grouping of specimens by habitat within geographic areas, which might have provided some insight into the sources of the morphologic vari-

TABLE 3.—Correlations of population mean values of individual characers with the first three principal components of interpopulation phenetic variation among 16 characters of *Euderma maculatum*

Character	No.	Principal components I	II	III
External				
Total length	1	0.712	−0.652	−0.261
Length of body	2	0.889	−0.370	−0.268
Length of tail	3	−0.574	−0.818	0.029
Length of hind foot	4	0.969	0.244	0.020
Length of ear	5	0.877	0.273	−0.396
Weight (in g)	6	0.975	0.077	−0.210
Length of forearm	7	0.988	−0.141	−0.055
Cranium				
Greatest length	8	0.857	−0.385	0.341
Greatest depth	9	0.910	−0.034	0.412
Basal length	10	0.696	−0.707	0.126
Palatal length	11	0.056	−0.963	0.263
Length of toothrow	12	0.557	0.816	0.156
Zygomatic width	13	0.943	0.299	0.146
Interorbital width	14	0.088	0.973	0.214
Mandible				
Depth of mandible	15	0.975	−0.063	0.213
Length of mandible	16	0.979	0.059	−0.196
Percent of phenetic variance explained		65.19	29.23	5.58

ation. Because of the diversity of habitats and the large geographic region encompassed by each population, considerable morphologic variation could be masked. However, the southern population of *E. maculatum* was large, the western population was small, and the northern and central populations were intermediate in body size.

The amount of geographic variation in *Euderma maculatum* may indicate there is little exchange of individuals among populations, and that populations of this bat are clumped as indicated by the distribution of specimen collection sites. While it is tempting to account for at least some of this geographic variation in terms of isolation of populations, not enough data exist to accurately determine the geographic range or habitats occupied by this species. This bat occurs from 57 m below sea level (Grinnell, 1910) to 3230 m above sea level (Reynolds, 1981) and in habitats ranging from desert to montane coniferous forest (Findley and Jones, 1965; Handley, 1959). Specimens of *E. maculatum* have been collected most often in dry, rough, desert terrain such as the Chihuahuan Desert in Big Bend National Park, Texas (Easterla, 1972). Until we know more about this rare species, it will be difficult to accurately assess the reasons for the degree of morphologic variation detected here.

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