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Taxonomic Review of the Pallid Bat, Antrozous pallidus (Le Conte)

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The vespertilionid subfamily Nyctophilinae is represented in North America and Cuba by the single genus *Antrozous*, which is endemic to the New World. Three species have been recognized: *A. pallidus*, widely distributed throughout the western and southwestern United States and México south to the Tranverse Volcanic Cordillera; *A. dubiaquercus*, known from Honduras, Veracruz, Jalisco, and the Tres Marias Islands off the western coast of México; and *A. koopmani*, known only from Cuba.

A. pallidus is easily distinguished from other North American vespertilionids by the large ears, broad wings, distinctive shape of its nose, pallid to blond coloration, and the possession of only four lower incisors. When originally described, it was placed in the genus *Vespertilio* (Le Conte, 1856). Allen (1862) later arranged *pallidus* in a new genus, *Antrozous*, which he distinguished from *Vespertilio* based on differences in the snout, skull, ears, and, most importantly, the lower incisors.

Geographic variation in *A. pallidus* was first analyzed by Miller (1897), who examined 123 specimens and recognized two subspecies, *A. p. pallidus* and *A. p. pacificus*. The western subspecies, *pacificus*, occurred west of the Sierra Nevada and was described by Merriam (1897) as larger and darker than *pallidus*. Later, two additional subspecies were described—*A. p. cantwelli* from eastern Oregon, southeastern Washington, and northern Nevada (Bailey, 1936), and *A. p. obscurus* from the coastal foothills and adjacent intermontane valleys of northeastern México (Baker, 1967).

Several other continental taxa were originally designated as species. *A. minor* was described by Miller (1902) from southern Baja California, but it was later relegated to a race of *A. pallidus* by Goldman (1951). Another species, *A. bunkeri*, was described from Kansas by Hibbard (1934), but it was also subsequently reduced to a subspecies of *A. pallidus* by Morse and Glass (1960).

In this study, we used univariate and multivariate statistical techniques to identify patterns of variation in morphologic variables associated with pallid bats. Specifically, we have attempted to 1) determine and assess patterns of morphological variation among populations of *A. pallidus*; 2) assess the degree of nongeographic variation in this species; 3) review the taxonomic status of the named subspecies of *A. pallidus*; and 4) document the geographic distribution of each recognized subspecies. Also included is a review of the fossil history of the subfamily Nyctophilinae, with special reference to the genus *Antrozous*, as well as comments on the taxonomic status of *A. dubiaquercus* and *A. koopmani*.

Much of the information presented in this paper has been taken from an unpublished monograph of the genus *Antrozous* prepared earlier by one of us (Martin, 1974). Subsequently, however, additional specimens from certain critical localities have been examined, and study of this material, together with a more refined statistical analysis, has produced substantially different conclusions from those originally reached by Martin.

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Materials and Methods

Measurements and samples.—We examined 1830 museum specimens, recording standard external measurements (TL, total length; TA, tail length; HF, hind foot length; and EL, ear length) as well as the following additional measurements: FOR, forearm length (from the posterior extremity of the olecranon process of the ulna to the distal extremity of the carpals); MET, metacarpal III (greatest length of metacarpal III including the carpals when wing is folded); PH I, phalanx I (greatest length of phalanx I of the third digit, measured at the junction of the fusion of the epiphyses); PH II, phalanx II (greatest length of phalanx II of the third digit); GSL, greatest length of skull (including the incisors); PC, postorbital constriction (least width); ZB, zygomatic breadth (greatest width across the zygomata measured at right angles to the long axis of the skull); CB, cranial breadth (greatest breadth across the skull through the mastoid region); PL, palatal length (shortest distance from the most anterior portion of the palatal margin to the posterior edge of the palate, not including the spine); MXTR, maxillary toothrow (greatest length of the maxillary toothrow, excluding the incisors); WAM, molar width (greatest width across the molar row as measured from the outer margins of the third upper molars); MNL, mandibular length (distance between the anteriormost portion of the lower jaw to a perpendicular line drawn through the posteriormost projections of the condyles); MNTR, mandibular toothrow (greatest length of the toothrow of a single ramus, excluding the incisors); and CD, greatest depth of cranium (measured from the highest point of the sagittal crest to a horizontal line drawn at the ventralmost protuberant portion of the auditory bullae). Animals with phalangeal epiphyses fused to diaphyses were considered adults and were the only specimens measured. All measurements are in millimeters.

Specimens examined from approximately 350 localities were plotted on a map and subsequently combined into 84 numbered geographic groups (Fig. 1), each having enough specimens to yield meaningful statistics and being small enough in geographic extent to include potentially interbreeding populations and a relatively homogenous environment.

Color analysis.—We selected seven specimens, representing a wide range of colors in *A. pallidus*, as standards for dorsal coloration and assigned them numbers as follows: *00*—pale throughout, with a light tinge of overhairs (TCWC 15360, female, 18 mi. W Fallon, Churchill Co., Nevada); *02*—pale, but with a definite expression of brownish overhairs (TCWC 15354, female, 37 mi. NW Safford, Graham Co., Arizona); *04*—pale blond, fairly continuous coloration throughout (UU 6700, female, Notom, Wayne Co., Utah); *06*—strongly blond with some rusty brown overhairs, bright (TCWC 2824, female, Maguayes, Río Pilon, Nuevo Leon, México); *08*—strongly blond with a considerable amount of rusty brown to dark brown overhairs, bright (TCWC 15369, female, 10 mi. SE Santa Maria, Santa Barbara Co., California); *10*—dull dusky brown throughout, color fairly uniform with some brightness (UA 2018, female, 3 mi. E Aravaipa, Graham Co., Arizona); *12*—dusky brown with a profusion of dark brown overhairs (UI 43290, male, N El Monte, Los Angeles Co., California).

We compared all specimens to these standards and assigned each the appropriate number. Due to the subtle nature of color variation, intermediate values were occasionally required and sometimes combinations of several numbers were necessary. For purposes of graphical display, the standards and combinations thereof were grouped into three major color classes as follows: A) pale, often with brownish overhairs (numbers 00 and 02); B) pale blond to uniform pale dusky brown, often with brownish overhairs, somewhat intermediate to classes A and C (04 and 06); and C) strongly blond and bright, usually with dark overhairs (08, 10, and 12). Ventral coloration was categorized as follows: A) pale to buffy white; B) buffy white with a slight blondish tinge; and C) strongly blond, sometimes with a brownish tinge.

Statistical analysis.—Individual and secondary sexual variation were analyzed with the statistical analysis system (SAS) designed and implemented by Barr and Goodnight (Service, 1972). Means were calculated for each character in representative samples 10 and 61, and a t-test was used to test for differences between sexes. Coefficients of variation (CV) were calculated to determine the extent of variability for each character.

Statistical analyses of geographic variation involved a variety of univariate and multivariate techniques. Standard univariate statistics (mean, range, standard deviation, standard error, coefficient of variation) were calculated for each character in every sample. North-south and east-west transects were constructed between certain grouped localities, and modified Dice-Leraas diagrams (Dice and Leraas, 1936) for the variable GSL were drawn to assess univariate patterns of variation. Five north-south transects were established as follows: *Transect A*, from northern California to southern Baja California (samples 5-13, 22, 82-83); *Transect B*, from eastern Washington to southern Baja California (samples 1-4, 14, 16-17, 19, 21-22, 24-25, 13, 82-83); *Transect C*, from northeastern Utah to southern Sonora (samples 26, 44, 32, 37, 50, 39, 51, 53, 68-70); *Transect D*, from northeastern New Mexico and western Oklahoma to north-central Jalisco (samples 65-66, 56, 58-61, 73-75, 84, 81); *Transect E*, from Kansas to Querétaro (samples 67, 64, 63, 76-80). Three west-east transects were established as follows: *Transect F*, from north-central California to Kansas (samples 7, 16-18, 20, 28, 30, 32, 44-46, 66-67); *Transect G*, from southwestern California to north-central Texas (samples 12, 22, 24-25, 39-41, 51-52, 54-56, 64); and *Transect H*, from north-central Baja California to central Texas (samples 13, 68-71, 60-63, 73).

Several multivariate statistical programs were used to assess the variation among samples. Principal components analysis, performed using the NTSYS programs developed by Rohlf and Kispaugh (1972), was used to summarize as much of the variation in the data as possible in a few dimensions. The first two principal components were extracted from a matrix of correlation among characters, and projections of the samples onto these components were made. A MANOVA-Canonical analysis program in SAS was used to assess the degree of divergence

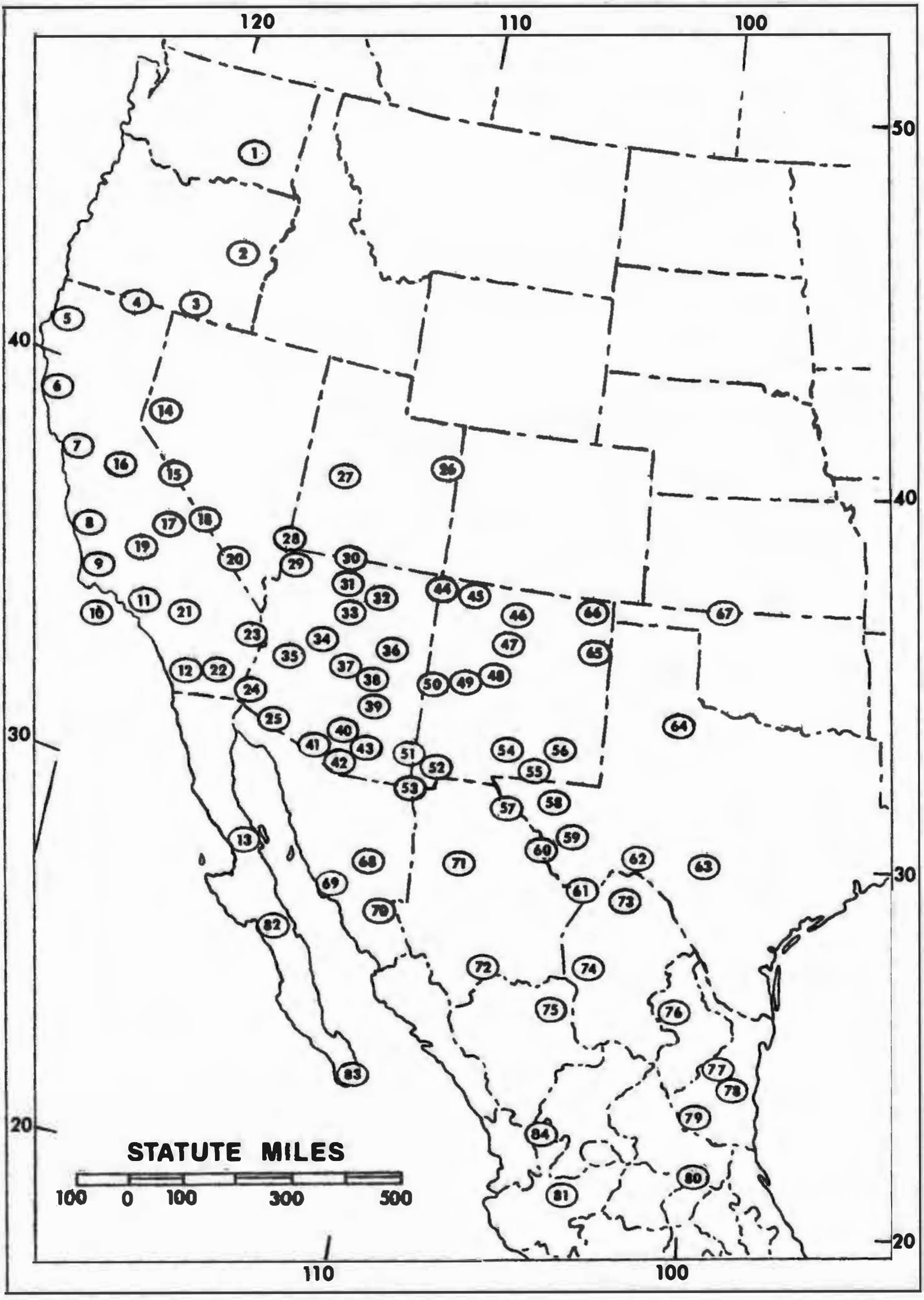

FIG. 1.—Geographic localities of 84 samples used in analysis of geographic variation in *Antrozous pallidus*.

among samples from selected geographic regions. This procedure maximizes the existing variability, such that an a priori assumption must be made that no misclassified individuals are present within the data set. A set of canonical variates was calculated and the centroid for each sample was plotted on the first two canonical variates. An equiprobability ellipse (under an assumption of bivariate normality), representing a single standard deviation, was drawn around the centroid of each sample.

Anatomy.—Selected features of postcranial osteology and soft anatomy were examined in some specimens. These were analyzed and drawn to scale with the aid of a camera lucida. Dental features of 81 specimens of *A. pallidus* and five *A. dubiaquercus* were examined and compared with the teeth of a fossil *Antrozous* from the upper Pliocene of Texas. Standard univariate statistics were computed and analyzed for these dental features.

Diagnosis

External characters.—A relatively large, pale to blond-colored vespertilionid bat with large ears; external measurements include total length, 92-135; ear length from notch, 21-37; length of forearm, 45-62; face distinct, with end of muzzle decidedly truncate and nostrils opening forward; rhinarium scroll-shaped and elevated into horseshoe-shaped ridge across nares; glandular swellings (termed pararhinal glands) present behind rhinarium on each side of muzzle; eyes relatively large; ears large, widely separated, more than half as broad as long, extending considerably beyond nose when laid forward; pinna rhomboidal, obliquely attached at base, rounded at tip, and with 9-11 horizontal striae along posterolateral half; narrow strip of hair, extending from the base halfway to the tip, present on anterodorsal rim of pinna; two narrow bands of hair, extending parallel to long axis of ear, present inside the pinna; tragus slender, tapered distally, rounded at tip, and serrated along outer edge; wing and tail membranes generally thick and leathery; wings proportionately broad, with third metacarpal only slightly longer than fifth; wingspread ranging from 360-390; wing membranes attached at base of toes; interfemoral membrane (uropatagium) attached at base of terminal caudal vertebrae; extreme tip of tail extending beyond uropatagium; calcar terminating in small, distinct lobe just short of middle of free edge of uropatagium; free border of uropatagium considerably longer than calcar; flight membranes naked and dark gray, with a slight vinaceous tinge; feet proportionately large, broad, and about half as long as tibia; five toes armed with large claws and sprinkled with few sparse hairs on dorsal surface; pelage of moderate length and medium texture; dorsal hairs longer (usually 5-6) and separated to greater degree than ventral hairs (usually 3-4); scantily haired area (interscapular patch) present between shoulders; dorsal pelage usually bicolored (a single annual molt occurs during summer); ventral pelage essentially uniform in color; considerable geographic variation in color pattern.

Skull.—Typically vespertilionid in appearance; braincase high, smooth; rostrum relatively large, more than half as long as braincase; basisphenoidal pits absent; interorbital region deep and lacking special concavities or convexities; palate broad; zygomatic arch relatively strong; mandible strong and heavy; middle ear cavity relatively large; tympanic ring large and almost covering cochleae; sagittal region varying from slightly depressed or flattened to abruptly squared or distinctly heightened.

Dentition.—Dental formula, I 1/2, C 1/1, P 1/2, M 3/3, total 28; upper incisors unicuspid, simple, well developed, and crowded against canines; lower incisors trilobed, subequal, strongly imbricated, and crowded; upper canine well developed, with a small basal cusp; lower canine possessing acute basal cusp approaching second premolar; single upper premolar large and close to canine; first lower premolar small and closely wedged between canine and larger second premolar; molars not peculiar and of typical tuberculosectorial type; last upper molar narrow, forming a transverse plate; hypoconid of last lower molar distinct and elongated.

Postcranial skeleton.—Sternum with T-shaped manubrium; xiphoid process with distinct heavy keel projecting anteroventrally from center-line of manubrium; mesosternum slightly keeled ventrally; 11 ribs (six sternal, three vertebrocostal, and two attaching only to vertebrae); first rib stout and attaching to manubrium via costal cartilage; first three ribs somewhat anteroposteriorly compressed but others strongly flattened dorsoventrally; last two ribs much thinner than others; spinal column with seven cervical, 11 thoracic, five lumbar, four sacral, and eight or nine caudal vertebrae; scapula normal, with clavicle long and bending slightly forward; pelvic girdle comparatively large with somewhat flattened ventral tuberosity on ischium; pubis stout.

Penis and baculum.—Baculum laterally angular, almost saddlelike, with tip pointed and base truncate, grooved ventrally and weakly convex or flattened dorsally; baculum wedge-shaped dorsally, widening from broad base to greatest width at midpoint, then gradually tapering to a truncate tip narrower than base; long axis of baculum tilted 45° from long axis of penis so that distal end lies closer to dorsal surface of penis than proximal end; penis an unusually hairy, trilobate structure with distal third exhibiting large degree of lateral expansion and dorsoventral compression; dorsally exposed urethral canal present on penis.

Karyotype.—Diploid number, 46; fundamental number, 50; six metacentric to submetacentric and 38 acrocentric autosomes; X-chromosome, submetacentric; Y-chromosome, acrocentric.

Fossil History

The paleontological record of nyctophiline bats, including *Antrozous*, is limited primarily to the Pleistocene, although one fossil has been recovered from the Pliocene. Most of the known fossils are representative of the extant species *A. pallidus*, which is known from five Pleistocene deposits: Papago Springs Cave, Arizona (Skinner, 1942); Isleta Caves, New Mexico (Harris and Findley, 1964); Potter Creek Cave, California (Stock, 1918); the McKittrick tar seeps, California (Schultz, 1938); and Newport Bay Mesa, Los Angeles Basin, California (Miller, 1971). White (1969) discovered skull fragments of nyctophiline bats from an early Pleistocene (late Blancan) deposit in the

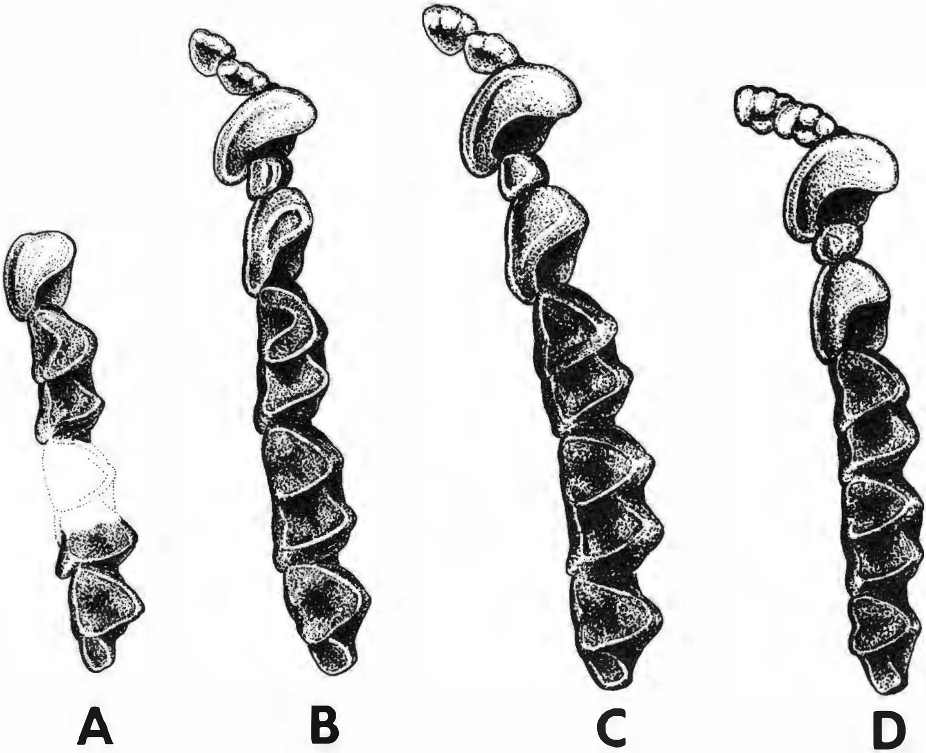

FIG. 2.—Comparison of the right mandibular toothrow in North American nyctophiline bats. (A) Pliocene *Antrozous* (MID 8675), Scurry Co., Texas; (B) *A. p. pallidus* (TNHC 5099), Cimarron Co., Oklahoma; (C) *A. p. pacificus* (TCWC 15370), Santa Barbara Co., California; and (D) *A. (Bauerus) dubiaquercus* (TCWC 11232), Veracruz, Mexico.

Anza-Borrego Desert of California, and, upon comparison with selected nyctophiline bats, he established a new genus and species, *Anzanycteris anzanensis*.

Dalquest (1978) reported a pallid bat (Midwestern University, no. 8675, Collection of Fossil Vertebrates) from the Beck Ranch local fauna, Scurry Co., Texas, which is late Pliocene (early Blancan) in age. The single specimen, an old adult with well worn dentition, is represented by a fragment of the right mandible. It is herein depicted morphologically and compared with recent specimens of *A. pallidus* and *A. (Bauerus) dubiaquercus*.

The second premolar and first and third molars are complete in the lower jaw of the fossil (Fig. 2); only the posterior third of the second molar is present, and the incisors, canine, and first premolar are missing. Length of m3 is distinctly shorter than that of m1. The second lower premolar is short and broad. The entoconids are strongly developed, especially in m2, and protrude more distinctly than in recent specimens of *Antrozous*. The molars are similar to those of *A. pallidus* but exhibit more strongly pronounced entoconids. The last lower molar resembles that in *A. pallidus*, especially in the

TABLE 1.—*Comparison of three dental characters of the Pliocene* Antrozous *from Beck Ranch with selected samples of Recent* A. pallidus. *The geographic locality for each sample appears to the left and is followed by the sample size in parentheses. The series of numbers for each character consists of: mean, range (in parentheses), and one standard deviation of the mean. All measurements are in millimeters. See text for description of characters.*

Sample	Dental characters		
	p2-m3	m1	m2
Pliocene specimen	6.30	1.90	1.60
California: Santa Barbara Co. (13)	7.34(7.10-7.60)0.20	2.10(1.90-2.30)0.11	1.92(1.80-2.10)0.08
Nevada: Churchill Co. (8)	6.64(6.35-6.90)0.17	1.88(1.80-2.00)0.00	1.78(1.60-1.90)0.11
Kansas: Barber Co. (6)	6.74(6.50-6.85)0.13	1.93(1.90-2.00)0.05	1.78(1.65-1.90)0.08
Oklahoma: Cimarron Co. (9)	6.62(6.30-6.75)0.16	1.91(1.80-2.00)0.08	1.68(1.50-1.80)0.09
New Mexico: Catron Co. (4)	6.45(6.30-6.60)0.13	1.85(1.75-1.90)0.07	1.68(1.60-1.80)0.10
Texas: Culberson Co. (12)	6.27(6.10-6.40)0.13	1.78(1.70-1.90)0.08	1.59(1.50-1.70)0.09
Texas: Brewster Co. (13)	6.06(5.80-6.40)0.19	1.79(1.65-1.90)0.09	1.59(1.50-1.70)0.07
Chihuahua (8)	6.19(5.90-6.50)0.19	1.73(1.60-1.80)0.08	1.62(1.40-1.75)0.12

shape of the talonid. The p2 appears shorter than in most specimens of *A. pallidus* examined, but this character might be unreliable due to considerable tooth wear in the fossil. Although dental measurements of the fossil also compare closely with specimens of *A. dubiaquercus*, distinct differences are noted in the shape of talonid of m3, which is approximately half the length of the trigonid in the fossil; in *A. dubiaquercus* the structures are approximately equal in length (Fig. 2).

Three measurements were used in comparing the fossil with eight samples of *A. pallidus* (see Table 1). These are: greatest length from the anteriormost portion of p2 to the posteriormost projection of m3 (p2-m3); greatest length of the first lower molar (m1); and greatest length of the last lower molar including the talonid (m3). In the first character, the measurement of the fossil fits best within the range of *A. pallidus* from Texas and México. The length of m1 in the fossil is nearest that of larger pallid bats from Nevada, Kansas, and Oklahoma but is much smaller than measurements of specimens from western California. In the length of m3, the Pliocene specimen compares best with *A. pallidus* from the southwestern United States and México.

Our analysis indicates that the jaw fragment and teeth of the fossil are virtually indistinguishable from those of modern *A. pallidus*, although more complete material might show that the Blancan bat is specifically different. We suggest that the slight difference between the Blancan specimen and those of Recent *A. pallidus* is a reflection of minor phenetic change that has occurred within the species since Blancan time. We would argue further that, although documentation of such change is of interest to evolutionary biologists, taxonomic recognition of such minor variations is unwarranted. The Pliocene specimen, however, is of interest because it extends the known history of the genus and species back to early Blancan times.

Nongeographic Variation

Individual and sexual variation were examined in two widely separated samples of *A. pallidus* (Table 2). Sample 10 (Santa Cruz Island, California) represents a single population, whereas sample 61 (southern Brewster and Presidio counties of the Big Bend in Texas) is a compilation of bats from 17 different but adjacent localities.

Individual Variation

Coefficients of variation (CV's) of external body measurements were more variable than cranial measurements in both samples. CV's of external measurements ranged from 2.01 (forearm of males, sample 10) to 11.85 (hind foot of males, sample 61). CV's of cranial measurements ranged from 1.55 (skull length of females, sample 61) to 4.31 (palatal length of females, sample 61). CV's of most cranial measurements ranged between 1 and 3, and, with the exception of postorbital constriction and palatal length, all measurements had values of less than 3.4. CV's were slightly greater in sample 61 than in sample 10 for almost every measurement of both sexes. The mean CV's of females were slightly higher than those of males in both samples. However, an *F*-test did not reveal significant differences in variance estimates between sexes of any character at either locality.

Analyses of individual variation in bats by Hayward (1970), Smith (1972), and Davis (1973) have shown that CV's of most characters range between 1 and 4. Hayward (1970) considered characters with CV's from 1.4 to 2.9 to be most stable in *Myotis velifer*, and Smith (1972) showed that CV's of 5 or greater were unusually high in mormoopid bats. In this study, all external measurements except forearm length had relatively high CV's and, consequently, they were not used in analyses of geographic variation. Forearm length and all cranial measurements had sufficiently small CV's to be useful in making geographic comparisons.

A considerable amount of dorsal color variation within samples is evident in *A. pallidus*. All three major color classes (A, B, and C) are represented in most samples. Some variation in color probably is the result of molting sequences. The degree of darkness in some specimens is a reflection of the percentage of dark overhairs to paler underhairs, which undergoes a certain amount of seasonal change. The distal portion of the dorsal hair becomes paler and the proximal portion becomes more yellowish in worn pelage (Orr, 1954).

Secondary Sexual Variation

Only one character (length of phalanx I of third digit) showed a significant difference between sexes in the Big Bend sample. With the exception of length of tail, females averaged slightly larger than males in external measurements, and in five of the 10 cranial measurements. No statistically significant differences were recorded between the sexes for any character in the

TABLE 2.—*Analysis of secondary sexual variation in two samples of* Antrozous pallidus. *See text for abbreviations of measurements. Significant t-values are indicated by an asterisk.*

Character	Males				t-value	Females			
	N	Mean±1 SD	Range	CV		N	Mean±1 SD	Range	CV
Big Bend, Texas									
Total length	51	105.82±4.97	94.0-115.0	4.69	−1.72(0.09)	34	107.85±5.79	92.0-120.0	5.37
Tail length	51	44.00±4.14	30.0- 51.0	9.40	0.25(0.80)	34	43.76±4.23	28.0- 51.0	9.67
Hind foot length	51	10.92±1.29	9.0- 15.0	11.85	−1.09(0.28)	34	11.20±0.98	9.0- 13.0	8.73
Ear length	50	27.92±2.49	21.0- 32.0	8.92	−0.10(0.92)	34	27.97±1.87	25.0- 32.0	6.67
Forearm length	51	50.68±1.48	47.6- 54.3	2.93	−0.90(0.37)	36	50.98±1.56	47.5- 54.3	3.06
Phalanx I	51	14.55±0.72	13.1- 16.6	4.96	−2.17(0.03)*	36	14.89±0.69	13.4- 16.5	4.66
Phalanx II	51	13.80±0.80	12.4- 16.1	5.82	−1.02(0.31)	36	13.97±0.74	12.8- 15.4	5.28
Metacarpal III	51	45.99±1.31	43.0- 49.2	2.86	−0.94(0.35)	36	46.29±1.64	42.1- 50.7	3.54
Greatest length of skull	50	19.72±0.37	18.8- 20.4	1.86	0.88(0.38)	31	19.65±0.30	19.2- 20.2	1.55
Postorbital constriction	51	3.80±0.15	3.4- 4.1	3.91	1.10(0.27)	35	3.76±0.16	3.5- 4.2	4.28
Zygomatic breadth	49	11.82±0.27	11.3- 12.4	2.26	−1.39(0.17)	33	11.90±0.27	11.4- 12.6	2.29
Cranial breadth	50	9.42±0.21	9.0- 9.8	2.24	−1.84(0.07)	31	9.50±0.15	9.2- 9.8	1.62
Palatal length	39	6.91±0.29	6.3- 7.4	4.15	−0.43(0.67)	20	6.94±0.30	6.4- 7.5	4.31
Length maxillary toothrow	52	6.46±0.14	6.1- 6.8	2.23	0.12(0.91)	35	6.45±0.16	6.0- 6.8	2.52
Width across molars	52	7.46±0.17	7.2- 7.8	2.34	−0.88(0.38)	34	7.49±0.21	7.1- 8.0	2.85
Mandibular length	52	13.82±0.33	12.8- 14.4	2.37	0.36(0.72)	35	13.80±0.36	13.1- 14.8	2.60
Length mandibular toothrow	52	7.19±0.20	6.6- 7.6	2.84	−1.28(0.20)	35	7.24±0.19	6.8- 7.6	2.62
Greatest depth of cranium	50	8.52±0.25	7.8- 9.1	2.92	1.07(0.29)	31	8.45±0.28	7.8- 9.1	3.32

TABLE 2.—*Continued.*

Santa Cruz Island, California									
Total length	16	118.62±3.74	111.0-124.0	3.15	−0.98(0.33)	23	119.87±4.00	112.0-125.0	3.34
Tail length	16	44.00±2.31	41.0- 47.0	5.25	−1.13(0.26)	23	45.00±2.95	39.0- 50.0	6.56
Hind foot length	16	14.38±0.62	14.0- 16.0	4.31	−0.38(0.70)	23	14.48±0.95	12.0- 16.0	6.54
Ear length	16	30.00±0.73	28.0- 31.0	2.43	−1.29(0.20)	23	30.35±0.88	28.0- 32.0	2.92
Forearm length	16	55.02±1.10	53.2- 57.4	2.01	−1.94(0.06)	23	55.75±1.21	54.0- 58.2	2.18
Phalanx I	16	15.98±0.54	15.2- 17.0	3.38	−0.23(0.82)	23	16.03±0.71	14.6- 17.2	4.46
Phalanx II	16	14.77±0.84	12.6- 16.0	5.73	0.53(0.59)	23	14.63±0.71	13.2- 15.6	4.83
Metacarpal III	16	51.30±1.22	49.2- 53.8	2.37	−0.90(0.37)	23	51.65±1.21	49.4- 53.7	2.34
Greatest length of skull	13	22.36±0.35	21.8- 23.2	1.57	0.61(0.54)	18	22.26±0.54	21.1- 23.0	2.43
Postorbital constriction	16	4.13±0.14	3.8- 4.3	3.27	0.12(0.91)	23	4.13±0.14	3.9- 4.4	3.29
Zygomatic breadth	16	13.16±0.27	12.5- 13.6	2.08	0.14(0.88)	20	13.14±0.39	11.9- 13.6	2.99
Cranial breadth	16	10.52±0.24	9.9- 10.9	2.33	0.35(0.73)	19	10.50±0.17	10.2- 10.8	1.61
Palatal length	16	8.20±0.29	7.5- 8.5	3.59	0.85(0.40)	23	8.11±0.34	7.2- 8.6	4.16
Length maxillary toothrow	13	7.51±0.14	7.2- 7.7	1.94	1.04(0.30)	19	7.45±0.14	7.2- 7.7	1.82
Width across molars	16	8.29±0.23	7.8- 8.7	2.75	−0.62(0.54)	22	8.34±0.26	7.6- 8.7	3.14
Mandibular length	16	15.85±0.40	14.9-16.6	2.55	1.27(0.21)	23	15.69±0.38	14.8- 16.3	2.39
Length mandibular toothrow	12	8.42±0.18	8.2- 8.7	2.14	0.42(0.68)	19	8.39±0.16	8.1- 8.7	1.89
Greatest depth of cranium	13	9.16±0.26	8.6- 9.4	2.79	−0.60(0.55)	16	9.22±0.28	8.8- 9.6	3.01

Santa Cruz Island sample, although forearm length ($P \leq .06$) approached significance. In all external measurements save length of phalanx II of third digit, females averaged slightly larger than males. Males averaged larger than females in all cranial measurements except molar width and cranial depth.

Williams and Findley (1979) reported that in most vespertilionid bats females are generally larger than males, with differences in body size and forearm length being greater than differences in skull dimensions. Those authors suggested that increased energy demands during pregnancy could be the primary factor in the selection for larger size in females. For *A. pallidus*, they reported that females averaged from four to five per cent larger than males. Our results, however, do not corroborate completely their findings. Generally, we found that females tend to average slightly larger than males in external measurements, whereas males tend to average slightly larger than females in most cranial measurements. There also appears to be some geographic variation in the magnitude and extent of these differences. Williams and Findley (1979) reported statistically significant differences between the sexes for two characters of pallid bats—length of head and body and the ratio of head and body length to forearm length which we did not consider.

Although Morse and Glass (1960) treated the sexes separately in studying variation in *A. pallidus* from the northeastern part of its range, we found sexual differences to be slight and, for the most part, nonsignificant. Therefore, we grouped males and females in each sample for the purpose of analyzing geographic variation.

Geographic Variation

Size

Univariate analysis.—Patterns of univariate variation along five north-to-south and three west-to-east transects for greatest length of skull, as depicted by Dice-Leraas diagrams, are illustrated in Figs. 3 and 4. Other measurements follow the same general pattern of geographic variation, and these are presented and discussed in detail by Martin (1974).

The largest pallid bats are from the Coastal Range of western California (samples 5-11), the Kansas-Oklahoma border (67), and Jalisco (81). The smallest bats occur in a contiguous area from Baja California (13, 82, 83) northward to southwestern California (22) and southern Nevada (18, 20) thence eastward through southern Arizona (24-25, 37, 39-41) and New Mexico (51-52) into southern Trans-Pecos, Texas (59-62). Bats of intermediate size occupy the remainder of the species range.

Smooth clines are rare in most measurements, and clinal increases from south to north and west to east are evident only in localized parts of the range. Morse and Glass (1960) noted a gradual, clinal increase from west to east in pallid bats, but we found this to be valid only for certain characters in selected eastern samples, and it did not hold true throughout the range of the species. Orr and Silva Taboada (1960) suggested that *A. pallidus* follows

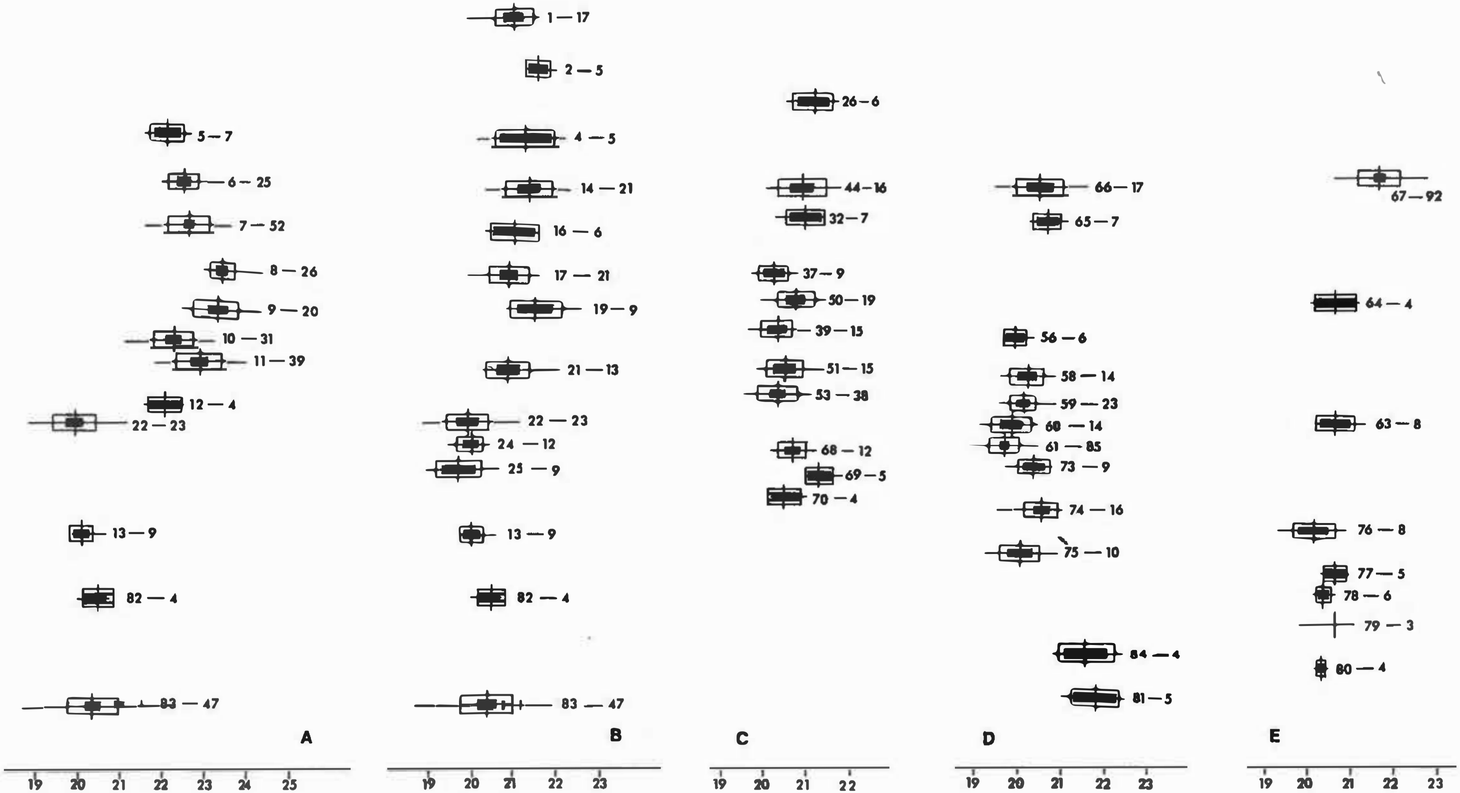

FIG. 3.—North to south clinal variation, expressed in Dice-Leraas diagrams along five transects (A-E), in greatest length of skull in selected samples of *Antrozous pallidus*. The horizontal line represents the range; vertical line, mean; open rectangle, one standard deviation; closed rectangle, two standard errors of the mean. The first number to the right of the grams is the sample number; the second number is the sample size. See Fig. 1 for location of samples. See text for description of transect locations.

Bergman's Rule in a general way, but our data support this notion only in a few instances. Instead, north-to-south clines often are broken and erratic, suggesting that populations of this species are somewhat demic in nature.

Several distinct morphological discontinuities occur in various parts of the range. An area of extreme morphological differentiation separates bats from the California Coast Range, which are large, from those to the east along the slopes of the Sierra Nevada, which are markedly smaller in size. Samples in the southern half of the Central Valley (19), Mojave Desert (21), Imperial Valley (22), Baja California (13, 82, 83), and southwestern Arizona (24-25) exhibit the most pronounced degree of differentiation from specimens in western California (7-12). The magnitude of the morphological break is reflected in the Dice-Leraas diagrams for greatest length of skull (Figs. 3A; 4G), which show a distinct morphological step separating sample 12 in southwestern California from adjacent localities in southwestern California (22) and Baja California (13). Differences of this same magnitude occur in all measurements and indicate a high degree of concordancy of character shifts in this geographic region.

Another area of distinct morphological differentiation occurs between the small-sized bats from Baja California and those from the western Mexican tableland, which average larger in size (Fig. 4H). This would suggest that there is no interbreeding of populations across the Gulf of California. Strong morphological shifts also separate specimens along the southwestern slopes of the Sierra Madre Occidental in north-central Jalisco (81) and Nayarit-Zacatecas (84) from samples in the Mexican Plateau (70-76) and in the vicinity of the Sierra Madre Oriental (76-80). Jalisco and Nayarit-Zacatecas specimens are significantly larger than those of the other samples in most measurements (Fig. 3D). Additionally, a break occurs in certain characters between specimens from Kansas (67) and those from the closest samples in Texas (64), Oklahoma (66), and New Mexico (65). Individuals in sample 67 average larger in size than those in the adjacent samples (Figs. 3E; 4F).

Another zone of differentiation separates samples in the southern Trans-Pecos and Stockton Plateau (58-62) of Texas from those in surrounding areas. Beginning with sample 58 from the Guadalupe Mountains, a clinal decrease in size is evident southward into the Big Bend region (59-61; Fig. 3D). However, a significant character shift separates the Trans-Pecos samples as well as those from the Sacramento Range of New Mexico (55 and 56) from samples to the southeast in west-central Texas (63-64) and eastern New Mexico (65). Bats from the Trans-Pecos and Stockton Plateau are significantly smaller in size than those comprising adjacent samples (Figs. 3D; 4H).

Morphological changes of lesser magnitude and agreement occur among samples along the western California coast (6-12), and some degree of clinal shifting occurs between samples from northwestern California (5 and 6) and those in the northern Great Basin region (1-4). Minor character shifts also separate samples 32-34 and 44-47 north of the Mogollon Rim and Black

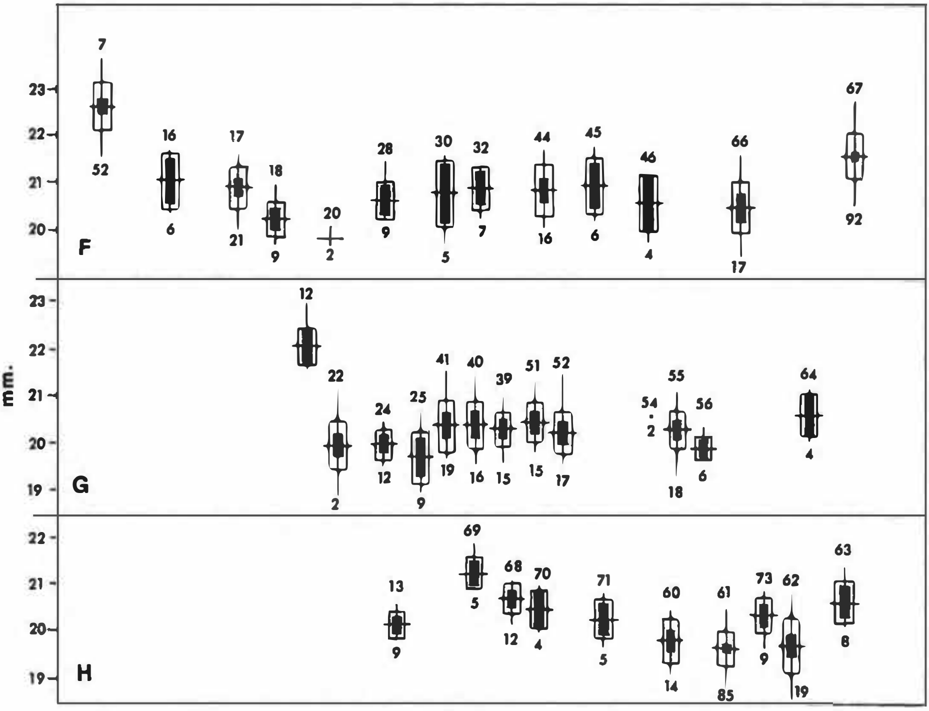

FIG. 4.—West to east variation, expressed in Dice-Leraas diagrams along three transects (F-H), for greatest length of skull in selected samples of *Antrozous pallidus*. For explanation of symbols, see Fig. 3. The number above each gram is the sample number; the one below each gram is the sample size.

Range in Arizona and New Mexico from samples 36-38 and 48-50 to the south of those regions (Fig. 3C).

Multivariate analyses.—The first three principal components were computed from the matrix of correlation among the 11 characters. The first principal component expresses 85 percent of the phenetic variation, the second 6.7, and the third 2.2. Two-dimensional plots of the first and second components, which account for 91.7 percent of the variation, are shown in Fig. 5. There is little distortion in distances when reducing the 11-dimensional character matrix to two dimensions. Loadings, which indicate the correlations of characters with the first two principal components, are given in Table 3. From these results, it is evident that component I is essentially a general size factor with high correlations for all characters. With respect to positioning of samples along component I, those containing specimens that were smallest overall are located on the far left; from that point, samples are arranged in ascending order relative to size, with those consisting of the largest individuals on the far right of the plot. Because component I accounts for 85 percent of the variation, it may be taken to represent overall size, and projections of localities on this component can be used to reflect such differences among samples.

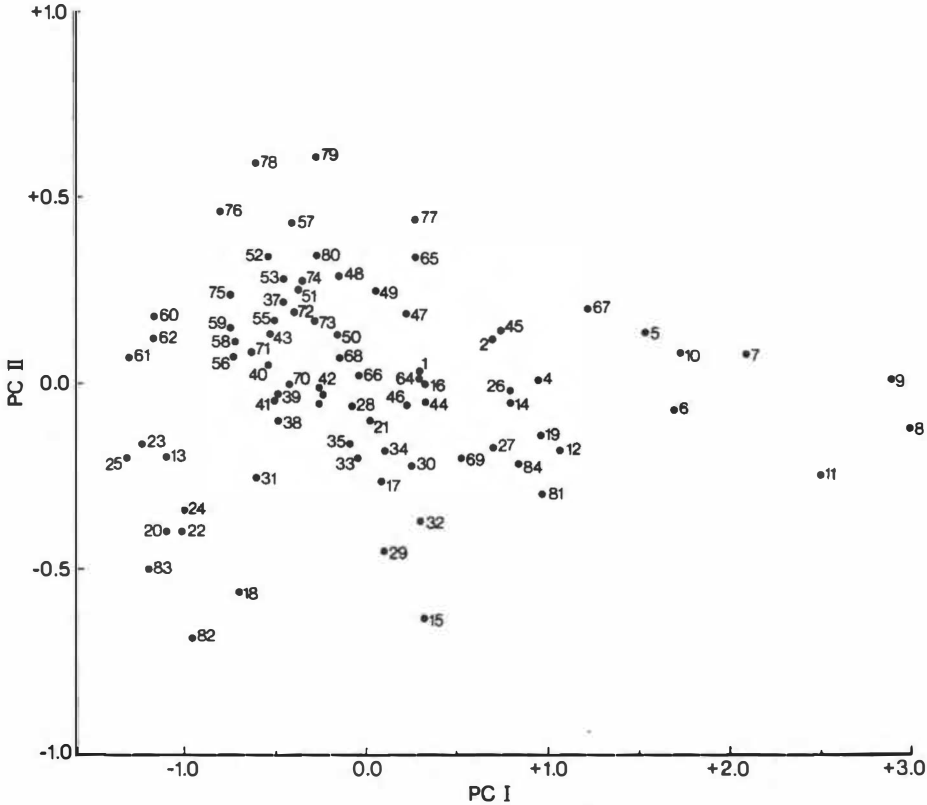

FIG. 5.—Two-dimensional projections of the 84 samples of *Antrozous pallidus* onto the first two principal components.

Component II has high positive loadings for postorbital constriction and cranial depth and a high negative loading for palatal length (Table 3). Samples with positive scores for this component tend to have wider postorbital regions, deeper skulls, and shorter palates than do samples with negative scores. There is little separation of samples representing the larger-sized bats (those to the right in Fig. 5) along component II; however, the positioning of samples of the smallest bats in size (to the left in Fig. 5) along this component reveals that most samples with positive scores are from east of the Continental Divide, whereas most of those with negative scores are from west of the Continental Divide. A similar geographic segregation of samples representing intermediate-sized bats also is seen along component II. Generally, those samples with positive scores for this component (wide postorbital region, deep skull, and short palate) are from the southern part of the range of the species, whereas those with negative scores (narrower postorbital region, shallower skull, longer palate) are primarily from the northern half of the range.

TABLE 3.—*Character loadings on the first two principal components of interlocality phenetic variation in* Antrozous pallidus.

Character	Principal components I	Principal components II
Forearm length	0.906	0.061
Greatest length of skull	0.976	−0.093
Postorbital constriction	0.720	0.631
Zygomatic breadth	0.959	0.072
Cranial breadth	0.953	0.136
Palatal length	0.895	−0.356
Length of maxillary toothrow	0.967	−0.183
Width across molars	0.944	−0.049
Mandibular length	0.975	−0.149
Length of mandibular toothrow	0.971	−0.186
Greatest depth of cranium	0.870	0.289

Multivariate analysis, as did univariate analysis, revealed three major geographic regions of morphological differentiation in pallid bats. The area of greatest differentiation is in the extreme western portion of the range of *A. pallidus*, in Baja California, California, Nevada, and Arizona. A second major region of differentiation is in the south-central United States in an area including Kansas, Oklahoma, Texas, and New Mexico. The third region of significance is in western Mexico (an area including the states of Jalisco, Nayarit, Zacatecas, and Sonora). In order to evaluate variational patterns in these three regions, we subjected selected samples in each region to MANOVA-Canonical analysis.

Results of the MANOVA-Canonical analysis for samples from the south-central United States are graphically depicted in Fig. 6. In this analysis, vector I accounts for 70 percent of the variance and vector II, 12 percent. Only one major hiatus, which separates sample 67 (Kansas-Oklahoma border) from the remaining samples, is evident in the graph. The ellipse surrounding the mean of that sample does not overlap that of any other. In all measurements, bats of sample 67 are significantly larger than those from nearby localities. Samples 64 (High Plains of Texas) and 65 (northeastern New Mexico), which were comprised of too few individuals to allow for the construction of ellipses, are positioned in the hiatus between the ellipse of sample 67 and those from other samples. Overlap exists among the ellipses for samples from New Mexico and Texas, and these are arranged in a size gradient beginning with smaller bats (samples 60 and 61 from southern Trans-Pecos, Texas) on the far left of the graph through samples of slightly increasing size (from northern Trans-Pecos and New Mexico) toward the right.

Results of the MANOVA-Canonical analysis for samples from the western portion of the range of *A. pallidus* are graphically depicted in Fig. 7. Separation is optimal along canonical vector I, which accounts for 81 percent of the variance and is heavily influenced by size; bats represented by samples on

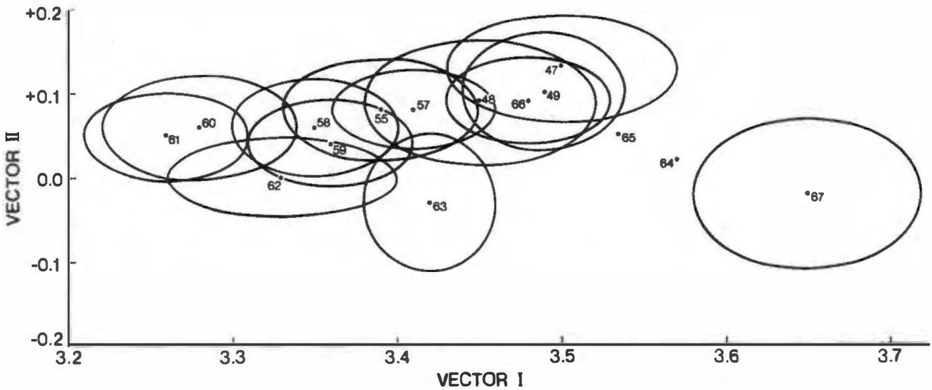

FIG. 6.—Projection of sample means plus or minus one standard deviation for the first two canonical variates in samples of *Antrozous pallidus* from the eastern portion of its range (see Fig. 1 for sample localities). Numbers represent samples used in the study of geographic variation. Ellipses represent one standard deviation around the mean. Single dots are samples represented by three or fewer specimens.

the left of the figure are small and those of samples to the right are progressively larger. There is little separation of samples along vector II, which accounts for only 8 percent of the variance. There are three distinct groupings of samples in Fig. 7: 1) a group of samples of small bats (Group I), which inhabits the desert areas of Baja California, extreme southeastern California, southern Nevada, and southwestern Arizona; 2) samples of large bats (Group III) from extreme western California, which are the largest of all *pallidus*; and 3) a grouping of medium-sized samples (Group II) from eastern and southern California, western Nevada, and the mountainous and plateau regions of central and northern Arizona. All three size groups occur in California. The largest bats occupy the Pacific Coast Range of California (samples 6-11), the smallest bats occur in the Colorado Desert of extreme southeastern California (samples 22-23), and bats of the medium group occupy the Sierra Nevadas (15-17), San Joaquin Valley (16, 19), and extreme southwestern California (12). There is virtually no evidence that intergradation occurs where the ranges of the large and small pallid bats approach one another in southern California (compare, for example, the position of samples 11 and 22 in Fig. 7). Evidence of intergradation among large and medium-sized bats is seen in sample 5 (Klamath Mountains) in northern California. Evidence of intergradation among small and medium-sized bats is seen in samples from the mountain regions of central and southern Arizona (38-41) and in sample 21 from the Mojave Desert of southern California.

The MANOVA-Canonical analysis results for samples from the Mexican mainland (excluding Baja California) are geographically depicted in Fig. 8. Vector I accounts for 50 percent of the variance and vector II, 23 percent. Separation is optimal along canonical vector I, with smaller bats positioned

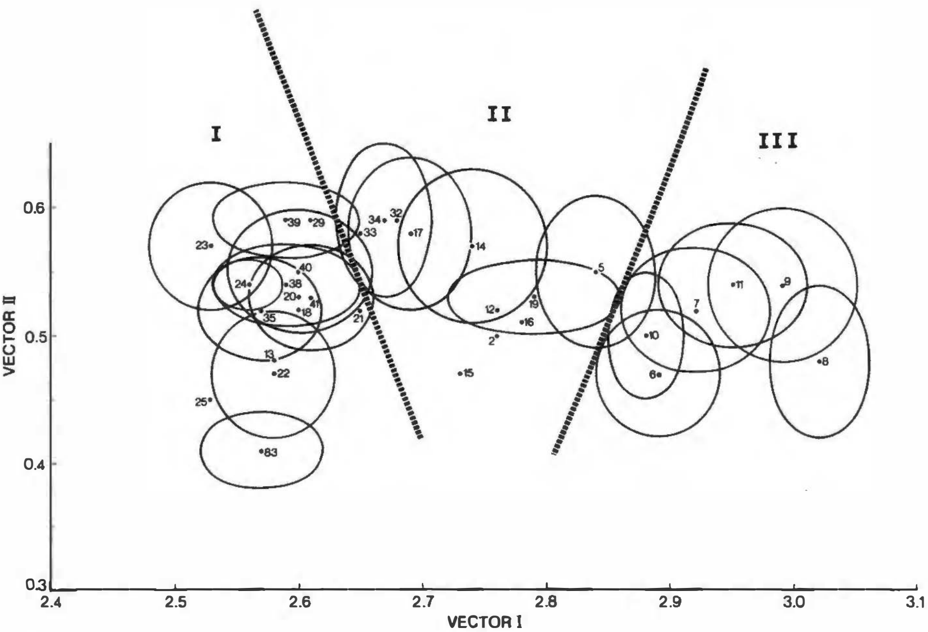

FIG. 7.—Projection of sample means plus or minus one standard deviation for the first two canonical variates in samples of *Antrozous pallidus* from the western portion of its range (see Fig. 1 for sample localities). For explanation of symbols, see Fig. 6. Dotted lines indicate areas of little or no overlap between standard deviations of one group and the means of another. See text for explanation of groups I, II, and III.

at the left of the figure and larger bats to the right. A major hiatus is evident in the graph, with samples 84 (Nayarit and Zacatecas) and 81 (Jalisco) being distinctly separated from the remaining Mexican samples. Sample 69 (from the coastal lowlands of southern Sonora) bridges the gap between samples 81 and 84 and the remaining samples. In virtually all cranial and external measurements, bats in samples 81 and 84 are markedly larger than those in the other samples. Separation is minimal along vector II, with sample 80 (Querétaro) segregating from other samples in northeastern México and sample 84 (Nayarit and extreme southwestern Zacatecas) segregating slightly from sample 81 (Jalisco).

Color

The expression of color in *A. pallidus* shows considerable geographic variation (Fig. 9). The darkest specimens occur throughout most of western California, parts of the northern Great Basin region, Baja California, and throughout most of México except for inland localities on the Central Plateau. Samples with high percentages of dark individuals also seem to occur near the periphery of the range of the species and along the seaward slopes of mountain ranges. Although most dark specimens tend also to be bright in hue, many individuals from the northern Great Basin and from eastern Méx-

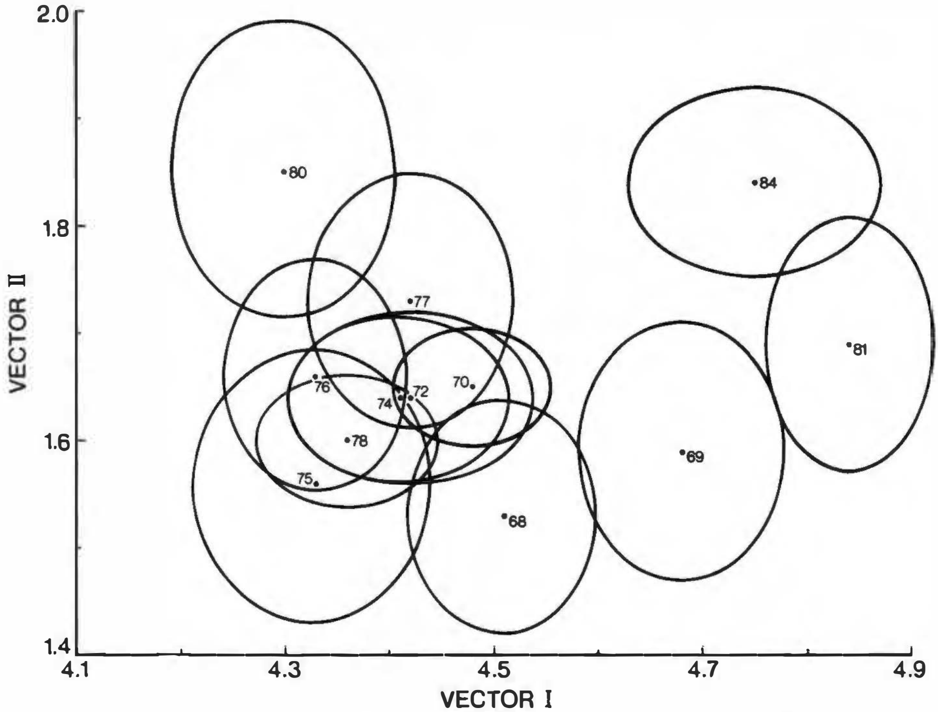

FIG. 8.—Projection of sample means plus or minus one standard deviation for the first two canonical variates in samples of *Antrozous pallidus* from the southern portion of its range (see Fig. 1 for sample localities). For explanation of symbols, see Fig. 6.

ico lack the intensity prevalent in bats from western California and the Baja Peninsula. Most specimens from the central part of the range average much paler in color, although varying numbers of dark individuals appear in many samples.

The palest specimens of *A. pallidus* occur with greatest frequency in arid desert regions of the southwestern United States and on the Mexican Plateau. Individuals from these areas also tend to lack the strongly bicolored pattern evident in bats from darker-colored populations. The paler coloration of bats living in arid areas is expected and presumably results from the selective advantages conferred by protective coloration, because arid regions generally have paler soils that contain less organic material (Findley and Traut, 1970).

Color of the venter shows much less variation than does that of the dorsum and tends to be either strongly blond or pale to buffy white (Fig. 9B). According to Orr (1954), the ventral pelage can become discolored due to frequent contact with urine and excrement in the roosts.

SUBSPECIES

In recognizing subspecies, we have followed Mayr's (1969:41) definition that "a subspecies is an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species." We believe that subspecies should be recognized only when strong evidence of phenetic breaks (presumably indicative of reduced gene flow) exist, thus imparting some biological meaning. Minor deviations from the overall pattern of variation should not be recognized formally.

Based on an assessment of geographic variation in *A. pallidus*, five distinct units can be identified, which in our opinion fit the above criteria; those five units are the continental subspecies of *A. pallidus* here recognized (see Fig. 10). Three of them are characterized by large size and have restricted geographic distributions. The largest individuals of the species are from the Coastal Range of western California and to this group the trinomial *Antrozous pallidus pacificus* applies. Another subspecies of large individuals is *Antrozous pallidus bunkeri*, which occupies a limited distribution along the Kansas-Oklahoma border. The third subspecies of large individuals occurs in western México in Jalisco, southwestern Zacatecas, Nayarit, and southern Sonora. As presently understood, those populations constitute an unrecognized subspecies, which is named and described beyond.

The two remaining subspecies are characterized by individuals of medium to small size and have more extensive geographic distributions. *Antrozous pallidus pallidus* is the most widely distributed of the five subspecies. It ranges from southern British Columbia and east of the Cascade Range throughout much of the Columbia Plateau and Great Basin, throughout the southwestern United States and south to south-central México. This subspecies displays a considerable degree of geographic variation with the largest individuals occurring in the northern portion of its range in Washington, Oregon, central California, and Nevada; the smallest individuals are from the Trans-Pecos region of Texas. This subspecies includes samples previously referred to *A. p. pallidus*, *A. p. cantwelli*, and *A. p. obscurus*. *Antrozous pallidus minor* is a subspecies comprised of the smallest pallid bats. It ranges from Baja California northward into extreme southwestern Arizona, southern California, and southern Nevada.

Accounts of Subspecies

Antrozous pallidus pacificus Merriam

1897. *Antrozous pallidus pacificus* Merriam, Proc. Biol. Soc. Washington, 11:180.
1918. *Antrozous pacificus*, Grinnell, Univ. California Publ. Zool., 17(12):352.
1924. *Antrozous pallidus pacificus*, Miller, Bull. U.S. Nat. Mus., 128:84.

Holotype.—U.S. National Museum, Biological Survey Collection, no. 29815; from Old Fort Tejon, 3200 ft., Tehachapi Mts., Kern Co., California. Type examined.

Distribution.—Along the Pacific Coast Ranges of western Oregon and California south to Los Angeles and San Bernadino counties.

Diagnosis.—Largest and darkest of the mainland subspecies of *A. pallidus*. Mean length of forearm varying from 55.1 to 57.9 in seven samples; mean

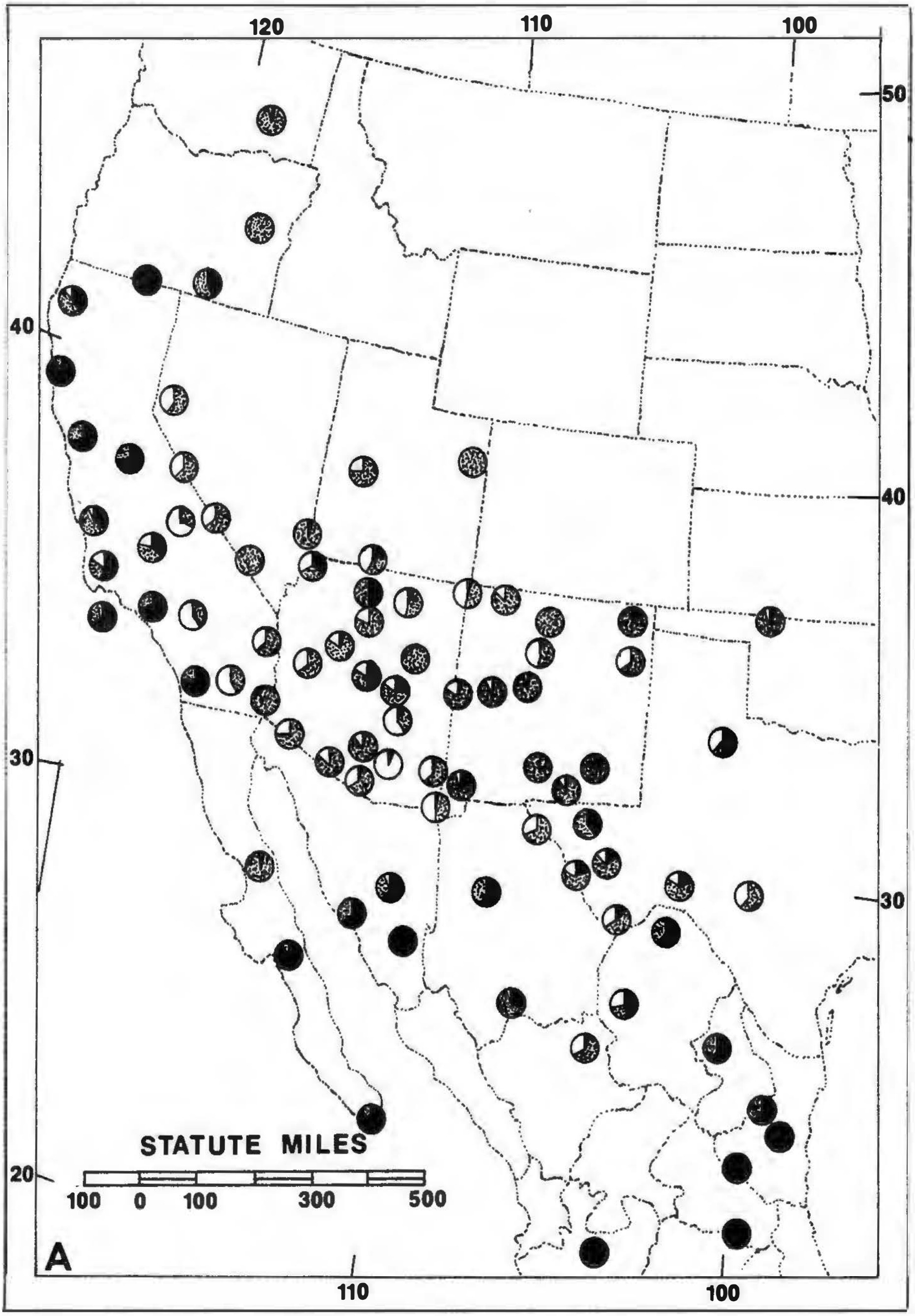

FIG. 9A.—Dorsal color variation in *Antrozous pallidus* showing the percentage of each sample which falls into the three major color classes described in the text. The darkest portion of each circle depicts darker bats (class C), the unshaded portion represents pale individuals (class A), and the stippled area indicates specimens of the intermediate color category (class B).

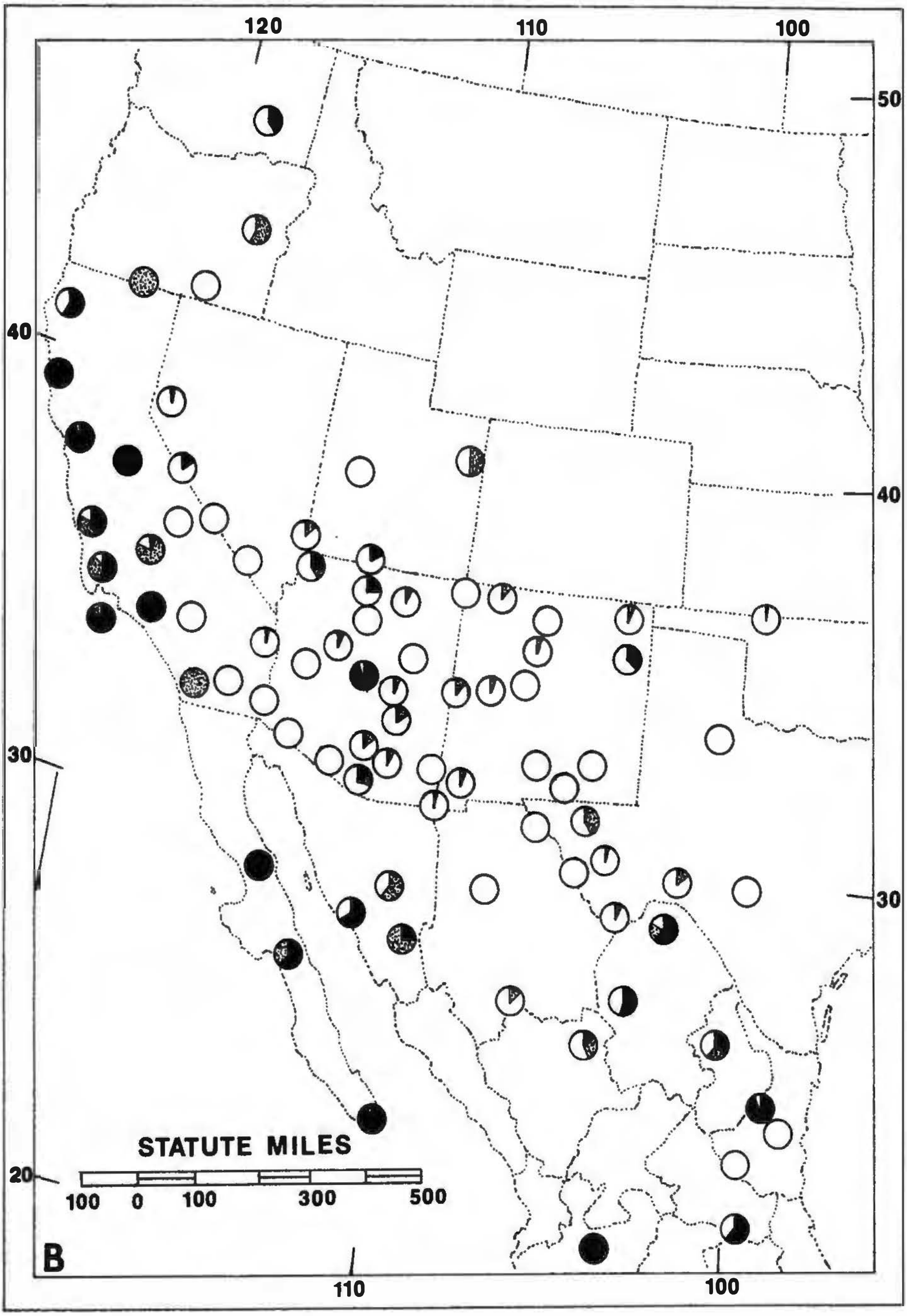

FIG. 9B.—Ventral color variation in *Antrozous pallidus* showing the percentage of each sample which falls into the three major color classes described in the text. The darkest portion of each circle depicts darker bats (class C), the unshaded portion represents pale individuals (class A), and the stippled area indicates specimens of the intermediate color category (class B).

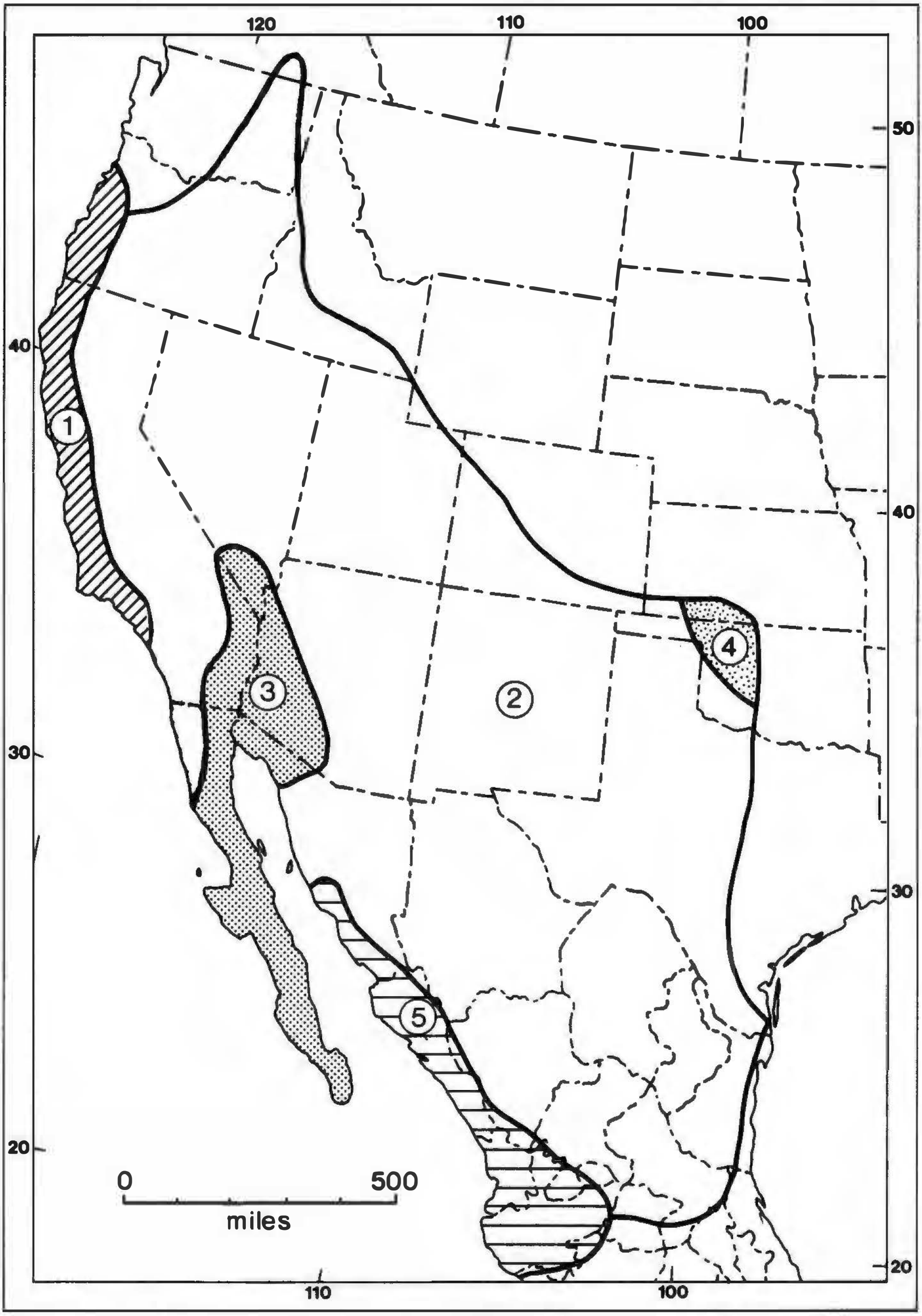

FIG. 10.—Geographic distribution of mainland subspecies of *Antrozous pallidus*: 1, *A. p. pacificus*; 2, *A. p. pallidus*; 3, *A. p. minor*; 4, *A. p. bunkeri*; 5, *A. p. packardi*.

length of skull in the same samples varying from 22.1 to 23.5; mean zygomatic breadth varying from 13.0 to 13.7; and length of maxillary toothrow varying from 7.4 to 8.0. Dorsal coloration medium to strong blond with dark overhairs; venter strongly blond with a brownish tinge.

Comparisons.—From *A. p. pallidus* in California, the Great Basin, and the Pacific Northwest, *pacificus* differs in its larger size (Appendix 1) and darker overall coloration. From *A. p. minor*, *pacificus* differs in larger size, both externally and cranially, but not in overall coloration. From *A. p. bunkeri*, *pacificus* is only slightly larger in size but much darker in coloration.

Remarks.—A relatively broad zone of intergradation between *A. p. pacificus* and *A. p. pallidus* is evident in specimens from samples where the Cascades, Sierra Nevada, and Coastal Ranges merge in northern California. Some degree of intergradation is also discernable in the Central California Valley, especially toward the south where the Tehachapi Mountains bridge the Coastal Ranges and the Sierra Nevada. In contrast, the transition in phenetic characteristics between *A. p. pacificus* (Group III on Fig. 7) and *A. p. pallidus* (Group II on Fig. 7) in southern California is abrupt. A possible explanation for this might be suggested by changing patterns of topography and vegetation in California during the Pliocene and Pleistocene. Large areas in central and southern California were covered by the sea in the late Pliocene to early Pleistocene at a time when the orogeny of the Sierra Nevada and Coast Ranges was just beginning (Smith, 1979). Based on an analysis of the herpetofauna, Peabody and Savage (1958) presented evidence that a corridor or island archipelago, located in the position of the present Pacific Coast Range, was formed and was connected to the mainland to the north but separated by a marine barrier strait from the mainland to the south in the vicinity of the Los Angeles Basin. The peninsula persisted until the second peak of Coast Range orogeny in mid-Pleistocene times (Peabody and Savage, 1958), and there is evidence that much, if not all, of the Los Angeles Basin was inundated until some time in the late Pleistocene. *A. p. pallidus* ranges along the southern California Coast and up the slope of the Sierra Nevada, and is differentiated from *A. p. pacificus* approximately in the position of this former marine barrier. We hypothesize that a northern element of pallid bats was an early migrant from the northern Great Basin and migrated westward and down this corridor. *A. p. pacificus* differentiated from this ancestral stock on the archipelago and was isolated from the southern mainland population by the wide marine strait for sufficient time to permit phenetic (and presumably genetic) divergence to take place. The warm, dry, climatic trends that followed allowed *A. p. pallidus* to move northward through mountain passes and into the San Joaquin Valley and bordering foothills. This explanation is similar to that postulated by Smith (1979) to explain the pattern of geographic variation in *Peromyscus californicus* in coastal California.

Specimens of *pacificus* from west-central California are the largest of the subspecies, and they exhibit a clinal decrease in size toward the north and south from the central part of the range. Specimens from Santa Cruz Island average smaller than those from adjacent samples on the California mainland.

Huey (1964:98) assigned specimens from near Santa Catalina and San Fernando in northwestern Baja California to *pacificus*. Although we did not examine those specimens, we feel certain they should be referred to *A. p. pallidus* inasmuch as pallid bats from just north of that area in San Diego County, California, are clearly referrable to that subspecies. Specimens from western Oregon are referred to *pacificus* on the basis of their assignment thereto by Bailey (1936:390).

Specimens examined (275).—Parenthetical numbers preceding locality designations refer to geographical samples used in the study of variation (see Fig. 2). CALIFORNIA. *Contra Costa Co.*: (07) Pinole, 2 (TCWC), 2 (UMMZ); (07) Berkeley, 1 (USNM); (07) Walnut Creek, 1 (CAS). *Humboldt Co.*: (05) Hoopa Indian Reservation, 8 (CAS). *Kern Co.*: (11) Fort Tejon, Old Fort Tejon, 3200 ft., Tehachapi Mts., 3 (FMNH), 3 (USNM). *Lake Co.*: (06) 5 mi. NE Lower Lake, 1 (FMNH); (06) Mirabel Mine, near Middleton, 19 (CAS). *Los Angeles Co.*: (11) Castaic, 1 (LACM); (11) Soledad Canyon, 2 (LACM), 3 (UI); (11) Old mine, Soledad Canyon, 2 mi. S Acton, 6 (LACM), 2 (UI); (11) Axusa, 4 (LACM), 1 (KU); (11) Near El Monte, 1 (UI); (11) 2 mi. E Monte, 1 (KU), 1 (UI); (11) Glendora, 1 (CU), 1 (USNM); (11) Pasadina, 1 (CAS); (11) San Dimas, 1 (KU); (11) Sierra Madre, 1 (KU), 7 (LACM); (11) Allhambra, 1 (USNM); (11) Palmas, 2 (LACM); (11) 0.5 mi. NW Louise Ave., Encino Park, 800 ft., 1 (LACM). *Marin Co.*: (07) Inverness, 1 (CAS); (07) Ross, 1 (CAS); (07) San Rafael, 1 (FMNH). *Mendocino Co.*: (06) Near Hearst, 3 (CAS). *Monterrey Co.*: (08) Lewis Creek, 1750 ft., 6 (LACM); (08) San Antonio Mission, 3 (UMMZ). *Napa Co.*: (06) Old Winery, 2 mi. NW St. Helena, 1 (FMNH). *San Bernadino Co.*: (11) Ontario, 1 (KU). *San Luis Obispo Co.*: (08) SE Cholamne, 1 (CAS); (08) 4.5 mi. NE Shandon, 1300 ft., 20 (CAS); (09) E part of county, Carissa Plains-Shandon area, 6 (CAS), 1 (USNM); (09) Painted Rock, 20 mi. SE Simmler, 1 (USNM). *San Mateo Co.*: (07) Belmont, 3 (CAS); (07) Woodside, 1 (CAS). *Santa Barbara Co.*: (09) 10 mi. SE Santa Maria, *ca.* 500 ft., 4 (TCWC); (09) 10 mi. NW New Cuyama, 3000 ft., 5 (TCWC); (09) 20 mi. WNW Santa Barbara, 500 ft., 4 (TCWC); (10) Stanton Winery, old winery, Santa Cruz Island, 77 (LACM), 5 (UI). *Santa Clara Co.*: (07) Attic of Encino Hall, Stanford University, Palo Alto, 28 (CAS); (07) San Jose, 14 (LACM); (07) Gilroy, 1 (CAS); (07) Bell Station, 4 (LACM). *Sonoma Co.*: (06) Cloverdale, 3 (CAS). *Ventura Co.*: (11) Fillmore, 2 (LACM).

Antrozous pallidus pallidus (Le Conte)

1856. *V[espertilio] pallidus* Le Conte, Proc. Acad. Nat. Sci. Philadelphia, 7:437.
1864. *Antrozous pallidus*, H. Allen, Smithsonian Misc. Coll., 7 (Publ. 165):68.
1936. *Antrozous pallidus cantwelli* V. Bailey, N. Amer. Fauna, 55:391; type locality Rogersburg, Asotin Co., Washington.
1967. *Antrozous pallidus obscurus* Baker, Southwestern Nat., 12:329-337; type locality Acuña, 800 m., Tamaulipas.

Holotype.—U.S. National Museum, Biological Survey Collection, no. 5467; from El Paso, El Paso Co., Texas. Type examined.

Distribution.—East of the range of *A. p. pacificus* from southern British Columbia and east of the Cascade Range throughout much of the Columbia Plateau and Great Basin, throughout the southwestern United States east of central Texas, and south to western and south-central México north of the Transverse Volcanic Cordillera.

Diagnosis.—A medium to small representative of *A. pallidus.* Mean length of forearm varying from 49.4 to 56.2 in 62 samples; mean length of skull in the same samples varying from 19.7 to 21.7; mean zygomatic breadth varying from 11.8 to 12.8; and length of maxillary toothrow varying from 6.5 to 7.3. Most specimens average less than 53 in forearm length, less than 21 in length of skull, less than 12.5 in zygomatic breadth, and less than 7 in length of maxillary toothrow. Color variable, from pale to strong blond to dark, with or without concentration of darker overhairs.

Comparisons.—For comparisons with *pacificus* and the new subspecies described beyond, see those accounts. Compared with *A. p. bunkeri, pallidus* is smaller in almost every external and cranial dimension (see Appendix 1). Only forearm length in samples from northern and southern California (4, 12), Utah (26, 27, 30), central Arizona (34), and northern New Mexico (45-47) exceeds that of *bunkeri* in size. Compared with *A. p. minor*, most samples of *pallidus* are significantly larger in almost every external and cranial dimension, although those from southern Trans-Pecos, Texas (60, 61, and 62) are similar in size to *minor.* In dorsal coloration, most specimens of *pallidus* are pale, with brownish overhairs; most of *minor*, strongly blond and bright, with dark overhairs.

Remarks.—Considerable geographic variation exists in *A. p. pallidus.* Specimens from most of the southwestern United States (excluding southern Trans-Pecos, Texas) and from México are medium in size. Specimens from southern Trans-Pecos, Texas average smallest in size. The largest representatives of *pallidus* are those from the Sierra Nevada, the Great Basin, and the Columbia and Colorado plateaus.

Pallid bats from eastern Oregon, southwestern Washington, and northern Nevada were described as a distinct subspecies, *A. p. cantwelli*, by Bailey (1936), primarily on the basis of color. Similarly, Baker (1967) assigned specimens from central Nuevo Leon southeastward to Querétaro, which were dark in dorsal coloration, to a different subspecies, *A. p. obscurus.* Our analysis, however, revealed that color alone does not accurately delineate those populations. Furthermore, it is impossible to distinguish populations referred to those subspecies using mensural characteristics. Consequently, *cantwelli* and *obscurus* are herein placed in synonymy with *A. p. pallidus.*

Specimens examined (1183).—Arizona. *Apache Co.*: (44) Canyon de Chelly National Monument, Canyon del Muerto at mouth of Black Rock Canyon, 5800 ft., 4 (UA). *Cochise Co.*: (43) Kiper Springs, Mescal, 5 (KU); (43) Whetstone Bridge overpass, 1 mi. NW Benson on Hwy. 86, 2 (UA); (43) 7.5 mi. S St. David, 2 (UA); (43) Bridge, 12.1 mi. S St. David by U.S. 80, 6 (UA); (43) Fairbank, 2 (UI); (43) Boquillas Ranch, 1.5 mi. S Fairbank, 6 (UI); (43) Fort Huachuca, 1 (USNM); (51) Mine, 15 mi. S San Simon, 4000 ft., 1 (UA); (51) 16 mi. S San Simon, 1500 ft., 1 (UA); (51) Paradise Mine, 1 mi. N Paradise, 5300 ft., 1 (UA); (51) 1.5 mi. N Paradise, 1 (AMNH), 1 (KU), 1 (MID), 5 (UA), 1 (UMMZ); (53) San Bernadino (Ranch), 1 (UI); (53) Watertank, 11 mi. E Douglas, base of Perilla Mts., 3 (UA). *Coconino Co.*: (30) House Rock Valley, 11 mi. E Jacob Lake, 1 (UI); (30) 6 mi. W, 5 mi. S Marble Canyon, Cliff Dwellers Lodge, 1 (UI); (30) 6.5 mi. W, 6 mi. S Marble Canyon, 2 (UI); (31) Bubbling Tank, S Rim Grand Canyon National Park, 1 (UI); (31) Tuba City, 1 (AMNH), 2 (USNM); (31) 5 mi. N Cameron, 1 (UI);

(33) Heiser Spring, Wupatki National Monument, 5500 ft., 5 (UA); (34) Twin Tanks, 30 mi. W Flagstaff, 1 (UA); (34) 28 mi. S, 9 mi. E Flagstaff, 1 (UNM). *Gila Co.*: (37) Wilbanks Ranch, Sierra Ancho, 7200 ft., 3 (KU), 5 (UI); (37) Natural drainages, 1 mi. S, 1 mi. SW Parker Creek Station, 4550 ft., 1 (UA); (38) San Carlos, 2 (LACM). *Graham Co.*: (38) San Carlos, 2 (LACM); (38) 37 mi. NW Safford, 2600 ft., 3 (TCWC); (39) Water hole, 3 mi. E Aravaipa, 1 (UA); (39) 6 mi. SSW Pima, Graham Mts., 34 (UI); (39) Central, 5 (USNM); (39) Camp Grant, 1 (USNM); (39) Stockton Pass Picnic Ground, Graham Mts., 1 (UI). (37) Jct. Fish Creek and Apache Trail, near Tortilla Flats, 1 (UA). *Mohave Co.*: (29) Vicinity Pipe Springs National Monument, 5000 ft., 1 (UA); (29) Pakoon Springs Ranch, vicinity of Grand Wash, 2400 ft., 1 (UA); (29) Nixon Springs, Mt. Trumbull, 6259 ft., 2 (UA); (29) Nixon Springs, Mt. Trumbull, 9 mi. ESE Trumbull P.O., 6500 ft., 1 (MNA); (29) 1 mi. W Toroweap Ranger Station, Grand Canyon National Monument, 4500 ft., 2 (UA). *Navajo Co.*: (32) Oraibi, Hopi Indian Reservation, 6000 ft., 3 (MVZ), 2 (USNM); (32) Keam's Canyon, 6200 ft., 2 (MVZ); (36) Silver Springs, 15 mi. SE Snowflake, 7 (KU); (40) Steam pump, SW end Catalina Mts., 1 (CAS); (40) Sabino Canyon, Santa Catalina Mts., 1 (LACM); (40) Canada de Oro Bridge, Interstate 10, 2 (MID); (40) Tucson, 1 (UA); (4) 2 mi. N, 7 mi. E Tucson, 3 (UA); (40) Hensley's Ranch, 13 mi. S Tucson, 1 (MVZ), 4 (UA); (40) West Twin Butte, 30 mi. S Tucson, 3400 ft., 1 (UA); (40) 0.5 mi. W Continental, 1 (UA); (42) Mine tunnel, mouth of Madero Canyon, 4 (UA). *Pinal Co.*: (40) Oracle, 3 (USNM). *Santa Cruz Co.*: (42) 7 mi. N Patagonia, 4 (CAS); (42) Stock Pond, 7 mi. NW Patagonia, 1 (UA); (42) 2 mi. W, 5 mi. N Patagonia, 1 (UA); (42) Circle Z Ranch, 5 mi. S Patagonia, 4 (UI); (42) Old bridge, Santa Cruz River, Hwy. 82, 5 mi. NE Nogales, 3 (UA); (42) Pena Blanca, Forest Camp, 1 (UI); (42) Pena Blanca Springs, 10 mi. WNW Nogales, 4800 ft., 1 (AMNH); (42) Memorial Stadium, Nogales, 6 (UI). *Yavapai Co.*: (34) Prescott National Forest, Walnut Creek Ranger District, Headquarters, 5250 ft., 1 (UA); (34) 2 mi. W Sedona, 6 (MNA); (34) 3 mi. W Sedona, 1 (MNA); (34) Prescott, 1 (AMNH); (34) Montezuma Well, 1 (USNM); (34) Camp Verde, 19 (CAS), 6 (KU), 1 (MVZ), 5 (UU).

California. *Fresno Co.*: (16) Fresno, 3 (USNM). *Inyo Co.*: (17) 2 mi. NW Independence, 15 (LACM); (17) Independence, 1 (MVZ); (17) Salt Camp, Saline Valley, 1100 ft., 1 (UMMZ); (17) New York Mt., 2 (USNM); (17) Lee Flat, 15 mi. N Darwin, 5200 ft., 1 (MVZ); (17) Coso Mts., 2 (FMNH). *Kern Co.*: (19) Weldon, 7 (MVZ); (19) Loraine, 2 (MHP); Joe Santos Ranch, 2.5 mi. NW Carneros Spring, 4 (CAS). *Modoc Co.*: (04) Cedarville, 3 (MVZ); (21) 10 mi. SE Victorville, 3200 ft., 8 (KU); (21) 15 mi. SE Victorville, 3200 ft., 1 (KU); (21) Morango Valley, 4 (LACM); (21) Little San Bernadino Mts., 1 (LACM). *San Joaquin Co.*: (16) Farmington, 3 (CAS). *Siskiyou Co.*: (04) T. H. Benton Estate, Butte Creek, 1 (MVZ); (16) Long Barn, 5000 ft., 1 (CAS). *San Diego Co.*: (12) Edgemoor Farm, Santee, 1 (MSU); (12) Santa Ysabel, 4 (USNM).

Colorado. *Archuleta Co.*: (45) Deep Canyon, 1 (UNM). *Mesa Co.*: (26) Colorado National Monument, East Monument Canyon, 4800 ft., 3 (CU). *Moffat Co.*: (26) Castle Park, Dinosaur National Monument, 1 (CU). *Montezuma Co.*: (44) Ashbaugh's Ranch, 2 (USNM).

Nevada. *Churchill Co.*: (14) Fallon, 4000 ft., 1 (MSU), 6 (USNM); (14) 2 mi. SW Fallon, 1 (MVZ); (14) 15 mi. W, 1 mi. S Fallon, 1 (MSU); (14) 14 mi. SW Fallon, 1 (MVZ); (14) 18 mi. W Fallon, 4200 ft., 7 (TCWC); (14) 3 mi. WSW Lahontan Dam, 4200 ft., 1 (MVZ); (14) Sand Springs, 13 mi. S, 20 mi. E Fallon, 3900 ft., 1 (KU), 1 (MSU); (14) Sand Springs, 24 mi. SE Fallon, 4200 ft., 1 (TCWC). *Esmeraldo Co.*: (15) 7 mi. N Arlemont, 5500 ft., 2 (MVZ); (15) Fish Lake, 4800 ft., 3 (MVZ); (15) South base Silver Peak Mts., 5500 ft., 1 (USNM). *Humboldt Co.*: (03) Quinn River Crossing, 1 (MVZ). *Lyon Co.*: (14) 2 mi. S, 18 mi. W Fallon, 7 (KU); (14) 9 mi. E, 2 mi. N Yerington, 4700 ft., 2 (MVZ).

New Mexico. *Bernalillo Co.*: (47) 21 mi. W, 2.5 mi. N, 1st and Central in Albuquerque, T. 10 N, R. 2 W, sec. 11, 17 (UNM); (47) 19.5 mi. W, 2.5 mi. S 1st and Central in Albuquerque, T. 10 N, R. 2 W, sec. 24, 1 (UNM); (47) 4.2 mi. W, 3.4 mi. N 1st and Central in Albuquerque, 37 (UNM); (47) Albuquerque, 1 (MHP), 1 (UNM); (47) Isleta Cave, 8 mi. W Isleta, 31 (UNM); (47) 7 mi. W, 1 mi. S Isleta, T. 8 N, R. 1 W, sec. 35, 2 (UNM); (47) Sandia Park, Sandia Mts., 3 (UNM); Tijeras, Tijeras Canyon, 9 (UNM); (47) Tijeras Canyon, 9 mi. E, 1.5 mi. S Albuquerque, T. 10 N, R. 4 E, sec. 26, 5700 ft., 1 (UNM); (47) Hell Canyon, Manzano Mts., 1 (UNM). *Catron Co.*: (50) Cottonwood Canyon, 13 mi. S Reserve, 1 (UNM); (50) 5 mi. NE

Glenwood, 4900 ft., 4 (TCWC); (50) State Fish Hatchery, Glenwood, 4 (UNM); (49) 8 mi. N, 6 mi. W Winston, mine shaft, Black Range, 13 (UNM); (49) Taylor Creek, 2 mi. NE Wall Lake, Black Range, 13 (UNM). *Chaves Co.*: (56) 18.5 mi. E, 4.5 mi. S Mayhill, 2 (UNM). *Colfax Co.*: (66) Springer, 2 (UNM). *Dona Ana Co.*: (54) Las Cruces, 1 (MID). *Eddy Co.*: (56) Carlsbad, 5 (USNM); (56) Mosley Springs, 11 mi. S, 10 mi. W Carlsbad, 2 (UNM). *Grant Co.*: (50) 14 mi. S, 6.5 mi. W Glenwood, 10 (UNM); (50) Silver City, 4 (USNM). *Hidalgo Co.*: (51) Old Valley View School, T. 24 S, R. 20 W, sec. 22, 5 (UNM); (51) Cave near bluffs, T. 29 S, R. 20 W, sec. 17, 1 (UNM); (52) T. 30 S, R. 16 W, NW ¼ sec. 34, 2 (UNM); (52) Tank at Double Adobe Creek, T. 31 S, R. 19 W, sec. 3, 3 (UNM); (52) Tank at OK Bar Adobe Canyon, T. 31 S, R. 19 W, sec. 24, 1 (UNM); (52) Sheridan Canyon, T. 31, R. 15 W, middle sec. 23, 10 (UNM); (52) Big Hatchet Mts., T. 31 S, R. 15 W, sec. 36, 5250 ft., 5 (UNM); (53) Clanton Canyon, Pelloncillo Mts., 1 (UNM); (53) Tank at entrance to Clanton Canyon, Peloncillo Mts., T. 32 S, R. 21 W, 1 (UNM); (53) Ace Robertson Ranch, T. 33 S, R. 21 W, sec. 20, 7 (UNM); (53) Guadalupe Mts., T. 33 S, R. 21 W, sec. 25, 8 (UNM); (53) Cloverdale Creek, 0.5 mi. NW Cloverdale picnic grounds, 2 (UNM); (53) T. 34 S, R. 18 W, NW ¼ sec. 1, 3 (UNM); (53) Wood Canyon, T. 33 S, R. 15 W, NW ¼ sec. 8, 2 (UNM); (53) Sycamore Well, T. 33 S, R. 14 W, SW ¼ sec. 31, 12 (UNM); (53) Sycamore Well, Alamo Huaco Mts., 1 (UNM). *Luna Co.*: (52) 27 mi. S Deming, 4000 ft., 2 (TCWC). *Otero Co.*: (54) White Sands National Monument, 1 (UI); (54) White Sands National Monument, 2 mi. W entrance, 1 (UA); (55) Alamo Mt., T. 26 S, R. 13 E, 10 (UNM); (55) Abandoned mine tunnel, Alamo Mt., T. 26 S, R. 13, 10 (UNM). *Quay Co.*: (65) 14.5 mi. E Tucumcari, 5 (KU). *Sandoval Co.*: (46) Jemez Springs, 1 (UNM); (46) South edge, Jemez Springs, 1 (KU); (46) Cochita Canyon, T. 17 N, R. 5 E, sec. 14, 1 (UNM); (47) Corrales, 3 (UNM); (47) Shallow Cave, T. 12 N, R. 5 E, sec. 22, Los Huertas Canyon, 7 (UNM); (47) Ellis Cave, T. 12 N, R. 5 E, NW ¼ sec. 33, 1 (UNM). *San Juan Co.*: (45) Marcelo Lucero Place, Pine River Canyon, 1 (UNM); (45) W side Pine River near Todosio Canyon, 1 (UNM); (44) 3 mi. E, 3 mi. S Farmington, 6 (UNM); (44) Galegos Canyon, 7.5 mi. S, 4 mi. E Farmington, 1 (UNM); (45) Gale Wash, 4 mi. E, 2 mi. S Bloomfield, 2 (UNM); (45) 8 mi. S, 4 mi. W Shiprock Peak, 1 (UNM); (44) 5 mi. N Newcomb, 2 (UNM); (44) Chuska Mts., 8 mi. W, 1 mi. S Sheep Springs, 1 (UNM); (45) Chaco Canyon National Monument, 1 (UNM). *Santa Fe Co.*: (46) 3 mi. S, 5.8 mi. E La Cienega, 3 (UNM). *Socorro Co.*: (48) 4.5 mi. E, 1 mi. N Socorro, 9 (UNM); (48) 5 mi. E, 1.5 mi. N Socorro, 1 (UNM); (48) 6.5 mi. W, 2 mi. S Socorro, 28 (UNM); (48) North fork Water Canyon, Magdalena Mts., 4 (UNM); (48) Water Canyon Cabin, Magdalena Mts., 6 (UNM); (49) Indian Butte, San Mateo Mts., 8000 ft., 3 (USNM); (49) Nogal Canyon, San Mateo Mts., 1 (MHP). *Union Co.*: (66) 8 mi. W Kenton, Oklahoma, in Union Co., New Mexico, 4 (UNM); (66) 3 mi. W, 6 mi. S Kenton, Oklahoma, in Union Co., New Mexico, 2 (UNM). *Valencia Co.*: (47) Laguna, 6 (USNM).

OKLAHOMA. *Cimarron Co.*: (66) Pigeon Cave, 2 mi. E, 0.5 mi. N Kenton, 1 (TNHC), (66) Tesequite Canyon, 1 mi. SE Kenton, 5 (NTSU), 3 (TNHC), 2 (USNM).

OREGON. *Baker Co.*: (02) Home, 3 (USNM). *Harney Co.*: (03) Catlow Cave, Catlow Valley, 1 (LACM), 4 (UMMZ). *Klamath Co.*: (4) Klamath, 1 (USNM). *Malheur Co.*: (02) 2 mi. NW Riverside, 2 (USNM). *Umatilla Co.*: (01) 17 mi. ENE Umatilla, 4 (KU).

TEXAS. *Brewster Co.*: (59) 10 mi. W Alpine, 3 (LACM); (59) Alpine, 1 (USNM); (61) 38 mi. S, 14 mi. E Marathon, 6 (UI); (61) Headquarters, Black Gap Wildlife Management Area, 2333 ft., 3 (MSU), 1 (TTU); (61) Black Gap Wildlife Management Area, 40 mi. SE Marathon, 1 (TTU); (61) Black Gap, 50 mi. SSE Marathon and vicinity, 4 (TCWC), 4 (TTU); (61) Black Gap Wildlife Management Area, 57 mi. S Marathon, 1 (TTU); (61) N base Rosillos Mts., 2 (UMMZ); (61) Terlingua Creek, 4 mi. E Terlingua, 2200 ft., 4 (TCWC); (61) Mouth of Santa Elena Canyon, 2100 ft., 1 (TCWC); (61) Oak Spring, W side Chisos Mts., 1 (UMMZ); (61) Grapevine Springs, Chisos quandrangle, 3000 ft., 2 (TCWC); (61) Oak Creek, Chisos Mts., 4000 ft., 2 (TCWC); (61) Chisos Mts., 1 (LACM); (61) Nails Ranch, E side Burro Mesa, 3500 ft., 4 (TCWC); (61) E base Burro Mesa, Big Bend, 3500 ft., 3 (MVZ); (61) 1.5 mi. NW Boquillas, 1 (UMMZ); (61) 4 mi. W Boquillas, 1 (USNM); (61) Boquillas Ranger Station, Big Bend National Park, 3 (TTU); (61) Johnson's Ranch, Rio Grande, 2100 ft., 3 (TCWC). *Brisco Co.*: (64) 6.1 mi. N, 0.1 mi. W Quitaque, 5 (TTU); (64) Los Lingos Canyon, 2 (TTU). *Culberson Co.*: (58) 4 mi. E Pine Spring

Camp, 2 (TCWC); (58) McKittrick Canyon, Guadalupe Mts. National Park, 13 (TCWC); (58) 35 mi. N Van Horn, 3700 ft., 1 (TCWC); (58) 25 mi. N Van Horn, 1 (TCWC); (58) 20 mi. E Van Horn, 1 (TCWC). *Deaf Smith Co.*: (65) 4.9 mi. S, 4.8 mi. E Glenrio, 4 (TTU). *El Paso Co.*: (57) El Paso, 2 (USNM); (57) McKelligon Canyon, El Paso, 4700 ft., 3 (KU); (57) Fort Bliss, 1 (UNM); (57) 8 mi. E Fabens, 4000-4200 ft., 4 (KU). *Haskell Co.*: (64) 8.5 mi. SW Rochester, 1 (MID). *Hudspeth Co.*: (57) Fort Hancock, 13 (USNM). *Jeff Davis Co.*: (59) Valentine school house, Valentine, 6 (TCWC); (59) Madera Canyon, 14 mi. NW Fort Davis, 6000 ft., 3 (TCWC); (59) Mouth of Madera Canyon, 4400 ft., 2 (TCWC); (59) 5.5 mi. NW Mt. Livermore, 6000 ft., 1 (TCWC); (59) Upper Limpia Canyon, 5 mi. E. Livermore, 1 (UMMZ); (59) Limpia Canyon, 3.5 mi. NE Fort Davis, Davis Mts., 2 (TTU); (59) Limpia Creek, 16 mi. NE Fort Davis, 4000 ft., 3 (TCWC); (59) Sawtooth Mts., 8 mi. S Hwy. 118 and 166, Davis Mts., 1 (TTU). *Kerr Co.*: (63) Camp Mystic, 24 mi. NNW Kerrville, 15 (TCWC); (63) 8 mi. SW Kerrville, Turtle Creek, 1 (TCWC). *Kimble Co.*: (63) 8 mi. E Junction, 6 (MID). *Presidio Co.*: (60) 9 mi. W Valentine, ZH Canyon, 1 (TCWC); (60) ZH Canyon, Sierra Vieja Mts., 2 (TTU); (60) 11 mi. W Valentine, 4 (TNHC); (60) 8 mi. NE Candelaria, 7 (TCWC); (60) Pinto Canyon, 45 mi. SW Marfa, Chinati Mts., 4 (TCWC); (60) T.W. Shelly Ranch, Pinto Canyon, Chinati Mts., 2 (TTU); (60) 14 mi. E Ruidosa, Pinto Canyon, Chinati Mts., 1 (TTU); (60) Harper Ranch, 37 mi. S Marfa, 4000 ft., 1 (TCWC); (60) 12 mi. E Ruidosa, Chinati Mts., 5000 ft., 1 (TCWC); (60) Chinati Rancho, 28 mi. NW Presidio, 4 (TCWC); (61) 5 mi. SE Bandera Mesa, 29 (MID); (61) La Mota Ranch, 63 mi. S Marfa, 4 (TNHC); (61) 15 mi. E Redford, 1 (MID); (61) 30 mi. SSE Redford, 8 (MID); (61) 2 mi. W Lajitas, 3 (MID). *Reeves Co.*: (59) 3 mi. WNW Toyahvale, 14 (MID). *Terrell Co.*: (62) 13 mi. S Sheffield, 1 (TNHC); (62) 15 mi. SW Sheffield, 2 (MID); (62) 21 mi. S Sheffield, 1 (TNHC); (62) 2 mi. N Dryden, 6 (TCWC). *Uvalde Co.*: (63) Cal Newton's Ranch, 25 mi. NW Uvalde off Hwy. 55, 2 (TCWC). *Val Verde Co.*: (62) Juno, 14 (MID); (62) Fisher's Fissure, 2 mi. W Langtry, 2 (TTU); (62) Comstock, 8 (USNM).

Utah. *Grand Co.*: (26) Moab, 1 (USNM). *Kane Co.*: (30) Rock Creek Canyon, 1 (AMNH). *Millard Co.*: (27) Volcanic Cave west of Meadow, 1 (UU). *San Juan Co.*: (30) 1 mi. NE Navajo Mt. Trading Post, 6000 ft., 2 (UU); 1 mi. S Kern Spring, 1 (UNM); Beaver Creek, 5000 ft., 1 (AMNH). *Servier Co.*: (27) 2 mi. E Annabella, 4 (UU). *Uintah Co.*: (26) Willow Creek, 5250 ft., 25 mi. S Ouray, 2 (UU). *Washington Co.*: (28) 2 mi. W Pine Valley, 6400 ft., 1 (UU); (28) Middleton, 2.5 mi. NE St. George, 1 (UU); (28) Beaver Dam Wash, 8 mi. N Utah-Arizona border, 2800 ft., 3 (UU); (28) Terry's Ranch, Beaver Dam Wash, 2 (UU); (28) Beaver Dam, 5 mi. N Utah-Arizona border, 1 (USNM). *Wayne Co.*: (27) Notom, 6200 ft., 3 (UU).

Washington. *Asotin Co.*: (01) Rogersburg, 1 (KU), 4 (USNM); (01) Bly, 1000 ft., 1 (KU), 2 (USNM). *Douglas Co.*: (01) Douglas Creek, 1.5 mi. NW Moses Cowlee, 1 (UNM). *Grant Co.*: (01) Drumhilder Ranch House, 9.5 mi. S Neppel, 2 (UMMZ). *Whitman Co.*: (01) Almota, 4 (USNM).

Chihuahua. (53) San Francisco, 5100 ft., 3 (KU); (53) 2 mi. S, 5 mi. W San Francisco, 5500 ft., 3 (KU); (53) 11.1 mi. SE Nuevo Casas Grandes, 3 (UNM); (57) 5.5 mi. N Samalayuca, 1 (UI); (57) 37 mi. S, 3 mi. W Cd. Juárez, 4350 ft., 3 (KU); (57) 8 mi. ESE Los Lamentos, 1400 m., 1 (KU); (71) 5 mi. N Cerro Campaña, Sierra del Nido, 5600 ft., 2 (MVZ); (71) 5 mi. N Chihuahua, 4700 ft., 3 (MVZ); (61) Consolación, 5100 ft., 3 (KU); (70) La Republica, 3900 ft., 4 (UA); (74) Sierra Almagre, 12 mi. S Jaco, 5400 ft., 1 (KU); (72) 2 mi. SE Parral, 6300 ft., 8 (TCWC); (72) Navarro, 72 km. W by road from Hidalgo de Parral, 6100 ft., 10 (LACM).

Coahuila. (62) Rio Grande, 17 mi. S Dryden, Terrell Co., Texas, in Coahuila, 600 ft., 2 (KU); (61) 10 mi. S, 5 mi. E Boquillas, 1500 ft., 1 (KU); (73) 70 mi. NW Muzquiz, Rancho Encantada, Sierra del Carmen, 8 (TNHC); (73) Fortin, Rancho las Margaritas, 3300 ft., 1 (KU); (73) Las Margaritas, 2800-2900 ft., 8 (KU), 3 (MSU); (73) 27 mi. NE Muzquiz, Rancho Mariposa, 1 (TNHC); (74) 18 mi. S, 14 mi. E Tanque Alvarez, 4000 ft., 6 (KU); (74) mi. N San Isidro, 16 mi. N Ocampo, 3 (KU); (74) 34 mi. W Cuatro Cienegas, ruins, 1 (UI); (74) 4 mi. N Acatita, 3699 ft., 4 (KU); (74) Las Delicias, 1 (AMNH), 15 (FMNH); (76) 5.1 mi. SSE Bella Union, 6500 ft., 1 (TCWC).

Durango. (72) Navarro, 72 km. W, on Vergel Road, from Hidalgo de Parral, Chihuahua, 3 (UA); (72) Río Sestin, 1 (AMNH); (72) Paraje Seco, 1 (LACM); (75) 3 mi. E Conejos, 4000 ft., 2

(MSU); (75) 7 mi. N Campaña, 3750 ft., 1 (MSU); (75) 37 mi. W Mapimi, 5500 ft., 7 (MSU); (75) Cave, 10 mi. S Lerdo, 4500 ft., 2 (CAS); (75) 1 mi. N Chorro, 6450 ft., 3 (KU).

NUEVO LEON. (76) Ojo de Agua, 2.5 mi. SW Sabinas Hidalgo, 1500 ft., 2 (TCWC); (76) Villa de Garcia, 3 (UNM); (76) 4 mi. S Monterrey, 1 (UI); (76) Rancho Rodeo, 7.3 mi. S Santa Catarina, 1 (MVZ); (76) Huasteca Canyon, 17 mi. SW Monterrey, 4500 ft., 1 (TCWC); (77) Aramberri, 3600 ft., 2 (KU).

QUERÉTARO. (80) Jalpan, 3 (USNM); (80) Cadereyta, 2100 m., 3 (UMMZ); (80) 1 mi. N Peña Blanca, 1 (TCWC); (80) 8.2 mi. S Peña Blanca, 1 (TCWC).

SAN LUIS POTOSI. (79) Cave at El Salto, 1750 ft., 1 (KU); (80) 3 mi. E Río Verde, 3400 ft., 3 (TCWC).

SONORA. (25) 33 mi. W Sonoyta, 1 (UI); (25) Tajitos, Hwy. 2, (UA); (53) Pilares, 1 (UMMZ); (68) 2 mi. by rd. S Moctezuma, 1 (UNM); (68) 28 mi. by rd. E Mazatan, 1 (UNM); (68) El Novillo, on Rio Yaqui, 4 (UNM); (68) Rancho Banachari, 10 mi. N Matape, 2700 ft., 6 (MVZ); (70) 9.5 mi. W Nuri, 1 (UNM); (70) Aduana, 1 (TTU).

TAMAULIPAS. (77) San Carlos Mts., 1.5 mi. NW Tinaja, 3 (TCWC); (78) 5 mi. S Jimenez, 11 (LSU); (78) 67 km. S Cd. Victoria, vicinity Santa Isabel, Hwy. 85, 2 (TTU); (78) Acuña, 2650 ft., 3 (MSU); (79) Tula, 6 (UMMZ).

Antrozous pallidus bunkeri Hibbard

1934. *Antrozous bunkeri* Hibbard, J. Mamm., 15:227-228
1960. *Antrozous pallidus bunkeri*, Morse and Glass, J. Mamm., 41:10-15

Holotype.—University of Kansas, Museum of Natural History, no. 9302; from 7 mi. S Sun City, Barber Co., Kansas (according to Jones *et al.*, 1967, the type locality is actually 4.5 mi. S and ¼ mi. E of the center of Sun City). Type examined.

Distribution.—From Barber County, Kansas, south to the western end of the Wichita Mountains in Greer County, Oklahoma.

Diagnosis.—A relatively large (see Appendix 1), pale-colored representative of *A. pallidus*. The majority of specimens averages more than 54 in forearm length, more than 21.5 in skull length, more than 12.7 in zygomatic breadth, more than 10.0 in cranial breadth, and more than 7.0 in maxillary toothrow length. Color pale blond to uniform pale dusky brown dorsally; pale to buffy white ventrally.

Comparisons.—For comparisons with *A. p. pacificus*, *A. p. pallidus* and the subspecies described herein as new, see those accounts. From *A. p. minor*, *bunkeri* differs in larger overall size (Appendix 1) and paler coloration.

Remarks.—Populations referred to *bunkeri* are associated with outcrops of the Blaine Gypsum formation of Oklahoma and Kansas, where rocky bluffs and caverns provide suitable roosting sites. This subspecies is apparently isolated from other populations of the species by hundreds of miles of unsuitable habitat in the form of featureless prairie that is completely devoid of rocky prominences and canyons. Considerable confusion has existed regarding the geographic range of *bunkeri*. In the past 40 years various authors (Hibbard, 1934; Blair, 1939; Burt, 1945; Findley, 1954; Morse and Glass, 1960; Packard and Judd, 1968; Lechleitner, 1969; Dalquest and Roth, 1971; Armstrong, 1972) have shifted its subspecific boundary back and forth from Kansas throughout parts of Oklahoma and into Colorado and north-central Texas. Our multivariate analysis (Fig. 6) of pallid bats from east of the Continental Divide in the United States clearly shows sample 67 from the southern Great Plains (herein referred to *bunkeri*) to be significantly different from other samples in this geographic area, and for this reason we recognize it as a distinct taxon.

Two different theories can be proposed to account for the isolation and evolution of *A. p. bunkeri* in the gypsum cave region of Kansas and Oklahoma. One theory, proposed by Handley (1959) to account for an isolate of *Plecotus townsendii* in the same geographic area, suggests that bats such as *Antrozous* and *Plecotus* were distributed across the continent during the Sangamon interglacial, and, with development of the Wisconsin glacial stage, retreated southwestward as winters became colder; remnant populations were left behind in cave regions of the southern Great Plains. An alternative theory, proposed by Humphrey and Kunz (1976), postulates that the Wisconsin glacial climate of the southern Great Plains involved short summers and long winters, with moisture somewhat greater, and temperatures cooler in summer and warmer in winter than exist today. These authors postulated that bats such as *Plecotus* and *Antrozous* spread across North America during the Wisconsin glacial period when winter weather was mild and at a time when these bats did not need caves as hibernacula to survive harsh winters. Caves did not develop in the southern Great Plains until the late Wisconsin, and they were subsequently occupied by bats as refugia from the severe and otherwise intolerable post-Pleistocene winters. Populations in areas void of caves were eliminated because they could not survive the severe winters without such shelter. Assuming that *A. pallidus* is similar in certain physiological and behavioral characteristics to *P. townsendii*, the isolation of *A. p. bunkeri* from *A. p. pallidus* to the south and west occurred during Holocene times; thus *bunkeri* is much younger than previously suspected.

The status of *A. p. bunkeri* is presently unknown. Twente (1955) estimated the number of bats of this subspecies in Barber County, Kansas, and adjacent Woods County, Oklahoma, to be between 200 and 400. The "Natural Bridge" south of Sun City, which is the type locality, collapsed in 1962, and no specimens have been taken there in recent years; also, local ranch hands "burned out" the colony at May Cave in Barber County, and several subsequent visits there and to a nearby barn produced only one living pallid bat (Jones *et al.*, 1967).

Specimens examined (152).—KANSAS. (67) *Barber Co.*: Natural Bridge Cave, 4-7 mi. S Sun City, 3 (FMNH), 87 (KU), 2 (MSU), 4 (MVZ), 2 (TCWC), 1 (TTU), 4 (UMMZ), 6 (USNM); (67) Aetna, May's Cave and vicinity, 4 (KU), 2 (LACM), 13 (MHP), 4 (TNHC), 2 (UMMZ), 1 (UNM), 3 (USNM), 1 (UU).

OKLAHOMA. (67) *Woods Co.*: Owl Cave, Alabaster Caverns State Park, 6 (CU), 7 (USNM).

Antrozous pallidus minor Miller

1902. *Antrozous minor* Miller, Proc. Acad, Nat. Sci., Philadelphia, 54:389.

1951. *Antrozous pallidus minor,* Goldman, Smithsonian Misc. Coll., 115:356.

Holotype.—U.S. National Museum, Biological Survey Collection, no. 79096; from Comondú, Baja California. Type examined.

Distribution.—From southern Baja California northward through the Colorado Desert of southeastern California and southwestern Arizona, and thence northward into southern Nevada.

Diagnosis.—A relatively small (see Appendix 1), dark-colored representative of *A. pallidus*. Mean forearm length varying from 49.6 to 51.9 in 11 samples; mean length of skull in the same samples varying from 19.8 to 20.5; mean zygomatic breadth varying from 11.7 to 12.2; and mean length of maxillary toothrow varying from 6.4 to 6.8. Color variable, from pale dusky brown, with brownish overhairs, to strongly blond and bright with dark overhairs.

Comparisons.—For comparisons with other subspecies, see accounts thereof.

Remarks.—Hall (1981:237) restricted the distribution of *minor* to the lower half of the Baja Peninsula. Our multivariate analysis of the western samples of *pallidus* (Fig. 7) revealed that Baja samples together with those from southeastern California, southwestern Arizona, and southern Nevada (Group I in Fig. 7; herein referred to *minor*) form a close, cohesive grouping that is markedly differentiated from samples from central Arizona, western Nevada, and southern California (Group II in Fig.7; herein referred to *pallidus*).

The range of *minor* approaches that of *pallidus* in San Diego County, California, where the two subspecies occur within 16 miles of one another. The morphological differences between them are such that it appears intergradation either does not occur or is extremely reduced. There is virtually no overlap in external and cranial measurements between *minor* (sample 22) and *pallidus* (sample 12); however, the sample size for the latter is much smaller in comparison to the former (Appendix 1). Evidence of intergradation between *minor* and *pallidus* is much more extensive in other geographic regions and is evident in specimens from samples where their ranges contact one another in southern Nevada (sample 18), central Arizona (samples 37, 38, and 39), and southern Arizona (samples 40 and 42). Specimens of *minor* from the type locality and throughout southern Baja are much brighter and darker in dorsal coloration than are those from California and Arizona.

A. p. minor probably evolved from a Pleistocene isolate of *pallidus* in southern Baja California. During the late Pliocene, pallid bats probably occupied the desert woodland and scrub habitats of northeastern Baja. At times of glacial maxima during the Pleistocene, temperatures in Baja became lowered, humidity increased, and desert environments were replaced by sage scrub and chaparral communities in the southern Cape region (Savage,1960). Subhumid coniferous woodlands expanded in the northwest coastal and montane area and oak woodland-chaparral communities dominated the entire central peninsula (Savage, 1960). Desert faunal elements, such as *A. pallidus*, probably survived in these isolated, marginal thorn scrub or chaparral refugia in the Cape region. At the heights of glacial recession, desert conditions were reconstituted from these marginal communities and desert elements expanded their range northward to include the Colorado, Arizona, and Sonora desert areas (Savage, 1960).

Specimens examined (203).—Arizona. *Maricopa Co.*: (35) 1 mi. W Aguilla, 6 (UI); (35) 4 mi. SE Wickenburg, 4 (UI); (35) 13.5 mi. S, 3.5 mi. W Aquilla, 3 (UI). *Mohave Co.*: (23) Old Clark Ranch barn, 6 mi. N Kingman, 3 (UA); (23) 1 mi. S Kingman, 3600 ft., 2 (TCWC), 1 (UA); (23) Twin Mills, 5 mi. SE Kingman, 7 (UI); (23) Fort Mohave, 1 (USNM). *Pima Co.*: (25) 10 mi. N Ajo, 1 (UA); (25) Bates Well, Organ Pipe Cactus National Monument, 1 (UI); (25) Papago Well, 1 (UI); (41) 11.5 mi. E, 1 mi. N Topawa Reservoir, 10 (UI); (41) Elkhorn Ranch, Sabino Canyon, 23.5 mi. N Sasabe, 7 (UI); (41) Garcias' Represso, 2 mi. E Sasabe, 1 (UA); (41) Leach Lake, Sasabe, 1 (UA). *Yavapai Co.*: 9 mi. N Wenden, 12 (UI); (35) Kearnsey Moore Mine, N side Harquahala Mts., 10 mi. E Wenden, 5 (UI); (35) Carmelita Mine, S side Harquala Mts., 12 mi. ESE Wenden, 2 (UI); (24) Mohare Wash, 14 mi. S, 5 mi. E Ehrenburg, 1 (UI); (24) Castle Dome Mts., 1 (UA); (24) Yuma, 1 (UA), 2 (USNM); (25) Tinajas Altas, 4 (CAS).

California. *Imperial Co.*: (22) Kane Springs, 3 (LACM); (24) Palo Verde, 1 (LACM); (24) 15 mi. S, 4 mi. E Palo Verde, 5 (LACM); (24) 8 mi. E Picacho, Colorado River, 1 (MVZ). *Inyo Co.*: (18) Furnace Creek Ranch, Death Valley, -198 ft., 2 (MVZ). *Riverside Co.*: (23) Riverside Mts., 35 mi. N Blythe, 1 (KU); (23) N end McCoy Mts., 3 (LACM). *San Bernadino Co.*: (20) Ivanpah, 2 (USNM); (20) 2.5 mi. SW Kelso, 2100 ft., 1 (MVZ); (23) Earp, 3 (LACM). *San Diego Co.*: (22) 11 mi. S, 1.5 mi. E Borrego Springs, 11 (MVZ); (22) Vallecito, 6 (MVZ); (22) Vallecito Stage Station, 1500 ft., 1 (MSU), 2 (MVZ); (22) Agua Caliente Spring, 3 (MSU).

Nevada. *Clark Co.*: (20) Corn Creek Ranch, 26 mi. N Las Vegas, 1 (USNM); (20) Corn Creek, 1 (MVZ). *Nye Co.*: (18) 6 mi. N Beatty, 3400 ft., 2 (TCWC); (18) Ash Meadows, 2.5 mi. W Devil's Hole, 2173 ft., 9 (MVZ).

Baja california. (13) Mina la Fortuna, 2 mi. N Laguna Seca Chapala, 2350 ft., 8 (MVZ); (13) El Barril, 1 (UA); (82) San Ignacio, 500 ft., 1 (MVZ); (82) Santa Rosalillito, SE end Bahia de Concepción, 25 ft., 3 (MVZ); (82) Comondú, 5 (USNM); (83) El Carrizalito, 5 mi. N Santiago, 1400 ft., 29 (MVZ); (83) Miraflores, 225 m., 2 (AMNH), 8 (KU), 2 (MVZ); (83) Santa Anita, 1 (USNM); (83) San Lucas, 8 (USNM).

Antrozous pallidus packardi, new subspecies

Holotype.—Adult female, skin and skull, Museum of Natural History, University of Kansas no. 103684; 12 mi. W Encarnación de Diaz, 5600 ft., Jalisco, obtained on 5 October 1965 by P. L. Clifton, original number 9544. The holotype skin is in excellent condition. The skull and mandible are in good condition except that the left auditory bulla is detached from the skull.

Distribution.—Along the western slopes of the Sierra Madre Occidental in southwestern Zacatecas, Jalisco, northeastern Nayarit and southern Sonora.

Diagnosis.—A relatively large (see Appendix 1), dark-colored representative of *A. pallidus*. Selected measurements of the holotype are length of forearm, 55.4; greatest length of skull, 22.4; postorbital constriction, 3.9; zygomatic breadth, 13.2; cranial breadth, 10.2; length of palate, 7.8; length of maxillary toothrow, 7.2; width across molars, 8.2; length of mandible, 15.6; length mandibular toothrow, 8.1; and depth of cranium, 9.1. The majority of specimens averages more than 55 in forearm length, more than 21.5 in skull length, more than 12.5 in zygomatic breadth, more than 10 in cranial breadth, and more than 7 in maxillary toothrow length. Dorsal coloration is blond and bright, usually with dark overhairs; ventral coloration is strongly blond, sometimes with a brownish tinge.

Comparisons.—*A. p. packardi* approaches *pacificus* in size and color, but differs in having a shorter and narrower skull (see measurements in Appendix 1) and is not as strongly blond or dark in dorsal coloration. Compared with *pallidus* from México, *packardi* is significantly larger in all external and cranial measurements, and the sagittal crest is much more prominent. Compared with *bunkeri*, *packardi* is similar in size (Appendix 1) but much darker in coloration. Compared with *minor*, *packardi* is larger in external and cranial measurements (Appendix 1), but not noticeably different in color from representatives of *minor* from Baja California.

Remarks.—Characters of this subspecies are best developed in those bats occupying the Sierra Madre Occidental in Zacatecas, Jalisco, and Nayarit. In Jalisco the subspecies is reported to prefer dry, open, upland areas where there is a permanent source of water (Watkins *et al.*, 1972). Pallid bats have not been recorded from Sinaloa, although Hall (1981:237) and Villa-R. (1967) included the northern half of this state within the probable range of the species. If pallid bats do occur along the western slope of the Sierra Madre Occidental in Sinaloa, they likely are referable to *packardi*.

Five specimens from the lowlands near Guaymas, Sonora, appear to be intergrades of *packardi* and *pallidus*. They resemble *packardi* in having a mean zygomatic breadth greater than 12.5, a mean cranial breadth of more than 10.0, and a mean maxillary toothrow of more than 7.0. They resemble *pallidus* in having a mean forearm length of 53.7 and a mean greatest skull length of 21.2. Overall, they resemble *packardi* more than they do *pallidus* and are herein referred to the former subspecies. Pallid bats from the mountainous slopes of central Sonora (samples 68, 70) are clearly nearer *pallidus* than *packardi* in characteristics (note the position of these samples in the graph in Fig. 8). On the southern edge of the Mexican Plateau the nearest known specimens of *pallidus* to any of *packardi* are from northern Querétaro, which is more than 150 miles east of the type locality of *packardi* in Jalisco. Pallid bats have not been collected in the intervening area and, hence, it is difficult to determine the eastern limits of the range of *packardi*, as well as determining if and where intergradation occurs between *packardi* and *pallidus* in southern México. The Querétaro specimens of *pallidus* are noticeably smaller than those of *packardi* and there is no overlap between the two in most measurements.

A. p. packardi probably evolved from a Pleistocene isolate of *pallidus* in southwestern México. The Sierra Madre Occidental is not continuous in this area; instead, low passes and a gradual slope from the Mexican Plateau to the lowlands allow faunal interchange between the lowlands of the Pacific coast and the plateau. Pallid bats probably traversed these dispersal routes to establish populations in western Jalisco and Nayarit. The major climatic shifts that took place in southwestern México in the Pleistocene caused the elevational depression of temperate habitats, perhaps as much as 1000 meters, during glacial stages so that a coniferous forest, characterized by mesic and pluvial conditions, was continuous over most of the Sierra Madre Occidental (Duellman, 1965). The vertical shifts in climate and vegetation during this time would have closed dispersal routes for pallid bats and effectively isolated those populations along the coastal slopes of the Sierras from those inhabiting the Mexican Plateau. With the onset of drier, xeric conditions during postglacial times the dispersal routes gradually reopened and pallid bats dispersed eastward toward the plateau.

Etymology.—*A. p. packardi* is named for the late Robert L. Packard in recognition of his research on mammals in the southwestern United States and México.

Specimens examined (17).—SONORA. (69) Bahia de San Carlos, N Guaymas, 1 (LACM); (69) 2 km. SW Maytorena, NE Guaymas, 4 (LACM). NAYARIT. (84) Rancho Viejo, 13 km. SW Santa Teresa, 1 (USNM); (84) Arroyo Taberna, 2 mi. WNW Mesa del Nayar, 4900 ft., 1 (USNM). ZACATECAS. (84) 18 km. N San Juan Capistrano, 1100 m., 1 (MSU); (84) 5 km. NE San Juan Capistrano, 1330 m., 1 (MSU). JALISCO. (81) 12 mi. W Encarnación de Diaz, 5600 ft., 2 (KU); (81) 1.5 mi. WNW Amatitan, 4100 ft., 1 (KU); (81) Santa Cruz del Valle, Guadalajara, 5 (AMNH).

Antrozous pallidus koopmani Orr and Silva Taboada

1960. *Antrozous koopmani* Orr and Silva Taboada, Proc. Biol. Soc. Washington, 73:83-86.

Holotype.—California Academy Sciences, no. 11846; from Cueva del Hoyo Garcia, Municipio de San Juan y Martinez, Provincia de Pinar del Rio, Cuba. Type examined.

Distribution.—Known only from six scattered localities on the island of Cuba.

Diagnosis.—Size large compared with that of mainland subspecies of *A. pallidus*. Characterized by long tail (greater than 55 mm); large skull (greatest length more than 23 mm and zygomatic breadth more than 12.9); long maxillary toothrow (greater than 7.6); well-developed sagittal crest; proportionately large temporal and orbital fossae resulting from elongation of the cranium rather than the rostrum.

Comparisons.—From *A. p. pacificus*, *koopmani* differs in having a considerably longer skull, a shorter width across molars, and a much shorter mandible (Table 4).

A. p. koopmani averages larger than *A. p. minor* and *A. p. pallidus* in all external and cranial measurements. There is no measurement overlap between *koopmani* and *minor* in skull length, length of maxillary toothrow, and length of mandibular toothrow. There is no measurement overlap between *koopmani* and *pallidus* in skull length (Table 4).

From *A. p. bunkeri*, *koopmani* averages larger in all measurements except width across molars, postorbital constriction, cranial breadth, and length of mandible. Measurement overlap does not occur in skull length and length of maxillary toothrow (Table 4).

From *A. p. packardi*, *koopmani* averages larger in all measurements except length of mandible, with measurement overlap lacking in total

TABLE 4.—*Selected measurements for subspecies of* Antrozous pallidus. *Mean, followed by one SD, extremes in parentheses, and N (in column for* A. koopmani *only). The English translation of the cranial variates measured by Silva Taboada (1976, 1979) appear parenthetically with the stub headings below. See materials and methods section for definition of variates measured.*

Variate	*A. p. bunkeri* N=26	*A. p. minor* N=121	*A. p. pacificus* N=151	*A. p. packardi* N=15	*A. p. pallidus* N=505	*A. p. koopmani*
Total length	119.42±6.74(106-129)	112.00±5.27(98-125)	117.98±6.36(101-135)	119.36±3.32(113-124)	112.36±5.85(92-135)	125.50(125-126)2
Tail length	48.04±3.85(40-56)	45.27±3.87(34-58)	43.07±4.90(35-56)	48.45±4.32(41-54)	44.42±3.90(28-58)	55.50(55-56)2
Hind foot length	13.76±1.45(11-19)	11.77±0.89(10-13)	13.89±1.45(10-19)	12.27±1.62(10-15)	11.90±1.56(7-16)	13.85(13.1-14.6)2
Ear length	28.23±1.61(26-31)	29.41±2.15(25-34)	29.63±1.79(24-34)	30.09±1.44(28-33)	28.30±2.61(25-35)	31.00(31-31)2
Forearm length	54.20±2.04(49.35-58.30)	50.50±1.71(45.50-55.60)	56.68±2.03(52.30-64.30)	54.79±1.59(52.20-57.50)	52.88±2.06(47.10-58.60)	56.70(54.90-58.50)2
Greatest length of skull (occipito-incisive length)	21.56±0.55(20.60-22.55)	20.18±0.52(18.75-21.70)	22.82±0.59(21.55-24.35)	21.52±0.59(20.90-22.55)	20.52±0.62(18.70-22.65)	23.30(23.00-23.60)2
Zygomatic breadth (zygomatic width)	13.03±0.38(12.40-13.70)	11.92±0.34(10.75±12.95)	13.37±0.36(12.50-14.35)	12.82±0.44(12.30-13.65)	12.26±0.36(11.25-13.75)	13.40(12.90-14.10)5
Length maxillary toothrow (canine-molar length, upper)	7.12±0.16(6.85-7.40)	6.65±0.19(6.20-7.10)	7.69±0.26(7.15-8.45)	7.18±0.20(6.90-7.50)	6.78±0.28(6.05-7.65)	7.80(7.6-8.0)3
Width across molars (molar width)	8.32±0.28(7.70-8.80)	7.59±0.24(6.90-8.15)	8.50±0.26(7.80-9.35)	8.14±0.22(7.80-8.55)	7.84±0.30(7.10-8.65)	8.30(8.10-8.40)5
Mandibular length	15.16±0.35(14.40-15.80)	14.20±0.36(13.15-15.25)	16.22±0.48(15.05-17.50)	15.28±0.31(14.75-15.75)	14.41±0.49(12.55-16.20)	15.10(14.90-15.30)2
Postorbital constriction (postorbital width)	4.05±0.14(3.70-4.30)	3.71±0.17(3.25-4.10)	4.11±0.16(3.70-4.50)	3.89±0.11(3.75-4.10)	3.89±0.17(3.40-4.35)	3.96(3.80-4.20)5
Cranial breadth (mastoid width)	10.54±0.26(10.00-10.90)	9.48±0.26(8.80-10.10)	10.69±0.32(9.30-11.45)	10.08±0.28(9.75-10.85)	9.78±0.31(8.70-10.80)	10.52(10.00-11.00)4
Length mandibular toothrow (canine-molar length, lower)	8.10±0.17(7.80-8.55)	7.46±0.20(7.00-7.90)	8.58±0.30(8.00-9.55)	7.97±0.31(7.65-8.30)	7.60±0.30(6.40-8.50)	8.60(8.50-8.70)2

length, tail length, skull length, length of maxillary toothrow, and length of mandibular toothrow (Table 4).

Remarks.—Antrozous koopmani was described from a single skull lacking mandibles taken from a cave in the Pinar del Rio Province of western Cuba (Orr and Silva Taboada, 1960). The skull was described by Orr and Silva Taboada as large but with proportionally small teeth when compared with *A. pallidus*. The combined temporal and orbital fossae were diagnosed as proportionately large resulting from elongation of the cranium rather than the rostrum, and the sagittal crest was described as well developed.

Subsequently, Silva Taboada (1976) discovered nine additional specimens from western and eastern Cuba, including two live adult females as well as other specimens recovered from owl pellets. Although we have not examined Silva Taboada's specimens, which are deposited in the Institute of Zoology, Academy of Sciences of Cuba, his elaborate descriptions of the external and cranial features of *koopmani* as well as the inclusion of a list of selected measurements (many of which are identical to those we took for *A. pallidus*) have allowed us to make additional detailed comparisons of *A. koopmani* and *A. pallidus*.

The general description of the external appearance (including color), skull, and teeth of *A. koopmani* given by Silva Taboada (1976, 1979) is virtually identical to that given earlier in this paper for *A. pallidus*. *A. koopmani* has two lower incisors on each side of the lower jaw that are essentially similar to those of *A. pallidus* in structure, placement, and proportions, and this confirms its inclusion in *Antrozous* instead of *Bauerus*. Comparisons of the skulls of representative specimens of the subspecies of *A. pallidus* with published photographs of the skull of *A. koopmani* (Silva Taboada, 1979; plates 3-5K, 6-7H) revealed no obvious differences in the shape or proportions of the cranium or lower jaw between these two taxa. The size and shape of the sagittal crest is well developed in *A. koopmani*, but this structure shows no greater development than that of medium-sized *A. pallidus* from the southwestern United States. Because both live specimens of *koopmani* were females, nothing is known of the penis or baculum.

Apparently, the major distinction between *koopmani* and *pallidus* is the larger size of the former which, according to Orr and Silva Taboada (1960), greatly exceeds that of *A. p. pallidus* and even that of the largest individuals of *A. p. pacificus*. Silva Taboada (1976) noted in particular that the length of the tail in *koopmani* was considerably longer than the published measurements of this character for *A. pallidus*.

We compared the mean and extreme for 13 of Silva Taboada's (1976, 1979) external and cranial measurements of *A. koopmani* with the mean and extremes of the same measurements for 818 adult specimens of the five nominal subspecies of *A. pallidus* recognized herein (Table 4). *A. koopmani* averages larger than all subspecies of *pallidus* in eight of 13 measurements, namely total length, length of tail, length of ear, length of forearm, greatest length of skull, zygomatic breadth, length of maxillary toothrow, and length of mandibular toothrow. However, in all 13 measurements the extremes of variation in specimens of *koopmani* are encompassed within the extremes of at least one of the subspecies of *pallidus*. The measurements of *koopmani* fall within the range of measurements for all 13 characters of *A. p. pacificus*, for 12 characters of *A. p. pallidus*, for 11 characters of *A. p. bunkeri*, for eight characters of *A. p. packardi*, and for nine characters of *A. p. minor*. These results indicate that *koopmani* is most similar in size to *A. p. pacificus*, which is the largest of the subspecies of *A. pallidus*. With the exception of length of tail (in which only one specimen examined of *pacificus* has a tail length that reaches 56) and length of the mandible, there is considerable overlap in the measurements of *koopmani* and *pacificus*. Only two specimens of *pacificus* have mandibular lengths that are less than 15.3, which is the upper limit of this measurement in *koopmani*.

The results of our comparisons indicate that *A. koopmani* is much less distinct from *A. pallidus* than previously suspected. The size differences between the two taxa are of a magnitude that are generally characteristic of subspecific rather than specific distinctions. For this reason, we herein arrange *koopmani* as a subspecies of *A. pallidus*, even though it is separated by over 900 miles, most of which are across the Gulf of México, from the nearest populations of *A. pallidus*. The classification of allopatric populations is often subject to considerable disagreement among taxonomists. In such cases it is difficult to apply a modern biological species concept. Mayr (1969) discusses the different philosophies of classifying allopatric populations and proposes some rules that can be used to describe their taxonomic status, one of which is the amount of morphological difference between the most divergent subspecies of a species as an indicator of how much morphological difference may evolve without acquisition of reproductive isolation. Application of this criterion reveals that the morphological distinctions between *A. koopmani* and *A. pallidus* are of no greater magnitude than are the differences between the two most divergent subspecies of *pallidus* (*A. p. minor* and *A. p. pacificus*; see Table 4).

Based on accounts by Silva Taboada (1976, 1979), *A. p. koopmani* is one of the rarest bats in Cuba. Only three specimens have been taken alive: two obtained by C. T. Ramsden in Guantanamo in 1920 under unknown circumstances and one captured (that subsequently escaped) by Silva Taboada and K. F. Koopman in Pinar del Río in 1956. The other specimens were recovered from owl pellets and fossil excavations. Specimens have been documented from both eastern and western Cuba, suggesting that the species is uniformly distributed over the island.

Orr and Silva Taboada (1960) speculated that the genus *Antrozous* could have arrived in Cuba originally from Yucatan, from which the island presently is separated by about 125 miles of water. However, no bats of the genus *Antrozous* have been taken on the Yucatan Peninsula nor south of a point 550 miles north of the Isthmus of Tehuantepec. Recent discoveries of *A.* (*Bauerus*) *dubiaquercus* in southern Veracruz (Pine, 1966, 1967) and in Honduras (Pine *et al.*, 1971) show that *A. p. koopmani* occurs closer geographically to *A. dubiaquercus* than to *A. pallidus*. Baker and Genoways (1978) made no comment on the zoogeographic status of *koopmani* other than "its ancestors evidently reached Cuba from the west."

Records of occurrence (from Silva Taboada, 1979).—*Pinar del Río:* Consolación del Norte; San Juan y Martinez. *La Habana*: Caimito del Guayabal; Jaruco; San Antonio de los Baños. *Oriente*: Caney; Guantanamo.

Comments on *Bauerus dubiaquercus*

Antrozous dubiaquercus was named by Van Gelder (1959) on the basis of specimens from the Tres Marias Islands, Nayarit, and placed into a separate subgenus (*Bauerus*) from other species in the genus. This species is similar to *A. pallidus*, but is dark brown, has shorter, narrower ears, and usually has an additional set of spicule-like lower incisors. Pine (1966, 1967) described *A. meyeri* from Veracruz and Honduras, but it was subsequently reduced to subspecific status under *dubiaquercus* (Pine *et al.*, 1971).

Comments.—White (1969) proposed that *Bauerus* be recognized as a separate genus from *Antrozous* based on the presence of an extra lower incisor in *dubiaquercus*. Pine *et al.* (1971) noted that the presence of a third lower incisor in *Bauerus* is not constant and proposed that *Antrozous* and *Bauerus* are best arranged as subgenera. Pine *et al.* (1971) also noted that the two species share several penile characteristics not found in other New World vespertilionids, indicating that *Antrozous* is a monophyletic taxon. Engstrom and Wilson (1981), primarily on the basis of differences in the karyotype of *dubiaquercus* (2N=44; FN=52) and *pallidus* (2N=46; FN=50), arranged *Bauerus* as a distinct genus, noting that intrageneric karyotypic variation in vespertilionid bats is uncommon. We have examined several specimens, including complete skeletons of *A. dubiaquercus*, and offer the following comparisons with *A. pallidus*, which bear on the systematic relationships of these species.

Pine *et al.* (1971) described the penes of *A. pallidus* and *A. dubiaquercus* using organs extracted from dry study skins. Subsequently, we have examined the phalli of both of these species from fluid-preserved specimens and have recorded additional characteristics not previously noted. The penis of *pallidus* is an unusual trilobate, hairy structure with the distal third exhibiting a large degree of lateral expansion and dorsoventral compression (Fig. 11). A dorsally exposed urethral canal also is present, which was not mentioned by Pine *et al.* (1971) and, to our knowledge, this characteristic has not been reported previously in the order Chiroptera. The penis of *dubiaquercus* is structured on the same general plan as that of *pallidus*, but it is much narrower and with a much less flattened median area (Fig. 11). There is some expansion of the distal tract, but distinct lobes are not present as in *pallidus*. The organ is nearly twice as long as wide in *dubiaquercus*, whereas the length and greatest width measure approximately the same in *pallidus*. The penis of *dubiaquercus* is distinctly more pubescent than that of *pallidus*. A dorsally exposed urethra is also evident in *dubiaquercus*, but the

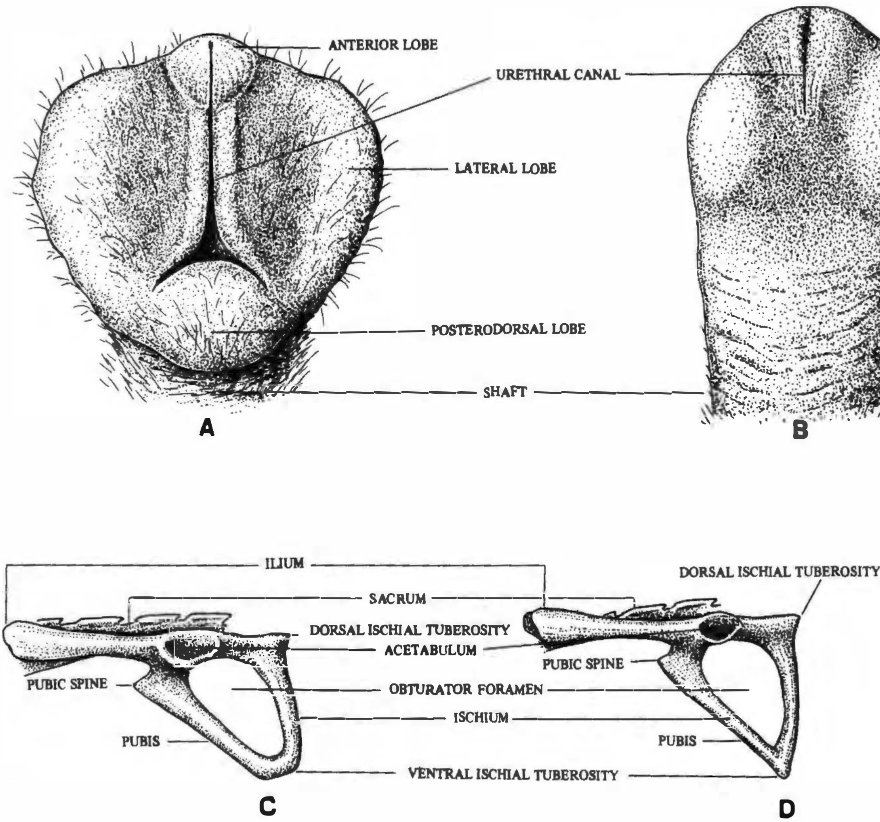

FIG. 11.—(A) Dorsal view of the penis of *Antrozous pallidus*. Note the urethral canal which opens dorsally. (B) Dorsal view of the penis of *A. (Bauerus) dubiaquercus* (AMNH 180840). (C) Lateral view of the left side of the pelvis of *A. pallidus*. (D) Lateral view of the left side of the pelvis of *A. (Bauerus) dubiaquercus*.

exposed portion of the structure is less than half the length of the exposed urethra in *pallidus*.

The pelvic girdles of *dubiaquercus* and *pallidus* compare favorably with those of other vespertilionid bats (see Vaughan, 1970), but there are some differences betweeen the two species. In *pallidus*, the ventral tuberosity of the ischium is somewhat flattened, the pubis is quite stout, and the pubic spine is pronounced; in *dubiaquercus*, the pubis is comparatively thinner and lighter, the ventral tuberosity is distinctly pointed, and the pubic bone is less pronounced (Fig. 11). The differences in the structure of the pelvic girdle of the two species might reflect adaptations associated with the peculiar terrestrial feeding habits of *A. pallidus*, with its more robust pelvis providing a slightly greater increase in the areas for muscle attachment along the lateral surface of the pelvis. Similarly, White (1969) related the "bulldog-like" upturning of the cheek teeth in *dubiaquercus* in contrast to the downturning in *pallidus* to feeding strategy with *dubiaquercus* possibly taking food exclusively in flight using the "bulldog" effect to obtain a stronger hold on larger insects. Unfortunately nothing is known of the food habits of *dubiaquercus* so possible adaptations relating to described skeletal differences remain merely hypotheses. However, it is well known that *pallidus* alights on the ground to capture insect prey (Barbour and Davis, 1969).

Differences between *dubiaquercus* and *pallidus* in the structure of the pelvic girdle and cheekteeth suggest that the two species may exploit different feeding strategies. Furthermore, examination of the phalli of fluid-preserved specimens reveals additional differences between them not previously reported by Pine *et al.* (1971). These differences, together with the chromosome differences between the two species, are approximately of the same magnitude as those found among most genera of vespertilionid bats. Hence, we agree with White (1969) and Engstrom and Wilson (1981) that *Bauerus* is best considered a genus distinct from *Antrozous*.

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APPENDIX 1.—Mean external and cranial measurements for 84 samples of five subspecies of *Antrozous pallidus*. See text for abbreviations of measurements and see Fig. 2 for sample localities.

Sample (N)	FOR	GSL	IC	ZB	CB	PL	MXTR	WAM	MNL	MNTR	CD
Antrozous pallidus pacificus											
5(7)	56.51	22.13	4.08	13.04	10.47	7.96	7.41	8.27	15.65	8.15	9.20
6(26)	55.10	22.51	4.08	13.15	10.39	8.10	7.55	8.35	15.82	8.41	9.12
7(54)	56.41	22.65	4.10	13.27	10.73	8.11	7.59	8.44	16.09	8.46	9.37
8(27)	57.24	23.49	4.14	13.72	10.94	8.63	7.95	8.66	16.70	8.85	9.57
9(20)	57.93	23.32	4.19	13.55	10.87	8.58	7.87	8.70	16.48	8.83	9.54
10(39)	55.45	22.30	4.13	13.15	10.51	8.15	7.48	8.32	15.76	8.40	9.19
11(45)	57.52	22.92	4.09	13.46	10.64	8.39	7.80	8.50	16.36	8.72	9.36
Antrozous pallidus pallidus											
1(19)	53.17	21.12	4.02	12.37	9.97	7.66	7.04	8.02	14.88	7.88	8.71
2(5)	53.75	21.67	4.12	12.55	9.96	7.80	7.15	8.15	15.16	7.96	8.79
3(3)	50.95	—	4.00	12.48	—	7.40	7.00	8.30	14.70	7.98	—
4(5)	56.01	21.33	3.94	12.71	10.38	7.62	7.28	8.20	15.26	8.06	9.01
16(6)	53.46	21.08	3.97	12.59	10.02	7.53	7.13	7.94	14.90	7.88	8.72
17(22)	53.71	20.92	3.81	12.30	9.77	7.62	7.01	8.00	14.63	7.82	8.84
19(9)	54.44	21.59	3.98	12.82	10.14	7.86	7.34	8.18	15.34	8.16	8.92
21(14)	52.51	20.88	3.87	12.38	9.88	7.53	6.98	7.91	14.61	7.76	8.80
12(4)	56.16	22.08	3.98	12.83	9.88	7.91	7.25	8.29	15.35	8.18	8.93
14(22)	54.25	21.46	3.92	12.66	10.06	7.84	7.22	8.14	14.98	8.01	9.21
15(6)	53.54	21.26	3.73	12.50	9.90	7.78	7.13	8.03	15.19	8.02	8.66
26(6)	55.58	21.15	3.96	12.67	10.03	7.57	7.10	8.43	15.16	8.17	8.93
27(8)	55.26	21.41	3.90	12.48	9.92	7.73	7.21	8.15	15.11	8.15	9.05
28(8)	52.86	20.69	3.82	12.26	9.66	7.75	6.79	7.79	14.34	7.68	9.16
30(5)	55.19	20.83	3.84	12.30	9.75	7.92	6.95	8.01	14.61	7.79	8.97
29(7)	53.60	20.76	3.71	12.05	9.54	7.53	6.91	7.86	14.39	7.75	8.70
31(3)	53.60	20.23	3.80	11.80	9.53	7.35	6.78	7.85	14.23	7.60	8.45
32(7)	54.48	20.99	3.83	12.26	9.94	7.85	7.06	8.10	14.73	7.89	8.70
33(9)	54.02	20.79	3.87	12.13	9.68	7.56	6.98	7.96	14.61	7.81	8.68
34(42)	54.49	20.79	3.81	12.43	9.83	7.58	6.90	7.95	14.66	7.80	8.85
36(7)	52.45	20.33	3.91	12.07	9.71	7.43	6.91	8.01	14.36	7.76	8.66
37(9)	52.04	20.23	3.93	12.28	9.68	7.27	6.72	7.66	14.24	7.54	8.81
38(16)	51.95	20.37	3.81	12.14	9.71	7.35	6.70	7.84	14.37	7.54	8.70
39(17)	52.81	20.33	3.88	12.05	9.65	7.24	6.73	7.75	14.29	7.66	8.67
40(16)	52.71	20.43	3.82	12.17	9.73	7.13	6.61	7.79	14.30	7.47	8.71
43(21)	52.17	20.36	3.89	12.18	9.73	7.28	6.64	7.71	14.28	7.45	8.71
42(30)	52.65	20.57	3.83	12.38	9.83	7.34	6.71	7.90	14.48	7.56	8.78
44(16)	54.44	20.93	3.92	12.31	9.78	7.66	7.09	8.08	14.78	7.88	8.98
45(6)	55.67	21.01	4.04	12.48	10.07	7.52	7.15	8.30	15.05	8.02	8.82
46(5)	54.65	20.65	3.84	12.41	9.98	7.55	6.89	8.12	14.64	7.80	8.94
66(8)	53.33	20.54	3.90	12.31	9.89	7.37	6.84	8.04	14.59	7.77	8.76
47(93)	54.54	20.73	3.96	12.40	9.97	7.44	6.92	8.05	14.59	7.77	8.94
65(8)	53.04	20.70	4.06	12.58	9.94	7.48	6.87	8.11	14.73	7.78	8.92
48(46)	53.15	20.50	3.97	12.29	9.90	7.27	6.77	7.89	14.43	7.60	8.85
49(32)	53.51	20.58	3.98	12.32	9.91	7.46	6.85	7.98	14.48	7.68	8.95
50(19)	53.04	20.65	3.91	12.28	9.81	7.38	6.76	7.93	14.40	7.59	8.85
51(16)	53.07	20.48	3.94	12.11	9.76	7.21	6.72	7.70	14.31	7.57	8.81

Appendix 1.—*Continued.*

52(22)	51.95	20.28	3.94	12.20	9.76	7.13	6.61	7.73	14.26	7.41	8.83
53(41)	51.93	20.34	3.94	12.27	9.77	7.21	6.66	7.78	14.28	7.48	8.80
54(8)	53.75	20.10	3.92	12.32	10.10	7.40	6.75	8.02	14.60	7.75	8.20
55(19)	52.86	20.34	3.90	12.19	9.74	7.15	6.71	7.84	14.29	7.46	8.69
56(6)	52.39	19.98	3.84	12.16	9.57	7.13	6.59	7.73	14.17	7.43	8.63
64(6)	53.42	20.68	3.91	12.79	10.00	7.35	6.94	8.28	14.85	7.83	8.76
58(17)	52.65	20.26	3.87	12.05	9.64	7.17	6.57	7.63	14.23	7.38	8.61
57(14)	52.92	20.30	3.98	12.25	9.79	7.03	6.65	7.88	14.16	7.48	8.80
59(26)	52.15	20.18	3.87	12.05	9.70	7.19	6.55	7.65	14.03	7.38	8.64
60(17)	50.89	19.85	3.82	11.86	9.46	7.01	6.50	7.49	13.61	7.27	8.72
62(23)	49.40	19.75	3.85	12.02	9.38	6.97	6.54	7.57	13.95	7.35	8.59
63(13)	52.40	20.66	3.87	12.48	9.86	7.37	6.81	7.80	14.47	7.63	8.64
61(92)	50.84	19.70	3.79	11.85	9.45	6.92	6.45	7.47	13.81	7.21	8.50
68(12)	51.79	20.70	3.88	12.57	9.95	7.22	6.82	7.93	14.53	7.66	8.74
70(4)	52.18	20.49	3.86	12.30	9.66	7.20	6.81	7.80	14.44	7.56	8.66
71(5)	51.76	20.29	3.80	12.10	9.84	7.16	6.60	7.64	14.24	7.45	8.83
72(24)	52.11	20.48	3.90	12.23	9.77	7.21	6.71	7.75	14.27	7.53	8.82
73(13)	52.67	20.41	3.89	12.34	9.69	7.18	6.80	7.93	14.20	7.64	8.89
74(30)	52.99	20.55	3.92	12.28	9.66	7.06	6.76	7.84	14.19	7.51	8.80
75(13)	51.66	20.07	3.90	12.10	9.61	7.14	6.63	7.45	14.13	7.49	8.80
76(8)	51.93	20.18	3.89	12.08	9.68	6.67	6.58	7.59	14.11	7.34	8.91
77(5)	53.81	20.66	3.99	12.29	9.80	7.16	6.80	7.74	14.35	7.60	9.03
78(17)	51.69	20.37	4.02	12.25	9.73	6.85	6.69	7.50	14.18	7.33	8.85
79(6)	54.44	20.67	4.08	12.10	9.77	6.95	6.76	7.71	14.28	7.49	8.83
80(8)	54.15	20.34	4.08	12.08	9.71	7.36	6.75	7.70	14.32	7.71	8.61
					Antrozous p. bunkeri						
67(95)	54.48	21.69	4.04	13.11	10.57	7.74	7.13	8.37	15.28	8.14	9.11
					Antrozous p. packardi						
81(5)	56.01	21.80	3.86	12.90	10.11	7.69	7.34	8.16	15.45	8.18	8.91
84(4)	55.72	21.54	3.89	12.70	9.96	7.68	7.22	8.10	15.25	8.08	9.15
69(5)	53.68	21.25	3.86	12.79	10.16	7.68	7.98	8.16	15.05	7.77	8.95
					Antrozous p. minor						
18(9)	51.93	20.26	3.66	12.01	9.59	7.46	6.82	7.68	14.41	7.60	8.46
20(3)	50.13	19.85	3.72	11.68	9.33	7.43	6.68	7.48	14.17	7.50	8.50
23(19)	51.21	19.76	3.72	11.76	9.38	7.03	6.54	7.55	13.86	7.38	8.51
22(25)	49.73	19.98	3.72	11.90	9.50	7.35	6.70	7.51	14.32	7.47	8.39
35(31)	50.85	20.08	3.77	12.05	9.52	7.23	6.68	7.67	14.11	7.48	8.58
24(12)	51.69	20.03	3.63	11.85	9.50	7.25	6.65	7.65	14.04	7.46	8.51
25(9)	50.11	19.76	3.70	11.96	9.36	7.11	6.44	7.47	13.92	7.29	8.48
41(19)	51.66	20.42	3.82	12.22	9.72	7.20	6.74	7.82	14.33	7.59	8.68
13(9)	49.63	20.13	3.82	11.72	9.36	7.25	6.71	7.56	13.99	7.46	8.40
82(4)	50.31	20.50	3.61	11.96	9.41	7.36	6.80	7.55	14.46	7.58	8.35
83(47)	49.88	20.36	3.64	11.84	9.96	7.22	6.59	7.51	14.18	7.37	8.39