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SYSTEMATIC REVIEW OF THE ANTILLEAN BATS OF THE *NATALUS MICROPUS*-COMPLEX (CHIROPTERA: NATALIDAE)

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ABSTRACT

Nongeographic and geographic morphometric variation in Antillean populations of bats of the *Natalus micropus*-complex were analyzed using univariate and multivariate statistical techniques. Samples of males and females from Jamaica and the Dominican Republic revealed females to be significantly larger than males in three measurements and males were significantly larger than females in two measurements. Generally, low coefficients of variation were found in samples of both sexes. The highest value obtained was 5.7 for length of phalanx 1 (digit III) in the sample from Old Providence Island. Two species—*Natalus micropus* and *N. tumidifrons*—were recognized within this complex. The chief difference between the species was the larger overall size of *N. tumidifrons*. *N. tumidifrons* is confined to the Bahamas and is considered to be monotypic. Two subspecies are recognized in *N. micropus* with the nominate subspecies occurring on Old Providence Island, Jamaica, and Hispaniola, and *N. m. macer* on Cuba and the Isle of Pines.

INTRODUCTION

The bats of the genus *Natalus* belong to the monotypic family Natalidae. In the West Indies members of the genus occur on the Greater and Lesser Antilles, the Bahamas, and Old Providence Island (off the

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Caribbean coast of Nicaragua). On the continental mainland they occur from Mexico to Brazil as well as on the coastal islands of Trinidad and Curaçao, off the northern coast of South America. Beginning with the description of *Natalus stramineus* by Gray in 1838, the taxonomic history of the family Natalidae has been characterized by a degree of confusion for most of the first century of chiropteran classification. During this period, the genus *Natalus*, usually allied with *Furipterus* and *Thyroptera*, was variously placed in the Phyllostomidae, Vespertilionidae, Emballonuridae, and Noctilionidae. In 1899 Miller, supported by conclusions of H. Allen (1892, 1894), proposed the Natalidae as a family containing *Chilonatalus* and *Amorphochilus* in addition to the above genera. In the same paper, Miller (1899) also reviewed the taxonomic history of the family up to that date. Miller (1906) described and added the new genus *Phodotes* to the family and a year later (Miller, 1907) grouped it with *Natalus*, *Chilonatalus*, and *Nyctiellus* in the Natalidae, placing *Furipterus* and *Amorphochilus* in the Furipteridae, and *Thyroptera* in the Thyropteridae.

Based on anatomical characteristics, Winge (1941) relocated the Natalidae as a division (Natalini) of the Vespertilionidae, including the genera "*Natalis*," *Thyroptera, Myzopoda, Amorphochilus*, and *Furia* (*Furipterus*), and suggesting also that they originated in the Old World. The taxonomic arrangement by Miller (1907) was reevaluated by Simpson (1945), who modified it by reducing *Chilonatalus* and *Phodotes* to subgenera of *Natalus*, thus leaving the Natalidae with two genera (*Natalus* and *Nyctiellus*). In perhaps the most significant contribution after Miller (1899, 1907), Dalquest (1950) discussed the taxonomic status of the genera of Natalidae and concluded that there was only a single genus in the family, *Natalus*, with three subgenera, *Natalus* (including *Phodotes*), *Chilonatalus*, and *Nyctiellus*. In his review, Dalquest also predicted the reduction of some nominal species within the genus to subspecific level. This arrangement was followed by Cabrera (1957), who, in addition to *Phodotes*, suggested that *Chilonatalus* was inseparable from *Natalus* even as a subgenus.

Although Hall and Kelson (1959) suggested that the nominal forms of the subgenus *Chilonatalus* (Miller, 1898)—*Natalus micropus* (Dobson, 1880) from Jamaica, *N. brevimanus* (Miller, 1898) from Old Providence Island, *N. tumidifrons* (Miller, 1903) from the Bahamas, and *N. macer* (Miller, 1914) from Cuba and Isle of Pines—might be only subspecific forms of *micropus*, they were treated as distinct species by these authors. Later, Varona (1974) without presenting any additional evidence treated all of these forms as subspecies of *N. micropus* and adopted the suggestion of Cabrera (1957) to not recognize the subgenus *Chilonatalus*. Finally, this arrangement has been followed by Hall (1981) without additional consideration.

In the last revision of natalid bats (Goodwin, 1959), only the larger forms belonging to the subgenus *Natalus* were included. Recently Kerridge and Baker (1978) have pointed out the need for a revision of the taxonomic status of the bats of *Natalus micropus*-complex. The aims of this study were to analyze in detail variation throughout the geographical range of the group. Univariate and multivariate analyses were used to examine the relationship among the populations involved.

METHODS AND MATERIALS

A total of 229 specimens was examined during this study. Most of them were conventional museum specimens preserved as skins and skulls, and specimens in alcohol with skulls removed. Additional material examined included complete skeletons, skin only, skull only, and complete fluid-preserved specimens.

External and cranial measurements were taken by means of dial calipers. All measurements are given in millimeters. Measurements were taken as follows: *length of forearm*—from the posteriormost projection of the elblow to the anteriormost portion of the wrist joint with the wing flexed; *length of metacarpal III*—distance from the wrist to the distal end of the third metacarpal; *length of the phalanx 1 (digit III)*—distance from the proximal to the distal end of the first phalanx of digit III; *greatest length of skull*—greatest distance from the anteriormost projection of the incisors to the posterior portion of the occipital bone; *condylobasal length*—distance from the posteriormost projection of exoccipital condyles to the anteriormost projection of premaxillae; *zygomatic breadth*—greatest width across zygomatic arches at right angles to logitudinal axis of cranium; *postorbital breadth*—least width across postorbital constriction, measured at right angles to the long axis of the 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; *length of maxillary toothrow*—distance from the posterior lip of alveolus of M^3 to the anterior lip of alveolus of canine; *breadth across upper molars*—greatest distance from labial margins of the upper molars at the widest point; *depth of braincase*—distance from the line along the flat part of the braincase to a line on the midventral part of the cranium touching the palate and the basioccipital.

Based on their geographical distribution, all adult specimens examined were grouped in five samples for males and females as follows: Bahamas; Cuba, including Isle of Pines; Jamaica; Dominican Republic; Old Providence Island. Statistical analyses were performed on an IBM-360 computer at Carnegie-Mellon University and a DEC-10 computer at the University of Pittsburgh. Univariate analyses were performed using the UNIVAR program. This program yields standard statistics (mean, range, standard deviations, standard error of the mean, variance, and coefficient of variation), and employs a single classification analyses of variance (ANOVA; F-test, significance level 0.05) to test for significant differences between or among means (Sokal and Rohlf, 1969). In addition, multivariate analyses were performed for both sexes to determine the degree of divergence among samples. Stepwise discriminant analysis and canonical analysis (BMDP7M, Dixon and Brown, 1977) perform a multiple discriminant analysis in a stepwise manner, selecting the variable entered by finding the variable with the greatest F value. The F value for inclusion was set at 0.01, and the F value for deletion was set at 0.05. Canonical coefficients were derived by multiplying the coefficient of each discriminant function by the mean of each corresponding variable. The program also classifies individuals, placing them with the group that they are nearest to on the discriminant functions.

RESULTS

Nongeographic Variation

Two kinds of nongeographic variation are discussed—secondary sexual variation and individual variation. Because of the limited size of the samples available, variation with age could not be analyzed.

Secondary sexual variation.—Using single classification analysis of variance, males were tested against females of two geographical samples (Jamaica and Dominican Republic) to learn if the sexes were significantly different in the characters studied. The results of these analyses (Table 1) demonstrated that in the 12 external and cranial measurements tested, females were significantly larger than males in two measurements (length of forearm and length of metacarpal III) in specimens from both samples and in one measurement (length of phalanx 1, digit III) in specimens from the Dominican Republic. The means for females averaged 0.1 mm larger in condylobasal length in specimens from both islands, and in length of phalanx 1 (digit III) and greatest length of skull in specimens from Jamaica and Dominican Republic, respectively. Of the remaining seven measurements, the sexes averaged the same in four (zygomatic breadth, postorbital breadth, length of maxillary toothrow, and breadth across upper molar). Males from both samples were significantly larger than females in depth of braincase, and in breadth of braincase in specimens from Jamaica. Males from the Dominican Republic were also 0.1 mm larger than females in mastoid breadth.

In conclusion, specimens from both samples reveal secondary sexual variation in size, and therefore, males and females were treated separately for analysis of geographic variation.

Individual variation.—In general, low coefficients of variation were found for all the characters studied in both sexes in samples from Jamaica and Dominican Republic (Table 1), as would be expected for minute-sized bats (Long, 1968, 1969) such as *Natalus*. Although external measurements generally have relatively high individual variation, depth of braincase (CV, 1.9 to 4.2) was found to vary most among the 12 external and cranial characters studied. The remaining measurements had coefficient values of 3.8 or less.

In the analysis of geographical variation of all samples (Table 2), additional coefficients of variation were obtained. For all samples, variation in external measurements was found to be higher (1.6 to 5.7) than in cranial measurements (0.9 to 4.2). The highest individual variation was found in length of metacarpal III (5.6) and length of phalanx 1 (digit III) (5.7), both from the Old Providence Island sample. Of cranial measurements, depth of braincase (1.2 to 4.2), postorbital constriction (1.8 to 4.2), and breadth across upper molar (1.9 to 4.2)

Table 1.—*Secondary sexual variation in external and cranial measurements of samples of the* Natalus micropus-*complex from Jamaica and the Dominican Republic. Statistics given are number, mean, two standard errors, range, coefficient of variation and F_s value. Means for males and females that are significantly different at* P < *0.05 level are marked with an asterisk.*

Locality	Sex	N	Mean	(Range) + 2 SE	CV	(F_s)
			Length of forearm			
Jamaica	♂	21	34.0	(32.5–35.2) + 0.31	2.1	8.269*
Jamaica	♀	41	34.6	(32.6–36.1) + 0.21	1.9	
Dominican Republic	♂	32	32.9	(30.6–34.4) + 0.28	2.4	7.296*
Dominican Republic	♀	11	33.6	(32.6–35.3) + 0.50	2.5	
			Length of metacarpal III			
Jamaica	♂	21	31.8	(30.2–33.1) + 0.32	2.3	15.541*
Jamaica	♀	41	32.6	(30.8–34.1) + 0.25	2.4	
Dominican Republic	♂	32	30.7	(29.2–31.9) + 0.25	2.3	4.113*
Dominican Republic	♀	10	31.2	(30.5–32.4) + 0.44	2.2	
			Length of phalanx 1 (digit III)			
Jamaica	♂	21	13.6	(12.7–14.3) + 0.20	3.4	1.770
Jamaica	♀	41	13.7	(12.6–15.2) + 0.16	3.7	
Dominican Republic	♂	32	12.9	(12.1–13.6) + 0.15	3.3	9.056*
Dominican Republic	♀	10	13.4	(12.6–14.2) + 0.30	3.6	
			Greatest length of skull			
Jamaica	♂	16	14.3	(13.9–15.0) + 0.13	1.8	0.226
Jamaica	♀	38	14.3	(14.0–14.8) + 0.06	1.3	
Dominican Republic	♂	31	14.1	(13.6–14.5) + 0.07	1.5	2.697
Dominican Republic	♀	11	14.3	(13.9–14.6) + 0.11	1.3	
			Condylobasal length			
Jamaica	♂	13	12.4	(12.1–12.9) + 0.11	1.5	0.782
Jamaica	♀	33	12.5	(12.1–12.8) + 0.67	1.5	
Dominican Republic	♂	31	12.4	(12.2–12.7) + 0.05	1.2	0.814
Dominican Republic	♀	11	12.5	(12.3–12.7) + 0.09	1.2	
			Zygomatic breadth			
Jamaica	♂	13	6.5	(6.3–6.6) + 0.04	1.2	0.245
Jamaica	♀	35	6.5	(6.0–6.7) + 0.05	2.2	
Dominican Republic	♂	30	6.5	(6.1–6.7) + 0.05	2.1	0.064
Dominican Republic	♀	10	6.5	(6.1–6.6) + 0.10	2.4	
			Postorbital breadth			
Jamaica	♂	16	2.6	(2.5–2.9) + 0.05	3.8	0.006
Jamaica	♀	39	2.6	(2.5–2.8) + 0.02	2.7	
Dominican Republic	♂	32	2.7	(2.5–2.9) + 0.03	3.3	0.507
Dominican Republic	♀	11	2.7	(2.6–2.9) + 0.06	3.8	
			Breadth of braincase			
Jamaica	♂	16	6.0	(5.8–6.2) + 0.06	2.1	7.149*
Jamaica	♀	38	5.9	(5.7–6.1) + 0.03	1.6	
Dominican Republic	♂	32	6.0	(5.7–6.3) + 0.05	2.4	2.347
Dominican Republic	♀	11	6.0	(5.8–6.2) + 0.07	2.0	

Table 1.—*Continued.*

Locality	Sex	N	Mean	(Range) + 2 SE	CV	(F_s)
			Mastoid breadth			
Jamaica	♂	12	6.3	(6.2–6.4) + 0.05	1.4	0.085
Jamaica	♀	33	6.3	(6.1–6.5) + 0.04	1.6	
Dominican Republic	♂	32	6.4	(6.2–6.6) + 0.04	1.9	1.073
Dominican Republic	♀	10	6.3	(6.2–6.5) + 0.06	1.5	
			Length of maxillary toothrow			
Jamaica	♂	15	5.9	(5.7–6.1) + 0.05	1.6	0.027
Jamaica	♀	38	5.9	(5.7–6.1) + 0.04	1.9	
Dominican Republic	♂	31	5.9	(5.6–6.1) + 0.04	1.9	2.092
Dominican Republic	♀	11	5.9	(5.8–6.0) + 0.04	1.1	
			Breadth across upper molars			
Jamaica	♂	16	4.3	(4.1–4.4) + 0.05	2.2	0.163
Jamaica	♀	38	4.3	(4.0–4.6) + 0.04	3.0	
Dominican Republic	♂	31	4.4	(4.2–4.6) + 0.03	2.0	0.625
Dominican Republic	♀	11	4.4	(4.2–4.5) + 0.05	2.0	
			Depth of braincase			
Jamaica	♂	16	5.0	(4.8–5.2) + 0.06	2.5	8.744*
Jamaica	♀	38	5.0	(4.7–5.2) + 0.03	3.0	
Dominican Republic	♂	32	5.0	(4.7–6.2) + 0.07	4.2	6.025*
Dominican Republic	♀	11	4.8	(4.7–5.0) + 0.06	1.9	

length of maxillary toothrow (females) were the characters with least overlap. The remainder of the characters, 10 for males and two for females, showed the samples studied grouping in non-overlapping subset.

Because the population *Natalus* from the Dominican Republic was not previously known, we compared samples from the Jamaica and Dominican Republic populations with the following results (Table 1). Males from Jamaica were significantly larger than males from the Dominican Republic in the three external measurements and 0.2 mm larger in greatest length of skull, whereas males from the Dominican Republic were 0.1 mm larger than the Jamaica sample in postorbital breadth, mastoid breadth, and breadth across upper molars. In the remaining five measurements, both samples averaged the same. In the case of females, Jamaican populations were significantly larger from those of the Dominican Republic in four measurements (length of forearm, length of metacarpal III, length of phalanx 1 (digit III), and depth of braincase. In three of the remaining measurements (postorbital constriction, breadth of braincase, and breadth across upper molars), females from the Dominican Republic averaged 0.1 mm larger than those

Table 2.—*Geographic variation in external and cranial measurements of 10 samples (five samples of males, and five samples of females) of the* Natalus micropus*-complex. Statistics given are sample size, mean, two standard errors of the mean, range, coefficient of variation, F-value, critical F-value, and results of SS-STP analysis showing nonsignificant subsets. Groups of means not significantly different at the 5% level are marked ns.*

Sex and locality	N	Mean ± 2 SE	Range	CV	F_s / F	Results SS-STP		
		Length of forearm						
Male								
Bahamas	6	34.1 ± 0.49	33.2–34.7	1.8	12.18	I		
Jamaica	16	34.0 ± 0.38	32.5–35.2	2.3	2.76	I		
Dominican Republic	32	32.9 ± 0.28	30.6–34.4	2.4			I	
Old Providence	8	32.5 ± 0.60	30.7–33.4	2.6			I	
Cuba	8	32.7	32.2–33.1					
Female								
Jamaica	37	34.6 ± 0.22	32.6–36.1	2.0	19.58	I		
Dominican Republic	11	33.6 ± 0.50	32.6–35.3	2.5	2.76		I	
Old Providence	4	33.1 ± 0.53	32.3–33.5	1.6			I	I
Cuba	5	32.4 ± 0.70	31.0–32.9	2.4				I
Bahamas	2	33.5	33.5					
		Length of metacarpal III						
Male								
Bahamas	6	32.2 ± 0.59	31.0–33.1	2.3	9.884	I		
Jamaica	16	31.8 ± 0.39	30.2–33.1	2.4	2.76	I		
Dominican Republic	32	30.7 ± 0.25	29.2–31.9	2.3			I	
Old Providence	8	30.3 ± 1.20	26.2–31.4	5.6			I	
Cuba	8	31.3	30.3–32.4					
Female								
Jamaica	37	32.7 ± 0.26	30.8–34.1	2.5	16.001	I		
Old Providence	4	31.5 ± 0.59	30.6–31.9	1.9	2.76		I	
Dominican Republic	10	31.2 ± 0.44	30.5–32.4	2.2			I	
Cuba	5	30.8 ± 0.72	30.0–32.1	2.6			I	
Bahamas	2	33.0	32.8–33.2					
		Length of phalanx 1 (digit III)						
Male								
Bahamas	6	14.7 ± 0.34	14.3–15.3	2.8	30.161	I		
Jamaica	16	13.6 ± 0.23	12.9–14.3	3.4	2.76		I	
Dominican Republic	32	12.9 ± 0.15	12.1–13.6	3.3				I
Old Providence	8	12.8 ± 0.51	11.2–13.8	5.7				I
Cuba	8	13.9	13.6–14.6					
Female								
Cuba	4	14.3 ± 0.52	13.7–14.9	3.6	3.740	I		
Jamaica	37	13.7 ± 0.17	12.6–15.2	3.9	2.76	I	I	
Old Providence	4	13.4 ± 0.39	13.0–13.8	2.9		I	I	
Dominican Republic	10	13.4 ± 0.30	12.6–14.2	3.6			I	
Bahamas	2	14.7	14.4–14.9					

Table 2.—*Continued.*

Sex and locality	N	Mean ± 2 SE	Range	CV	F_s F	Results SS-STP		
		Greatest length of skull						
Male								
Bahamas	6	15.6 ± 0.20	15.2–15.9	1.6	71.264	I		
Jamaica	16	14.3 ± 0.13	13.9–15.0	1.8	2.76		I	
Dominican Republic	31	14.1 ± 0.07	13.6–14.5	1.5			I	I
Old Providence	8	13.9 ± 0.18	13.5–14.3	1.9				I
Cuba	2	14.6	14.4–14.8					
Female								
Jamaica	37	14.3 ± 0.06	14.0–14.8	1.3	4.903	I		
Dominican Republic	11	14.3 ± 0.11	13.9–14.6	1.3	2.76	I	I	
Cuba	5	14.2 ± 0.38	13.5–14.6	3.0		I	I	
Old Providence	3	13.8 ± 0.55	13.3–14.2	3.4			I	
Bahamas	2	15.6	15.4–15.8					
		Condylobasal length						
Male								
Bahamas	6	13.8 ± 0.12	13.6–14.0	1.1	136.135	I		
Jamaica	13	12.4 ± 0.11	12.1–12.9	1.5	2.76		I	
Dominican Republic	31	12.4 ± 0.05	12.2–12.7	1.2			I	
Old Providence	5	12.2 ± 0.15	12.1–12.5	1.4			I	
Cuba	1	12.6						
Female								
Cuba	4	12.7 ± 0.17	12.5–12.9	1.3	2.339	ns		
Old Providence	3	12.5 ± 0.29	12.3–12.8	2.0				
Jamaica	33	12.5 ± 0.07	12.1–12.8	1.5				
Dominican Republic	11	12.5 ± 0.09	12.3–12.7	1.2				
Bahamas	2	13.7	13.6–13.8					
		Zygomatic breadth						
Male								
Bahamas	6	7.1 ± 0.08	7.0–7.3	1.4	56.297	I		
Dominican Republic	30	6.5 ± 0.05	6.1–6.7	2.1	2.76		I	
Jamaica	13	6.5 ± 0.04	6.3–6.6	1.2			I	
Old Providence	8	6.4 ± 0.09	6.3–6.7	2.0			I	
Cuba	2	6.7	6.6–6.7					
Female								
Old Providence	3	6.5 ± 0.07	6.5–6.6	0.9	0.416	ns		
Dominican Republic	10	6.5 ± 0.10	6.1–6.6	2.4				
Cuba	4	6.5 ± 0.16	6.3–6.7	2.5				
Jamaica	34	6.5 ± 0.05	6.0–6.7	2.1				
Bahamas	2	7.3	7.2–7.4					

Table 2.—*Continued.*

Sex and locality	N	Mean ± 2 SE	Range	CV	F_s F	Results SS-STP		
			Postorbital breadth					
Male								
Bahamas	6	2.8 ± 0.04	2.8–2.9	1.8	11.259	I		
Dominican Republic	32	2.7 ± 0.03	2.5–2.9	3.3	2.76		I	
Jamaica	16	2.6 ± 0.05	2.5–2.9	3.8			I	
Old Providence	8	2.6 ± 0.05	2.5–2.7	2.5			I	
Cuba	2	2.8	2.7–2.8					
Female								
Dominican Republic	11	2.7 ± 0.06	2.6–2.9	3.8	1.944	ns		
Jamaica	37	2.6 ± 0.02	2.5–2.8	2.7				
Old Providence	3	2.6	2.6					
Cuba	5	2.6 ± 0.10	2.4–2.7	4.2				
Bahamas	2	2.9	2.8–2.9					
			Breadth of braincase					
Male								
Bahamas	6	6.4 ± 0.06	6.3–6.5	1.2	21.145	I		
Dominican Republic	32	6.0 ± 0.05	5.7–6.3	2.4	2.76		I	
Jamaica	16	6.0 ± 0.06	5.8–6.2	2.1			I	
Old Providence	8	5.8 ± 0.08	5.7–6.0	2.0				I
Cuba	2	5.9	5.8–5.9					
Female								
Dominican Republic	11	6.0 ± 0.07	5.8–6.2	2.0	1.613	ns		
Jamaica	37	5.9 ± 0.03	5.7–6.1	1.6				
Old Providence	3	5.9 ± 0.07	5.8–5.9	1.0				
Cuba	4	5.9 ± 0.17	5.7–6.1	3.0				
Bahamas	2	6.4	6.3–6.4					
			Mastoid breadth					
Male								
Bahamas	5	6.9 ± 0.09	6.8–7.0	1.5	42.536	I		
Dominican Republic	32	6.4 ± 0.04	6.2–6.6	1.9	2.76		I	
Jamaica	12	6.3 ± 0.05	6.2–6.4	1.4			I	
Old Providence	3	6.2 ± 0.12	6.1–6.3	1.6			I	
Cuba	1	6.5						
Female								
Dominican Republic	10	6.3 ± 0.06	6.2–6.5	1.6	0.331	ns		
Cuba	4	6.3 ± 0.08	6.2–6.4	1.3				
Jamaica	33	6.3 ± 0.04	6.1–6.5	1.6				
Old Providence	2	6.3 ± 0.10	6.2–6.3	1.1				
Bahamas	2	7.0	6.8–7.1					

Table 2.—*Continued.*

Sex and locality	N	Mean ± 2 SE	Range	CV	F_s F	Results SS-STP		
			Length of maxillary toothrow					
Male								
Bahamas	6	6.6 ± 0.11	6.4–6.8	2.1	81.235	I		
Jamaica	15	5.9 ± 0.05	5.7–6.1	1.6	2.76		I	
Dominican Republic	31	5.9 ± 0.04	5.6–6.1	1.9			I	
Old Providence	8	5.8 ± 0.05	5.7–5.9	1.3				I
Cuba	3	6.0	5.9–6.1					
Female								
Cuba	5	6.0 ± 0.07	5.9–6.1	1.4	3.681	I		
Dominican Republic	11	5.9 ± 0.04	5.8–6.0	1.1	2.76	I	I	
Jamaica	37	5.9 ± 0.04	5.7–6.1	1.9			I	
Old Providence	4	5.8 ± 0.05	5.8–5.9	0.9			I	
Bahamas	2	6.7	6.6–6.7					
			Breadth across upper molars					
Male								
Bahamas	6	4.9 ± 0.08	4.8–5.0	2.0	63.730	I		
Dominican Republic	31	4.4 ± 0.03	4.2–4.6	1.9	2.76		I	
Old Providence	8	4.3 ± 0.12	4.0–4.5	3.8			I	
Jamaica	16	4.3 ± 0.05	4.1–4.4	2.2			I	
Cuba	3	4.5	4.5–4.6					
Female								
Dominican Republic	11	4.4 ± 0.05	4.2–4.5	2.0	1.636	ns		
Old Providence	3	4.4 ± 0.13	4.3–4.5	2.6				
Cuba	5	4.3 ± 0.16	4.1–4.5	4.2				
Jamaica	37	4.3 ± 0.04	4.0–4.6	3.0				
Bahamas	2	4.9	4.9					
			Depth of braincase					
Male								
Bahamas	6	5.1 ± 0.08	5.0–5.3	2.0	3.819	I		
Jamaica	16	5.0 ± 0.06	4.8–5.2	2.5	2.76	I	I	
Dominican Republic	32	5.0 ± 0.07	4.7–6.0	4.2		I	I	
Old Providence	6	4.8 ± 0.08	4.7–5.0	2.0			I	
Cuba	2	4.8	4.7–4.8					
Female								
Jamaica	37	5.0 ± 0.03	4.8–5.2	1.9	9.470	I		
Dominican Republic	11	4.8 ± 0.06	4.7–5.0	1.9	2.76		I	
Cuba	4	4.8 ± 0.15	4.7–5.0	3.1			I	
Old Providence	3	4.7 ± 0.07	4.7–4.8	1.2			I	
Bahamas	2	5.1	5.1					

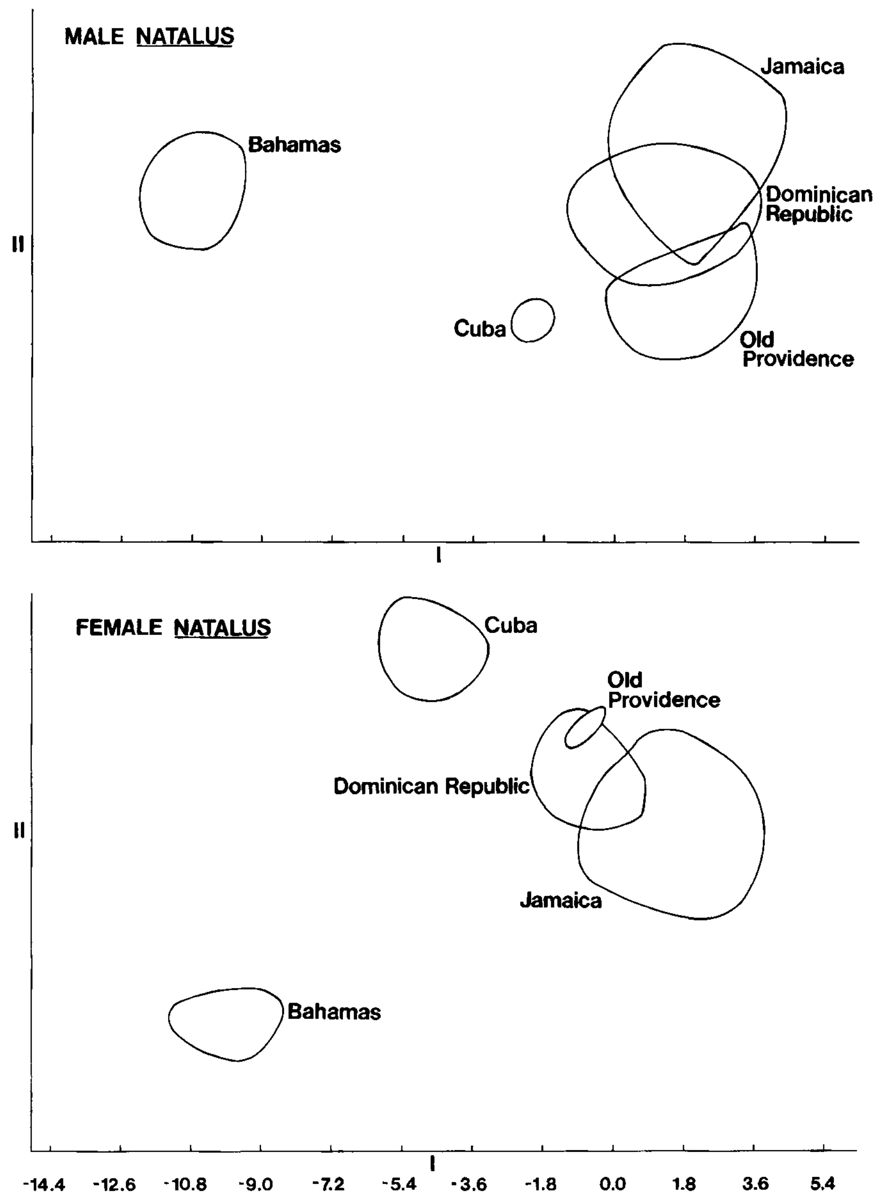

Fig. 1.—Two-dimensional projection of the first two canonical variates of male (upper) and female (lower) samples of the *Natalus micropus*-complex, based on a classification of variance-covariance among three external and nine cranial measurements.

Table 3.—*Variables used in discriminant function analysis of males and females of the* Natalus micropus-*complex. Characters are listed in order of their usefulness in distinguishing groups, with the character with the greatest between-groups variance and the least within-groups variance being selected first. The statistics are recalculated at each step.*

Step	Character	F-value	U-statistic
	Males		
1)	Condylobasal length	102.20	0.0952
2)	Length of phalanx 1 (digit III)	7.49	0.0555
3)	Breadth across upper molars	5.27	0.0367
4)	Length of forearm	3.04	0.0281
5)	Depth of braincase	2.88	0.0217
6)	Mastoid breadth	2.32	0.0175
7)	Postorbital breadth	1.21	0.0154
8)	Length of maxillary toothrow	1.13	0.0137
9)	Length of metacarpal III	1.38	0.0119
10)	Zygomatic breadth	0.62	0.0110
11)	Breadth of braincase	0.88	0.0100
12)	Greatest length of skull	0.62	0.0093
	Females		
1)	Length of maxillary toothrow	25.94	0.2881
2)	Length of forearm	23.53	0.0874
3)	Length of phalanx 1 (digit III)	6.79	0.0521
4)	Mastoid breadth	5.71	0.0328
5)	Condylobasal length	3.75	0.0235
6)	Greatest length of skull	2.94	0.0178
7)	Depth of braincase	4.86	0.0116
8)	Breadth of braincase	1.97	0.0095
9)	Length of metacarpal III	1.44	0.0081
10)	Zygomatic breadth	1.29	0.0070
11	Postorbital breadth	0.66	0.0065
12)	Breadth across upper molars	0.45	0.0061

from Jamaica, whereas the samples averaged the same in the other five.

Multivariate Analyses.—Canonical analyses provides a procedure for graphically representing phenetic relationship among samples with the characters weighted by variance-covariance analysis. Examination of the two-dimensional plots of the male and female samples of the *micropus*-complex presented in Fig. 1 reveals two distinct groups well separated on the first variate. In the males, the Bahamas sample is found on the left side of the plot, whereas those from Jamaica, the Dominican Republic, Old Providence Island, and Cuba are grouped on the right. In this latter group, Cuba is found close to the other three samples but is separated from them on Variate I, whereas the other samples overlap. In the females, the sample from the Bahamas is found

Table 4.—*Classification matrix for male and female samples of the* Natalus micropus-*complex, based upon the discriminant functions of 12 morphometric characters. Values indicate the number of individuals classified into each group.*

Sample	Classification groups 1	2	3	4	5
Males					
1) Jamaica	8	1	0	1	0
2) Dominican Republic	2	27	0	0	0
3) Cuba	0	0	1	0	0
4) Old Providence	0	0	0	3	0
5) Bahamas	0	0	0	0	5
Females					
1) Jamaica	30	0	0	0	0
2) Dominican Republic	0	9	0	0	0
3) Cuba	0	0	4	0	0
4) Old Providence	0	1	0	1	0
5) Bahamas	0	0	0	0	2

at the bottom of the left side of the plot, and those from Jamaica, the Dominican Republic, Old Providence Island, and Cuba, diagonally opposite, are clustered higher at the right side of the plot. The sample from Cuba is found at the top middle of the plot on Variate I, separated from the cluster of samples from Jamaica, the Dominican Republic, and Old Providence Island. The sample from the Bahamas is widely separated from Cuba on Variate II.

The amount of total dispersion accounted for male and female samples of the *micropus*-complex, respectively, was 85.4 and 61.7% for Variate I, and 7.8 and 24.2% for Variate II. In Table 3, characters used in this analysis are listed from the most useful to the least useful in discriminating groups. Characters with high positive canonical coefficients for Variate I (values greater than 1.5) were, in decreasing order of values, depth of braincase for males, and length of forearm, and condylobasal length for females. Those with high negative values include, ordered as above, condylobasal length, breadth across upper molars, and mastoid breadth for males, and mastoid breadth, length of maxillary toothrow, and postorbital breadth for females. In Variate II, positive values of more than 1.5 were, in decreasing order of value, depth of braincase, length of maxillary toothrow, and zygomatic breadth for males, and mastoid breadth for females. The characters with high negative values were postorbital breadth, breadth across upper molars, and greatest length of skull for males, and breadth of braincase, zygomatic breadth, mastoid breadth, and condylobasal length for females.

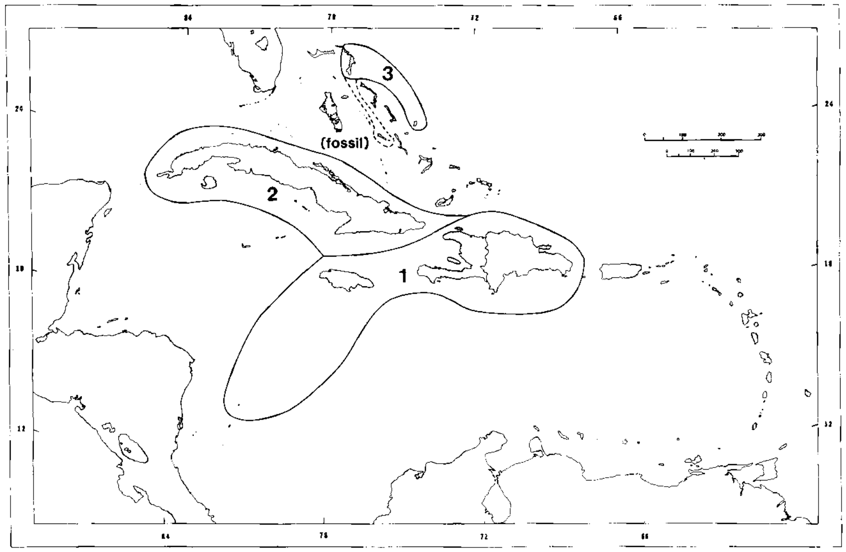

Fig. 2.—Map showing distribution of *Natalus micropus* and *N. tumidifrons*. 1) *N. m. micropus*; 2) *N. m. macer*; 3) *N. tumidifrons*.

A similar arrangement of the geographical relationship of the samples offered by the canonical analysis (Fig. 1) is suggested in the distribution of individuals by the classification matrix (Table 4). This analysis shows that of the individuals in the sample from Jamaica, two males are misclassified with specimens from the Dominican Republic and Old Providence, two males from the Dominican Republic are misclassified with the Jamaican sample, and a female from Old Providence is misclassified with the sample from the Dominican Republic. The remaining specimens including all the specimens from Cuba and the Bahamas involved in this analysis are classified in their proper group.

Taxonomic Conclusions

Based on our interpretations of the univariate and multivariate analyses, we consider that the *Natalus micropus*-complex represents two morphologically distinct species, *Natalus micropus* from Cuba, Jamaica, Hispaniola (Dominican Republic and Haiti), and Old Providence Island, and *N. tumidifrons* from the Bahama Islands. *Natalus tumidifrons* is clearly distinquishable from the several populations of *N. micropus* on the basis of larger size. In six characters for males and seven for females of the 12 characters studied, there was no overlap between the two species in the range of measurements when compared by sex.

Natalus tumidifrons is considered to be monotypic, whereas two subspecies are recognized within *N. micropus*. *N. m. micropus* occurs on Jamaica, Old Providence Island, and Hispaniola and *N. m. macer* occurs on Cuba and the Isle of Pines (see discussion below for distinguishing characters).

SYSTEMATIC ACCOUNTS

Genus *Natalus* Gray

1838. *Natalus* Gray, Mag. Zool. Bot., 2:496, December.

Type species.—*Natalus stramineus*

Natalus tumidifrons Miller, 1903

1903. *Chilonatalus tumidifrons* Miller, Proc. Biol. Soc. Washington, 16:119, September 30.
1950. *Natalus (Chilonatalus) tumidifrons*, Dalquest, J. Mamm., 31:443, November 21.
1974. *Natalus micropus tumidifrons*, Varona, Acad. Cien. Cuba, p. 32.

Holotype.—Adult male, in alcohol with skull removed, USNM 122024, obtained near Sandy Point, Watling Island [=San Salvador Island], Bahamas, by J. H. Riley on 12 July 1903; original number 157.

Measurements of holotype.—Length of forearm, 33.5; length of metacarpal III, 32.8; length of phalanx 1 (digit III), 14.4; greatest length of skull, 15.4; condylobasal length, 13.6; zygomatic breadth, 7.2; postorbital breadth, 2.9; breadth of braincase, 6.3; mastoid breadth, 6.8; length of maxillary toothrow, 6.6; breadth across upper molars, 4.9; depth of braincase, 5.1.

Distribution.—Bahama Islands: Watling and Great Abaco islands (Fig. 2). Also known as fossil from Great Exuma (Koopman et al., 1957).

Diagnosis.—Distinguished by large cranial size from the closely related *N. micropus*.

Comparisons.—Skull and teeth are larger in *Natalus tumidifrons* than in *Natalus micropus*. Occurring allopatrically both species can be clearly separated by cranial measurements (Table 2). Comparing the sexes of the two species separately there is no overlap in the following measurements: greatest length of skull, condylobasal length, zygomatic breadth, breadth of braincase (females only), mastoid breadth, length of maxillary toothrow, and breadth across upper molars. Standard statistics are given in Table 2.

Remarks.—The relationship of the insular populations of the genus *Natalus*, and the differences found between *N. tumidifrons* and *N. micropus* suggest a pattern comparable to other West Indian chiropteran taxa. Similar cases are represented by the genus *Pteronotus* with the sympatric species *P. macleayii* and *P. quadridens* in the Greater Antilles (Smith, 1972) and by the two allopatric species of the genus *Brachyphylla* (Swanepoel and Genoways, 1978) in the Greater Antilles, Lesser Antilles, and the Bahamas.

Specimens examined (59).—WATLING ISLAND [=San Salvador Is.]: N. Victoria Hill, 2 (USNM); no specific locality, 7 (USNM). GREAT ABACO ISLAND: no specific locality, 3 (2 FMNH, 1 AMNH); Marsh Harbor, Israel's Point, 47 (MCZ).

Natalus micropus

Distribution.—This species occurs on Cuba, Isle of Pines, Hispaniola (Dominican Republic), Jamaica, and Old Providence Island (Fig. 2).

Diagnosis.—Smaller cranially than the closely related *Natalus tumidifrons*, making it one of the smallest species of the genus.

Comparisons.—See account for *Natalus tumidifrons*.

Remarks.—Varona (1974) and Hall (1981) have proposed that *brevimanus* from Old Providence Island and *macer* from Cuba and Isle of Pines represent only subspecies of *micropus*, which was originally described from Jamaica. A univariate comparison (Table 2) of these geographical populations, including a sample of the previously unreported population from the Dominican Republic, indicates that the population from Cuba and Isle of Pines averaged larger than the samples from Jamaica, Dominican Republic, and Old Providence Island in length of phalanx 1 (digit III), length of maxillary toothrow, and condylobasal length. Although the males available from Cuba and Isle of Pines were not enough to be entered in the analyses, the means in the female sample averaged smaller than the other three populations in length of forearm, length of matacarpal III, postorbital breadth, and breadth of braincase. The multivariate analyses (Fig. 1) showed the samples from Jamaica, Dominican Republic, and Old Providence Island clustered at the right side of the plot separated from the population from Cuba and Isle of Pines on Variate I in both males and females.

In order to better understand the relationship of the populations of *Natalus micropus*, additional multivariate analyses of these populations were performed excluding *Natalus tumidifrons* from the Bahamas. This showed the sample from Cuba well separated from the other populations on Variate I in the females and on Variate I and II in the males. The populations from Jamaica, Dominican Republic, and Old Providence Island were grouped together and overlapping, with the Dominican Republic intermediate. The classification matrix indicated that 100% of the individuals from Cuba (both sexes) could be correctly identified using only two characters—length of forearm and length of phalanx 1 (digit III).

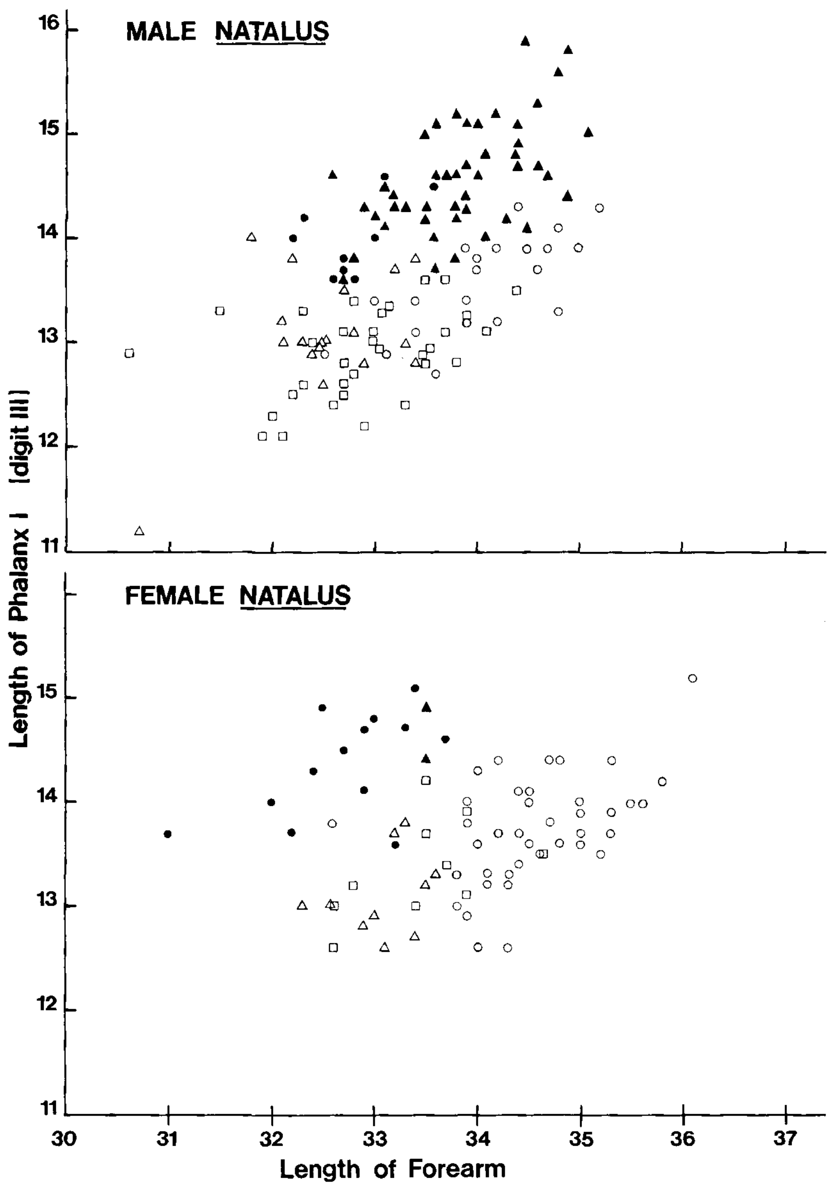

Fig. 3.—Bivariate plot of values of length of forearm and length of phalanx 1 (digit III) to show the relationship of samples of the *Natalus micropus*-complex. Open circles are specimens from Jamaica; closed circles from Cuba; open triangles from Old Providence Island; closed triangles from the Bahamas; open squares from Dominican Republic.

Because of the results of the classification analyses, we prepared a bivariate plot of length of forearm and length of phalanx 1 (digit III) of all samples, to determine the range of variation among them. Using only these two external measurements allowed us to include data for many specimens not used in the multivariate analyses. The bivariate plots (Fig. 3) show the Cuban samples of males and females are distinguishable from the samples from Jamaica, Dominican Republic, and Old Providence Island on the basis of these two characteristics. The specimens of *Natalus micropus* from Cuba have a longer phalanx 1 (digit III) and relatively shorter forearm than other populations of *Natalus micropus*. In these characteristics, the Cuban population is more similar to *N. tumidifrons* than other populations of *N. micropus*. Based on results of this analysis of geographic variation in *Natalus micropus*, we believe that the relationship among these populations is best represented by considering them to be two subspecies.

Natalus micropus micropus Dobson, 1880

1880. *Natalus micropus* Dobson, Proc. Zool. Soc. London, p. 443, October.
1898. *Natalus (Chilonatalus) brevimanus* Miller, Proc. Acad. Nat. Sci. Philadelphia, 50:328, July.
1907. *Chilonatalus brevimanus*, Elliot, Field Columbian Mus., Zool. Ser., 7:525.
1907. *Chilonatalus micropus*, Miller, Bull. U.S. Nat. Mus., 57:185.
1907. *Chilonatalus brevimanus*, Miller, Bull. U.S. Nat. Mus., 57:185.
1950. *Natalus (Chilonatalus) micropus*, Dalquest, J. Mamm., 31:443, November 21.
1950. *Natalus (Chilonatalus) brevimanus*, Dalquest, J. Mamm., 31:443, November 21.
1974. *Natalus micropus brevimanus*, Varona, Acad. Cien. Cuba, p. 31.
1974. *Natalus micropus micropus*, Varona, Acad. Cien. Cuba, p. 32.

Holotype.—Adult male, skin and skull, BMNH 80.12.14.1 from Kingston, Jamaica, obtained by G. E. Dobson.

Measurements of holotype.—Length of forearm, 33.5; greatest length of skull, 14.5; condylobasal length, 13.3; zygomatic breadth, 2.6; mastoid breadth, 6.3; length of maxillary toothrow, 6.1; breadth across upper molars, 4.4.

Distribution.—Jamaica, Hispaniola (Dominican Republic), and Old Providence Island (Fig. 2).

Comparisons.—*Natalus micropus micropus* is distinguishable from *Natalus micropus macer* by size differences in external measurements. In a bivariate plot (Fig. 3) male and female samples of *micropus* are separable from male and female samples of *macer* by a combination of the length of forearm (shorter) and length of phalanx 1 (digit III) (longer).

Remarks.—The population described as *brevimanus* (Miller, 1898) was considered a distinct species for a long time until it was recently reduced to a subspecies of *N. micropus* by Varona (1974). It is worthy of note that when this population was originally reported from Old

Providence Island, it was referred to *N. micropus* (Allen, 1890). Based upon our study, we do not believe that this population should be given subspecific designation. Individuals from Old Providence Island averaged smaller than others in many measurements, but the range of measurements overlapped with those from Jamaica and particularly Hispaniola.

The specimens reported herein from the Dominican Republic are the first known from the island of Hispaniola. In many characteristics the population was intermediate to, and overlapping with, those from Jamaica and Old Providence Island. The finding of *Natalus micropus micropus* on the island of Hispaniola gives additional evidence of the relative close faunal relationship of this island and Jamaica.

Specimens examined (142).—DOMINICAN REPUBLIC: Cueva No. 2 Los Patos, Barahona Province, 30 (UPS); Cueva Vicente, Samana Province, 14 (4 AMNH, 10 UPS). JAMAICA: Balaclava, 3 (AMNH); Kingston, 1 (BMNH); Moneague, 1 (USNM); Montego Bay, 2 (USNM); Port Antonio, 5 (USNM); St. Clair Cave, 2 mi S Ewarton, St. Catherine Parish, 53 (33 CM, 19 TTU, 1 AMNH); no specific locality, 2 (USNM). OLD PROVIDENCE ISLAND: no specific locality, 31 (28 USNM, 2 FMNH, 1 AMNH).

Natalus micropus macer Miller, 1914

1914. *Chilonatalus macer* Miller, Proc. Biol. Soc. Washington, 27:225, December.
1950. *Natalus (Chilonatalus) macer*, Dalquest, J. Mamm., 31:443, November 21.
1970. *Natalus micropus macer*, Viña Bayes and Deas Diaz, Acad. Cien. Cuba, Ser. Espelol. Carsol., 24:7.
1974. *Natalus micropus macer*, Varona, Acad. Cien. Cuba p. 32.

Holotype.—Adult female, in alcohol with skull removed, USNM 113724 from Cueva de la Majana, Baracoa, Cuba, obtained by William Palmer on 6 February 1902; original No. 699.

Measurements of holotype.—Length of forearm, 32.8; length of metacarpal III, 31.0; greatest length of skull, 14.3; condylobasal length, 12.8; zygomatic breadth, 6.7; postorbital breadth, 2.6; breadth of braincase, 6.1; mastoid breadth, 6.2; length of maxillary toothrow, 6.1; breadth across upper molars, 4.2; depth of braincase, 4.9.

Distribution.—Cuba and Isla de Pinos (Fig. 2).

Comparisons.—See account for *Natalus micropus micropus*.

Remarks.—When the population from Cuba was first reported, it was regarded as *N. micropus* (Miller, 1904; Allen, 1911), but was later named as a distinct species (Miller, 1914). More recently, this population was considered a subspecies of *N. micropus*. The current study supports this status proposed by Viña Bayes and Deas Diaz (1970) and Varona (1974) and adopted by later authors (Silva, 1979; Hall, 1981).

Specimens examined (28).—CUBA: Cueva de los Paredones, Ceiba del Agua, La Habana Province, 1 (AMNH); Finca Quinones, Pinar del Rio Province, 1 (MCZ); San Vicente, Pinar del Rio Province, 5 (4 AS, 1 AMNH); Cueva de la Majana, Baracoa, Oriente Province, 6 (2 USNM, 2 MCZ, 2 AMNH); Guantanamo, Oriente Province, 7 (USNM). ISLA DE PINOS: Cueva de Punta Brava, 8 (4 FMNH, 4 AMNH).

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