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Fossil Chiroptera from Cave Deposits in Central Cuba, with Description of Two New Species (Genera *Pteronotus* and *Mormoops*) and the First West Indian Record of *Mormoops megalophylla*

(Pp. 33—74, pls. II—IV, 2 text-figures)

Quirópteros Fósiles de Depósitos Cavernarios en la Región Central de Cuba, con Descripciones de Dos Nuevas Especies (Géneros *Pteronotus* y *Mormoops*) y el Primer Récord Antillano de *Mormoops megalophylla*

Kopalne nietoperze z osadów jaskiniowych środkowej Kuby, z opisem dwu nowych gatunków (rodzaje *Pteronotus* i *Mormoops*) i pierwszym stwierdzeniem *Mormoops megalophylla* na Antylach

Abstract. Fossil remains of bats discovered in two caves in Central Cuba are described. Only cavernicolous bats were represented. Three layers were recognized in the deposits, from which the remains of 15 species of bats (genera *Pteronotus*, *Mormoops*, *Macrotytus*, *Monophyllus*, *Brachyphylla*, *Phyllonycteris*, and *Natulus*) were recovered. Two of these (*Pteronotus pristinus* and *Mormoops magna*) are described as new, and a third one (*Mormoops megalophylla*) is recorded for the first time from the Antillean region. Chronocline variation consisting in an increase in size is demonstrated for 9 of the 13 species represented by adequate samples.

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INTRODUCTION

It is well established that fossil sequences contribute importantly to the understanding of various aspects of the evolution of a fauna. Unfortunately, very little progress has been achieved in this connection as regards West Indian Chiroptera, the major component of the mammalian fauna in the subregion. Only the bat fauna of Jamaica has been profitably discussed from this point of view (KOOPMAN and WILLIAMS 1951; WILLIAMS 1952); but an equivalent knowledge is almost completely lacking for the remaining islands.

Bat-bearing fossil deposits recently discovered in Cuban caves constitute the subject of this report. These collections are unparalleled, qualitatively and quantitatively, by any of the fossil deposits previously discovered in the West Indies, and the inferable age of the fossils adds considerable interest to the findings. Therefore, it is hoped that this report will represent a substantial addition to current knowledge of the evolution of the chiropteran fauna of the West Indies.

THE CAVES AND THE FOSSIL DEPOSITS

The „Motel Las Cuevas” (The Caves Motel) is a well known tourist center, located on a conspicuous miocene limestone hill (180 m above sea level and 6 km from the coast) at the city of Trinidad, in southern Las Villas Province (central Cuba). The motel is so named because it is built on top of a complex cave system of several kilometers of underground galleries, referred to by speleologists as the Trinidad cave system. Bat-bearing fossil deposits were discovered in two of the contiguous caves that compose the system, locally known as „Cueva de los Masones” (Masones Cave) and „Cueva del Jagüey” (Jagüey Cave). The deposits were located in sections of these caves into which access was not possible in historic times until 1967, when it was provided with the aid of dynamite while the caves were being conditioned for the exploitation of bat guano by the Organic Fertilizers Division.

Masones Cave

Masones Cave has a linear extension of 800 m and its entrance opens at 143 m above sea level. In 1968 the cave was to the fullest extent exploited for bat guano. The fossil deposits were located in one of the inner chambers, approximately 200 m from the entrance of the cave, and 14 m below the level of the entrance, representing the deepest point of the cave. The chamber is roughly rectangular, 15 by 6 m, the ceiling approximately 10 m high, and is reached through a narrow, steep gallery communicating with the central gallery of the cave. The depth of the guano from the lowest point of the present floor

was 4 m, as judged by a clearly marked line around the walls of the chamber (as well as by statements of men who had worked in the extraction). At various elevations below this level hundreds of small patches of guano containing bones still remained in the fissures and concavities of the wall.

The main fossil deposit of this chamber was a wall pocket (approximately 1 m above the lowest point of the chamber floor) of undisturbed material 1.3 m wide by 1.5 m high, with an average depth of 0.3 m from the outer surface to the inner wall of pocket. The rock section forming the ceiling of the pocket is part of a large structural shelf on the wall of the chamber. Internally the pocket communicates through a vertical passage with the top of the structural shelf, which is approximately on a level with the upper layers of the former guano deposit that filled the chamber to a depth of 4 m (see above). As a consequence, after the removal of the pocket deposit, there was room for a man to climb through the passage and reach the top of the shelf. For the upper layers of the pocket deposit, evidence of sedimentological origin through this passage is unquestionable.

Jagüey Cave

Jagüey Cave has a linear extension of 1,700 m and its entrance opens at 139 m above sea level. The cave has not been exploited for bat guano as yet (1973), although it has been conditioned for that purpose since 1968.

Jagüey Cave has two levels of galleries. At several places on the floor of the upper level, sink holes of varying sizes communicate with the lower level. Bat guano is almost absent on the upper level, but enormous deposits occur throughout the lower level. The fossil deposits were located in the deepest chamber of the lower level. Distance of this chamber from the cave entrance is 110 m, and the corresponding difference in elevation is 58 m; it is irregular in form, with an average diameter of 14 m. On a considerable extent of the floor surface and its subsurface (less than 40 cm deep), particularly near walls, skeletal remains of bats were concentrated in incredible numbers and formed a continuous mass of millions of bones in a loose matrix composed of mineralized guano and moderately coarse calcareous debris. The effect of flooding on this material was obvious everywhere and in some places gave the impression of a „river” of bones that once flowed down to the chamber.

MATERIALS AND METHODS

On October 2, 1969, the left half (approximately 65 cm) of the pocket deposit of Masones Cave was excavated to a depth of 1 m from the upper layer, and the osteological material obtained was called Collection Aa. Data on this excavation are shown in table 1. The majority of the small bone-bearing patches of guano found at different elevations on the walls of the chamber were also collected on the same date, and this material was called Collection B. On October 28, the right half of the pocket deposit was excavated (also to a depth of 1 m)

TABLE 1

Stratigraphic data of the wall pocket deposit of Masones Cave (Collection Aa)

LAYER			MATERIAL EXCAVATED			OSSEOUS CONTENT		
No.	Depth (cm)	Thickness (cm)	Dry Weight (kg)	Humidity (%)	Matrix	Num-ber*	Bones/kg	Description**
M4	surface	8	5.96	48.2	A very dark (<i>in situ</i>), moist material composed of recent (but not fresh) guano, charcoal (roughly cubic particles up to 2 cm in length), and coarse calcareous debris (average diameter of larger fragments, 2 cm)	735	123.3	Relatively uniform yellow (OO Y-14-5°)***, not fragile, and of a general appearance resembling fresh specimens. Metallic sound described for material from M1 and M2, lacking
M3	8	15	—	—	Very coarse calcareous debris (fragments up to 10 cm in diameter), charcoal (as in M4), and abundant minute shells of land snails, <i>Chondropoma</i> (<i>Chondropomorus</i>) <i>delatrenum</i> (d'ORBIGNY)	—	—	Extremely scanty and fragmentary
M2	23	53	36.44	40.9	A reddish brown (<i>in situ</i>), moderately compact (but loose when handled) material composed of mineralized guano and fine to moderately coarse calcareous debris	492	13.5	Stained light brown (average color, 0-8-8°), mineralized and extremely fragile (limb bones producing a noticeable metallic sound when gently tossed against a hard surface)
M1	76	24	15.86	38.4	Same as for M2, except color, which is dark gray	191	12.0	Same as for M2

* Refers to the total number of the following skeletal elements: complete cranium, rostral portion, mandibular ramus, humerus, radius, femur, and tibia.

** Detached from matrix and air dried.

*** „Colour Atlas” (VILLALOBOS and VILLALOBOS 1947).

to obtain a greater sample of crania and mandibles, and these were designated Collection Ab. On November 21, after removal of the rocks accumulated at the bottom of the pocket deposit during the exploitation of guano, excavation of the deposit was continued below the 1 m limit established in the October 2 excavation until a final depth of 1.5 m was reached (representing the lower limit of layer M1). Again, mostly crania and mandibles were recovered, and these were merged into Collection Ab.

On November 26, a trench was excavated in the chamber of Jagüey Cave where the surface-subsurface accumulations of bone were discovered. A flat area of the floor, not reached by these accumulations, was selected as an adequate site for the excavation. The trench, 3 m long by 1 m wide, was excavated until the structural floor of the chamber was reached at a depth of 2.7 m. Except for the clay at the surface level, a detailed examination failed to disclose a definite stratigraphy in this trench. Only faintly defined and discontinuous strata could be detected in the otherwise homogeneous material. Nevertheless, a complete vertical section, 50 by 50 cm, was removed on the basis of a somewhat arbitrary stratigraphy (table 2), and the osteological material recovered was called Collection C. At the same time, the surface and subsurface accumulations of bone were sampled at several places where fossils were exposed, and this material was designated Collection Da. On November 28 sampling was repeated to increase the number of crania and mandibles, and these were called Collection Db.

After removal from deposits, all material was packed in tightly closed polyethylene bags, and brought to the laboratory. Representative samples were separated to determine moisture content. To detach bones from matrix, heaps of material were gently laid by hand on a fine mesh screen and washed with water by spraying with moderate pressure. Skeletal remains were then collected and allowed to air dry. Only rarely were specimens incrustated with lime. The general appearance of the various skeletal materials thus processed is described in tables 1 and 2.

All skeletal material was carefully sorted to separate complete and partial crania (rostra), complete and partial lower jaws (rami), and the four long appendicular bones (only if complete): humerus, radius, femur, and tibia. The remaining skeletal elements were discarded. Only presumably adult specimens, as suggested by complete ossification, were selected. As a rule, crania of immature bats were seldom preserved, but mandibles and limb bones of young bats were common. The resultant 6,205 bones were identified by color markings with respect to deposits and layers. Distribution of total fossil material by collections is shown in table 3, and relative frequencies of osteological elements among collections are shown in fig. 1. All fossil material was deposited in the Institute of Zoology, Cuban Academy of Sciences.

Neontological material from the collections of the Academy of Sciences was used in comparisons, and is designated in tables and graphs, as well as in the text, by the notation R (Recent). For each taxon, cranial samples were balanced

TABLE 2
Stratigraphic data of the Jagüey Cave trench (Collection C)

LAYER			MATERIAL EXCAVATED			OSSEOUS CONTENT		
No.	Depth (cm)	Thickness (cm)	Dry Weight (kg)	Humidity (%)	Matrix	Number*	Bones/kg	Description**
13	surface	12	36.74	23.3	Exclusively clay (light gray)	—	—	Lacking
12	12	11	8.84	33.5	A reddish brown (<i>in situ</i>) material composed of moderately coarse calcareous debris and mineralized guano. The same applies to the rest of the layers	15	1.7	Degree of preservation quite similar to that in layers M1 and M2 of the Masones deposit, producing the same metallic sound described for said layers, but ranging from the average color of the older Masones layers (0—8°)*** to a very dark brown (OOS—3—10°). The same applies to the rest of the layers, as well as to material from the surface-subsurface accumulations of bone
11	23	29	34.54	32.4		146	4.2	
10	52	27	18.08	34.5		63	3.5	
9	79	19	23.59	35.0		35	1.5	
8	98	28	22.22	36.5		25	1.1	
7	126	10	6.92	39.8		32	4.6	
6	136	11	8.83	39.9		15	1.7	
5	147	16	10.74	40.0		51	4.8	
4	163	15	10.55	39.7		75	7.1	
3	178	15	8.18	40.7		25	3.1	
2	193	16	7.42	46.2		36	4.9	
1	209	61	80.97	39.3		73	0.9	
		270	277.62	37.0		591	2.1	

* Refers to the total number of the following skeletal elements: complete cranium, rostral portion, mandibular ramus, humerus, radius, femur, and tibia.

** Detached from matrix and air dried.

*** „Colour Atlas” (VILLALOBOS and VILLALOBOS 1947).

as far as possible by equivalent assembling of specimens of each sex from western, central, and eastern Cuba. Post-cranial material, on the other hand, was prepared from specimens collected in central Cuba, except for *Natalus macer* which combines specimens from eastern Cuba and the Isle of Pines. Although sexual dimorphism occurs in several of the taxa, males and females were combined in all neontological samples to facilitate comparisons with the fossil material. Nevertheless, pertinent examples of secondary sexual variation are described and illustrated.

Statistics computed for all fossil and neontological samples, according to respective deposits, layers, and taxa, included arithmetic mean, standard deviation, standard error, coefficient of variation, and observed range. For each

TABLE 3

Distribution of total fossil material (N = 6,205) by collections

Collection	Subcollection	Layer(s)	Bones*
A. Masones Cave wall pocket deposit (see Table 1)	a	M4	735
		M2	492
		M1	191
	b	M4	12
		M2	279
		M1	18
B. Masones Cave wall patches of bone-bearing guano			1,113
C. Jagüey Cave trench (see Table 2)		1—12	591
D. Jagüey Cave surface-subsurface bone accumulations	a		2,409
	b		365

* Refers to the total number of the following skeletal elements: complete cranium, rostraportion, mandibular ramus, humerus, radius, femur, and tibia, except for Collections Ab and Db which contain only crania and mandibular rami.

taxon, fossil samples from different deposits and layers, as well as corresponding neontological samples, were compared by means of Student's *t*-test. The .05 level of statistical significance was chosen for all comparisons between means. The measurements selected for statistical treatment were greatest length of skull, length of mandible, and length of humerus, the skeletal element occurring most frequently in all fossil deposits (fig. 1). Measurements were taken in millimeters with dial calipers and with the aid of a stereoscopic magnifier. The length of the skull was measured from the posteriormost projection of the occiput to the anteriormost projection of the premaxilla (except in *Mormoops*, in which this measurements was taken from the occipital condyles instead of the occiput). The length of the mandible was measured from the tip of the symphysis to the posteriormost projection of the condyle. The humerus was measured from the

outermost projection of the greater tuberosity to the equivalent projection of the distal articular surface.

I know of no published work on West Indian fossil or subfossil Chiroptera in which the limb bones were treated as extensively as in the present report. Certainly, the cranium is the most important skeletal element for taxonomic and statistical analyses but usually is the least frequently encountered element in most fossil deposits, as is clearly appreciated in fig. 1. In the absence of crania,

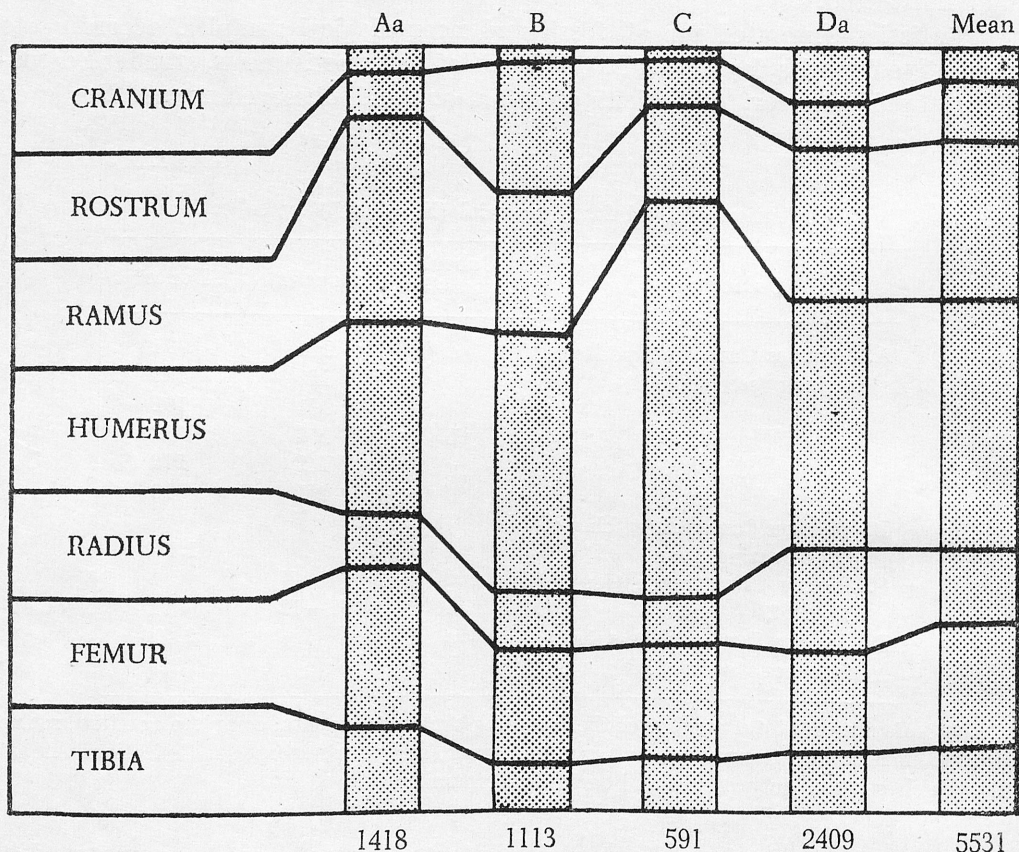


Fig. 1. Bar diagram representing relative frequencies of osteological elements among four fossil collections. Height of bar 100%. Notation on top of bar refers to corresponding collection (table 3); number on bottom indicates size of collection. Complete mandibles are counted as separate rami. Subcollections Ab and Db were excluded because only crania and mandibles were collected (see text)

mandibles — which occurred in the deposits more frequently than most limb bones except the humerus — are secondarily the best taxonomic indicators. Nonetheless, limb bones amplify the size of samples for quantitative analyses, and as well may increase the number of species detected in fossil material, although certain pairs of species (*Pteronotus fuliginosus* — *P. macleayi*), and even genera (*Erophylla* — *Phyllonycteris*), are extremely difficult to distinguish

on the basis of limb bones. Had only crania and mandibles been considered in this study, several species would not have been detected in some of the layers. Obviously, conclusions and inferences on the temporal ranges of these taxa would have been misleading. I found a study of limb bones to be useful and therefore emphasize their importance for others who may have occasion to examine similar fossil material in the future.

RESULTS

Within the four major collections of fossils herein considered 15 species of bats were identified, two of which represent undescribed taxa¹. These are shown in table 4 where it may be observed that 13 of the 15 species occurred in both caves, while 11 occurred in all four collections, suggesting a general picture of faunal continuity throughout the layers.

In no taxon could metrical or morphological differences be detected between samples from layers M1 and M2 of the wall pocket deposit of Masones Cave (Collection A), or between these samples and those from patches of bone-bearing guano at different elevations throughout the walls of the chamber (Collection B), except for material corresponding to the surface level marked on the walls; this latter is indistinguishable from material representing the surface layer (M4) of the pocket deposit. In accordance with these findings, all available specimens from layers M1 and M2, as well as those from the wall patches of guano below the former surface layer of the chamber deposit, were combined for statistical analyses and are identified by the notation M12. Likewise, specimens from wall patches corresponding to the surface layer of the chamber deposit were merged into those from layer M4 of the pocket deposit.

Remnant portions of a layer averaging 15 cm in depth, very similar in composition to layer M3 of the pocket deposit (see table 1), were found in wall patches underlying the surface level of the Masones chamber deposit. This evidence indicates that layers M4 and M3 were the surface and subsurface layers of the deposit that filled the whole chamber to a depth of 4 m prior to the exploitation of guano, and that their presence at a lower level (surface and subsurface layers of the pocket deposit) is the result of sequential overflowing and pouring through the vertical passage of the structural wall shelf described previously (see „Masones Cave”). On the other hand, layers M1 and M2 of the pocket deposit must have sedimented laterally and may represent the midlower section of the former chamber deposit, as the basal limit of the pocket deposit was about 1 m higher than the lowest point of the present floor of the chamber.

As regards Jagüey Cave, no significant differences were found in any taxon throughout the layers of the trench excavated in the deepest chamber (Collection

¹ In addition, ophidian vertebrae (possibly *Epicrates*) were found in layer M2 (Collection A), together with some remains (fragmentary coccyx, vertebrae, scapulae, and a femur) of an apparently undescribed species of capromyid rodent.

C), or between these samples and those from the surface-subsurface accumulations of bone at the same chamber (Collection D). Specimens from these two sources were also combined and are designated by the notation J. Most samples from layer J, however, differed significantly when compared to those from layers M12 and M4 of the Masones deposit.

It was stated before (see „Jagüey Cave”) that guano is almost absent on the upper level of Jagüey Cave, whereas huge deposits occur throughout the lower level, to which the upper level is connected by sink holes. On the basis of these circumstances, as well as of the flooded nature of the surface accumula-

TABLE 4

Distribution of taxa among fossil collections

Taxa	Masones cave				Jagüey cave	
	Collection A			Collection B	Collection C (1—12)	Collection D
	M1	M2	M4			
Mormoopidae						
<i>Pteronotus</i> sp.	X	X				X
<i>P. fuliginosus</i>		X	X	X	X	X
<i>P. macleayi</i>	X	X	X	X	X	X
<i>P. parnelli</i>	X	X	X	X	X	X
<i>Mormoops</i> sp.				X		
<i>M. blainvillei</i>			X		X	X
<i>M. megalophylla</i>	X	X		X	X	X
Phyllostomatidae						
<i>Macrotus waterhousei</i>					X	X
<i>Monophyllus redmani</i>	X	X	X	X	X	X
<i>Brachyphylla nana</i>	X	X	X	X	X	X
<i>Erophylla sezekorni</i>	X	X	X	X	X	X
<i>Phyllonycteris poeyi</i>	X	X	X	X	X	X
Natalidae						
<i>Natalus major</i>	X	X	X	X	X	X
<i>N. macer</i>	X	X	X	X	X	X
<i>N. lepidus</i>	X	X	X	X	X	X

tions of bone at the lower level, it is concluded that the guano deposits of Jagüey Cave were originally on the upper level of the cave and were subsequently washed down through sink holes to the lower level. Accordingly, materials herein designated by the notation J may be regarded as the product of redeposition. The absence of a definite stratigraphy for the trench, where bones were uniformly distributed along the vertical section of a homogeneous matrix (see table 2), further supports this assumption.

As a result of the above comparisons, three basic layers, M12, M4, and J, were statistically (but not qualitatively) recognized in the fossil deposits. All statistically significant differences between samples from these layers, as well as between these samples and the corresponding neontological ones,

on the basis of the three variates studied, are documented in table 5. *Erophylla* and all three species of *Natalus* were excluded from the table because significant differences were not detected among fossil samples of these taxa, and they appear to be indistinguishable from their present-day representatives. Also excluded were two other species herein described as new (genera *Pteronotus* and *Mormoops*) because these were represented in the deposits by material quantitatively inadequate for statistical treatment. Consequently, of the 13 species tested, 9 (69 %) varied significantly within the fossil layers and/or with respect to corresponding neontological samples.

A detailed inspection of table 5 reveals that whenever samples from layer M4 differed significantly from samples of either of the two other fossil layers (M12 or J), M4 samples had the larger mean value. Likewise, a larger mean value was invariably characteristic of J samples that differed significantly from M12 samples. In other words, samples from layer J were not, in any case, significantly smaller than those from M12 or larger than those from M4. As a consequence, several taxa were represented in the deposits by large (M4) and small (M12) specimens in Masones Cave, while specimens from contiguous Jagüey Cave were either statistically intermediate in size or indistinguishable from specimens of one or the other of the Masones layers. On the other hand, neontological samples were significantly larger than corresponding fossil samples from layer M4, except in two taxa where the respective samples were indistinguishable.

Any plausible interpretation of the phenomenon described above presupposes the discontinuous and alternate availability of access to the caves where the fossils were deposited. Obviously, had access to both caves been synchronously available throughout the temporal span involved in the deposition of the fossils, all three fossil layers would have been represented in both caves. The relative position in time of the fossil layers is, thus, inevitably linked to the evolutionary history of the caves themselves. In an attempt to ascertain that history, at least in its major respects, collaboration was requested from sedimentologists and speleologists of the Institute of Geography (Academy of Sciences).

On March, 1970, eight stratigraphic profiles exposed during previous extractions of guano in four of the caves composing the Trinidad cave system (Masones and Jagüey caves included) were studied with the purpose of establishing the sedimentological sequence of the system. Sediments were correlated on the basis of their physical nature, chemical composition and topographical location. Fossils were not used in this connection because bone content of the majority of these sediments was scanty and fragmentary². Results of this work have been published (VIÑA and FUNDORA 1970), and the reader is referred to this paper for a general map of the caves, descriptions and illustrations of the stratigraphic profiles, a correlation chart of the sediments studied, and a postulated evolution-

² In my experience, except for material from surface and subsurface layers, fossils from deep guano deposits are well preserved only where they happen to enter wall pockets and fissures; otherwise, they are almost destroyed, apparently owing to compaction pressure of the deposits.

	J	29	21.2—23.3	22.27	0.53	2.38	R—M12	7.77	.001	5.61
	M12	18	21.2—22.8	22.03	0.54	2.45	M4—J	3.17	.01	2.71
							M4—M12	3.82	.001	3.76
<i>Pteronotus parnellii</i>										
Cranium	R	25	19.8—20.8	20.17	0.22	1.09	R—J	8.25	.001	2.58
	J	19	19.3—19.9	19.65	0.18	0.92	R—M12	2.30	.05	1.83
	M12	2	19.7—19.9	19.80	0.14	0.71				
Mandible	R	24	14.8—15.4	15.03	0.17	1.13	R—J	9.47	.001	2.73
	M4	2	15.0—15.2	15.10	0.12	0.79	R—M12	9.01	.001	2.99
	J	25	14.4—14.8	14.62	0.11	0.75	M4—J	5.92	.001	3.18
	M12	18	14.3—14.9	14.58	0.14	0.96	M4—M12	5.02	.001	3.44
Humerus	R	17	28.0—29.6	28.86	0.49	1.70	R—M4	2.22	.05	2.98
	M4	2	27.5—28.5	28.00	0.85	3.04	R—J	13.81	.001	5.79
	J	33	26.6—28.0	27.19	0.37	1.36	R—M12	11.54	.001	4.37
	M12	6	27.2—27.9	27.60	0.41	1.48	M4—J	2.83	.01	2.89
<i>Mormoops blainvilliei</i>										
Cranium	R	29	13.2—14.0	13.54	0.18	1.33	R—J	4.55	.001	1.77
	J	18	13.0—13.5	13.30	0.17	1.28				
Mandible	R	29	11.2—11.8	11.48	0.15	1.31	R—J	3.88	.001	1.48
	J	23	11.0—11.7	11.31	0.16	1.41				
Humerus	R	11	26.2—27.4	26.90	0.49	1.82	R—J	11.83	.001	4.20
	J	34	25.0—27.3	25.77	0.54	2.10				
<i>Mormoops megalophylla</i>										
Cranium	J	3	14.7—15.0	14.83	0.15	1.01	J—M12	6.27	.001	3.44
	M12	6	14.2—14.4	14.32	0.10	0.70				
Mandible	J	15	12.4—12.8	12.57	0.12	0.95	J—M12	15.11	.001	5.09
	M12	13	11.8—12.1	11.93	0.10	0.84				
Humerus	J	22	29.5—31.9	31.00	0.68	2.19	J—M12	7.21	.001	5.16
	M12	17	27.8—30.5	29.40	0.67	2.28				

TABLE 5 (Continued)

SAMPLES					COMPARISONS					
Variate	Notation	N	O.R.	X	s	V	Samples Compared	t	P	Per Cent Difference
<i>Macrotus waterhousei</i>										
Mandible	R	16	14.6—15.7	15.10	0.32	2.12	R—J	5.75	.001	5.03
	J	7	14.1—14.6	14.34	0.20	1.33				
<i>Monophyllus redmani</i>										
Cranium	R	28	21.2—22.2	21.81	0.24	1.10	R—J	4.96	.001	1.65
	J	32	20.8—22.0	21.45	0.32	1.49	R—M12	3.95	.001	1.97
	M12	6	21.1—21.8	21.38	0.24	1.12				
Mandible	R	26	13.8—14.5	14.20	0.23	1.62	R—J	8.45	.001	3.66
	J	22	13.4—14.0	13.68	0.19	1.39	R—M12	7.74	.001	3.87
	M12	20	13.2—14.1	13.65	0.25	1.83				
Humerus	R	19	19.4—22.0	20.69	0.81	3.92	R—J	9.23	.001	4.78
	J	52	18.2—21.4	19.70	0.74	3.76	R—M12	7.73	.001	3.82
	M12	38	18.4—21.3	19.90	0.74	3.72				
<i>Brachyphylla nana</i>										
Cranium	R	30	27.5—29.8	28.33	0.48	1.69	R—J	3.48	.001	1.48
	J	34	27.0—28.8	27.91	0.47	1.68	R—M12	6.81	.001	3.35
	M12	17	26.8—28.2	27.38	0.41	1.50	J—M12	3.96	.001	1.90
Mandible	R	30	17.9—19.5	18.73	0.34	1.82	R—J	4.21	.001	1.98
	J	32	17.7—19.2	18.36	0.36	1.96	R—M12	9.84	.001	4.91
	M12	21	17.4—18.5	17.81	0.31	1.74	J—M12	5.66	.001	3.00
Humerus	R	20	32.5—35.7	34.28	0.76	2.22	R—J	2.44	.02	1.75
	J	30	32.1—35.2	33.68	0.90	2.67	R—M12	6.86	.001	5.57
	M12	30	30.5—35.0	32.37	0.84	2.59	J—M12	5.87	.001	3.89

Phylloncycteris poeyi

Cranium	R	30	23.7—26.0	24.91	0.54	2.17	R—J	5.05	.001	2.77
	M4	26	24.0—26.0	25.04	0.47	1.88	R—M12	6.30	.001	3.85
	J	31	23.2—25.2	24.22	0.53	2.19	M4—J	6.16	.001	3.27
	M12	19	22.6—24.5	23.95	0.50	2.09	M4—M12	7.59	.001	4.35
Mandible	R	20	15.4—16.7	16.00	0.37	2.31	R—J	4.34	.001	2.94
	M4	24	15.4—17.1	16.08	0.41	2.55	R—M12	7.01	.001	4.56
	J	18	14.9—15.9	15.53	0.29	1.87	M4—J	4.82	.001	3.42
	M12	24	14.6—16.0	15.27	0.33	2.16	M4—M12	7.56	.001	5.04
Humerus							J—M12	2.68	.02	1.67
	R	21	26.9—29.8	28.28	0.73	2.58	R—J	5.18	.001	4.24
	M4	36	27.0—30.2	28.33	0.77	2.72	R—M12	9.05	.001	7.39
	J	40	25.3—28.8	27.08	0.92	3.40	M4—J	6.38	.001	4.41
	M12	31	24.5—27.6	26.19	0.87	3.32	M4—M12	10.68	.001	7.55
							J—M12	4.14	.001	3.29

of Jagüey Cave was also obstructed (as found in 1967). 4) Subsequently, a third cave entrance (the youngest in the cave system) was formed at the blind end of the Masones gallery (see no. 2 above), and this gallery was available again for bat colonization (this time from the opposite direction), thus allowing deposition of layer M4. 5) Finally, this third entrance was also obstructed (as found at present). At the same time, an internal collapse of huge rocks close to the chamber of the fossil deposits isolated the original blind section of the gallery into which access is not possible now. (This concealed section of the gallery was detected by the WENNER system of electrical prospecting. On the other hand, evidence for the postulated internal collapse is unquestionable at the southern side of the chamber containing the fossil deposits.)

The above scheme, representing the temporal sequence shown in fig. 2, implies that variation of the majority of the taxa involved throughout the temporal span concerned was chronoclinal in nature, consisting in an increase in size.

ACCOUNTS OF SPECIES

Family Mormoopidae

Pteronotus pristinus, new species (Plates II and III)

Holotype. — Cranium, with all molars, second premolars, and a left otic bone in place; No. 324.1, Instituto de Zoología, Academia de Ciencias de Cuba; „Cueva de los Masones” (layer M2), Trinidad, Las Villas Province; 2 October 1969. Probably of Pleistocene age.

Referred material. — Same time and place as the holotype: one rostral portion, two mandibular rami, and two tibiae. „Cueva de los Masones” (layer M1): one radius and one tibia. „Cueva del Jagüey” (surface-subsurface accumulations of bone = layer J): two crania (one in the collections of the Royal Ontario Museum: ROM 59132), six mandibular rami, and one humerus.

Diagnosis. — Largest known member of the subgenus *Chilonycteris* (*sensu* SMITH 1972).

Comparisons. — From *Pteronotus personatus*, *P. pristinus* may be distinguished primarily by the condition of the infraorbital canal (infraorbital foramen opening at the end of a short tubular canal in the latter), thus approaching the Antillean species *macleayi* and *fuliginosus*. *P. pristinus* more closely resembles *P. fuliginosus* than *P. macleayi* in a relatively shorter rostrum. This makes zygomatic breadth greater than half the length of the skull (incisors excluded) in *fuliginosus* and *pristinus*, whereas in *macleayi* it is equal to no less than half the length of the skull. The new species differs from *P. fuliginosus* in the shape of the braincase, which in *pristinus* is more rounded when viewed from above, and flatter in dorsal profile. From all three previously known members of the

subgenus, *P. pristinus* may be readily distinguished by the noticeable difference in size.

Measurements (of the holotype followed in parenthesis by those of the measurable specimens in referred material). — Maximum length of skull, 17.7 (17.3); zygomatic breadth, 9.0; breadth of braincase, 8.3 (7.8, 8.0); rostral breadth, 6.7 (6.8, 6.8); interorbital constriction, 3.4 (3.4); alveolar width across molars, 6.4 (6.2); alveolar width across canines, (4.8); length of mandible, (12.2, 12.3, 12.4, 12.6, 12.7); length of humerus (from greater tuberosity to distal articular surface), (25.5); length of tibia, (15.9, 16.2).

Remarks. — The discovery of a fourth species of *Pteronotus* in Cuba (as well as a third species of *Mormoops* described beyond) emphasizes the importance of the Greater Antillean region in the evolution and differentiation of mormoopids (SMITH 1972: 120). Interestingly enough, all four species of *Pteronotus* occurred together in layers M12 and J.

Pteronotus fuliginosus torrei (ALLEN)
(plates II and III)

Specimens examined (91). — M12: 2 crania, 7 rostra, 7 rami³, 10 limb bones. J: 8 crania, 1 rostrum, 11 rami, 27 limb bones. M4: 1 cranium, 4 rami, 13 limb bones.

Remarks. — A significant difference was found between samples J and R. Samples M12 and M4 do not differ from J, but samples from those layers are small (table 5). Upper and lower molars are almost invariably preserved. The last premolars are common, and in two specimens both upper premolars are present. These are the first fossil specimens of this species so far collected.

*Pteronotus macleayi macleayi*⁴ (GRAY)
(plates II and III)

Specimens examined (274). — M12: 8 crania, 31 rostra, 21 rami, 50 limb bones. J: 10 crania, 8 rostra, 19 rami, 59 limb bones. M4: 4 crania, 3 rostra, 29 rami, 32 limb bones.

Remarks. — No significant differences in skull length were found between any of the fossil and neontological samples. In lengths of mandible and humerus, however, samples M12 and J differed significantly from samples M4 and R, the latter samples further differing in length of humerus (table 5). Both upper and lower molars and premolars are exceedingly well preserved in most specimens. These specimens represent the first fossil record of *P. macleayi*.

³ Throughout these accounts complete mandibles are counted as separate rami.

⁴ Original spelling of specific names (*macleayi*, *parnellii*, *blainvillii*, and *waterhousii*) is emended in accordance with Opinions of the International Commission of Zoological Nomenclature.

Pteronotus parnelli parnelli (GRAY)
(plates II and III)

Specimens examined (245). — M12: 2 crania, 4 rostra, 25 rami, 44 limb bones. J: 19 crania, 11 rostra, 36 rami, 91 limb bones. M4: 1 cranium, 3 rami, 9 limb bones.

Remarks. — No differences were found between samples M12 and J, but both differed significantly from sample R. The few specimens from M4 are indistinguishable from R, except for the humerus (table 5). In the majority of specimens upper and lower last premolars and all molars are present. In one specimen from layer M12 the complete upper dentition was preserved on the right side. Occurrence of *P. parnelli* in the deposits represents the first fossil record for Cuba.

Additional fossil records of *P. parnelli* in the West Indies. — Jamaica (*parnelli*): KOOPMAN and WILLIAMS 1951: 21; WILLIAMS 1952: 172. La Gonave (*gonavensis*): KOOPMAN 1955: 110. Puerto Rico (*portoricensis*): ANTHONY 1918: 344; REYNOLDS *et al.* 1953: 2; CHOATE and BIRNEY 1968: 404.

Mormoops blainvillei LEACH
(plate III)

Specimens examined (144). — J: 20 crania, 13 rostra, 30 rami, 72 limb bones. M4: 1 rostrum, 6 rami, 2 limb bones.

Remarks. — Significant differences were found between samples J and R. Sample M4 (only mandibles) was intermediate between, but not significantly different from, the two other samples (table 5). In a great majority of specimens the second upper premolar (and frequently also the first) is preserved with all the molars. Lower jaws of two also possessed all three premolars. These are the first fossil specimens of *M. blainvillei* known from Cuba.

Additional fossil records of *M. blainvillei* in the West Indies. — Little Exuma: KOOPMAN 1951: 229. Jamaica: KOOPMAN and WILLIAMS 1951: 7. Hispaniola: MILLER 1929a: 8. La Gonave: KOOPMAN 1955: 110. Puerto Rico: ANTHONY 1918: 347; CHOATE and BIRNEY 1968: 404.

Mormoops megalophylla megalophylla PETERS
(plates III and IV)

Specimens examined (125). — M12: 8 crania (one in the collections of the Royal Ontario Museum: ROM 59130), 2 rostra, 17 rami, 35 limb bones. J: 8 crania (one in the collections of the Royal Ontario Museum: ROM 59131), 2 rostra, 17 rami, 36 limb bones.

Remarks. — Skulls from layers M12 and J were compared with continental forms of this species by Karl F. KOOPMAN. According to KOOPMAN (personal communication), the Cuban fossil seems indistinguishable from the living *M. m. megalophylla* of Mexico and Central America, although specimens from

layer J average larger in cranial measurements. The occurrence of this species in Cuba represents the first record for the West Indian subregion.

Specimens of *M. megalophylla* from Pleistocene deposits in Florida were reported by RAY et al. (1963). Measurements of mandibular rami and limb bones were given by these authors in comparison with recent specimens (*M. m. senicula*). Their „total length of mandibular ramus”, however, was measured from tip of symphysis to angular process. On the other hand, the length of the humerus included the distal spinous process (as implied in their table of measurements) and most likely was measured from the lesser tuberosity. These measurement definitions depart radically from those given in the present report (see „Materials and Methods”). For that reason, measurements shown in table 5 for the mandible and the humerus of the Cuban *M. megalophylla* are disproportionately smaller than the corresponding measurements given by RAY et al. (*op. cit.*) for the Florida specimens, whereas their measurements for the lengths of radius and femur (where ambiguity in measurement is less likely to occur) are in perfect agreement with those recorded for Cuban fossil radii and femora from layer J (tibiae were not found in the Cuban deposits). The Cuban fossil mandibles and humeri were thus remeasured in accordance with the above authors, and all available data were assembled in table 6, where it may be observed that the Cuban specimens of *M. megalophylla* from layer J are clearly referable to the fossil specimens from Florida.

Among material from layer M12, two humeri of *Mormoops* were found which are distinctly larger and heavier than the series of *megalophylla* from the same layer. The smaller of the two specimens (a left humerus) is perfectly complete and measures 33.4 mm in length (measurement taken as in table 6); the larger (a right humerus) lacks the distal spinous process, and its estimated length (based on the ratio calculated for the smaller specimen) is 33.6 mm. These values are well above the range of variation shown in table 6 for 17 humeri of *M. megalophylla* from layer M12, and even above the maximum value of the larger specimens from layer J. Accordingly, these conspicuously robust humeri represent a third, undescribed species of *Mormoops* which may be known as

Mormoops magna, new species
(plate III)

Holotype. — Left humerus; No. 344.1, Instituto de Zoología, Academia de Ciencias de Cuba; „Cueva de los Masones” (wall patches of bone-bearing guano = layer M12), Trinidad, Las Villas Province; 2 October 1969. Probably of Pleistocene age.

Paratype. — Right humerus, lacking distal spinous process; No. 344.2, Instituto de Zoología, Academia de Ciencias de Cuba; collected at the same time and place as the holotype.

Diagnosis. — Humerus like in *Mormoops megalophylla*, but larger and stouter.

TABLE 6

Measurements (in mm) of skeletal elements of *Mormoops megalophylla*

Element	Fossil (Cuba) (Layer M12) Mean (Range) N	Fossil (Cuba) (Layer J) Mean (Range) N	Fossil (Florida) (RAY et al. 1963) Mean (Range) N	Recent (<i>M. m. senicula</i>) (RAY et al. 1963) Mean (Range) N
Ramus	12.50 (12.3—12.7) 9	13.23 (12.8—13.5) 11	13.15 (13.1—13.2) 2	12.93 (12.7—13.3) 3
Humerus	30.01 (28.6—31.2) 17	32.08 (31.3—32.9) 15	32.25 (31.7—32.8) 2*	31.85 (31.7—32.0) 2
Radius	48.30 (47.7—48.9) 2	51.77 (51.5—52.1) 3	51.60 (50.7—52.1) 6	51.35 (51.2—51.5) 2
Femur	24.29 (23.8—25.1) 10	25.93 (25.2—26.8) 3	25.98 (25.7—26.2) 3	25.75 (25.4—26.1) 2

* The smallest (31.2) of the three values given by RAY et al. (*op. cit.*) was omitted because a note in their table of measurements states that the specimen lacks the distal spinous process (pertinence of this process discussed in text).

Measurements (of the holotype and paratype followed in parenthesis by those of 17 specimens of *M. megalophylla* from the same layer). — Length of humerus (from outermost projection of greater tuberosity to equivalent projection of distal articular surface), 32.6, 32.8 (27.8—30.5); lateral diameter at middle of shaft, 1.8, 1.8 (1.5—1.6); width of proximal epiphysis, 4.2, 4.1 (3.5—3.7).

Remarks. — The holotype and paratype of *Mormoops magna* are significantly larger than specimens of *M. megalophylla* from layer M12, and even larger than those from layer J ($P < .001$). The types of *M. magna* have not been compared with mainland forms of *M. megalophylla*, but their larger size with respect to said forms may be inferred from the fact that — on the basis of condylobasal length — specimens of *megalophylla* from layer J are as large (table 5) as those of the largest geographic race of the species (*M. m. carteri*), according to measurements given by SMITH (1972: 113)⁵.

Although a specific diagnosis based on such limited material would seem inadequate under most circumstances, the occurrence of the specimens together with specimens of *megalophylla* in the wall patches of Masones Cave renders the specific distinctness of *M. magna* unquestionable.

Family Phyllostomatidae

Subfamily Phyllostomatinae

Macrotus waterhousei minor GUNDLACH in PETERS

Specimens examined (17). — J: 1 cranium, 4 rostra, 9 rami, 3 limb bones.

Remarks. — Only mandibular rami were adequate for statistical analysis. The fossil and the neontological sample differed significantly (table 5). The four rostral portions retain all teeth in one or both sides, except the canines and incisors. The last premolar and all molars are present in the lower jaws, two of which also possess the second premolar.

Additional fossil records of *M. waterhousei* in the West Indies. — Little Exuma (*compressus*): KOOPMAN 1951: 229. Great Exuma (*compressus*): KOOPMAN et al. 1957: 165. Cuba (*minor*): ANTHONY 1919: 637; ARREDONDO 1970: 136. Isle of Pines (*minor*): PETERSON 1917: 361. Jamaica (*jamaicensis*): WILLIAMS 1952: 172. Hispaniola (*waterhousei*): MILLER 1929a: 8, 1929b: 4. La Gonave (*waterhousei*): KOOPMAN 1955: 110. Puerto Rico (*waterhousei*): CHOATE and BIRNEY 1968: 404.

⁵ It may be observed that an exception was made with the genus *Mormoops* in the manner of measuring the length of the skull (see „Materials and Methods”); as a result, measurements shown in table 5 for greatest length of cranium in members of the genus *Mormoops* are equivalent to condylobasal length as defined by SMITH (1972:6).

Subfamily *Glossophaginae**Monophyllus redmani clinedaphus* MILLER

Specimens examined (1,739). — M12: 24 crania, 122 rostra, 161 rami, 599 limb bones. J: 84 crania, 22 rostra, 93 rami, 629 limb bones. M4: 1 ramus, 4 limb bones.

Remarks. — Samples M12 and J are statistically indistinguishable and both differ significantly from sample R (table 5). Most crania and mandibles lack teeth but within them all upper teeth, except incisors, are represented.

Living populations of *Monophyllus* in Cuba are noticeably dimorphic. In females the premaxilla tends to be narrow and projects forward, whereas in males this region is broader and more rounded anteriorly. As a consequence, females average larger in length of skull, and smaller in alveolar width across canines, than males. Moreover, in females the mandible is conspicuously slender and almost straight, whereas in males it is much broader, with a convex lower profile (plate III). To my knowledge secondary sexual variation in *Monophyllus* has not been previously recorded.

On the basis of the above dimorphism, an attempt was made to determine the sex among 83 crania recovered from layer J. Each specimen was tentatively separated as to sex by inspection, and then results were tested against the ratio (of skull length to width across canines) calculated from the neontological sample. On only two were data from measurements inconclusive, although the specimens could be readily diagnosed by inspection. A sex ratio of 46 males to 37 females was estimated for the fossil sample. A record of monthly random sampling of living individuals in a cave at Guayos (central Cuba) during 1968—1969 resulted in a sex ratio of 55 males to 53 females, a ratio not unlike that of the fossil specimens.

Additional fossil records of *Monophyllus* in the West Indies. — Cuba (*redmani clinedaphus*): KOOPMAN and RUIBAL 1955: 3. Jamaica (*redmani redmani*): KOOPMAN and WILLIAMS 1951: 20; WILLIAMS 1952: 172. La Gonave (*redmani clinedaphus*): KOOPMAN 1955: 110. Puerto Rico (*redmani portoricensis*): ANTHONY 1918: 349; REYNOLDS et al. 1953: 2; SCHWARTZ and JONES 1967: 12; CHOATE and BIRNEY 1968: 406. Puerto Rico (*plethodon frater*): ANTHONY 1917: 565; SCHWARTZ and JONES 1967: 16; CHOATE and BIRNEY 1968: 405.

Subfamily *Phyllonycterinae**Brachyphylla nana* MILLER

Specimens examined (1,118). — M12: 17 crania, 39 rostra, 87 rami, 125 limb bones. J: 173 crania, 24 rostra, 133 rami, 511 limb bones. M4: 2 crania, 6 rami, 1 limb bone.

Remarks. — A significant difference was determined between samples M12 and J, as well as between samples J and R (table 5). The great majority of crania and mandibles are edentulous. The last premolar, however, is surprisingly frequent in both jaws and not uncommon on both sides.

Additional fossil records of *Brachyphylla* in the West Indies. — Cuba (*nana*): ANTHONY 1919: 638; KOOPMAN and RUIBAL 1955: 3; ARREDONDO 1970: 135, 136; MAYO 1970: 41. Isle of Pines (*nana*): PETERSON 1917: 361. Jamaica (*pumila*): KOOPMAN and WILLIAMS 1951: 12. Hispaniola (*pumila*): MILLER 1929a: 9. Puerto Rico (*cavernarum*): ANTHONY 1918: 352; REYNOLDS et al. 1953: 3; CHOATE and BIRNEY 1968: 406. Antigua (*cavernarum*): WING et al. 1968: 182.

Erophylla sezekorni sezekorni (GUNDLACH)

Specimens examined (152). — M12: 5 rostra, 2 rami, 5 limb bones. J: 31 crania, 8 rostra, 15 rami, 70 limb bones. M4: 16 limb bones.

Remarks. — No significant differences could be detected among fossil samples of this species, or between these and the corresponding neontological samples. The whole series of fossil crania and mandibles is almost completely edentulous.

Additional fossil records of *Erophylla* in the West Indies. — Great Exuma (*sezekorni planifrons*): KOOPMAN et al. 1957: 166. Cuba (*sezekorni sezekorni*): KOOPMAN and RUIBAL 1955: 4; ARREDONDO 1970: 135. Jamaica (*sezekorni syops*): KOOPMAN and WILLIAMS 1951: 20. Hispaniola (*bombifrons santacristobalensis*): MILLER 1929a: 10.

Phyllonycteris poeyi GUNDLACH

Specimens examined (1,690). — M12: 20 crania, 111 rostra, 120 rami, 185 limb bones. J: 153 crania, 32 rostra, 77 rami, 425 limb bones. M4: 28 crania, 42 rostra, 126 rami, 371 limb bones.

Remarks. — Samples M12 and J differed significantly from samples M4 and R in length of the skull. In mandibular length and the length of the humerus, however, significant differences were found as well between samples M12 and J (table 5). Although most specimens were edentulous, molars were occasionally present, but premolars were seldom preserved. One cranium and one mandible from layer J possessed a complete dentition.

KOOPMAN (1952: 257) indicated that „males of *P. poeyi* tend to have heavier more robust skulls than do females”. I think this is the only reference in the literature to sexual dimorphism in the genus *Phyllonycteris*. Indeed, the Cuban species exhibits a significant sexual dimorphism favoring males in length of skull ($P < .01$ in sample R), and the average alveolar width across the canines is proportionately smaller in females. Moreover, the mandible is much broader in males at the interval between the last molar and the rise of the coronoid process. As these differences are readily seen, sexing of fossil skulls was attempted by inspection, as well as by tests against the ratio calculated for sample R from

variates indicated above. Results were as follows: 8 males and 23 females in sample J, and 7 males and 21 females in sample M4. Sex ratios determined by random sampling of live *Phyllonycteris* in four Cuban caves (13 ♂♂—94♀♀, 207 ♂♂—524♀♀, 1 ♂—23♀♀, and 13 ♂♂—19♀♀) represent an average ratio of 0.35, which is similar to those estimated for the fossil samples: J, 0.35; M4, 0.33.

Additional fossil records of *Phyllonycteris* in the West Indies. — Cuba (*poeyi*): ANTHONY 1919: 641; KOOPMAN and RUIBAL 1955: 4; ARREDONDO 1970: 135, 136. Jamaica (*aphylla*): KOOPMAN and WILLIAMS 1951: 16. Hispaniola (*obtusa*): MILLER 1929a: 10. Puerto Rico (*major*): ANTHONY 1917: 567; CHOATE and BIRNEY 1968: 409.

Family Natalidae

Natalus major primus ANTHONY (plates III and IV)

Specimens examined (227). — M12: 1 cranium, 24 rostra, 26 rami, 33 limb bones. J: 21 crania (two in the collections of the Royal Ontario Museum: ROM 59133 and ROM 59134), 23 rostra, 44 rami, 54 limb bones. M4: 1 limb bone.

Remarks. — The Cuban representative of this species was previously known only by fragments of a rostrum and four mandibular rami. Therefore, 22 nearly complete skulls listed above represent the first known crania of this fossil form. Morphologically, the specimens support GOODWIN'S (1959: 10) allocation of the Cuban *primus* as a subspecies of *N. major*.

Significant differences were not detected between samples from layers M12 and J in any of the variates studied. The last two premolars and all molars are exceptionally well preserved in both jaws throughout the fossil series. The one complete cranium from layer M12 retains all teeth on both sides except the incisors.

Additional fossil records of *N. major* in the West Indies. — Cuba (*primus*): ANTHONY 1919: 642; KOOPMAN and RUIBAL 1955: 4; GOODWIN 1959: 10. Jamaica (*jamaicensis*): KOOPMAN and WILLIAMS 1951: 17.

Natalus macer (MILLER) (plate III)

Specimens examined (270). — M12: 3 rostra, 21 rami, 46 limb bones. J: 10 crania, 17 rostra, 55 rami, 101 limb bones. M4: 1 cranium, 4 rami, 12 limb bones.

Remarks. — Significant differences were not found between any of the samples studied. Except for the incisors, the upper and lower teeth are frequently preserved. These remains represent the first fossil specimens of *N. macer* to be collected in Cuba.

Additional fossil records of *N. (Chilonatalus)* in the West Indies. — Great Exuma (*tumidifrons*): KOOPMAN et al. 1957: 167.

Natalus lepidus (GERVAIS)
(plate III)

Specimens examined (94). — M12: 3 rostra, 17 rami, 14 limb bones. J: 3 crania, 3 rostra, 4 rami, 26 limb bones. M4: 15 rami, 9 limb bones.

Remarks. — No significant differences were determined in any of the comparisons of samples. Molars were preserved in all partial and complete crania and mandibles, and premolars were also occasionally present. These are the first fossil specimens of *N. lepidus* for Cuba.

Additional fossil records of *N. lepidus* in the West Indies. — Great Exuma: KOOPMAN et al. 1957: 167.

DISCUSSION

Age of the fossil deposits

In the experience of speleologists (and in my own experience) the occurrence of charcoal strata in Cuban caves is a common phenomenon. VIÑA and FUNDORA (1970) found charcoal to be abundant in several of the stratigraphic profiles studied by them in the Trinidad cave system (including Masones and Jagüey caves), and it was found as well in layers M3 and M4 of the Masones pocket deposit (see table 1). These charcoal layers were regarded by VIÑA and FUNDORA (*op. cit.*) as evidence of the occurrence of alternate dry and humid periods during past geological times. The above authors postulate that superficial charcoal beds were deposited during periods of intensive drought, as a result of huge regional fires, and were subsequently washed down through sink-holes and cave entrances during pluvial periods of high intensity. Significantly enough, *Chondropoma delatreanum* — a terrestrial mollusk represented in layer M3 by hundreds of minute shells (table 1) — is a tree-dweller of humid forests in Cuba at present. That only charcoal and minute shells should have reached the deposits, while presumable heavier components of these exogenous sediments did not, is understandable considering that the pocket deposit was located at approximately 200 m from the entrance of the cave.

On the above considerations, the fossil layers are regarded as representing whole cave populations or demes that were doomed to extinction as a consequence of accidents (regional fires, floods, obstruction of cave entrances) correlated with radical climatic fluctuations. Thus, the isolation of the deposits by obstruction of the access to the respective cave chambers is interpreted as the result of intensive speleogenetic activity correlated with increased rainfall. These circumstances set the thanatocenoses off from bat-bearing fossil deposits so far made known from the Antilles, which, according to a general consensus, originated as a result of owl predation. (Incidentally, large-scale industrial exploitation of bat guano, as it is currently practiced in Cuba, may be viewed as an occasional aid to paleontological research.)

The occurrence in Cuba of alternate dry and humid periods during Pleistocene times was recently substantiated by GRANA (1968) and MAYO (1969), from studies of cave sediments in eastern and western Cuba, respectively, as well as by NUÑEZ et al. (1968), on the basis of surface sediments. On the other hand, *Mormoops megalophylla* was recorded from a Pleistocene deposit in Florida (RAY et al. 1963). Since mormoopids are not equipped physiologically to occupy temperate areas because of their sensitivity to cold (VAUGHAN and BATEMAN 1970: 234), the former northward extension of the range of *M. megalophylla* must have occurred during one of the warm stages of the Pleistocene. Correspondence between specimens of *M. megalophylla* from the Florida deposit and Cuban specimens of that species from layer J (see „Accounts of Species”) suggests that this layer may well represent such a stage of the Pleistocene. In view of the paleoclimatic and faunal evidence, a late Pleistocene age may safely be postulated for the older layers of the Masones and Jagüey deposits.

Comparison with other West Indian Deposits

A pattern of temporal (chronocline) variation similar to that described earlier in this report (see „Results”) has not been conclusively demonstrated previously for the Chiroptera of the West Indies. In the „Accounts of Species” the known West Indian fossils of the taxa involved were reviewed. In an overwhelming majority authors repeatedly commented on the lack of difference between fossil and living specimens of those insular populations. Aside from these taxa, fossil specimens of *Noctilio*, *Tonatia*, *Glossophaga*, *Artibeus*, *Stenoderma* (including *Phyllops* and *Ariteus*), *Desmodus*, *Eptesicus*, *Tadarida*, *Eumops*, and *Molossus* have been collected in the West Indies, but no differences were found between fossil specimens from different layers, or between these and neontological specimens, in any of the respective species or subspecies from these islands (*Tonatia*, *Desmodus*, and *Stenoderma rufum anthonyi* are known only as fossils in the West Indian subregion).

Aside from the Chiroptera, the only reference I know of which discusses a similar pattern of variation in a West Indian mammal is by CHOATE and BIRNEY (1968), who reported the insectivore *Nesophontes* from cave deposits in Puerto Rico. Although a stratigraphic record was not kept, pertinent comments by these authors (*op. cit.*: 401—402) deserve to be quoted: „Specimens of *N. edithae* from Cueva de Clara can be assigned to one or the other of two categories, regardless of age, on the basis of size. However, no qualitative characters were found to distinguish specimens of the two categories... Specimens from Cueva del Perro are almost intermediate in some measurements between the two size categories represented in Cueva de Clara... It is difficult to explain the predominance of large and small individuals in one cave and of intermediate-sized individuals in another cave only a short distance from the first. Probably this phenomenon has resulted from allochronic differentiation and sequential deposition of fossils in various caves.” Surprisingly, no significant differences

were found by the above authors (*op. cit.*: 406) in quantitatively adequate samples of fossil *Brachyphylla* from „Cueva de Clara”, or between these and samples from „Cueva del Perro”, probably owing to differences in rates of evolution in these two mammalian orders.

Nevertheless, it would be unwise to assume that such a peculiar pattern of variation, affecting six widely distributed West Indian chiropteran genera is limited exclusively to the Cuban populations. Under these circumstances, then, it is reasonable to seek an explanation for the observed discrepancy in the fossil deposits themselves.

The bat-bearing fossil deposits known to date from caves in the West Indies are the result of owl predation (ANTHONY 1918, 1919; MILLER 1929a, 1929b; KOOPMAN and WILLIAMS 1951; WILLIAMS 1952; KOOPMAN 1952, 1955; KOOPMAN and RUBAL 1955; MAYO 1970). The faunistic composition of these deposits, both qualitatively and quantitatively, conforms generally to the known food preferences of West Indian owls. Larger osseous elements occasionally present may be credited to several species of giant owls that once were extant in the West Indies (WETMORE 1922, 1937; BRODKORB 1969; ARREDONDO 1972). Moreover, most deposits have been found in cave entrances and vestibules.

Instead, the Masones and Jagüey fossil deposits originated from remains of whole bat populations that perished within these caves at different epochs (see preceding section). These deposits were located at 200 m and 110 m, respectively, from the nearest entrances, and the only other remains associated with the bats were a few vertebrae (possibly *Epicrates*) and post-cranial bones of a single capromyid rodent (see footnote 1); but *Epicrates* and *Capromys* are frequent wanderers of the deepest recesses of caves in Cuba. Furthermore, only cave-dwelling bats occurred in the deposits.

WILLIAMS (1952: 175) appropriately emphasized that „terrestrial deposits quite different from those which contain bats... are known in Jamaica”, and — it may be added — in Cuba (BROWN 1913; ALLEN 1917; KOOPMAN 1958a; FISCHER 1970, 1971; FISCHER and STEPHAN 1971a, 1971b) and Puerto Rico (WILLIAMS and KOOPMAN 1951) as well. These deposits are generally regarded as significantly older than any of the unconsolidated materials from cave entrances, and their faunistic composition (crocodyles, large ground birds, and sloths, among others) implies that owls did not contribute to their formation. But, as stated above, no bats were recovered from such deposits. The Cuban record of *Desmodus* (KOOPMAN *op. cit.*) would seem to represent an exception; but the occurrence of this vampire bat in the deposit (no other bat remains were found) together with its presumed preys is just what would be expected.

It may be concluded, then, that the imperfectly known history of faunal succession in West Indian Chiroptera has been derived almost exclusively from deposits composed of ancient owl pellets. An analysis of circumstances determining the formation and preservation of these deposits is in order.

1. Owl predation upon bats is highly selective taxonomically. A review of the literature covering all known fossil and subfossil records of West Indian

Chiroptera from owl pellet deposits, including records from fresh pellets (too extensive to be included here), confirms that only species of the noninsectivorous subfamilies *Glossophaginae*, *Stenodermatinae*, and *Phyllonycterinae* are abundantly represented in the respective deposits. The remaining taxa are poorly represented, or do not occur in the deposits. The relatively frequent occurrence of *Macrotus waterhousei* in such deposits, as well as in fresh owl pellets, would seem to contradict the above generalization; but foraging behavior and flight characteristics set this species off from insectivorous bats proper. Fragility has been invoked to explain the absence of small and delicate species from bat-bearing fossil deposits (KOOPMAN and WILLIAMS 1951: 21). However, fragility is inconsequential in fossil deposits which were not originated as a consequence of owl predation. The smallest and more delicate bats of the West Indies, *Natalus lepidus*, *N. macer*, *Pteronotus fuliginosus*, and *P. macleayi*, were abundantly represented in the Masones and Jagüey fossil deposits. The first two species were known as fossils from a single mandibular ramus each, whereas fossil specimens of both species of *Pteronotus* were previously unknown. On the other hand, specimens of these taxa have not been recovered from fresh owl pellets. Except for *N. macer*, however, these are common, highly colonial species. Pertinent observations (to be published elsewhere) suggest that incidence of owl predation upon bats depends fundamentally on the foraging behavior (including aerodynamic characteristics) of the particular bat species. In fact, bats constitute a small part of the owl's diet (not exceeding ten per cent in recent deposits examined in Cuba).

2. Not all caves contain suitable roosting sites for owls. A considerable number of caves occur in Cuba, for example, but relatively few are inhabited by owls. Owls seem to prefer relatively ample cave vestibules with a twilight zone. Comparing cave deposits in Cuba and Puerto Rico, ANTHONY (1919: 627) states: „I believe that it is more than mere coincidence that bones are found in greatest abundance in the large caves where the top has fallen in, admitting light”.

3. The majority of cave entrances and vestibules must have been extensively flooded during the Pleistocene, either by heavy rains or by fluctuations of sea level in those caves located in coastal regions. Some of the most studied bat-bearing fossil deposits were taken from caves fronting the sea (ANTHONY 1919; WILLIAMS 1952).

4. Burial practices, as well as cave inhabitation, by some groups of Greater Antillean aborigines must have represented an additional source of disturbance of deposits at cave entrances in pre-Columbian times. Indeed, some of the bat-bearing deposits have been described as partially kitchen-midden in nature (KOOPMAN 1955; REYNOLDS et al. 1953).

In summary, the selective nature of owl predation and the unsuitability of most cave entrances as roosting sites for owls must have influenced the number, composition, and size of deposits originally formed. The great majority of these deposits may have been obliterated during the Pleistocene because of climatic

factors. Consequently, deposits that have endured till historic times — many of which have been largely disturbed by human action — probably do not represent great antiquity, a condition that may possibly account for the lack of difference between recent specimens of bats and corresponding fossil specimens from such deposits.

Temporal variation of taxa

The position in time of the Masones and Jagüey fossil layers implies that during the temporal span in question phyletic evolution of the majority of the taxa involved consisted fundamentally in an increase in size. Demonstration of this evolutionary trend for these same species on other islands of the Greater Antilles must have been precluded hitherto by deficient fossil records (see preceding section). Since the operation of BERGMANN'S effect could not account for the observed pattern of variation (because of pronounced climatic fluctuations evidenced in the stratigraphic sequence), consideration of the possibility, among others, that size may have varied as a response to insular habitats seemed pertinent.

The problem of the effect of insularity on the size of bats was recently attacked by KRZANOWSKI (1967), who concluded that the Chiroptera living on islands more often decrease in size than increase. Nonetheless, the majority of the New World insular bats included in KRZANOWSKI'S survey occur on continental islands off the coasts of Central and northern South America and thus limit his coverage of actual West Indian Chiroptera. Therefore, a closer examination of the bat fauna of the West Indies proper is warranted. To this end, the four largest islands of the Greater Antilles were selected to test size relationships between bats from smaller and larger islands. These islands are ecologically comparable, differ greatly in area, and contain 70 per cent of the entire West Indian bat fauna.

The corresponding comparisons are summarized in table 7. These data show conclusively that in a group of ecologically comparable islands of the West Indies body size of bats tends to be smaller in larger islands and larger in smaller islands, which strongly suggests that KRZANOWSKI'S (*op. cit.*) generalization does not hold for this insular area. On the other hand, this pattern of variation affords indirect evidence of the postulated lack of antiquity of most fossil deposits from the Greater Antilles (see preceding section) because, hypothetically, the rate of evolution must have been greater in the smaller islands.

Interestingly, an absolute majority of the extinct species and subspecies of Chiroptera endemic to the Greater Antilles have attained maximum size at their corresponding taxonomic levels. Thus, *Monophyllus plethodon frater*, *Stenoderma rufum anthonyi*, and *Natalus major primus*, respectively, are the largest known subspecies; *Pteronotus pristinus* is considerably larger than any of the other species in the subgenus; *Mormoops magna* and *Phyllonycteris major* are the largest known members in their respective genera. Hypothetically, once

maximum body size has been reached it could become disadvantageous to the species in the event of radical ecological changes such as those of the Pleistocene.

The case of *Stenoderma rufum* in Puerto Rico would seem to represent an exception to the above hypothesis because a living subspecies occurs on the island. Actually, the recently described fossil subspecies *S. r. anthonyi* was regarded as a probable precursor to the considerably smaller extant subspecies *S. r. darioi* (CHOATE and BIRNEY 1968: 408—409). However, aside from a noticeable difference in size, relevant structural characters distinguish both forms (contrary to the pattern of temporal variation discussed), whereas the living subspecies differs from the nominate subspecies that occurs in the Virgin Islands exclusively in colour of pelage (HALL and TAMSITT 1968: 3). Moreover, fossils

TABLE 7
Relations of size in Greater Antillean Chiroptera*

Taxa	Cuba	Hispaniola	Jamaica	Puerto Rico
<i>Pteronotus fuliginosus</i>	1	3	2	3
<i>Pteronotus macleayi</i>	1		3	
<i>Pteronotus parnelli</i>	3	1	3	2
<i>Macrotus waterhousei</i>	1	3	2	
<i>Monophyllus redmani</i>	2	2	3	1
<i>Artibeus jamaicensis</i>	1	3	3	3
<i>Stenoderma**</i>	2	1	2	3
<i>Brachyphylla</i>	2	1		3
<i>Erophylla bombifrons</i>		1		3
<i>Erophylla sezekorni</i>	1		3	
<i>Natalus (Natalus)</i>		1	3	
<i>Natalus (Chilonatalus)</i>	1		3	
<i>Eptesicus fuscus</i>	2	2	1	3
<i>Lasiurus borealis</i>	2	1	3	1
<i>Tadarida brasiliensis</i>	2	3	2	1
<i>Molossus molossus</i>	1	2	2	3
Number of taxa compared	14	13	14	11
Taxa of minimum size	7	6	1	3
Taxa of maximum size	1	4	8	7
Approximate area (km ²)	105,000	77,700	11,700	8,800

* Tabulation is based on published records and measurements for taxa of the four largest islands of the Greater Antilles. Forms known only as fossils are excluded. All chiropteran taxa (except those that do not vary in size) occurring at least in two of the islands under consideration are listed at left. For each taxon size rank is indicated numerically: minimum size, 1; intermediate in size, 2; and maximum size, 3.

** Including *Phyllops* and *Ariteus*.

of the subspecies *darioi* are unknown. Consequently, on geographic grounds and from degree of differentiation among subspecies, *S. r. darioi* may be regarded as an invader from the Virgin Islands after the niche was vacated by the extinction of *S. r. anthonyi*. It may be argued that Puerto Rico and some of the

Virgin Islands were connected by dry land up until recently, but this is what would be expected in the case of such weakly differentiated subspecies as *darioi* and *rufum*.

Comparison of fossil and recent faunas

The following comparisons between fossil and recent faunas are based on the assumption that the fossil layers represent unbiased samples of actual circumstances at the time of deposition of the fossils. The foregoing discussion suggests that this is a reasonable assumption. On the other hand, the distribution and relative abundance of the majority of recent bats of Cuba are satisfactorily known at present (in press).

Of the mormoopids, *Pteronotus pristinus* is the first extinct taxa of the family so far discovered, and probably was not represented by large populations. *M. megalophylla* was abundant before becoming synchronous with *M. blainvillei* (in layer J), which appears to have arrived in the caves much later (see fig. 2). On the other hand, the absence of *Pteronotus fuliginosus* from layer M1 points to the possibility that it could have been the latest of the four species of the genus to colonize the caves.

Macrotus was represented in the deposits only by scanty remains from layer J. *Macrotus* is a facultative cave-dweller, always occurring in unstable cave environments (usually near entrances). Therefore, its absence from the older layers does not exclude the possibility of its earlier occurrence in the cave, particularly when the location of the deposits with respect to cave entrance is considered.

Of the anthophilous bats of Cuba (glossophagines and phyllonycterines), *Monophyllus* appears to have been at one time the most abundant (not exceeded in quantity of remains by any other species in the deposits), whereas at present it is the most uncommon of the group. *Erophylla* seems to have always been, as it is today, much less abundant than *Brachyphylla* and *Phyllonycteris*.

Of the natalids, populations of *N. macer* appear to have been formerly as abundant as those of *N. lepidus*. A most remarkable shift has operated since then, favoring the absolute predominance of *N. lepidus* at present. Significantly, displacement of *N. tumidifrons* by *N. lepidus* in the Bahamas was postulated by KOOPMAN et al. (1957: 170). On the other hand, the occurrence of *N. major* in layer M4 seems to support the currently accepted hypothesis of lateness of extinction.

Fifteen species of extant Cuban bats roost in caves (SILVA and PINE 1969: 16). Ten are exclusively cave-dwellers and invariably occupy the most stable environments in areas less influenced by the external environment. These 10 species occurred in the deposits, together with four other extinct bats of the genera *Pteronotus*, *Mormoops*, and *Natalus*, presumably also exclusive cave-dwellers as bats of these genera are not known to live outside of caves in Cuba or elsewhere. Therefore, simultaneous inhabitation of a cave by 13 strictly cav-

ernicolous bats (*Mormoops blainvillei* was lacking in layer M12, and *M. magna* in layer J) may have been common at the time of deposition of the older fossil layers. This number is especially significant, because at present in Cuba the simultaneous occurrence of the 10 obligatory cave-dwellers in a single cave is unknown. Only one cave is known where nine occur together; in another, eight; seven have been found in a few caves, and six is not uncommon in caves throughout the island. In fact, 12 (obligatory plus facultative cave-dwellers) is the greatest number of species known to occur simultaneously in Cuban caves. Consequently, the aggregation reflected by fossils suggests that in Cuba at a former time cave habitats were more efficiently exploited (probably to saturation).

Three species disappeared in the sequence from layers M1 to M4. Aside from apparent shifts in the relative abundance of taxa, replacements of one taxon by another — such as the well documented *Tonatia-Macrotus* sequence in Jamaica (KOOPMAN and WILLIAMS 1951) — seems not to have occurred. Therefore, the rather extensive faunal continuity throughout the stratigraphic sequence may be regarded as representing deme extinctions (during periods of climatic severity) and recolonizations from refugia within Cuba. Chronoclines may thus indicate that — during the segment of phyletic evolution represented by the fossil layers — considerable time was required for recolonization or that, more likely, access to these caves was not available during lengthy periods as a consequence of speleogenetic activity, an alternative consistent with the observed evidence. Hypothetically, fossil layers statistically intermediate with respect to the Masones and Jagüey layers could be found in other Cuban caves.

The fact that fossil layers were statistically recognized in the deposits suggests the feasibility of a relative chronology if similar fossil deposits should turn up in Cuba. Eventually, such a chronology could be tested by correlations based on a few carbon-datings. On the other hand, the occurrence in all the fossil layers of all four pollinivorous bats of Cuba (*Monophyllus*, *Brachyphylla*, *Erophylla*, and *Phyllonycteris*) implies that representative samples of the contemporaneous floras are contained in the matrix of said layers. This affords the possibility of tracing vegetational changes throughout the temporal span in question from studies of fossil pollen, a most suggestive avenue of further research.

Consideration of the probable role represented by cave habitats in the evolution of the Greater Antillean bat fauna evokes the following speculations: A number of Greater Antillean bats are currently regarded to be poorly differentiated from their mainland relatives and, therefore, may represent the latest arrivals in the archipelago (KOOPMAN 1958b). The better differentiated living forms (presumably the earliest arrivals) are represented by seven endemic genera and two subgenera (comprising 15 species), and five nonendemic genera and two subgenera (comprising seven endemic species). Of the 22 actual endemic species of the Greater Antilles, 15 (of the genera *Pteronotus*, *Mormoops*, *Monophyllus*, *Brachyphylla*, *Erophylla*, *Phyllonycteris*, and *Natalus*) are obligatory cave-dwellers, whereas only four species (of the genus *Stenoderma*: including *Phyllops* and *Ariteus*) are strictly tree-dwellers. Of the remaining three species,

one (*Tadarida minuta*) roosts in palms and houses; another (*Eptesicus lynni*) is known from caves and must be a facultative cavernicole as all other members of the genus in the Antilles; and of the third (*Antrozous koopmani*), its roosting habits are unknown. The Greater Antilles constitute one of the important karstic regions of the world, and caves are incredibly numerous (4,000 already known in Cuba) throughout the region. The superiority of cave roosting over any other type of roosting habit in bats is obvious. Caves afford, among other advantages, the development of quantitatively strong populations and also provide maximum protection during reproductive cycles and hurricane seasons. Accordingly, extinction must have been greater in tree-dwelling bats than in cave-dwellers at all times but especially during the Pleistocene.

We may assume that the reason for obligatory cave-dwelling bats forming a decided majority of the Greater Antillean endemic species at present is that cave habitats favored their preservation. But as bats in Central and northern South America are historically sylvan (HERSHKOVITZ 1969), the original colonizations of the Greater Antilles must have been mainly by tree-dwelling bats, ⁶ most of which — because of the very nature of their roosting habit — disappeared after periods of radical climatic changes such as those of the Pleistocene. Such a process would explain why at present „the bat fauna (of the Greater Antilles) is poorer than would be expected on the basis of the ecology” (KOOPMAN 1958 b: 435). The extant fauna may thus represent a deficit between rates of extinction and immigration, considering that water gaps may be significant barriers to bat dispersal (KOOPMAN 1970). Although more cave-dwellers than treedwellers are known in the Greater Antilles as extinct taxa, this is probably due to the roost peculiarities and correlated gregariousness of the latter having reduced the possibility of their preservation as fossils; only those tree-dwellers incorporated to cave entrance deposits through owl predation must have had a chance to be preserved, and the low probability of preservation of such deposits was substantiated earlier in this discussion. Finally, none of the weakly differentiated taxa, generally regarded as the latest invaders, can be assigned to the group of obligatory cave-dwellers. (Except for *Pteronotus parnelli*, at present only endemic species are exclusive cave-dwellers in the Greater Antilles.) A few are facultative cavernicoles, but most live in trees or their present-day alternatives of houses and other man-made structures.

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⁶ According to the general consensus of Cuban botanists, at least 85 per cent of the territory of the Island was originally covered by broad-leaf forests.

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LITERATURE CITED

- ALLEN, G. M. 1917. New fossil mammals from Cuba. *Bull. Mus. Comp. Zool.* **61**: 1—12.
- ANTHONY, H. E. 1917. Two new fossil bats from Porto Rico. *Bull. Amer. Mus. Nat. Hist.* **37**: 565—568.
- . 1918. The indigenous land mammals of Porto Rico, living and extinct. *Mem. Amer. Mus. Nat. Hist. new ser.* **2**: 331—435.
- . 1919. Mammals collected in eastern Cuba in 1917. With descriptions of two new species. *Bull. Amer. Mus. Nat. Hist.* **41**: 625—643.
- ARREDONDO, O. 1970. Dos nuevas especies subfósiles de mamíferos (*Insectivora: Nesophontidae*) del Holoceno Precolombino de Cuba. *Mem. Soc. Cien. Nat. La Salle* **30**: 122—152.
- . 1972. Nueva especie de ave fósil (*Strigiformes: Tytonidae*) del Pleistoceno superior de Cuba. *Bol. Soc. Venezolana Cien. Nat.* **29**: 415—431.
- BRODKORB, P. 1969. An extinct Pleistocene owl from Cuba. *Quart. J. Florida Acad. Sci.* **31**: 112—114.
- BROWN, B. 1913. Some Cuban fossils. *Amer. Mus. J.* **13**: 221—228.

- CHOATE, J. R., and E. C. BIRNEY. 1968. Sub-Recent *Insectivora* and *Chiroptera* from Puerto Rico, with the description of a new bat of the genus *Stenoderma*. J. Mamm. **49**: 400—412.
- FISCHER, K. 1970. Quartärpaläontologische Grabungsexpedition 1967 in Cuba. Wiss. Zeitschr. Humboldt Univ. Berlin **19**: 232—236.
- . 1971. Riesenfaultiere (*Megalonychidae*, *Edentata*, *Mammalia*) aus dem Pleistozän der Pio-Domingo-Höhle in Kuba. Wiss. Zeitschr. Humboldt Univ. Berlin **20**: 609—673.
- , and B. STEPHAN. 1971a. Ein flugfähiger Kranich (*Grus cubensis* n. sp.) aus dem Pleistozän von Kuba — Eine Osteologie der Familie der Kraniche (*Gruidae*). Wiss. Zeitschr. Humboldt Univ. Berlin **20**: 541—592.
- . 1971b. Weitere Vogelreste aus dem Pleistozän der Pio-Domingo-Höhle in Kuba. Wiss. Zeitschr. Humboldt Univ. Berlin **20**: 593—607.
- GOODWIN, G. G. 1959. Bats of the subgenus *Natalus*. Amer. Mus. Nov. **1977**: 1—22.
- GRAÑA GONZÁLEZ, A. 1968. Notas sobre los sedimentos de la Cueva Velette, Mayarí, Oriente. Acad. Cien. Cuba. Ser. Espeleol. Carsol. **4**: 1—10.
- HALL, E. R., and J. R. TAMSITT. 1968. A new subspecies of the red fig-eating bat from Puerto Rico. Life Sci. Occas. Pap. Roy. Ontario Mus. **11**: 1—5.
- HERSHKOVITZ, P. 1969. The evolution of mammals on southern continents. VI. The Recent mammals of the Neotropical Region: A zoogeographical and ecological review. Quart. Rev. Biol. **44**: 1—70.
- KOOPMAN, K. F. 1951. Fossil bats from the Bahamas. J. Mamm. **32**: 229.
- . 1955. A new subspecies of *Chilonycteris* from the West Indies, and a discussion of the mammals of La Gonave. J. Mamm. **36**: 109—113.
- . 1958a. A fossil vampire bat from Cuba. Breviora **90**: 1—4.
- . 1958b. Land bridges and ecology in bat distribution on islands off the northern coast of South America. Evolution **12**: 429—439.
- . 1970. Zoogeography of bats. In About bats. Edited by B. H. SLAUGHTER and D. W. WALTON. J. Graduate Res. Center, Southern Methodist Univ. **39**: 29—50.
- , M. K. HECHT, and E. LEDECKY-JANECEK. 1957. Notes on the mammals of the Bahamas with special reference to the bats. J. Mamm. **38**: 164—174.
- , and R. RUBAL. 1955. Cave-fossil vertebrates from Camagüey, Cuba. Breviora **46**: 1—8.
- , and E. E. WILLIAMS. 1951. Fossil Chiroptera collected by H. E. ANTHONY in Jamaica, 1919—1920. Amer. Mus. Nov. **1519**: 1—29.
- KRZANOWSKI, A. 1967. The magnitude of islands and the size of bats (*Chiroptera*). Acta Zool. Cracoviensia **12**: 281—348.
- MAYO, N. A. 1969. Nueva especie de *Megalonychidae* y descripción de los depósitos cuaternarios de la Cueva del Vaho, Boca de Jaruco, La Habana. Mem. Facultad Cien., Univ. Habana. Ser. cien. biol. **3**: 1—58.
- . 1970. La fauna vertebrada de Punta Judas. In Sistema subterráneo de Punta Judas (A. GRAÑA GONZÁLEZ and J. IZQUIERDO BORDÓN). Acad. Cien. Cuba. Ser. Espeleol. Carsol. **30**: 1—45.
- MILLER, G. S., Jr. 1929a. A second collection of mammals from caves near St. Michel, Haiti. Smithsonian Misc. Collect. **81**: 1—30.
- . 1929b. Mammals eaten by indians, owls, and spaniards in the coast region of the Dominican Republic. Smithsonian Misc. Collect. **82**: 1—16.
- NÚÑEZ JIMÉNEZ, A., V. PANOŠ, and O. ŠTELCL. 1968. Carsos de Cuba. Acad. Cien. Cuba. Ser. Espeleol. Carsol. **2**: 1—47.
- PETERSON, O. A. 1917. Report upon the fossil material collected in 1913 by the Messrs. LINK in a cave in the Isle of Pines. Ann. Carnegie Mus. **11**: 359—361.
- RAY, C. E., S. J. OLSEN, and H. J. GUT. 1963. Three mammals new to the Pleistocene fauna of Florida, and a reconsideration of five earlier records. J. Mamm. **44**: 373—395.
- REYNOLDS, T. E., K. F. KOOPMAN, and E. E. WILLIAMS. 1953. A cave faunule from western Puerto Rico with a discussion of the genus *Isolobodon*. Breviora **12**: 1—8.

- SCHWARTZ, A., and J. K. JONES, Jr. 1967. Review of bats of the endemic Antillean genus *Monophyllus*. Proc. U. S. Natl. Mus. 124: 1—20.
- SILVA TABOADA, G., and R. H. PINE. 1969. Morphological and behavioral evidence for the relationship between the bat genus *Brachyphylla* and the *Phyllonycterinae*. Biotropica 1: 10—19.
- SMITH, J. D. 1972. Systematics of the chiropteran family *Mormoopidae*. Univ. Kansas Mus. Nat. Hist. Mis. Publ. 56: 1—132.
- VAUGHAN, T. A., and G. C. BATEMAN. 1970. Functional morphology of the forelimb of mormoopid bats. J. Mamm. 51: 217—235.
- VILLALOBOS DOMÍNGUEZ, C., and J. VILLALOBOS. 1947. Colour Atlas. El Ateneo. Buenos Aires.
- VIÑA BAYÉS, N., and C. FUNDORA MARTÍNEZ. 1970. Estudio preliminar de los sedimentos del sistema subterráneo de Trinidad, Las Villas. Acad. Cien. Cuba. Ser. Espeleol. Carsol. 26: 1—19.
- WETMORE, A. 1922. Remains of birds from caves in the Republic of Haiti. Smithsonian Misc. Collect. 74: 1—4.
- . 1937. Bird remains from cave deposits on Great Exuma Island in the Bahamas. Bull. Mus. Comp. Zool. 80: 427—441.
- WILLIAMS, E. E. 1952. Additional notes on fossil and subfossil bats from Jamaica. J. Mam m. 33: 171—179.
- , and K. F. KOOPMAN. 1951. A new fossil rodent from Puerto Rico. Amer. Mus. Nov. 1515: 1—9.
- WING, E. S., C. A. HOFFMAN, Jr., and C. E. RAY. 1968. Vertebrate remains from indian sites on Antigua, West Indies. Caribbean J. Sci. 8: 123—139.

RESUMEN

Se descubrieron depósitos de murciélagos fósiles en dos cuevas de la región central de Cuba como consecuencia de la explotación industrial del guano de murciélago. Es casi imposible que estos depósitos se originaran como resultado de la depredación por lechuzas (como ha sido el caso con los depósitos de murciélagos fósiles dados a conocer de las Antillas hasta la fecha) porque solamente se encontraron restos de murciélagos en dichos depósitos y éstos estaban situados a 110 y 200 m de las respectivas entradas de las cuevas, en lugares cuyo acceso se logró con la ayuda de dinamita. Además, sólo se hallaron murciélagos cavernícolas. La evidencia sustancial documentada en el texto sugiere que estos depósitos más bien constituyen los restos de demos enteros de murciélagos que perecieron dentro de las cuevas a consecuencia de accidentes correlacionados con períodos de severidad climática, presumiblemente en tiempos pleistocénicos, representando así un nuevo tipo de depósito fósil contentivo de murciélagos en las Antillas. Incidentalmente, la explotación industrial en gran escala del guano de murciélago, tal como se practica corrientemente en Cuba, puede verse como una ayuda ocasional a la investigación paleontológica.

Se reconocen tres capas en los depósitos, de donde se extrajeron restos de 15 especies de murciélagos (géneros *Pteronotus*, *Mormoops*, *Macrotus*, *Monophyllus*,

Brachyphylla, *Erophylla*, *Phyllonycteris*, y *Natalus*). De éstas, dos (*Pteronotus pristinus* y *Mormoops magna*) se describen como nuevas, y una tercera (*Mormoops megalophylla*) se reporta por primera vez de la región antillana.

En la mayoría de los táxones las muestras fósiles de diferentes capas son estadísticamente (pero no cualitativamente) distinguibles. Se demuestra variación cronoclinal consistente en un aumento de la talla en 9 de las 13 especies representadas por material cuantitativamente adecuado para el análisis estadístico. Se intenta explicar por qué no se han demostrado cronoclinos en estas mismas especies de depósitos fósiles previamente descubiertos en Cuba y en otros lugares de las Antillas Mayores. Esta discrepancia se interpreta como el resultado de la insuficiente antigüedad de los depósitos previos, sobre la base de un análisis de los factores que determinan la formación y preservación de depósitos originados a partir de antiguas regurgitaciones de lechuzas, de donde se infiere una baja probabilidad de duración hasta los tiempos históricos.

La operación del efecto de BERGMANN no pudo haber producido el patrón de variación temporal (cronoclinal) que se observa, por cuanto se evidencian fluctuaciones climáticas pronunciadas en la secuencia estratigráfica. Sin embargo, un análisis de las relaciones de talla entre los murciélagos recientes de las Antillas Mayores sugiere que la talla pudo haber variado como respuesta a los hábitats insulares, puesto que los murciélagos tienden a ser más pequeños en las islas mayores, y más grandes en las islas menores, dentro de este grupo de islas ecológicamente comparables.

Sólo tres especies desaparecieron durante el lapso en cuestión. Aparte de cambios aparentes en la abundancia relativa de los táxones, no parece haberse producido el reemplazo de un taxon por otro. Consecuentemente, la extensa continuidad faunística que se observa a través de la secuencia estratigráfica es considerada como representativa de extinciones de demos (durante períodos de severidad climática) y recolonizaciones desde refugios dentro de Cuba. Así, los cronoclinos pueden indicar que — durante el segmento de la evolución filética representado por las capas fósiles — se requería considerable tiempo para la recolonización, o que, más bien, el acceso a estas cuevas no estuvo disponible durante periodos de larga duración a consecuencia de la actividad espeleogenética, alternativa ésta consistente con la evidencia observada. Hipotéticamente, en otras cuevas cubanas pueden encontrarse capas fósiles estadísticamente intermedias con respecto a las que aquí se consideran.

El hecho de que en la mayoría de los táxones las muestras alocrónicas se distinguieran estadísticamente, sugiere la viabilidad de una cronología relativa, si se hallaran en Cuba depósitos fósiles similares. Eventualmente, tal cronología podría comprobarse mediante correlaciones basadas en unos pocos fechados de carbono. Por otra parte, la presencia en todas las capas fósiles de los cuatro murciélagos polívoros de Cuba (*Monophyllus*, *Brachyphylla*, *Erophylla*, y *Phyllonycteris*) implica que la matriz de dichas capas contiene muestras representativas de las floras contemporáneas. Esto proporciona la posibilidad de trazar los cam-

bios vegetacionales a través del lapso en cuestión mediante el estudio del polen fósil, avenida muy sugestiva para ulterior investigación.

La presencia de especies de murciélagos cavernícolas obligatorios en las dos capas fósiles más antiguas, en número significativamente mayor que el que actualmente se encuentra en las cuevas de Cuba, sugiere que en épocas anteriores los hábitats cavernarios fueron más eficientemente explotados (probablemente hasta la saturación). Porque de las 22 especies vivientes endémicas de las Antillas Mayores, 15 son cavernícolas obligatorios, se infiere que los hábitats cavernarios favorecieron su preservación. Pero como los murciélagos en Centroamérica y el norte de Suramérica son históricamente silváticos, se postula que las colonizaciones originales de las Antillas Mayores se caracterizaron por el predominio de especies arborícolas, la mayoría de las cuales — debido a la naturaleza misma del refugio seleccionado — desaparecieron a causa de radicales cambios climáticos, tales como los que se sucedieron durante el Pleistoceno. Esto explicaría la pobreza comparativa de la fauna reciente de murciélagos en las Antillas Mayores, con relación a la diversidad ecológica de esta región insular. La fauna reciente se considera, así, como representativa del déficit entre las tasas de extinción e inmigración, teniendo en cuenta que las extensiones marítimas pueden ser barreras significativas en la dispersión de los murciélagos. El hecho de que la mayoría de los táxones extintos de las Antillas Mayores sean murciélagos cavernícolas se interpreta como consecuencia de la reducida posibilidad de los arborícolas de preservarse como fósiles, por las peculiaridades de este tipo de refugio y por la concomitante disminución del gregarismo. Sólo aquellos arborícolas incorporados a depósitos cavernarios mediante la depredación por lechuzas tendrían oportunidad de preservarse, y la baja probabilidad de preservación de tales depósitos se consignó anteriormente en este resumen.

STRESZCZENIE

W dwu jaskiniach środkowej Kuby, w wyniku eksploatacji guana nietoperzy dla celów nawozowych, stwierdzono obecność warstw ze szczątkami nietoperzy. Szczątki te nie nagromadziły się w wyniku działalności sów (jak w znanych dotychczas stanowiskach kopalnych nietoperzy na Antylach), gdyż nie towarzyszyły im resztki innych zwierząt i znajdowały się one w odległości 110 i 200 m od otworów badanych jaskiń, w chodnikach, do których dostęp uzyskano dopiero po wysadzeniu skał. Dane przytoczone w tekście wskazują, że szczątki te pochodzą od całych populacji nietoperzy, które zginęły w jaskiniach w wyniku klęsk, prawdopodobnie pożarów, związanych z okresami suchego klimatu. Tak więc opisane znaleziska reprezentują nowy typ osadów z kośćmi nietoperzy na Antylach.

W osadach wyróżniono trzy warstwy, z których oznaczono szczątki 15 gatunków nietoperzy (rodzaje *Pteronotus*, *Mormoops*, *Macrotus*, *Monophyllus*, *Brachyphylla*, *Erophylla*, *Phyllonycteris* i *Natalus*). Dwa z nich (*Pteronotus pristinus* i *Mormoops magna*) są tu opisane jako nowe dla nauki, a trzeci (*Mormoops megalophylla*) został po raz pierwszy stwierdzony na Antylach.

W większości taksonów próbki kopalne z poszczególnych warstw różnią się statystycznie, choć nie jakościowo. Wykazano zmienność chronoklinálną wyrażającą się zwiększeniem rozmiarów dla 9 z 13 gatunków reprezentowanych w liczbie dostatecznej dla analizy statystycznej. Autor próbuje wyjaśnić, dlaczego w dotychczasowych badaniach dla tych samych gatunków z osadów Kuby i innych stanowisk na Antylach nie wykazano takiej zmienności rozmiarów w czasie. Wynika to stąd, że dotychczasowe stanowiska były młodsze, a także wiąże się z czynnikami określającymi osadzanie się i zachowanie osadów pochodzących ze zrzutek sów, które powodują, że szansa zachowania się tego typu osadów z dawniejszych okresów jest mała.

Działanie reguły BERGMANNA nie mogło być powodem stwierdzonej zmienności rozmiarów w czasie, gdyż osady dostarczają dowodów silnie zaznaczonych wahań klimatycznych w czasie ich tworzenia się. Analiza wielkości współczesnych nietoperzy Wielkich Antyli wskazuje natomiast, że wielkość ta ulega zmianom pod wpływem środowiska wyspowego tego archipelagu mimo podobnych warunków ekologicznych. Wielkość ciała nietoperzy jest z reguły mniejsza na dużych wyspach, większa na mniejszych.

Tylko trzy gatunki nietoperzy zniknęły w czasie objętym badaniami. Poza wyraźną zmianą we względnej liczebności poszczególnych taksonów nie stwierdzono zastępowania poszczególnych form przez inne. Ze względu na to autor sądzi, że stosunkowo duża ciągłość fauny w czasie tworzenia się osadów jest wynikiem wymierania populacji (w okresach niekorzystnego klimatu) i powtórnego zasiedlania przez nie terenu z refugium w obrębie Kuby. Chronoklinálna zmienność może więc wskazywać, że — podczas odcinka ewolucji, reprezentowanego w kopalnych osadach — trzeba było wiele czasu do powtórnej kolonizacji lub, co bardziej prawdopodobne, że dostęp do jaskini był dla nietoperzy zamknięty przez długie okresy w wyniku procesów rozwoju jaskiń. Ta druga hipoteza lepiej zgadza się z obserwowanymi faktami.

Fakt, że próbki osobników z różnego czasu są odróżnialne statystycznie u większości badanych gatunków, sugeruje możliwość stworzenia chronologii względnej podobnych kopalnych osadów, które mogą zostać wykryte na Kubie. Taka chronologia winna być sprawdzona w przyszłości przez skorelowanie jej z datowaniem opartym na ilości radioaktywnego izotopu węgla. Z drugiej strony występowanie we wszystkich warstwach osadów wszystkich czterech pyłkożernych gatunków nietoperzy Kuby (*Monophyllus*, *Brachyphylla*, *Erophylla* i *Phyllonycteris*) wskazuje, że reprezentatywne próbki ówczesnych flor zawarte są we wspomnianych warstwach. Wskazuje to na możliwość śledzenia zmian roślinności w omawianym okresie na podstawie pyłków kopalnych, co wydaje się szczególnie interesującym kierunkiem dalszych badań.

Występowanie w dwu starszych warstwach wyraźnie większej liczby gatunków nietoperzy, obligatorycznie związanych z jaskiniami, niż obecnie w jaskiniach Kuby wskazuje, że wówczas środowisko jaskiniowe było pełniej wykorzystywane przez nietoperze (być może aż do nasycenia) niż dziś. Ze względu na to, że 15 z 22 obecnych gatunków nietoperzy endemicznych dla Wielkich Antyli jest obligatoryjnie związane z jaskiniami, przypuszczać można, że było to środowisko korzystne dla ich zachowania się. Ponieważ jednak nietoperze Ameryki Środkowej i północnej części Ameryki Południowej są — historycznie biorąc — formami leśnymi, należy przyjąć, że większość z nich — ze względu na charakter ich schronień — zniknęła po okresach gwałtownych zmian klimatycznych, takich jak zachodzące w plejstocenie.

Ten proces przyczynił się do względnego ubóstwa fauny nietoperzy w stosunku do bogactwa ekologicznego, dającego się stwierdzić w dzisiejszej faunie Wielkich Antyli. Należy sądzić, że skład współczesnej fauny nietoperzy jest wynikiem różnicy między tempem wymierania i imigracji, biorąc pod uwagę, że przestrzenie wodne między wyspami mogą być istotnymi barierami dla rozprzestrzeniania się nietoperzy. Fakt, że wśród taksonów wymarłych nietoperzy na Wielkich Antylach jest więcej gatunków jaskiniowych niż leśnych, można wyjaśnić tym, że gatunki leśne ze względu na mniej masowe występowanie i charakter schronień miały mniej szans zachowania się w stanie kopalnym. Zachować się mogły jedynie osobniki przyniesione do osadów w pobliżu otworów jaskiń przez sowy, a jak wynika z danych w tekście pracy, tego typu osady mają małe prawdopodobieństwo zachowania się przez dłuższy czas.

Plate II

Fossil crania and mandibles of four species of the genus *Pteronotus*. From left to right: dorsal, occlusal, and lateral views of cranium, and lateral view of mandible. From top to bottom: *P. fuliginosus*, *P. macleayi*, *P. pristinus* (holotype), and *P. parnelli*. Approximately 2.7×

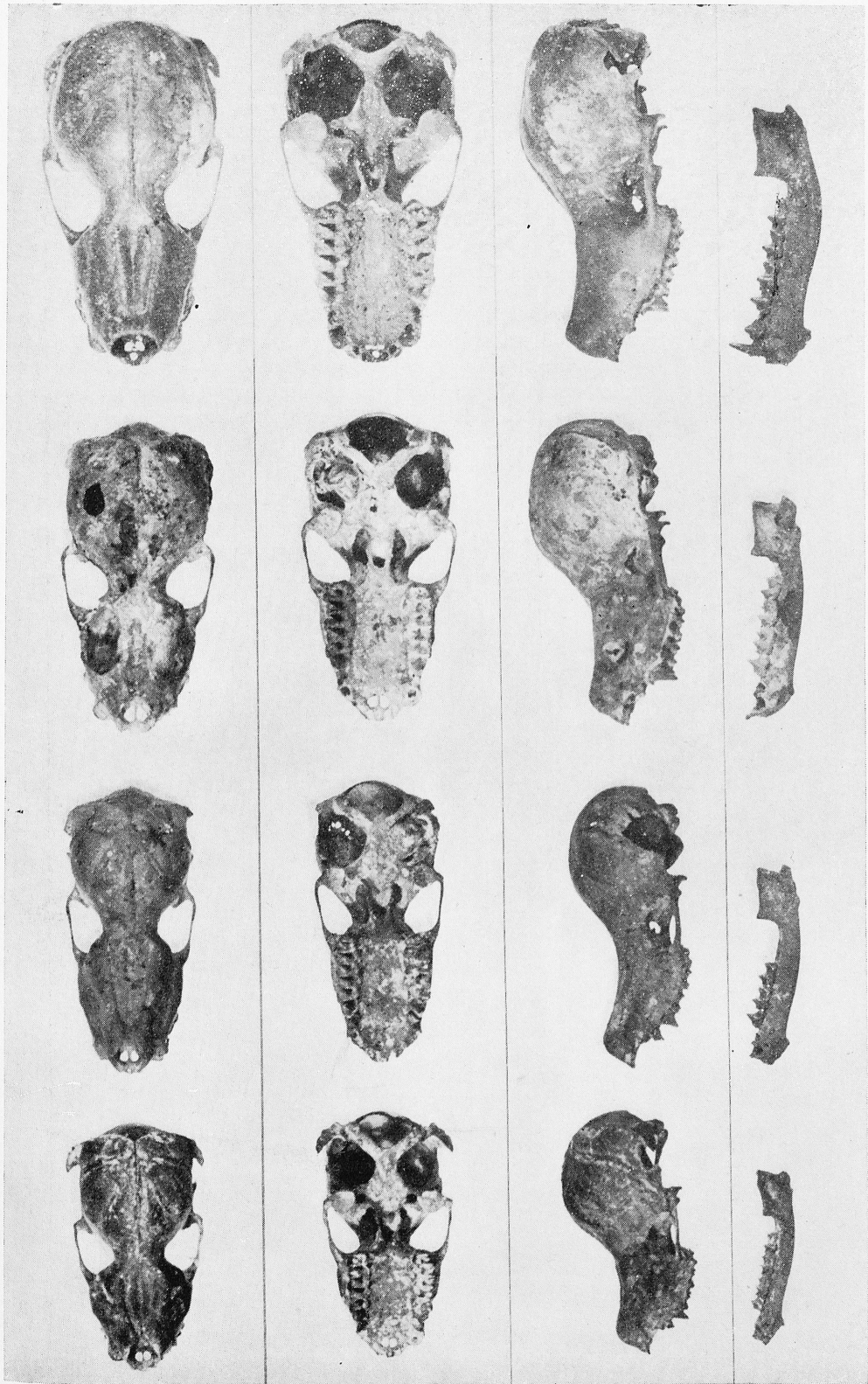


Plate III

Fig. 1. Anterior view of fossil humeri in species of the genera *Pteronotus* (right humerus), *Mormoops* (left humerus), and *Natalus* (right humerus). From left to right: *P. fuliginosus*, *P. macleayi*, *P. pristinus*, *P. parnelli*, *M. blainvillei*, *M. megalophylla*, *M. magna* (holotype), *N. lepidus*, *N. macer*, and *N. major*. Approximately $2.7\times$

Fig. 2. Sexual dimorphism in recent (left) and fossil (right) specimens of *Monophyllus redmani*. Lateral view of male (above) and female (below) mandibular ramus. Approximately $2.7\times$

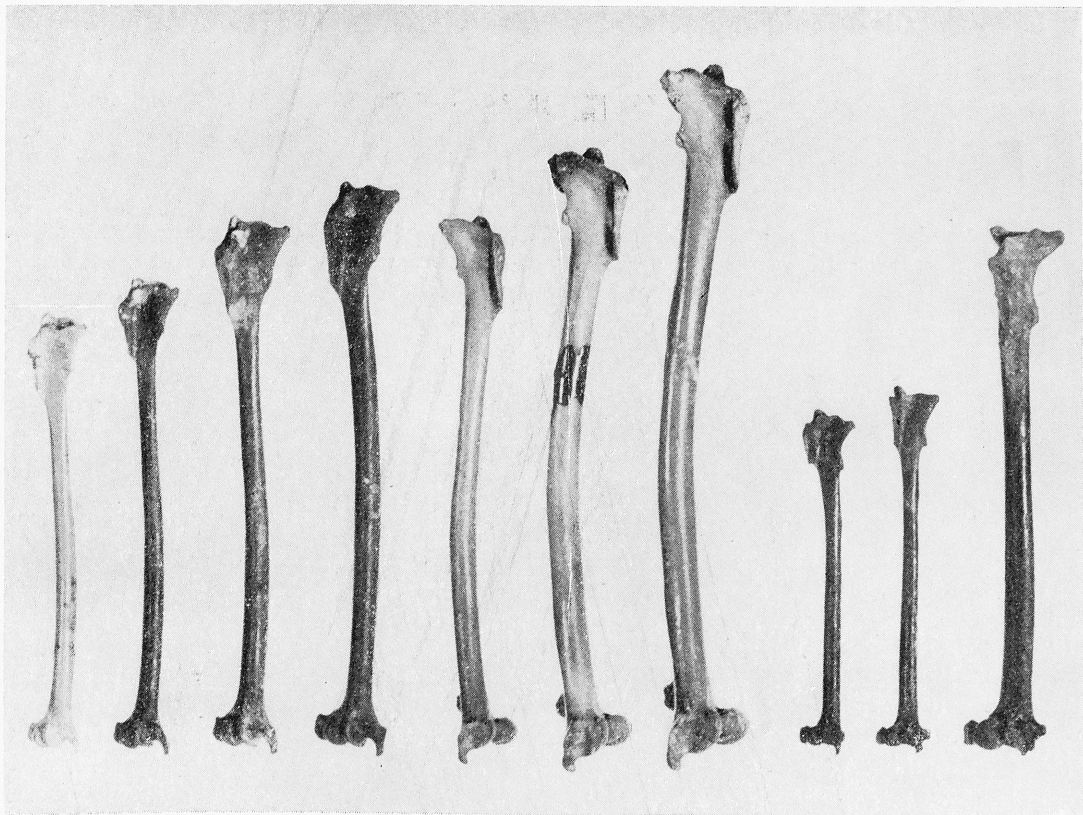


Fig. 1

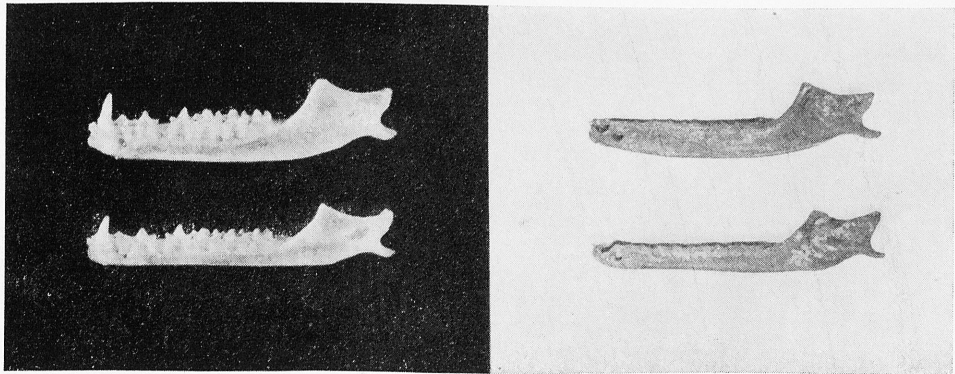
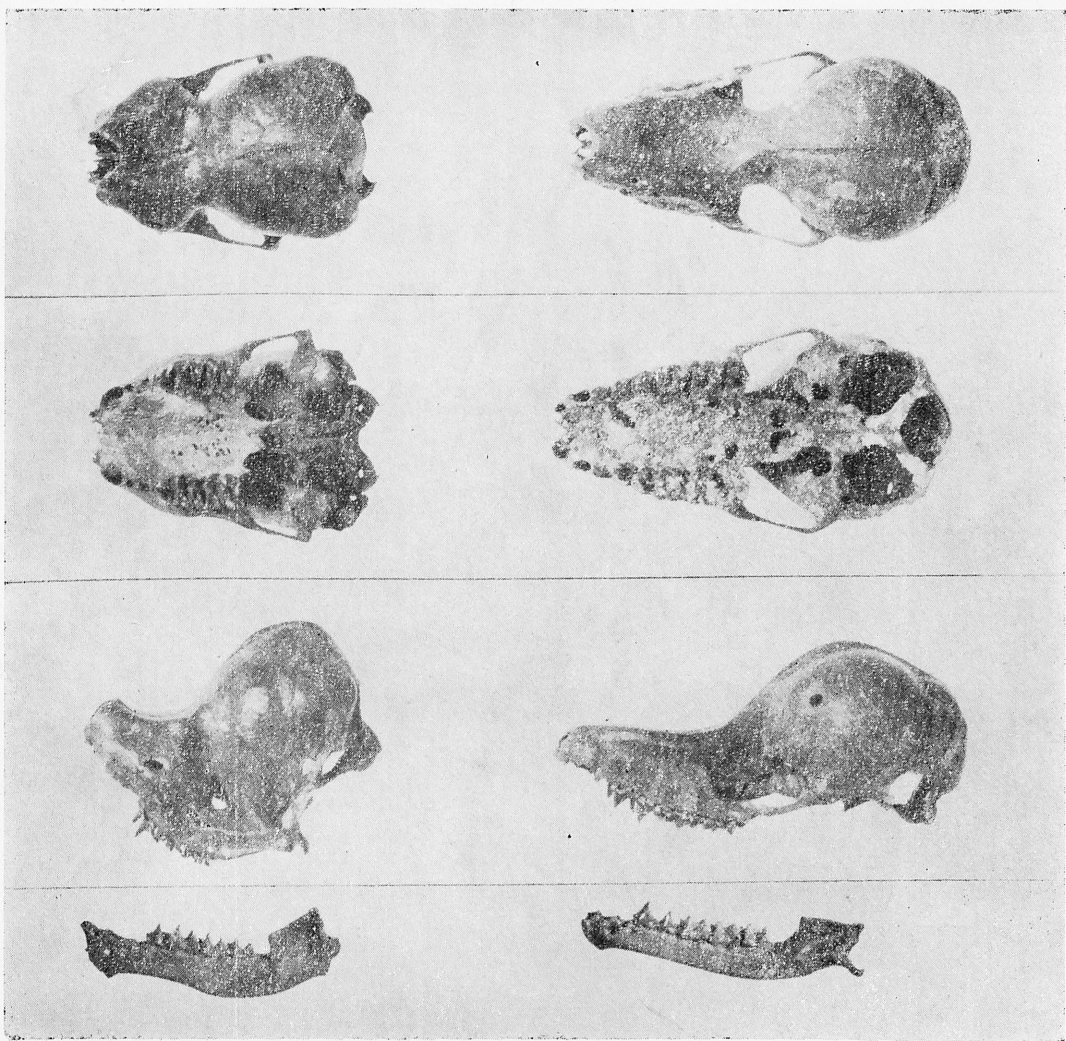


Fig. 2

Plate IV

Fossil crania and mandibles of *Mormoops megalophylla* (left) and *Natalus major* (right). From top to bottom: dorsal, occlusal, and lateral views of cranium, and lateral view of mandible.

Approximately 2.7×



Redaktor zeszytu: prof. dr K. Kowalski

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