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A Systematic Revision of *Macrotus* (Chiroptera)

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ABSTRACT

Among 810 specimens of bats of the genus *Macrotus* (Phyllostomatidae) that were studied are specimens representing populations both geographically and morphologically intermediate between the three nominal species recognized in recent years. Specimens from Sinaloa are intergrades between *Macrotus californicus* and *Macrotus mexicanus*, and specimens from Cuba are intergrades between *M. mexicanus* and *M. waterhousii*. Therefore, we conclude that a single species, *Macrotus waterhousii*, having seven subspecies, ranges from California south to Guatemala on the mainland and occurs on most West Indian islands east to Hispaniola. Secondary sexual dimorphism was not detected. Only adults were used in geographic comparisons. Individual variation is described. Various degrees of intra-specific differences are described, and the relevance of the subspecies concept is discussed. Synonymies, ranges, types, detailed comments, and lists of specimens are included in the Accounts of Subspecies.

INTRODUCTION

The big-eared, leaf-nosed bats of the genus *Macrotus* were revised by Rehn (1904), who recognized four species: *M. californicus*, *M. mexicanus*, *M. pygmaeus*, and *M. waterhousii*. Goodwin (1953, p. 246) indicated that the type (and only reported) specimen of *M. pygmaeus* is referable to

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Micronycteris megalotis mexicana, and one of us (Anderson) has verified this determination. Only one new name, *Macrotus waterhousii heberfolium* Shamel (1931, p. 252), has been proposed since 1904. The species and subspecies as treated by Rehn have been used by all subsequent authors, as is summarized by Hall and Kelson (1959, p. 101).

An attempt (by Anderson in 1956) to identify specimens from Chihuahua and northern Sinaloa (in the region of the boundary between the allopatric geographic ranges of *M. californicus* and *M. mexicanus* as then understood) led to a consideration of the relationships of these two species.

Initially, 10 specimens of *Macrotus californicus* from California and 10 of *Macrotus mexicanus* from Guerrero were compared visually, and a number of measurements were taken. *Macrotus mexicanus* had greater total length of skull, interorbital breadth, breadth of braincase, length of forearm, and total length. Measurements recorded from Sinaloan specimens were intermediate; some specimens were nearer *mexicanus*, some were nearer *californicus*, and some specimens resembled *mexicanus* in some characters and *californicus* in other characters. We concluded, tentatively, that *M. californicus* and *M. mexicanus* were conspecific and continued to gather data for a more adequate analysis of geographic variation.

The intergradation of two forms in the genus that are as distinct as typical *M. mexicanus* and *M. californicus* suggested that the status of the third allopatric species, *M. waterhousii*, should be studied also, especially since *M. waterhousii* Gray, 1843, antedates both *M. californicus* Baird, 1859, and *M. mexicanus* Saussure, 1860. The concurrent treatment of these three nominal species and their subspecies enables us to make all indicated nomenclatural changes at one time. Dr. Karl F. Koopman kindly informed us that his earlier study of *M. waterhousii* indicated its possible conspecificity with mainland *Macrotus*, although he had not gathered data to document this tentative conclusion. Hershkovitz (1951, p. 554) commented that "Specific distinction [of *M. waterhousii*] from *M. mexicanus* is doubtful." Some earlier authors, as is indicated in the synonymies, also had expressed the same opinion.

Nelson collaborated in the preliminary studies of specimens in the University of Kansas Museum of Natural History in 1958 and in subsequent years. Anderson studied selected specimens in other museums, made statistical calculations, and wrote the first draft of the manuscript.

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PROCEDURE AND METHODS

Cranial measurements were taken with dial calipers reading to tenths of millimeters, except that (in most specimens) the length of the auditory bullae and the breadth at the canines were measured with an eyepiece micrometer in a binocular microscope as was the length of the second upper premolar tooth (in five series only). All measurements are in millimeters. External measurements (see table 1) are those recorded by collectors, except the length of the forearm which was measured in dried or alcoholic specimens with calipers. Cranial measurements selected, after preliminary consideration of various measurements, as best showing geographic differences are:

TOTAL LENGTH OF SKULL: The maximum length from occiput to tips of incisor teeth (not, therefore, exactly parallel to the basicranial axis of the skull).

BREADTH OF BRAINCASE: At the lateral bulges posterodorsal to (and not including) the roots of the zygomatic processes of the squamosals.

TABLE 1
EXTERNAL MEASUREMENTS (IN MILLIMETERS) OF ADULT *Macrotus waterhousii*
(For each measurement and each group—a “group” is a sample from an area shown by a
corresponding letter in fig. 1—the mean and standard deviation are shown on one
line; the minimum and maximum are shown, in parentheses, on a second
line; and the number in each sample is shown on a third line.
Some of these data are omitted for small samples.)

Group	Total Length	Length of Tail	Length of Hind Foot	Length of Forearm
A (Baja California)	95.0 (90-98) <i>N</i> = 4	— (35-40) <i>N</i> = 3	— — <i>N</i> = 0	49.38±1.40 (46.0-52.0) <i>N</i> = 28
B (California)	94.3±3.0 (85-99) <i>N</i> = 58	36.3±2.2 (28-41) <i>N</i> = 58	13.8±1.1 (11-15) <i>N</i> = 58	49.33±1.27 (45.8-51.9) <i>N</i> = 58
C (Northern Sonora)	94.9±2.5 (87-100) <i>N</i> = 35	34.9±1.6 (30-37) <i>N</i> = 35	14.7±0.9 (12-15) <i>N</i> = 35	49.00±1.09 (47.2-51.0) <i>N</i> = 35
D (Southern Sonora)	94.7±2.4 (87-101) <i>N</i> = 41	33.8±2.4 (25-36) <i>N</i> = 41	14.5±1.5 (11-18) <i>N</i> = 41	48.99±2.01 (44.7-52.5) <i>N</i> = 41
E (Northern Sinaloa)	96.1±3.9 (87-103) <i>N</i> = 21	21.5±2.5 (29-39) <i>N</i> = 21	13.7±0.7 (13-15) <i>N</i> = 21	49.32±1.00 (47.5-51.0) <i>N</i> = 21
F (Southern Sinaloa)	93.1±4.8 (87-107) <i>N</i> = 15	33.3±3.3 (28-40) <i>N</i> = 15	13.1±1.1 (11-15) <i>N</i> = 15	49.40±0.93 (47.8-51.3) <i>N</i> = 15
G (Jalisco)	94.2±3.9 (86-100) <i>N</i> = 35	32.6±3.0 (27-39) <i>N</i> = 35	14.5±0.6 (13-16) <i>N</i> = 35	48.38±1.24 (46.3-51.8) <i>N</i> = 35
H (Guerrero, Morelos, Puebla)	99.5±5.1 (91-108) <i>N</i> = 17	37.0±1.3 (29-42) <i>N</i> = 17	13.1±1.3 (11-15) <i>N</i> = 17	51.29±2.03 (45.1-54.3) <i>N</i> = 17
I (Oaxaca)	100.5±3.2 (95-105) <i>N</i> = 15	36.6±2.1 (33-40) <i>N</i> = 15	14.1±1.0 (12-15) <i>N</i> = 15	51.29±1.04 (49.2-53.0) <i>N</i> = 15
J (Western Cuba)	99.5±4.1 (89-105) <i>N</i> = 12	33.9±2.7 (29-37) <i>N</i> = 12	14.5 (14-15) <i>N</i> = 2	51.21±1.27 (49.8-54.0) <i>N</i> = 19
K (Isle of Pines)	93.7±6.8 (77-108) <i>N</i> = 16	35.7±3.1 (30-38) <i>N</i> = 16	13.2±0.7 (13-15) <i>N</i> = 16	50.78±0.93 (48.9-52.6) <i>N</i> = 16
L (Eastern Cuba)	101.2±3.0 (96-106) <i>N</i> = 16	37.0±2.2 (34-41) <i>N</i> = 16	14.57 (13-15) <i>N</i> = 7	51.56±1.96 (45.1-54.7) <i>N</i> = 18
M (Western Bahamas)	— — <i>N</i> = 0	— — <i>N</i> = 0	— — <i>N</i> = 0	51.52 (49.5-53.6) <i>N</i> = 4

TABLE 1—(Continued)

Group	Total Length	Length of Tail	Length of Hind Foot	Length of Forearm
N (Jamaica)	104 (102-106) <i>N</i> = 3	37 (both 37) <i>N</i> = 2	— — <i>N</i> = 0	53.96 (52.5-54.8) <i>N</i> = 5
O (Hispaniola)	99.1±4.4 (93-108) <i>N</i> = 14	34.3±3.1 (30-38) <i>N</i> = 14	14.7±1.6 (12-16) <i>N</i> = 14	53.88±1.65 (50.5-56.8) <i>N</i> = 76
P (Eastern Bahamas)	— (100-107) <i>N</i> = 3	— (34-39) <i>N</i> = 3	— — <i>N</i> = 0	56.2 (55.0-58.0) <i>N</i> = 3

INTERORBITAL BREADTH: The standard breadth at the interorbital constriction.

BREADTH AT CANINES: Between the most lateral points of the upper canines.

LENGTH OF BULLA: The distance between two planes perpendicular to the basicranial axis of the skull and passing through the anteriormost and posterior-most points of the auditory bulla.

Although there are significant geographic differences in the length of the ear, as shown in figure 2, the measurement of the ear taken by the collector was not used because different collectors had taken the measurement in different fashions. Larger bullae were associated with larger ears, and, therefore, the length of the bulla was used.

Data from within each of 16 different areas were grouped for the computation of statistics. Statistics are given in tables 1 and 2, and statistics for selected measurements are graphed in figures 6 through 18. The 16 areas are shown in figure 1, where they are indicated by the letters A through P. Variation within each area was judged to be negligible.

Although 810 specimens are listed in the paragraphs on Specimens Examined in the subspecies accounts, we are aware of more than 450 additional specimens that are not listed because they were examined only superficially or not at all. These specimens were not used because we judged that other material was adequate to answer the specific questions we were attempting to answer.

THE CONCEPT OF SUBSPECIES

The measurements, thus analyzed, reveal three large areas of major geographic differentiation; the first includes groups A through E; the second includes groups F through L; and the third includes groups M through P (see fig. 1). These three major areas approximate the ranges of the three nominal species, until now recognized, except that popula-

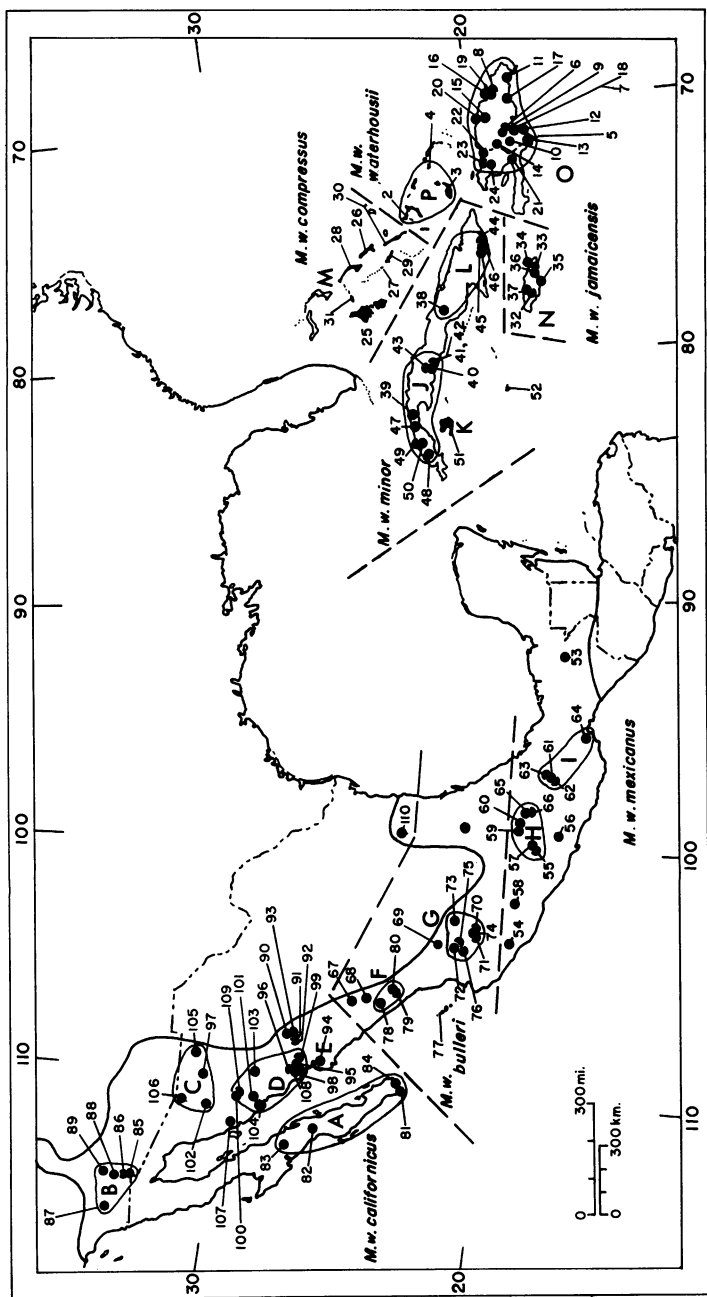


FIG. 1. Map showing the geographic ranges of *Macrotus waterhousii* and its subspecies. Heavy broken lines separate ranges of subspecies. Dots represent localities from which specimens have been examined by one or both of the authors. Other records from Yucatan and Guatemala are discussed in text. The number of each locality refers to the number with the designation of that locality in the text. A through P indicate areas from which samples were derived for statistical treatment. The northern and southern limits of the known range on the mainland are shown by heavy lines.

tions from Cuba and the Isle of Pines, formerly allied with other Caribbean *Macrotus* and therefore placed in *M. waterhousii*, seem closer morphologically to those from southern Mexico. Within each of these major areas, geographic variation is evident. The first major area exhibits greater homogeneity in the *Macrotus* from place to place than does the second, and the second major area exhibits greater homogeneity than the third. The amount of variability among specimens from any one locality does not differ appreciably from one region to another.

With these observations in mind, we could regard the bats studied as consisting of a single species with three subspecies. We do recognize only one species, but we choose to recognize more than three subspecies for the following reasons:

1. Until alleged differences can be evaluated conclusively, the nomenclaturally most conservative course of action is most desirable. In other words, when in doubt do not change the name.

2. The amounts of variability within different subspecies are more comparable if the third major area, and less certainly the second major area, are divided into more than one subspecies. This maintenance of somewhat comparable amounts of variability is regarded as pertinent, even though we realize that it is impossible to make subspecies precisely comparable in degree of intrasubspecific variability. Widespread and geographically varied species generally exhibit degrees of homogeneity and distinctness between subspecies and within subspecies. Nevertheless, within this pattern there are contiguous areas within which samples of *Macrotus* are morphologically similar to one another and are significantly different from samples from other such contiguous areas.

3. The main features of geographic variation certainly are made no less evident, and may in fact be emphasized, by the use of more than three subspecies names. The names, by themselves, do not convey any information about geographic variation. It may be assumed, however, upon examining a distribution map showing subspecies ranges, that the animals are more variable geographically in that part of their range where more subspecies have been recognized. Such an assumption is valid if one person or several persons with comparable concepts and knowledge of the species have decided what to recognize.

4. Subspecific names are convenient. It is easier to say *M. w. compressus* than to say "representatives of *Macrotus waterhousii* from the Bahama Islands north of Crooked Island" or even "northern Bahamian specimens."

Available material from the West Indies provides some new information on variation in *Macrotus* and warrants the nomenclatural reassign-

ment at the subspecies level of specimens from the southeastern Bahama Islands. Samples are still too small to permit conclusive statistical tests of the significance of some of the alleged differences between populations, and are too small to provide answers to other questions pertinent to the evaluation of subspecies. For example, we now know that specimens from Oriente Province in eastern Cuba are significantly larger than specimens from Pinar del Río and Las Villas provinces in western Cuba and from the Isle of Pines off western Cuba. These three western samples do not differ significantly in size. We may conclude that the clinal variation within Cuba from west to east is not uniform, but we have no basis on which to decide whether or not there is a "step" in the cline. By studying the few available specimens from each of several islands in the northern part of the Bahama Islands and other specimens from the southern islands, we learn that size is greater in those of *Macrotus* of more southern islands. As regards more detailed analysis, we cannot be certain, for example, whether or not any difference in size exists between specimens from New Providence Island and those from Long Island.

The distribution and variation of *Macrotus* on the mainland and on islands of varying sizes and varying distances apart are the results of an evolutionary "experiment" worthy of more detailed study. The fact that neither the last reviser of the genus in 1904 nor we have studied this experiment in greater detail is attributable to the amount of material available rather than to the use of inadequate methods or unsound theoretical doctrine. Faced with the usual situation of limited material, the systematist has several alternatives. He can give up, on the grounds that materials, time, and funds do not provide "the minimum required for the necessary high standard of taxonomic work" suggested by Pimentel ("1959" [1960], p. 152). He can obtain more material, as Pimentel also suggested, and most systematists attempt to do so. Or, he can learn what he can with the available resources, including such new material as he has been able to obtain. Probably his contribution to knowledge will be greatest if he does the last. In our study of *Macrotus* we have not used all available material and we have not exhausted the possibilities of the materials used. For example, we could have increased the cranial samples by extracting the skulls from additional specimens in preservative, and we could have used additional measurements. We have selected certain measurements and samples that would provide answers to certain questions.

We find no evidence in the literature that reveals any delay in the advance of knowledge of *Macrotus* as a result of the use of a concept of subspecies or the use of the trinomen. Much has been written recently

on methods of study of geographic variation and on the concept and the nomenclature of subspecies. See for example various articles and letters in the pages of the journal *Systematic Zoology* in the past five years. Certain abuses of the concept of subspecies have been overexaggerated in connection with proposals of new methods. Newer concepts and methods such as "numerical taxonomy" will be justified as they produce meaningful systematic results, and the concept of subspecies will continue in use as long as systematists find it to be useful. We have found it useful in our study of *Macrotus*.

Some of the above ideas on the nature of subspecies and some additional ideas have been expressed earlier by one of us (Anderson, 1959, p. 445).

The use of subspecies names does not necessarily imply that only one level of intraspecific variation has been studied or that only one level is important. In the dendrogram in figure 19 we have graphically illustrated our interpretation of the relative degrees of morphological differentiation between populations from areas shown by letters A through P in figure 1. Lines connected farther to the right indicate greater distinction. Samples A through D are not significantly different. Since various degrees of differentiation separate populations, the selection of a certain level for the recognition of subspecies is arbitrary. The numbers at the bottom of the dendrogram show the numbers of subspecies that would be recognized by the use of different levels of difference as subspecies criteria. Seven subspecies are recognized in this paper. The reasons for recognizing subspecies and for recognizing seven subspecies instead of three, which is probably the next most reasonable number, are discussed above. Symbols at the left of figure 19 are arrows showing postulated directions of gene flow. Dots by arrows represent over-water gaps. Double arrows are used where the effect of gene flow is judged to be greater in one direction than in the opposite direction. Wider arrows represent greater effective gene flow. For example, a wider arrow from O to P than in the reverse direction indicates that the probability of a bat's crossing from the larger land mass and larger population in Hispaniola (O) to the small islands of the southern Bahamas (P) is greater than the probability of movement in the opposite direction. Also, movement of the same number of individuals would have a greater effect on the gene pool of a smaller recipient population. Although the dendrogram separates E and F at a high level, it should be remembered that these areas are geographically close and presumably are occupied by interbreeding stocks of bats. Sample E is different from D because of this interbreeding.

In a few areas the estimated effects of gene flow differ from the observed morphological differences. The abrupt break between samples E and F

TABLE 2
CRANIAL MEASUREMENTS (IN MILLIMETERS) OF ADULT *Macrotus waterhousii*
(For each measurement and each group—a “group” is a sample from an area shown by a corresponding letter in fig. 1—the mean and standard deviation are shown on one line; the minimum and maximum are shown, in parentheses, on a second line; and the number in each sample is shown on a third line.)

Group	Length of Skull	Breadth of Braincase	Interorbital Breadth	Breadth at Canines	Length of Bulla
A (Baja California)	22.92±0.46 (22.1-23.7) N = 15	8.60±0.22 (8.2-9.1) N = 15	3.52±0.15 (3.2-3.7) N = 15	3.33±0.18 (3.0-3.7) N = 15	3.90±0.14 (3.6-4.1) N = 15
B (California)	23.30±0.34 (22.5-24.1) N = 58	8.93±0.18 (8.5-9.3) N = 58	3.53±0.11 (3.3-3.8) N = 58	3.35±0.14 (3.1-3.7) N = 58	3.91±0.10 (3.7-4.1) N = 56
C (Northern Sonora)	23.07±0.36 (22.2-23.7) N = 35	8.62±0.18 (8.3-9.1) N = 35	3.49±0.10 (3.3-3.8) N = 35	3.36±0.15 (3.1-3.7) N = 35	3.86±0.11 (3.7-4.1) N = 35
D (Southern Sonora)	23.16±0.37 (22.5-23.7) N = 41	8.62±0.19 (8.3-9.0) N = 41	3.57±0.19 (3.4-4.0) N = 41	3.44±0.16 (3.2-3.9) N = 41	3.79±0.17 (3.4-4.1) N = 41
E (Northern Sinaloa)	23.68±0.29 (23.2-24.2) N = 21	9.13±0.12 (9.0-9.4) N = 21	3.64±0.12 (3.4-3.9) N = 21	3.56±0.11 (3.4-3.7) N = 21	3.82±0.07 (3.7-4.0) N = 21
F (Southern Sinaloa)	23.73±0.34 (23.2-24.1) N = 15	8.91±0.21 (8.6-9.2) N = 15	4.09±0.12 (3.9-4.2) N = 15	3.78±0.13 (3.6-4.0) N = 15	3.59±0.11 (3.4-3.7) N = 15
G (Jalisco)	23.26±0.32 (22.6-23.9) N = 35	9.04±0.16 (8.8-9.4) N = 35	4.07±0.12 (3.8-4.3) N = 35	3.68±0.08 (3.5-3.9) N = 35	3.60±0.08 (3.4-3.7) N = 35
H (Guerrero, Morelos, Puebla)	23.88±0.56 (22.4-24.4) N = 17	9.30±0.20 (9.0-9.8) N = 17	4.06±0.12 (3.9-4.3) N = 17	3.88±0.18 (3.6-4.2) N = 17	3.59±0.06 (3.4-3.7) N = 17
I (Oaxaca)	24.38±0.44 (23.7-25.5) N = 28	9.24±0.27 (8.7-9.8) N = 28	4.05±0.12 (3.7-4.3) N = 28	3.81±0.13 (3.6-4.1) N = 28	3.56±0.08 (3.4-3.7) N = 28
J (Western Cuba)	23.72±0.25 (23.2-24.1) N = 19	8.92±0.13 (8.7-9.1) N = 19	4.11±0.11 (3.9-4.3) N = 19	3.55±0.13 (3.4-3.8) N = 19	3.57±0.10 (3.4-3.7) N = 19
K (Isle of Pines)	23.67±0.37 (22.9-24.2) N = 16	8.90±0.11 (8.7-9.1) N = 16	4.05±0.08 (3.9-4.2) N = 16	3.54±0.14 (3.3-3.8) N = 16	3.60±0.06 (3.5-3.7) N = 16
L (Eastern Cuba)	24.39±0.24 (23.9-24.8) N = 17	9.02±0.15 (8.8-9.2) N = 17	4.15±0.09 (4.0-4.3) N = 17	3.74±0.10 (3.6-3.9) N = 17	3.54±0.09 (3.4-3.7) N = 17
M (Western Bahamas)	25.08±0.39 (24.5-25.7) N = 13	9.44±0.17 (9.2-9.7) N = 13	4.30±0.12 (4.1-4.4) N = 13	3.85±0.18 (3.5-4.1) N = 13	3.72±0.13 (3.5-4.0) N = 13

TABLE 2—(Continued)

Group	Length of Skull	Breadth of Braincase	Interorbital Breadth	Breadth at Canines	Length of Bulla
N (Jamaica)	25.60 (25.2-26.1) <i>N</i> = 3	9.37 (9.3-9.5) <i>N</i> = 4	4.20 (4.1-4.3) <i>N</i> = 4	4.05 (3.9-4.2) <i>N</i> = 4	3.55 (3.5-3.6) <i>N</i> = 4
O (Hispaniola)	26.08±0.55 (25.1-26.9) <i>N</i> = 24	9.38±0.19 (9.0-9.6) <i>N</i> = 24	4.29±0.08 (4.1-4.4) <i>N</i> = 24	4.36±0.17 (4.0-4.6) <i>N</i> = 24	3.51±0.12 (3.3-3.8) <i>N</i> = 24
P (Eastern Bahamas)	26.70 (25.9-27.9) <i>N</i> = 5	9.38 (9.1-9.6) <i>N</i> = 5	4.36 (4.3-4.5) <i>N</i> = 5	4.30 (4.1-4.5) <i>N</i> = 5	3.56 (3.5-3.7) <i>N</i> = 5

(see figs. 17 and 18) is greater than we would have estimated on the assumption of a more or less continuously distributed population of *Macrotus* along the coastal area in Sinaloa. Two possible contributing causes are (1) secondary intergradation and (2) the narrowness of the occupied area and therefore smaller population size in Sinaloa than in the larger occupied regions to the north and to the south of Sinaloa. A more abrupt morphological gap separates Cuban *Macrotus* from surrounding insular populations to the eastward than would have been guessed, and a smaller morphological difference separates Cuban *Macrotus* from mainland *Macrotus* than would have been guessed.

NON-GEOGRAPHIC VARIATION

Understanding of geographic variation presupposes an understanding of variation with age, of differences between the sexes, and of the range of variation between individuals from a single population of the same age and sex.

Young individuals were recognized by their distinct phalangeal epiphyses. The presence of cartilage between shaft and epiphysis is evident in both dried skins and specimens in alcohol. Only individuals lacking this cartilage were used in the comparisons. Evident differences in the amount of wear on teeth do occur within samples of presumed adults. Individuals with the most worn teeth, however, are not in every case the largest individuals, and the samples of adults were not subdivided for statistical analysis in the geographic comparisons.

Males do not differ significantly from females in any measurement studied. Differences in mean values for 28 males and 30 females from California (sample B) were not statistically significant at the 95 per cent

confidence level; therefore, males and females were combined in all samples for statistical comparisons.

Variation occurs within samples of adults from single localities or groups of localities from small areas of uniform habitat and without evident barriers. This "individual variation" may be defined as the variation that remains when the effects of other sources of variation have been minimized. Other definitions are possible, but however it is defined, this variation cannot be eliminated, even in carefully controlled laboratory experiments with living organisms. The amount of variation in one sample of adults (B, from California) is shown for five cranial measurements and for the length of the forearm in figures 7, 9, 11, 13, and 15. These figures also correlate the measurements. In each of these graphs a weak positive correlation is apparent. The estimated coefficients of correlation are between 0.3 and 0.6. Larger individuals tend to be larger in all measurements. The breadth of the braincase and the breadth at canines perhaps tend to be greater, relative to the length of the skull, in larger individuals. The braincase in a young mammal generally, and probably also in a young *Macrotus*, is broader, relative to the length of the skull, than in the same animal as an adult. The relatively broader braincase in larger adults of *Macrotus* is thus not predicted from the assumption that the larger adults are the older adults. Therefore, the larger adults are not necessarily the older adults, as is noted above in connection with amount of wear on the teeth. The cranial measurements differ in their variability. The coefficients of variability calculated from the data in table 2 indicate that in most samples the length of the skull is the least variable, then in order of increasing variability the breadth of the braincase, the length of the bulla, interorbital breadth, and the breadth at the canines. External measurements, especially the length of the tail and hind foot, are in almost every case more variable than cranial measurements. Part of this greater variability results from the use of different techniques of measurement by different collectors. The coefficient of variation of the total length is usually no greater than the coefficients of the more variable cranial measurements.

GEOGRAPHIC VARIATION

Each of four cranial measurements and the length of the forearm are plotted against the length of the skull in figures 6 through 15. Figures 6, 8, 10, 12, and 14 show the correlations of averages for the above measurements in 16 samples from different geographic areas (see the corresponding letters A through P in fig. 1). Points representing geographically adjacent

samples, beginning with Baja California and California and then proceeding in a generally southeastward direction, are connected by lines. A trend to larger size toward the southeast is apparent in every measurement except the length of the bulla, which actually decreases. On each graph is plotted a line, on which any point has a value on the y axis equal to a certain stated percentage of its value on the x axis (except that in figures 14 and 15 the length of the skull as a percentage of the length of the forearm is indicated by the line marked 50%). Inspection of figure 6 reveals that the breadth at the canines, relative to the length of the skull, increases geographically. Figure 8 reveals the relative decrease in length of bulla that follows from the actual decrease in length of bulla mentioned above. Figure 10 reveals an abrupt change in the actual and relative interorbital breadth between samples E and F, and a relatively greater interorbital breadth in the samples showing greatest size than in the five samples showing least size. Figure 12 reveals that the relative breadth of the braincase decreases geographically with increasing size. Figure 14 reveals a high positive correlation (estimated coefficient of correlation about 0.9) and no important change in ratio of average values of length of forearm to length of skull. The major facts of geographic import evident in the graphs are the increase in most measurements and the decrease in the length of the bulla, as one proceeds southeastwardly, the break between samples E and F (most evident in fig. 10) and the differences between correlations geographically derived and those derived from a single sample. Statistics for three cranial measurements in each of 16 samples presented in figures 16, 17, and 18 are derived from data in table 2. The increase in size from northwest to southeast is again apparent in figures 16 and 18, as is the decrease in the length of the bullae (in fig. 17) and the break between samples E and F (in figs. 17 and 18).

On the basis of these data we conclude that all bats of the genus *Macrotus* should be referred to one species.

ACCOUNTS OF SUBSPECIES

Macrotus waterhousii waterhousii Gray

Macrotus Waterhousii GRAY, 1843a, p. 21. TROUESSART, 1897, p. 152.

Macrotus waterhousii: WAGNER, 1855, p. 640 (Haiti). DOBSON, 1878, p. 464 (three specimens from Hispaniola). ALLSTON, 1879, p. 38. REHN, 1904, p. 429.

Otopterus waterhousei: LYDEKKER, 1891, p. 673.

Macrotus waterhousei: ELLIOT, 1896, p. 82. KOOPMAN, 1955, p. 110.

Otopterus waterhousii: G. M. ALLEN, 1911, p. 227. J. A. ALLEN, 1908, p. 581. ELLIOT, 1904, p. 651 (photographs of skull); 1905, p. 508; 1907, p. 527.

Macrotus waterhousii waterhousii: MILLER, 1929, p. 8. HERSHKOVITZ, 1951, p. 554. HALL AND KELSON, 1959, p. 102.

Macrotus waterhousii heberfolium SHAMEL, 1931, p. 252. POOLE AND SCHANTZ, 1942, p. 132. KOOPMAN, HECHT, AND LEDECKY-JANECEK, 1957, p. 165. HALL AND KELSON, 1959, p. 101.

Macrotus waterhousii compressus: SHAMEL, 1931, p. 251 (part, specimens from Acklins Island only). KOOPMAN, HECHT, AND LEDECKY-JANECEK, 1957, p. 165 (part, specimens from Acklins, Crooked, and Great Inagua islands).

The type locality is Haiti. Mr. John Edwards Hill has kindly informed us that the holotype is a specimen in alcohol and bears registry number 55.12.26.278 of the British Museum (Natural History). It is a male, obtained originally from J. Hearne, Esq., and it was formerly in the collection of the Zoological Society of London.

The range includes Hispaniola and the southern Bahamas.

Specimens from Great Inagua Island, which is closer to the eastern tip of Cuba than to Hispaniola, are actually larger than any specimen from Hispaniola. The total lengths of the skulls of the two from Great Inagua are 27.2 and 27.9 mm. Geographic variation is evident within Hispaniola. Comparative total lengths of skulls from Haiti and from the Dominican Republic are: Haiti, mean of 12, 26.47 ± 0.10 s.e., range 25.6 to 26.9 mm.; Dominican Republic, mean of 13, 25.72 ± 0.12 s.e., range 25.1 to 26.6 mm. (t 4.87).

The discovery that the largest individuals are in western Hispaniola was unexpected on the dual hypothesis that (1) considering the West Indies in general, *Macrotus* are larger from more eastern areas, and (2) intergradation with smaller bats from Cuba would result in smaller bats from western than from eastern Hispaniola.

We draw the following conclusions: The clinal trends within the West Indies are not uniform. There is a distinct morphological discontinuity between *M. w. waterhousii* and its geographically nearest relatives on Cuba. The bats of the genus *Macrotus* in the southern Bahamas have been derived primarily from Hispaniola, with little if any contribution from Cuba. The effect of mixture of Cuban *Macrotus* with Hispaniolan *Macrotus* across the Windward Passage is not evident on the eastern side of the passage but is evident on the western side.

The single specimen from Providenciales Island, named *Macrotus waterhousii heberfolium* by Shamel, is not significantly different from Haitian specimens. Its distinctive characters were said to be (1) larger size, (2) tricolored rather than bicolored hair, and (3) broader, blunter nose leaf. The measurements of the type of *heberfolium* are smaller than those cited by Shamel: for example, length of forearm, 55.7 rather than 57.4 mm.; length of skull, 26.3 rather than 26.6; interorbital breadth, 4.4

rather than 4.6; breadth of braincase, 9.6 rather than 10. However, even if Shamel's measurements were correct, the difference in size from Haitian specimens is not significant. For example, five of 14 Haitian specimens exceed 26.6 mm. in length of skull.

When the fur of the type is dried and parted, a tricolored appearance is evident. Examination under magnification clearly shows that the basal smoky gray appearance is the result of a mixture of the dark unfaded



FIG. 2. *Left*: Dried study skin of *Macrotus w. californicus*, K.U. No. 45160, from 35 miles north of Blythe, Riverside County, California. *Right*: Skin of *M. w. mexicanus*, K.U. No. 66332, from 1 mile southeast of Apetlanca, Guerrero. Note the larger ears and paler pelage of *californicus*. The whitish nape patches evident on most study skins are not so on living bats. The skin of the interscapular and nape fold has comparatively sparse hair, and, when this skin is flattened and stretched in preparation, the white of the basal parts of the hairs becomes the dominant color.

tips of emerging hair with the whitish bases of the older hair. If the new hair is not considered, there is no significant difference in the color of the hair of the type of *heberfolium* when compared with that of *waterhousii* from Hispaniola. The dorsal hairs, being described, are not actually bicolored in other West Indian forms, for example *waterhousii*, as Shamel stated, but are tricolored. In unworn pelage there is usually a short pale tip in addition to the basal whitish band and the adjacent brownish band. In the type of *heberfolium* these pale tips are less distinct than in most but not all of 15 Hispaniolan specimens compared directly, and the basal

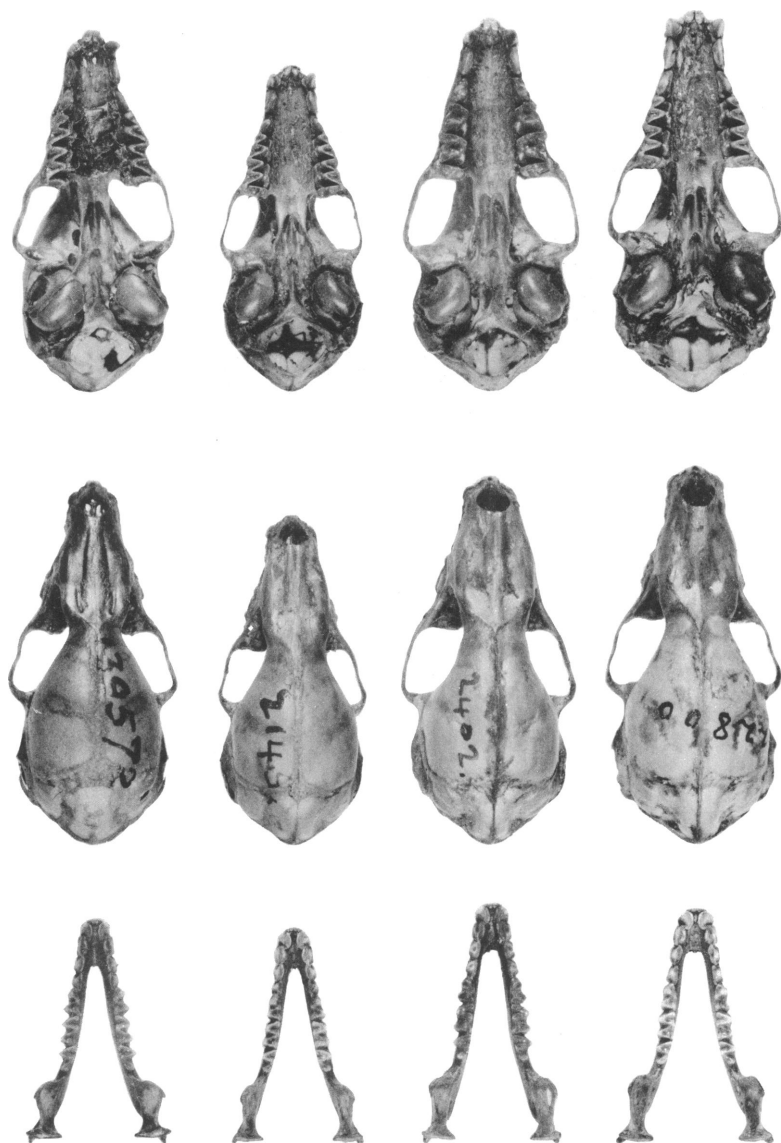


FIG. 3. Skulls of *Macrotus waterhousii* in ventral and dorsal views (some slightly tilted) and jaws in dorsal view, to show geographic variation. *Left to right*: A.M.-N.H. No. 139572, *M. w. californicus*, Fortuna Mine, Yuma County, Arizona; A.M.N.H. No. 2145, *M. w. bulleri*, San Pedro, Guadalajara, Jalisco, Mexico; A.M.N.H. No. 2402, *M. w. mexicanus*, Tehuantepec, Oaxaca, Mexico; A.M.N.H. No. 22800, *M. w. minor*, Santiago, Cuba. Photographed by Robert Logan in ultraviolet light. $\times 2$.

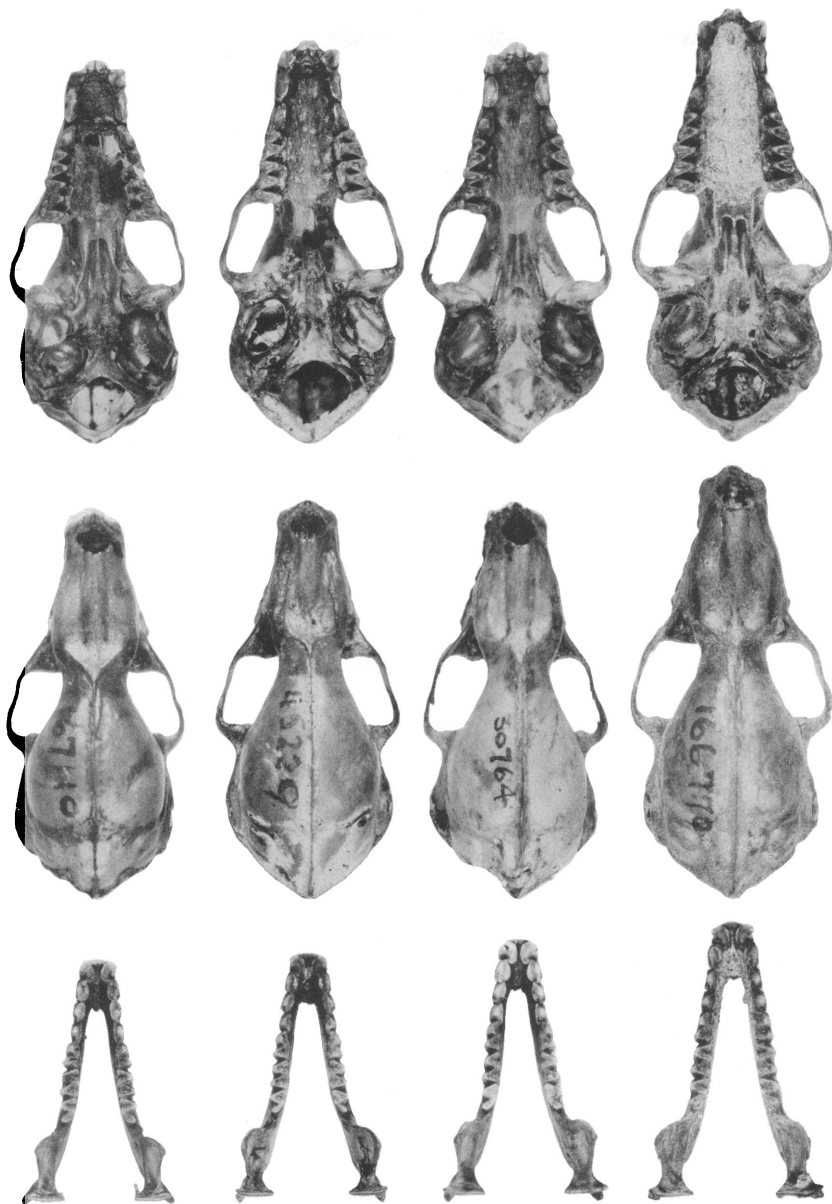


FIG. 4. Skulls of *Macrotus waterhousii* in ventral and dorsal views (some slightly tilted) and jaws in dorsal view, to show geographic variation. *Left to right*: A.M.-N.H. No. 167110, *M. w. compressus*, Great Exuma Island, Bahamas; A.M.N.H. No. 45229, *M. w. jamaicensis*, Oxford Cave, Balaclava, Jamaica; C.N.H.M. No. 30764, *M. w. waterhousii*, Port au Prince, Haiti; A.M.N.H. No. 166770, *M. w. waterhousii*, Great Inagua Island, Bahamas. Photographed by Robert Logan in ultraviolet light. $\times 2$.

whitish part makes up a greater proportion of the total length of the hair. These differences are attributable to wear, fading, and probably continued growth at the base of the hair.

The nose leaf of the type of *heberfolium* is not broader than, but is narrower than, most of the 15 individuals of *waterhousii* directly compared. The tip is not more bluntly rounded than that of some Hispaniolan specimens, for example, U.S.N.M. No. 217225. Also a slight asymmetry in the tip of the nose leaf of the type may indicate an earlier injury or an abnormality.

The distinctive characteristics of *M. w. waterhousii* reported by Rehn (1904, p. 429) who examined only one specimen were: (1) in comparison with *M. w. jamaicensis*, the upper tooth row is heavy and strongly crowded and the skull is large, 26.8 mm. in length; (2) in comparison with *M. w. compressus*, the first lower premolar is subquadrate in basal outline rather than "elongate-elliptical," and the anterior width of the rostrum is equal to the interorbital space rather than being narrower; (3) in comparison with *M. w. minor*, the size is larger and the general color is ochraceous brown or pale umber rather than dark umber or dark reddish brown; and (4) in comparison with Mexican and Central American forms, the foot is robust and the toes are strong. Rehn gave several paragraphs of descriptive details, most of which are not in comparative terms and are not diagnostic of the subspecies. All the above listed characters have some validity. Except for color, all the characters are correlated with large size if heterogonic growth patterns are considered. The size of the rostrum and of the teeth relative to the entire skull is greater in larger bats. The teeth are not only larger, but more crowded and angular (or in the case of the first lower premolar "subquadrate," as noted by Rehn). We have not made detailed notes on color, but our impression is that *waterhousii*, although variable in color, is on the average paler than *minor*, *jamaicensis*, and *compressus*. Large series would need to be assembled at one place for meaningful comparisons. The individual variation at one place often exceeds the average geographic differences in the West Indies. The age, sex, and geographic variation in the red and brown color "phases" need to be studied. One of the two specimens from Great Inagua Island is reddish and pale; the other is dark umber. Both were taken on January 29, and both are adults.

SPECIMENS EXAMINED: Total, 130. Localities are arranged alphabetically. Numbers preceding locality designations refer to the numbers in figure 1.

BAHAMA ISLANDS

- 1 Acklins Island, Salt Point, Jamaica Bay, two U.S.N.M.

- 2 Crooked Island, Gordon, one M.C.Z.
- 3 Great Inagua Island, Salt Pond Hill Cave, four A.M.N.H.
- 4 Providenciales Island, Caicos Group, one U.S.N.M.

DOMINICAN REPUBLIC

- 5 Beata Island, one C.M.
- 6 Bohechio, 4 kilometers southwest of Padre Las Casas, province of Azua, 20 M.C.Z.
- 7 Cabral, 10 kilometers south of El Firme, province of Barahona, two M.C.Z.
- 8 Caña Honda, 10 A.M.N.H.
- 9 Cueva de Ceboruco, Municipio San Juan de la Maguana, five M.C.Z.
- 10 Guayabal (2 to 3 kilometers west of), 16 M.C.Z.
- 11 La Romana (caves near River Chavon, east of), 10 A.M.N.H.
- 12 Los Patos, two A.M.N.H., one U.S.N.M.
- 13 Pedernales (7 kilometers east-southeast of), Cueva Jinagosa, one M.C.Z.
- 14 Pedro Santana, Cerro de San Francisco, province of San Rafael, five M.C.Z.
- 15 Peña (8 kilometers west-northwest of), Cueva del Limon, one M.C.Z.
- 16 Sanchez (cave near), one U.S.N.M.
- 17 San Domingo City, two C.N.H.M.
- 18 San Juan River (cave at Laguna, near the), 10 A.M.N.H.
- 19 San Lorenzo, Samana Bay, two U.S.N.M.
- 20 Sosua, 13 M.C.Z.

HAITI

- 21 Diquini Cave, Port au Prince, six C.N.H.M., four M.C.Z.
- 22 Fort Liberté, three U.S.N.M.
- 23 L'Acul (cave 3 miles west of), five U.S.N.M.
- 21 Port au Prince, two M.C.Z.
- 24 St. Michel, Cave I, two U.S.N.M.

Macrotus waterhousii compressus Rehn

Macrotus waterhousii compressus REHN, 1904, p. 434. G. M. ALLEN AND SANBORN, 1937, p. 226. POOLE AND SCHANTZ, 1942, p. 132. KOOPMAN, HECHT, AND LEDECKY-JANECEK, 1957, p. 165 (part, not including specimens from Acklins, Crooked, and Great Inagua islands). HALL AND KELSON, 1959, p. 101.

Macrotus waterhousei: J. A. ALLEN, 1890a, p. 170.

Macrotus waterhousii: MILLER, 1905, p. 381.

Otopterus waterhousii compressus: ELLIOT, 1905, p. 509. G. M. ALLEN, 1911, p. 228.

M[acrotus]. waterhousei compressus: KOOPMAN, 1951, p. 229.

The type locality is Eleuthera Island. The type specimen is U.S.N.M. No. 122484.

The range of the subspecies is the Bahama Islands from Long Island north to New Providence and Eleuthera islands or, in other words, the islands of the Grand Bahama Bank and Watling Island east of this bank. The bats from different islands are not known to differ significantly. Possibly larger samples would reveal differences.

Macrotus waterhousii compressus is compared with *M. w. waterhousii* above.

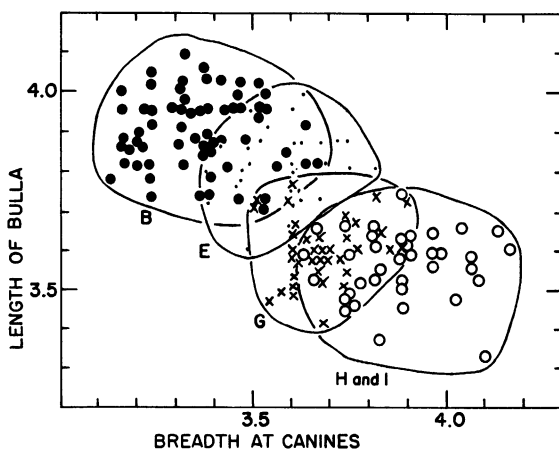


FIG. 5. Scatter diagram showing variation in length of bullae and breadth at canines of individuals in four samples of *Macrotus waterhousii* from areas shown in figure 1 by letters B, E, G, and H and I combined. Sample E is interpreted as representing a population of the same subspecies as sample B that has been modified by intergradation with populations represented by sample G.

In comparison with *M. w. minor*, *M. w. compressus* is larger in most measurements but not in the length of the forearm. The measurements and ratios of *compressus* shown in figures 5, 7, 9, 11, and 13 can in general be interpreted as being intermediate between those of *minor* and those of *waterhousii*. Slightly larger bullae and a relatively larger breadth of braincase and interorbital breadth than in either *minor* or *waterhousii* are evident. As is evident without measurement of the skulls, the relatively greater breadth in *compressus* is reflected in the breadth of the rostrum also. There is no reason to assume that a population derived from the mixing of small bats and large bats will be exactly intermediate in each characteristic. Probably *compressus* has been derived by colonization of the northern Bahamas by bats from both the southeast (*waterhousii*) and southwest (*minor*). This interpretation is slightly different from that of Koopman, Hecht, and Ledecy-Janecek (1957, p. 171), who postulated colonization from the southeast and differentiation "in the course of the spread north." On the whole, we agree with Koopman and his co-authors that *compressus* is slightly nearer *waterhousii* morphologically, but we judge that *compressus* is intermediate and that the difference between *compressus* and *waterhousii* is, in part, the result of a mixture with *minor* rather than entirely the result of differentiation after colonization of the northern Bahamas occurred.

SPECIMENS EXAMINED: Total, 54. Localities are arranged alphabetically. Numbers preceding locality designations refer to the numbers in figure 1.

BAHAMA ISLANDS

- 25 Andros Island, Conch Sound, one A.M.N.H.
- 26 Cat Island, Orange Creek, three M.C.Z.
- 27 Darby Island, Exuma Cays, one A.M.N.H.
- 28 Eleuthera Island, "4 miles south of Georgetown," two U.S.N.M.; Gregory Town, two U.S.N.M.
- 29 Great Exuma Island, Pigeon Cay, one A.M.N.H.; Isaacs Cay, one A.M.N.H.; George Town, one A.M.N.H.
- 30 Long Island, Fox's Cave, four C.N.H.M.; Hamilton's Cave, one C.N.H.M., 10 M.C.Z.; Morris Cave, one C.N.H.M.
- 31 New Providence Island, Nassau, one C.N.H.M., 21 M.C.Z., one U.S.N.M.; Nassau, Fort Charlotte, one C.M.; Winton (caves at), two A.M.N.H.

Macrotus waterhousii jamaicensis Rehn

Macrotus waterhousii jamaicensis REHN, 1904, p. 432. POOLE AND SCHANTZ, 1942, p. 133. HALL AND KELSON, 1959, p. 101.

Macrotis [*sic*]: GRAY, 1843b, p. 50 ("some specimens" from Jamaica).

Macrotus Waterhousei: GOSSE, 1851, p. 295 (habits, no preserved specimen or specific locality noted, illustration).

Macrotus Waterhousii: WAGNER, 1855, p. 640 (the part from Jamaica). TROUESART, 1897, p. 152 (the part from Jamaica).

Macrotus waterhousii: OSBURN, 1865, p. 74. DOBSON, 1878, p. 464 (nine specimens from Jamaica).

Otopterus waterhousii: ELLIOT, 1904, p. 652 (mentions Jamaica).

Otopterus waterhousii jamaicensis: ELLIOT, 1905, p. 508. G. M. ALLEN, 1911, p. 227.

Macrotus waterhousei: WILLIAMS, 1952, p. 172 (fossils, subspecific status uncertain).

The type locality is Spanish Town, Jamaica. The type specimen is U.S.N.M. No. 8553/37543.

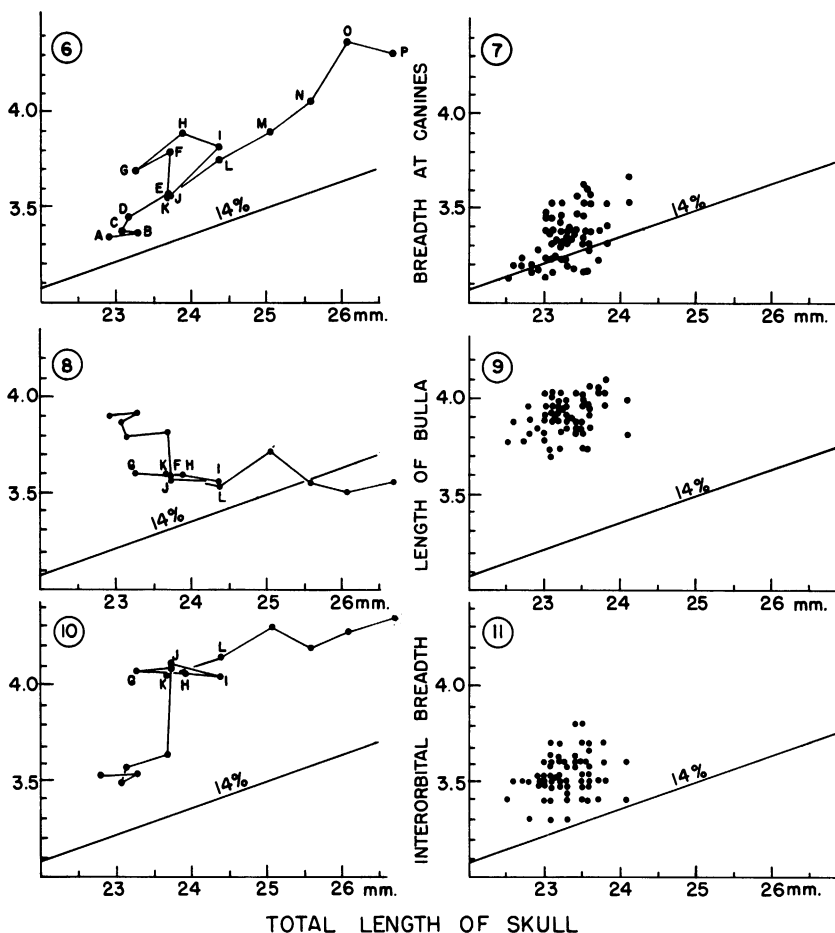
Macrotus waterhousii jamaicensis is known only from Jamaica.

A comparison with *M. w. waterhousii* is included in the account of that subspecies. In comparison with *M. w. minor*, its geographically nearest relative, *M. w. jamaicensis* is larger and perhaps darker. In size *jamaicensis* is intermediate between *minor* and *waterhousii*, but is closer to *waterhousii*.

SPECIMENS EXAMINED: Total, 14. Localities are listed alphabetically. Numbers refer to numbers in figure 1.

JAMAICA

- 32 Balaclava, Oxford Cave, one A.M.N.H.
- 33 Kingston, one U.S.N.M.
- 34 Port Antonio, four M.C.Z.
- 35 Portland Point Lighthouse, four C.N.H.M.
- 36 Spanish Town, two U.S.N.M.
- 37 Windsor, Trelawny Parish, two A.M.N.H.



FIGS. 6-11. Graphs showing correlations of length of skull (the abscissa in each graph) with three other cranial measurements. Graphs 6, 8, and 10 correlate average values of 16 samples from areas shown by corresponding letters in figure 1 and in other figures, where needed for clarification. Graphs 7, 9, and 11 correlate measurements of individuals in sample B only.

Macrotus waterhousii minor Gundlach in Peters

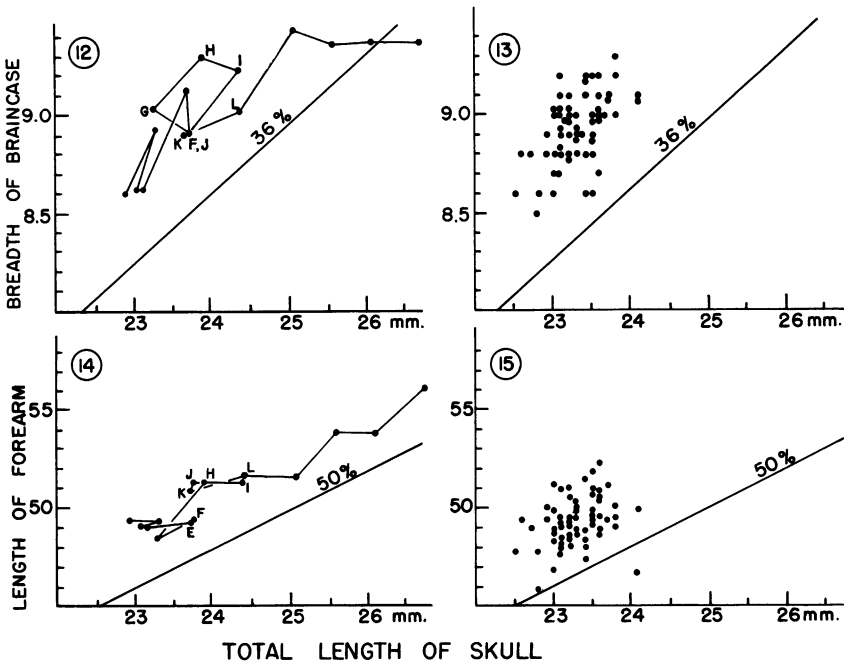
Macrotus minor GUNDLACH in Peters, 1865, p. 382.

M[acrotus] Waterhousei: GUNDLACH, 1873, p. 239 (Cuba).

Macrotus Waterhousii: TROUESSART, 1897, p. 152 (Cuba).

Macrotus waterhousii: DOBSON, 1878, p. 464 (part, Cuba). MILLER, 1904, p. 344 (Cuba and Isle of Pines).

Otopterus waterhousii: ELLIOT, 1904, p. 652 (mentions Cuba).



FIGS. 12-15. Graphs showing correlations of length of skull (the abscissa in each graph) with breadth of braincase and length of forearm. Graphs 12 and 14 correlate average values of the same 16 samples as are shown in figures 6, 8, and 10. Graphs 13 and 15 correlate measurements of individuals in sample B only.

Otopterus waterhousii minor: ELLIOT, 1905, p. 509. G. M. ALLEN, 1911, p. 227. *Macrotus waterhousii minor*: REHN, 1904, p. 435. ANTHONY, 1919, p. 637 (eastern Cuba). HALL AND KELSON, 1959, p. 102.

Macrotus waterhousei: KOOPMAN AND RUIBAL, 1955, p. 3 (subfossil fragments not referred to subspecies).

The type locality is western Cuba. No specimen has been designated as the type. The original description did not note the number of specimens; measurements cited could have come from one specimen.

Macrotus waterhousii minor is known from Cuba, the Isle of Pines, and Grand Cayman Island.

The original description in a paper by Peters began as follows: "2. *Macrotus minor* Gundlach n. sp." Nowhere in the paper was any explanation given for citing Gundlach. Accepting Peters' citation as evidence that Gundlach is alone responsible both for the name and the conditions that make it available, and complying with Article 50 of the International Code of Zoological Nomenclature (Stoll, 1961), we here recognize

Gundlach as the author. In compliance with Article 51 (C) of the Code, the citation of authorship should be "Gundlach *in* Peters."

Gundlach (1873, p. 239) noted that specimens from western Cuba were smaller than those from eastern Cuba, and mentioned that the western individuals of *minor* might be either a variety of, or a different species from, *waterhousii*. He said the eastern Cuban specimens were of the Jamaican type of *M. waterhousii*.

Macrotus waterhousii minor is compared in the above accounts with *M. w. waterhousii*, *M. w. compressus*, and *M. w. jamaicensis*. The larger size of specimens of *minor* from Oriente Province in eastern Cuba is the basis for our regarding them as intergrades with one or more of these larger subspecies. The fact that samples from different parts of western Cuba and from the Isle of Pines do not differ significantly has already been noted. Rehn (1904, p. 437) noted the difference in size between *minor* and the other subspecies in the West Indies. He noted also a "deeper coloration" of *minor* than of *jamaicensis*, a difference that we cannot verify for reasons noted in the account of *waterhousii*.

Rehn (1904, p. 436) also noted that *minor* had more marked furring on the proximal part of the inner border of the ear than did other West Indian subspecies. This we cannot verify. Any difference, if it exists, is too small to be established on the basis of the specimens at hand at the time of writing (by Anderson with the specimens of the American Museum of Natural History). Notes were not made of this character in specimens examined at other institutions.

Rehn (1904, p. 429) separated *M. waterhousii*, consisting of four West Indian subspecies, including *minor*, from the mainland forms by the "quite robust" rather than "rather slender" foot and the "strong" rather than "weak" toes. The Antillean bats, being in general larger, have larger feet and toes. Some Cuban specimens, however, are not distinguishable from some southern Mexican specimens on the basis of the size of the feet. Other measurements show that *minor* is intermediate between other, and larger, Antillean subspecies and *M. w. mexicanus* of the mainland. In fact, as noted above, *minor* resembles *mexicanus* more than *minor* resembles *waterhousii*. This intermediacy of *minor* on the average, the lack of any diagnostic character, and the actual overlap of measurements of *minor* and *mexicanus* are the bases for our regarding *mexicanus* as conspecific with the species *waterhousii* (as used by Rehn).

SPECIMENS EXAMINED: Total, 89. Localities are listed alphabetically. Numbers refer to numbers in figure 1.

CAMAGUEY PROVINCE, CUBA

38 Cubitas (Cueva del Indio, Sierra de), one M.C.Z.

HABANA PROVINCE, CUBA

- 39 About 4 miles south of San José de las Lajas, one A.M.N.H.

LAS VILLAS PROVINCE, CUBA

- 40 Cienfuegos, one M.C.Z.
 41 Cumanayagua, Mina Carlotta, 160 meters, eight U.M.M.Z.
 42 Guabairo Cave, Guabairo, two U.M.M.Z.
 43 Hormiguero, Cantabria Cave, two U.M.M.Z.
 41 Soledad, Vilche's Cave, two M.C.Z.; 2 miles southeast of Atkins Gardens, one U.M.M.Z.; Central Greenhouse of Atkins Gardens, one U.M.M.Z.

ORIENTE PROVINCE, CUBA

- 44 Daiquiri, 11 A.M.N.H.
 45 Santiago, two A.M.N.H., six M.C.Z., six U.S.N.M.; El Cobre (mine), one U.S.N.M.
 46 Siboney, two A.M.N.H.

PINAR DEL RÍO PROVINCE, CUBA

- 47 Guanajay (cave), one U.S.N.M.
 48 Luis Lazo, one M.C.Z.
 49 Pan de Guajaibon, near La Mulata, seven A.M.N.H.
 50 San Diego de los Baños, Mogote Cave, five U.S.N.M.

ISLA DE PINOS

- 51 Caballos Mountains, Kennan Caves, 19 C.M.; Casas Mountains, two C.M.; Nueva Gerona, two U.S.N.M.

GRAND CAYMAN ISLAND

- 52 Grand Cayman Island, five U.S.N.M.

Macrotus waterhousii mexicanus Saussure

Macrotus mexicanus SAUSSURE, 1860, p. 486. J. A. ALLEN, 1890b, p. 179. REHN, 1904, p. 437. NOVICK, 1963, p. 51 (orientation sounds).

Macrotus bocourtianus DOBSON, 1876, p. 436 (from Vera Paz, Guatemala); 1878, p. 467 (same four specimens from Guatemala). ALSTON, 1879, p. 38.

Macrotus Bocourtianus: TROUESSART, 1897, p. 152.

Otopterus bocourtianus: GAUMER, 1917, p. 292 (Yucatan). J. A. ALLEN, 1904, p. 236. ELLIOT, 1904, p. 654; 1905, p. 510; 1907, p. 528.

Otopterus mexicanus: MERRIAM, 1898, p. 18 (Morelos). ELLIOT, 1901, p. 420 (photographs of A.M.N.H. No. 2404); 1904, p. 653; 1905, p. 510; 1907, p. 528. J. A. ALLEN, 1904, p. 236.

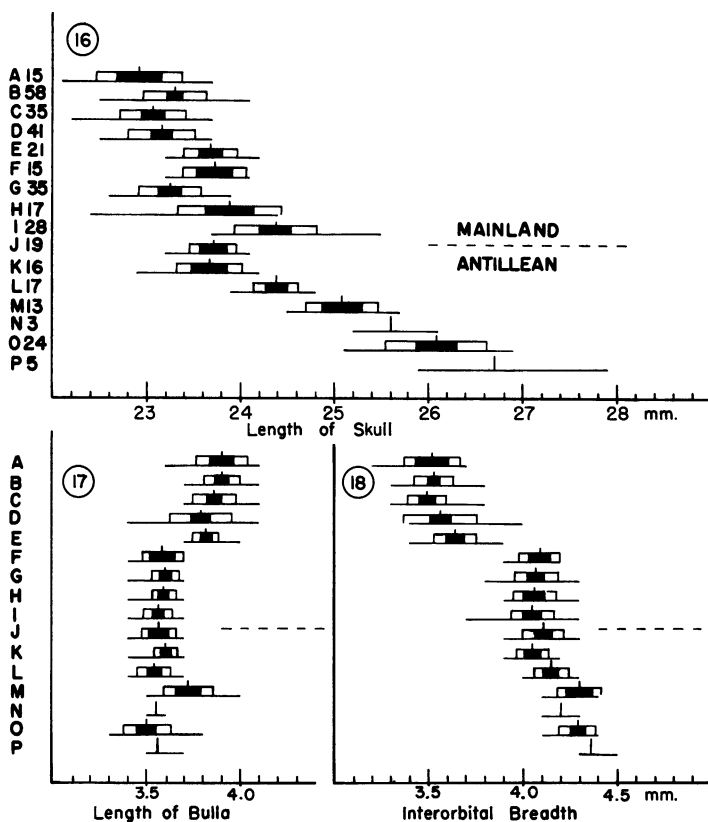
Macrotus californicus: TROUESSART, 1897, p. 152 (part, Mexico).

Macrotus waterhousii: DOBSON, 1878, p. 464 (part, Mexico). ALSTON, 1879, p. 38 ("Yautepec").

Otopterus [sic] *bulleri*: WARD, 1904, p. 653 ("Southern Puebla").

Macrotus mexicanus mexicanus: MARTÍNEZ AND VILLA, 1938, p. 344 (Morelos); 1940, p. 307 (Guerrero). DAVIS AND RUSSELL, 1952, p. 235 (Morelos); 1954, p. 67 (same records from Morelos). LUKENS AND DAVIS, 1957, p. 4 (Guerrero). MALAGA ALBA AND VILLA, 1956, p. 536 (summary of all records). HALL AND KELSON, 1959, p. 102 (compilation of distributional records). GRUMMON AND NOVICK, 1963, p. 363 (obstacle avoidance).

The type locality is Cuautla, near Yautepec, Morelos, Mexico. No specimen has been designated as the type.



FIGS. 16-18. 16. Variation of length of skull in 16 samples of *Macrotus waterhousii*. Geographic origin of each sample is indicated by letters corresponding to those in figure 1. The size of each sample is shown by a number at the left. For each sample the range is shown by a horizontal line; the mean, by a vertical line; one standard deviation each side of the mean, by boxes; and two standard errors each side of the mean are shown by a bar. A general, although uneven, increase in size is evident from west to east (top to bottom). 17. Statistics on length of bullae in the same 16 samples. 18. Statistics on interorbital breadth. In both length of bullae and interorbital breadth the greatest change occurs between sample E and sample F.

The range of *M. w. mexicanus* includes southern Mexico and northern Guatemala (see fig. 1).

The name *Macrotus bocourtianus* of Dobson (1876, p. 436) was based on four immature specimens from the "Paris Museum" in preservative. The largest of these four was designated as the type. The diagnostic characters of *bocourtianus* were said to be its size (being greater than that

of *Macrotus waterhousii*) and the extension of one and one-half distal vertebrae in the tail beyond the uropatagial margin rather than only one vertebra so extending. No subsequent author indicates that he re-examined the original four specimens, but several authors using Dobson's measurements have judged that neither size nor caudal extension of *bocourtianus* is sufficiently different from the measurements of specimens from southern Mexico to warrant even subspecific recognition of *bocourtianus*. We agree. Our data (see, for example, fig. 16) show that specimens from Oaxaca (group I) are significantly larger on the average than specimens from the region of the type locality of *M. w. mexicanus* (group H), but are not so large as *M. w. waterhousii*. The Oaxacan specimens are larger on the average than western Cuban specimens of *M. w. minor*, so that the increase in size from west to east that characterizes the species as a whole is interrupted between Oaxaca and Cuba.

A gap of about 700 miles separates Palenque, Chiapas, the easternmost locality from which we have examined a specimen of *mexicanus*, from the nearest localities in western Cuba where *minor* occurs. Gaumer (1917, p. 292) reported *Otopterus bocourtianus* from Yucatan, actually citing 10 different place names. He also published a photograph of a specimen that is identifiable as *Macrotus*. Gaumer (1917, p. 293) reported the following: "The long-eared bat lives in all parts of Yucatan, many times under granaries of corn, where it eats the insects that come from them; at other times it is found in caves that are not very dark. They emerge early and do not fly very high" (translation by Anderson). The above facts may be accepted with reasonable confidence as establishing the presence of *Macrotus* in Yucatan, even though the whereabouts of Gaumer's specimens is not known to us, and even though more recent collectors such as the University of Kansas field party of the summer of 1962 have not obtained additional specimens (verbal report of Dr. J. Knox Jones, Jr.). One specimen of *Macrotus*, in the Chicago Natural History Museum (C.N.H.M. No. 6490) bears the notation "Yucatan?" on the oldest label. No other data are present. This specimen "was received at the Field Columbian Museum in a small lot of skins and labeled Yucatan" (Elliot, 1904, p. 654).

A comparison of *M. w. mexicanus* with *M. w. minor* is given above. In comparison with *M. w. bulleri* to the west, *mexicanus* is larger, the dentition is less crowded, and the second upper premolar is longer and stronger as noted by Rehn (1904, p. 440). The length of the second upper premolar was measured in five samples to test the hypothesis that this measurement is smaller in *bulleri*. Samples used, numbers measured, means, standard errors, and ranges are:

Sample B, California	$N = 58, 1.80 \pm 0.001 (1.62-1.98)$
Sample E, northern Sinaloa	$N = 21, 1.81 \pm 0.016 (1.66-1.95)$
Sample G, Jalisco	$N = 35, 1.51 \pm 0.013 (1.44-1.66)$
Sample H, Morelos and vicinity	$N = 17, 1.78 \pm 0.019 (1.70-1.91)$
Sample I, Oaxaca	$N = 15, 1.75 \pm 0.018 (1.65-1.85)$

Sample G of *bulleri* clearly differs from samples H and I of *mexicanus*.

SPECIMENS EXAMINED: Total, 96. Localities are listed alphabetically. Numbers refer to numbers in figure 1.

CHIAPAS

53 Palenque, one C.N.H.M.

COLIMA

54 Colima, one U.S.N.M.

GUERRERO

55 1 mile southeast of Apetlanca, six K.U.

56 Chilpancingo, one M.V.Z.

57 Cueva Calicanto, 8 kilometers southeast of Teloloapan, 1400 meters, 10 K.U.

MICHOACAN

58 La Salada, five U.S.N.M.

MORELOS

59 Cuernavaca, four U.S.N.M.

60 San Gabriel, 970 meters, four K.U.

OAXACA

61 $4\frac{1}{2}$ kilometers north of Cuicatlan, 640 meters, nine K.U.

62 3 kilometers west-northwest of Dominguillo, 730 meters, four K.U.

63 Reyes, 4500 feet, one U.S.N.M.

64 Tehuantepec, 20 A.M.N.H., one C.N.H.M., one L.A.C.M.; 3 miles northwest of Tehuantepec, nine K.U.

PUEBLA

65 2 miles southeast of Izucar de Matamoros, 17 K.U.

66 1 mile east of Raboso, 4350 feet, two I.U.

Macrotus waterhousii bulleri H. Allen

Macrotus bulleri H. ALLEN, 1890, p. 73 (original description); 1894, p. 41. J. A. ALLEN, 1890b, p. 179.

Macrotus waterhousii: ALSTON, 1879, p. 207 (two specimens from Tres Marias Islands).

Macrotus californicus: J. A. ALLEN, 1889, p. 166 (first report of specimens later named *M. bulleri*).

Macrotus californicus Var. *Bulleri*: TROUESSART, 1897, p. 152.

Otopterus mexicanus: MERRIAM, 1898, p. 18 (52 specimens from the Tres Marias Islands). NELSON, 1899, p. 18 (Tres Marias Islands); J. A. ALLEN, 1904, p. 236 (specimens from Jalisco and Tres Marias Islands). ELLIOT, 1904, p. 653 (mentions Tres Marias Islands and Jalisco).

Otopterus bulleri: ELLIOT, 1904, p. 654; 1905, p. 510; 1907, p. 528.

Macrotus mexicanus bulleri: REHN, 1904, p. 439. MALAGA ALBA AND VILLA,

1956, p. 538 (old and new Mexican records). HALL AND KELSON, 1959, p. 102 (compilation of distributional records). JONES, "1963" [1964], p. 751 (Durango).

The type locality is Bolaños, Jalisco, Mexico. In 1889 J. A. Allen reported eight specimens consisting of skins and skulls and three additional skulls from Bolaños. These 11 specimens were entered in the catalogue of mammals at the American Museum of Natural History (skins, A.M.-N.H. Nos. 2002-2009; skulls alone, A.M.N.H. Nos. 1286-1288). The collector, Audley C. Buller, whose manuscript notes were quoted by J. A. Allen (1889, p. 166), stated that 14 specimens were captured. All were males.

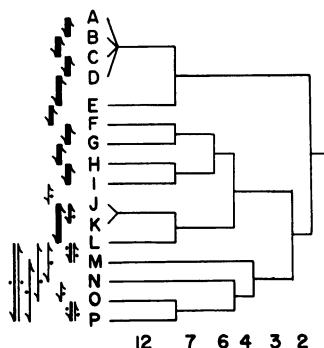
In 1890, Harrison Allen based the name *Macrotus bulleri* on at least eight, and possibly 10, of the same 11 specimens from Bolaños. No holotype was designated, and no lectotype has been selected until the present time. Eight of the 11 original specimens are still in the American Museum of Natural History. Two (A.M.N.H. Nos. 2004 and 2008) have been in the Chicago Natural History Museum since 1898, and one (A.M.N.H. No. 2005) was exchanged with Count Deria in 1907. The 10 specimens that we have examined are all immature, as judged by the presence of cartilaginous epiphyseal sutures of phalanges, or the development of the skull in the case of those specimens that are only skulls. A.M.N.H. No. 2007 (skin) and A.M.N.H. No. 1276 (skull) are herein selected as the lectotype, and in compliance with Recommendation 74C of the International Code of Zoological Nomenclature the following data are included: length of skull, 22.2 mm.; date of capture, July 6, 1889; collector, Audley C. Buller; original number, 29; sex, male; age, immature; catalogue numbers in Department of Mammalogy of the American Museum of Natural History, as noted above; nature of specimen, study skin and skull in moderately good condition.

A comparison with *M. w. mexicanus* is given above. The sample (G) of *M. w. bulleri*, for which data are cited there, includes only adults. The smaller size of the second upper premolar in *bulleri*, a diagnostic feature based originally on immature specimens only, is thus verified. Data for two samples of *M. w. californicus* are also cited above, and the second upper premolar is thereby also shown to be smaller in *bulleri* than in *californicus*.

More information in regard to the local distribution and abundance of *Macrotus* in the area between Jalisco and Morelos is needed before speculations about possible barriers or the pattern of intergradation between *bulleri* and *mexicanus* are warranted. The subspecies *bulleri* is not so distinct as *californicus*. Other judgments in regard to the distinctness of subspecies are reflected in figure 19.

Malaga Alba and Villa (1956, p. 538) referred three specimens in the collection of the Instituto de Biología and from a "Cueva cerca de Pinalito," Jacala, Hidalgo, to *bulleri*. They compared these specimens with specimens of *mexicanus* and noted that in both size and the form of the premolars the Hidalgan specimens agreed with *bulleri*. Only two specimens (Nos. 3628 and 3629) from Jacala could be found by Anderson in the Instituto de Biología in June, 1964. Both were in alcohol, and the skull had been removed from one. In size of the single bulla present, this specimen agrees with both *bulleri* and *mexicanus* rather than with *californicus*. The specimen was compared with *californicus* from Arizona and from Tamaulipas. In the form of the second upper premolar and in the

FIG. 19. Dendrogram indicating estimated levels of morphological differentiation between samples of *Macrotus* from areas shown by A through P in figure 1, and symbols (at left) showing the occurrence, direction, and estimated effectiveness of gene flow between areas. See text.



breadth at the canines, the specimen resembles *bulleri* rather than *mexicanus*. We lack knowledge of the presence or absence of *Macrotus* in the region between Jalisco and Hidalgo and again judge that it would be premature to speculate regarding distribution, abundance, barriers, amount of morphological differentiation, and other factors of evolutionary import. The specimens from Hidalgo were the first to be reported from the eastern part of Mexico north of Morelos (not considering the Yucatan Peninsula).

In 1959 Koopman and Martin (p. 10) reported specimens from southern Tamaulipas that extended the known range of the species northward significantly and that posed an interesting problem regarding geographic variation, which is discussed in the account of *M. w. californicus* below.

SPECIMENS EXAMINED: Total, 131. Localities are listed alphabetically. Numbers refer to numbers in figure 1.

DURANGO

67 Chacala, eight U.S.N.M.

68 Santa Ana, 12 kilometers east of Cosalá [Sinaloa], 1300 feet, five K.U.

HIDALGO

—¹ Jacala, two I.B.

JALISCO

69 Bolaños, eight A.M.N.H., two C.N.H.M., nine U.S.N.M.

70 El Salto, 11½ miles south and 10½ miles east of Guadalajara, one K.U.

71 22 miles west and 8 miles south of Guadalajara, four K.U.

72 10 miles west and 9 miles north of Magdalena, 14 K.U.

73 Northwest side of Río Verde, 12 miles south and 4 miles east of Yahualico, 5200 feet, two K.U.

74 San Pedro, near Guadalajara, four A.M.N.H.

75 1 mile northwest of Tequila, 4000 feet, 25 K.U.

76 4 miles north-northeast of Teuchitlán, 21 K.U.

NAYARIT

77 Maria Madre, Tres Marias Islands, six U.S.N.M.

SINALOA

78 3 miles southeast of Camino Real, 500 feet, one K.U.

79 Panuco, 22 kilometers northeast of Concordia, five K.U.

80 Copala, eight L.A.C.M., five M.C.Z.; 6 miles west of Santa Lucia, 5650 feet, one K.U.

Macrotus waterhousii californicus Baird

Macrotus Californicus BAIRD, 1859a, p. 116 (original description).

Macrotus californica BAIRD, 1859b, p. 4, pl. 1 (first notation, by inference, of the catalogue number of type).

Macrotus californicus: H. ALLEN, 1864, p. 3; "1893" [1894], pp. 33, 34 (reasons for rejecting *Otopterus*). TROUESSART, 1897, p. 152 (catalogue of names). REHN, 1904, p. 441. LYON AND OSGOOD, 1909, p. 290 (note loss of type specimen). J. GRINNELL, 1914, p. 269. H. W. GRINNELL, 1918, p. 252 (California, detailed synonymy). HOWELL, 1920, p. 172 (roosting habits, photograph of cave). G. M. ALLEN, 1922, p. 156 (Arizona). HUEY, 1925, p. 196 (food). BURT, 1934, p. 393 (Nevada); 1938, p. 19 (Sonora). DICE AND BLOSSOM, 1937, p. 17 (Arizona). HATFIELD, 1937, p. 96 (Nevada, behavior). ARNOLD, 1943, p. 103 (wintering in California). HALL, 1946, p. 129 (Nevada). REEDER AND COWLES, 1951, p. 390 (thermoregulation). MALAGA ALBA AND VILLA, 1956, p. 538 (summary of Mexican records). HALL AND KELSON, 1959, p. 103 (compilation of distributional records). VAUGHAN, 1959, p. 30 (natural history and morphology). COCKRUM, "1960" [1961], p. 32 (Arizona). BRADSHAW, 1961a, p. 117 (reproduction); 1961b, p. 679 (abstract, natural history); 1962, p. 645 (reproduction). MITCHELL, 1963, p. 543 (tolerance to ammonia). HUEY, 1964, p. 93 (Baja California).

Macrotis [*sic*] *californicus*: HARDY, 1949, p. 434 (Arizona).

Macrotus waterhousii: COUES AND YARROW, 1875, p. 80 (regarded both *M. californicus* and *M. mexicanus* as synonyms of *M. waterhousii*). DOBSON, 1878, p. 464 (one specimen from Cape St. Lucas). ALSTON, 1879, pp. 38, 207 (mentions California).

[*Otopterus*] *californicus*: ELLIOT, 1901, p. 420; 1904, p. 653; 1905, p. 509 (check list).

¹ This locality is an unnumbered dot on figure 1.

Otopterus californicus: STEPHENS, 1906, p. 276 (California).

Macrotus mexicanus bulleri: KNOBLOCH, 1942, p. 297 (Chihuahua).

Macrotus mexicanus: KOOPMAN AND MARTIN, 1959, p. 10 (Tamaulipas).

The type locality is Old Fort Yuma on the right bank of the Colorado River opposite the present town of Yuma, Arizona, and now in Imperial County, California. The type specimen, now lost, was U.S.N.M. No. 2347.

More is known about *M. w. californicus* than about any other subspecies of *Macrotus waterhousii*, as the citations in the above synonymy indicate. This knowledge is not summarized here, except as it is directly pertinent to the problem of specific status.

Geographic uniformity in the characters studied and measured is evident from the southern end of Baja California north to California, Nevada, and Arizona and thence south through Sonora. Evidence of intergradation with *M. w. bulleri* to the south appears in the sample (E, see fig. 5) from northern Sinaloa, and between northern and southern Sinaloa there is a distinct morphological break. The discrepancy between figures 5 and 17 in the ranges of lengths of the bullae for samples E and G results from the fact that figure 5 is based on all specimens for which both the length of the bullae and the breadth at the canines were known, and figure 17 is based only on specimens for which all five cranial dimensions were known.

In comparison with *M. w. bulleri*, *M. w. californicus* differs in having larger second premolars, as shown above in the account of *M. w. mexicanus*, and in having larger ears, larger auditory bullae, lesser breadth at canines, lesser interorbital breadth, and paler appearance of pelage, ears, and patagial membranes.

Ten specimens from Jaumave, Tamaulipas, have been referred, without identification as to subspecies, to *Macrotus mexicanus* by Koopman and Martin (1959, p. 10). These specimens extended the known range of the species on the east coast of Mexico northward from Hidalgo where Malaga Alba and Villa (1956, p. 538) had reported specimens referred to *Macrotus mexicanus bulleri*. The absence of specimens of *Macrotus* from the plateau of north-central Mexico (see fig. 1) and ecological considerations suggest that Tamaulipan *Macrotus* are nearest geographically, and might be expected to be nearest morphologically, to *Macrotus* occurring to the south of Tamaulipas. The latter is not the case. Comparisons of measurements, and of the specimens themselves, indicate that the Tamaulipan series is clearly nearer to *M. w. californicus*. In fact, when skulls from Tamaulipas are placed in a series of skulls from Arizona the two groups cannot be separated on the basis of the characters that are most diagnostic of *M. w. californicus*, or on any other morphological basis. The

same Tamaulipan skulls can be readily separated when placed with a series from Jalisco or Oaxaca.

Measurements of the four Tamaulipan specimens having intact skulls are: length of skull, 23.4, 23.0, 23.6, 23.5; breadth of braincase, 8.8, 8.7, 8.6, 8.5; interorbital breadth, 3.6, 3.5, 3.7, 3.6; breadth at canines, 3.4, 3.4, 3.4, 3.6; and length of bullae, 4.0, 4.1, 4.0, 4.0.

The Tamaulipan skins have ears that are comparable in size to those of Arizonan *californicus* and are perhaps slightly larger than those of Oaxacan *mexicanus*, as well as can be judged from dried specimens. Differences in color, like differences in ear size, are difficult to judge. In general the Tamaulipan series seems slightly darker and more reddish than *californicus*, and thus may approach the condition of *mexicanus* or *bulleri*. Color differences must be given less weight in the evaluation of relationships than the cranial characters, because color is not diagnostic for all individuals, even in series of undoubted *californicus* and *mexicanus*.

If the resemblances of Tamaulipan specimens are interpreted as indicative of actual genetic relationship rather than convergent development, how can the occurrence of *californicus* in Tamaulipas be explained? The most probable interpretation, in our judgment, is that during some warmer and drier period *Macrotus* was distributed across the continent in the region of the present international boundary, that changing conditions have removed it from this area, and that the Tamaulipan population is a relict one. *Leptoncycteris*, another tropical genus, still occurs in the boundary region as far west as the Big Bend and also to the west of the Sierra Madre Occidental.

SPECIMENS EXAMINED: Total, 296. Localities are listed alphabetically. Numbers refer to numbers in figure 1. There are hundreds of other specimens that were not examined or studied in detail. For example, we know of 350 specimens from Arizona, none of which were used in our study.

BAJA CALIFORNIA, MEXICO

- 81 Cape St. Lucas, four U.S.N.M.
- 82 Comondú, five U.S.N.M.
- 83 San Ignacio, six U.S.N.M.
- 84 Santa Anita, four U.S.N.M.

CALIFORNIA, UNITED STATES

- 85 Imperial County, Fort Yuma, 28 K.U.; 6 miles southwest of "Mt." Yuma, 10 K.U.
- 86 Imperial County, 3 miles north of Potholes, 250 feet, four K.U.
- 87 Riverside County, cave near Torres, two K.U.
- 88 Riverside County, 10 miles southwest of Ripley, two K.U.
- 89 Riverside County, Riverside Mountains, 35 miles north of Blythe, 22 K.U.

CHIHUAHUA, MEXICO

- 90 Barranca de Cobre, one U.S.N.M.

- 91 Batopilas, two U.S.N.M.
- 92 "Near Batopilas," 10 U.S.N.M.
- 93 La Bufa, two K.U.

SINALOA, MEXICO

- 94 12 miles north and 3 miles west of Los Mochis, 34 K.U.

SONORA, MEXICO

- 95 Alamos, one A.M.N.H.; Agua Marin, 1800 feet, 8.3 miles west of Alamos, two M.V.Z.; Alamos (Minas Nuevas, 5 miles north-northwest of), four U.I.; 4 miles north of Alamos, 1500 feet, 16 K.U.
- 96 Camoa, Río Mayo, 800 feet, eight U.S.N.M.
- 97 Chinipas, two K.U., 17 M.C.Z., 18 U.S.N.M.; 6 miles northeast of Chinipas, two U.S.N.M.
- 98 Chinobampo, six U.C.L.A.
- 99 Guirocoba, two L.A.C.M., seven U.C.L.A.
- 100 Hermosillo, one U.S.N.M.
- 101 Ortiz, one U.S.N.M.
- 102 Rancho Carrizo, two U.C.L.A.
- 103 San Javier, five U.C.L.A.
- 104 San José [de Guaymas], 15 miles north of Guaymas, 10 U.C.L.A.; $\frac{1}{2}$ mile northwest of San José de Guaymas, 25 feet, 16 K.U.
- 105 Santa Maria Mine, El Tigre Mountains, three U.M.M.Z.
- 106 Saric, three U.C.L.A.
- 107 Sierra Seri, La Libertad Ranch, one U.S.N.M.
- 108 Tesia, five U.C.L.A.
- 109 3 miles east of Willard railroad station, 1200 feet, 12 M.V.Z., eight U.C.L.A.

TAMAULIPAS, MEXICO

- 110 Jaumave, 10 U.M.M.Z.

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