SYSTEMATICS AND VARIATION OF

MYOTIS SUBULATUS (SAY)

By

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Thesis Adviser

Dean of the Graduate School

PREFACE

This research was carried out under the direction of Dr. B. P. Glass, as major advisor, and Drs. R. J. Miller and A. M. Stebler, who served on the graduate advisory committee, and gave aid throughout the study. Dr. G. A. Moore gave advice concerning systematics, Dr. R. D. Morrison concerning statistical analysis of the data and Mr. Bob Walls wrote the computer program. Drs. James S. Findley, Sydney Anderson, J. K. Jones, Jr., H. Gunderson, W. H. Burt, Wayne Davis, and D. F. Hoffmeister also assisted in various ways.

Grateful thanks are expressed to all of the above.

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A total of 519 specimens were examined in the course of this study. The sources of this material and the individuals making the loans are listed below. Grateful acknowledgement is extended to each of them.

Arizona: University of Arizona, (UA), E. Lendell Cockrum; California: California Academy of Science, (CAS), R. T. Orr; Long Beach State College, (LB), Ross Hardy; San Diego Society of Natural History, (SD), R. C. Banks; Museum of Vertebrate Zoology,

Berkeley, (MVZ), W. Z. Lidicker; Colorado: University of Colorado, (CU), H. G. Rodeck; Illinois: Southern Illinois University, (SIU), H. S. Stains; University of Illinois, (UI), D. F. Hoffmeister; Kansas: Kansas State Teachers College at Emporia, (KT), Dwight Spencer; University of Kansas, (KU), J. K. Jones, Jr.; Massachusetts: Museum of Comparative Zoology at Harvard, (MCZ), B. Lawrence; Michigan: University of Michigan Museum of Zoology, (UMMZ), W. H. Burt; Missouri: University of Missouri, (MU), W. H. Elder; New Hampshire: Dartmouth College Museum, (DA), W. W. Bowen; New Mexico: New Mexico Western College, (NM), B. J. Howard; University of New Mexico, (UNM), James S. Findley; New York: New York State Museum, (NY), E. M. Reilly; Oregon: Oregon State University, (OU), R. M. Storm; University of Oregon, (UO), J. H. Shotwell; Pennsylvania: Academy of Natural Sciences of Philadelphia, (ANSP), H. R. Roberts, Reading Public Museum and Art Gallery, (RP), S. C. Gundy; Texas: Baylor University, (BU), B. C. Brown; Fort Worth Childrens Museum, (FW), J. R. Preston; Texas Cooperative Wildlife Collections, (TCWC), W. B. Davis; Utah: Brigham Young University, (BYU), H. H. Frost; Weber College (WC), E. A. Jenne; Washington: University of Washington, (WSU), G. E. Hudson; United States National Museum, (USNM), D. H. Johnson, and A. M. Greenhall, (U. S. Fish & Wildlife Service). Alberta, University of Alberta, (UAC), Victor Lewin; British Columbia Provincial Museum of Natural History, (BCPM), C. J. Guiquet; University of British Columbia, (UBC), I. McT. Cowan; Ontario: National Museum of Canada, (NMC), P. M. Youngman; Royal Ontario Museum (ROM), R. L. Peterson.

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I. INTRODUCTION

This study was initially planned as a critical examination of intraspecific variation in the bat Myotis subulatus (Say). Specific objectives were to determine the geographic limits of the subspecies, to determine the degree of differentiation between subspecies, and, if possible, to identify the isolating factors responsible for geographic variation.

During the study a nomenclatural problem involving the validity of the species name Myotis subulatus became apparent. This secondary problem required solution before the proper assignment of names to subspecies could be attempted. The study therefore consists of two parts, first: a clarification of the status of the name Myotis subulatus, and second: an analysis of subspeciation within the species.

The subspecies concept has been discussed by many authors, among others, Mayr (1957), Burt (1954), and Anderson (1959), with differing viewpoints. The trinominal system has also been the object of considerable debate. Although a discussion of these concepts is not necessary here, such diversity of thought among taxonomists necessitates a statement of the criteria used in evaluating population relationships so that this work may be evaluated and compared with others.

The author feels that a subspecies may be defined as an isolated or partially-isolated population of a species showing tangible morphological differentiation from other populations. The author believes

that size of the area occupied by a distinct population should be considered in evaluating population relationships. If the area occupied is large, a hundred miles or more square, 75% differentiation between populations may be sufficient to merit trinomial distinction. However, if it is small, greater than 75% differentiation may be necessary, the percent necessary being roughly inversely proportional to area occupied by the population.

II. NOMENCLATURE OF THE SPECIES

The name subulatus was first applied to a North American Myotis by footnote in James' (1823) account of Long's expedition from Pittsburgh to the Rocky Mountains. Apparently James took the description directly from Say's field notes, and the description has been quite properly attributed to Say. The vicinity of La Junta, Colorado, on the Arkansas River near the mouth of the Purgatoire is usually given as the type locality. Actually the locality was several miles further up the Arkansas, as Long's party had that morning passed the Huerfano, about sixty miles above the Purgatoire, and had travelled twenty-six miles during the day. This would place the type locality on the banks of the Arkansas River, slightly east of the 104th meridian.

The type specimen is not mentioned in Say's notes as having been preserved, but in another footnote (James, ibid. p. 14) it was indicated that the type of the band-tailed pigeon and other natural history specimens acquired on this expedition were placed in the Philadelphia Museum. This collection, better known as Peale's Museum, was later destroyed by fire and the type of M. subulatus with it, if such ever existed.

Apparently there are no other collections of bats from southeastern Colorado, except for a single specimen of Myotis subulatus in the University of Colorado Museum, which was collected in 1938 in Bone Canyon, Baca County. This individual resembles M. subulatus

from Cimarron County, Oklahoma, which suggests that a bright brownish color is common to all these bats throughout the badlands of the contiguous parts of Colorado, New Mexico, and Oklahoma.

Extensive collections in the Oklahoma State University Museum from Cimarron County, Oklahoma (Glass and Ward, 1959) indicate that Myotis yumanensis and M. subulatus are the only species of the genus in the area. The single skull of M. lucifugus from Union County, New Mexico (Miller and Allen, 1928) was collected on Sierra Grande, which achieves an elevation of 8-9000 feet, 3-4000 feet higher than the badlands to the north and east. The specimen probably represents the eastern limit of range for M. lucifugus in New Mexico, and its existence there is not considered pertinent to the true identity of M. subulatus. The Sierra Grande specimen has been examined and the writer agrees with Harrison and Findley (1962) that it is properly identified.

Say's original description, as quoted by James (1823) reads as follows:

> "A small bat was shot this evening, during the twilight, as it flew rapidly in various directions, over the surface of the creek. It appears to be an immature specimen, as the molares are remarkably long and acute; the canines are very much incurved, and the right inferior one is singularly bifid at tip, the divisions resembling short bristles. This species is beyond a doubt distinct from the Caroline bat (V. Caroliniana, Geoff.) with which the ears are proportionally equally elongated, and, as in that bat, a little ventricose on the anterior edge, so as almost to extend over the eye, but the tragus is much longer, narrower, and more acute resembling that of the V. emarginatus, Geoff., as well in form as in proportion to the length of the ear. We call it V. subulatus, and it may be thus described. --Ears longer than broad, nearly as long as the head, hairy on the basal half, a little ventricose on the anterior edge, and extending to the eye; tragus elongated, subulate; the hair above blackish at base,

> tip dull cinereous; the interfermoral membrane hairy at base, the hairs unicoloured, and a few also scattered over its surface, and along its edge, as well as that of the brachial membrane; hair beneath black, the tip yellowish white; hind feet rather long, a few setae extending over the nails; only a minute portion of the tail protrudes beyond the membrane.
>
> Total length. . . . 2 9-10 inches.
> Tail. . . . . 1 1-5"

The remarks on hair color, foot size, digital setae, uropatagial hair, and flight characteristics fit Myotis yumanensis, not M. subulatus. The two cannot be confused on any of the physical characteristics named, and the former flies along watercourses, close to the surface (Glass and Ward, loc. cit.), and is rarely, if ever, seen flying silhouetted against the sky. M. subulatus, on the other hand, flies well above the ground, is readily silhouetted against the sky, and in the experience of those who have observed it, it is not in the habit of skimming the surface of streams (Glass, pers. comm.). To one familiar with the bats of these badlands the assumption seems inescapable that the bat Say collected was M. yumanensis. However, without a type specimen this cannot be proved.

If this assumption is correct, subulatus would by priority, be the oldest available name for M. yumanensis. However, the name subulatus has already been applied to M. lucifugus and M. keeni as well as to the species currently carrying the name. Another change would only compound confusion. Furthermore, the name M. yumanensis has stood valid and unchallenged for 101 years, ever since its original description in 1864. Therefore, it seems appropriate to suggest that the name subulatus should be suppressed under the plenary powers of the International Commission of Zoological Nomenclature, and the

name yumanensis be retained. The propriety of this action is reinforced by the lack of a type specimen of M. subulatus for final and decisive reference. A proposal to this effect is being submitted to the Commission.

The first available name for the species presently called subulatus is M. leibi (Audubon and Bachman, 1842), based on a specimen collected by Dr. Leib in Erie County, Ohio, cited in the original description as Erie County, Michigan (Miller and Allen, 1928). Henceforth in this discussion the name Myotis leibi will be used.

Available names for the presently recognized subspecies of M. leibi and Myotis l. ciliolabrum (Merriam, 1886) from Trego County, Kansas, and Myotis l. melanorhinus (Merriam, 1890) from Coconino County, Arizona.

The present study is concerned with a re-evaluation of the populations making up the species herein referred to as Myotis leibi and called M. subulatus by Miller and Allen (1928). The early taxonomic history of this species was thoroughly and accurately reviewed by Miller and Allen (ibid) and is not discussed any further in this review. The arrangement of subspecies at the time this study was undertaken was essentially like that of Miller and Allen (ibid), with the exception of range extensions of the subspecies.

Fig. 1, adapted from Hall and Kelson (1959), indicates the geographic extent of the subspecies of M. leibi as understood when the present study was initiated.

Fig. 2 indicates the geographic distribution of specimens examined in the present study. Noteworthy changes from the map of Hall and Kelson (1959) are the Wichita Mountains (Glass and Ward, 1959) and McCurtain County (unpubl.) records for Oklahoma, and the removal of

the single locality for Iowa. The Iowa specimen proves upon examination to be not M. leibi, but M. keeni. The species has also been taken in Michoacan, (Burt, 1961), Durango, (Baker, 1960), and Chihuahua, (Anderson, unpubl.) Mexico.

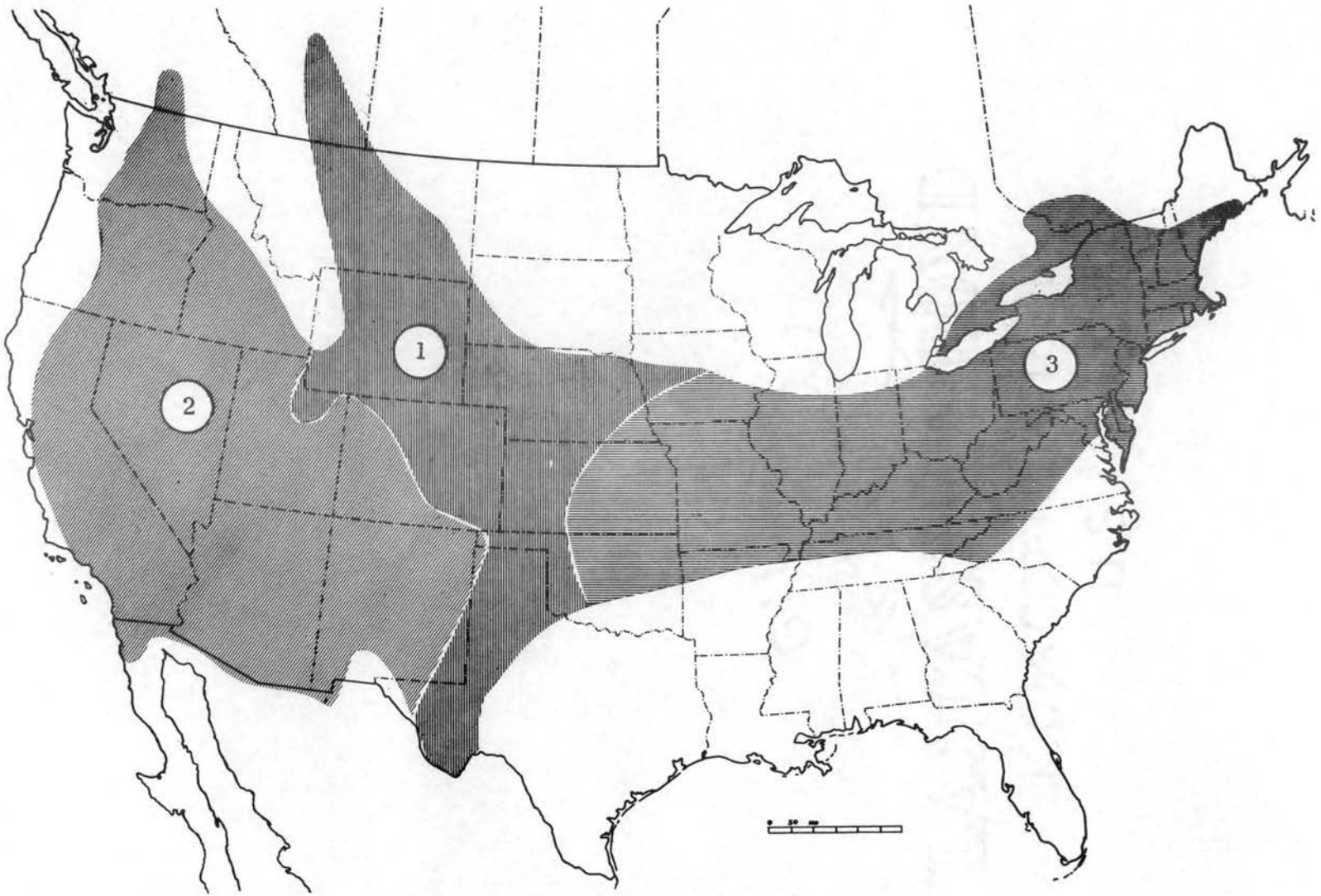

Fig. 1. Geographic distribution of Myotis subulatus (map adapted from Hall & Kelson 1959) based on published records through October 1957. 1: M. s. subulatus, 2: M. s. melanorhinus, 3: M. s. leibi.

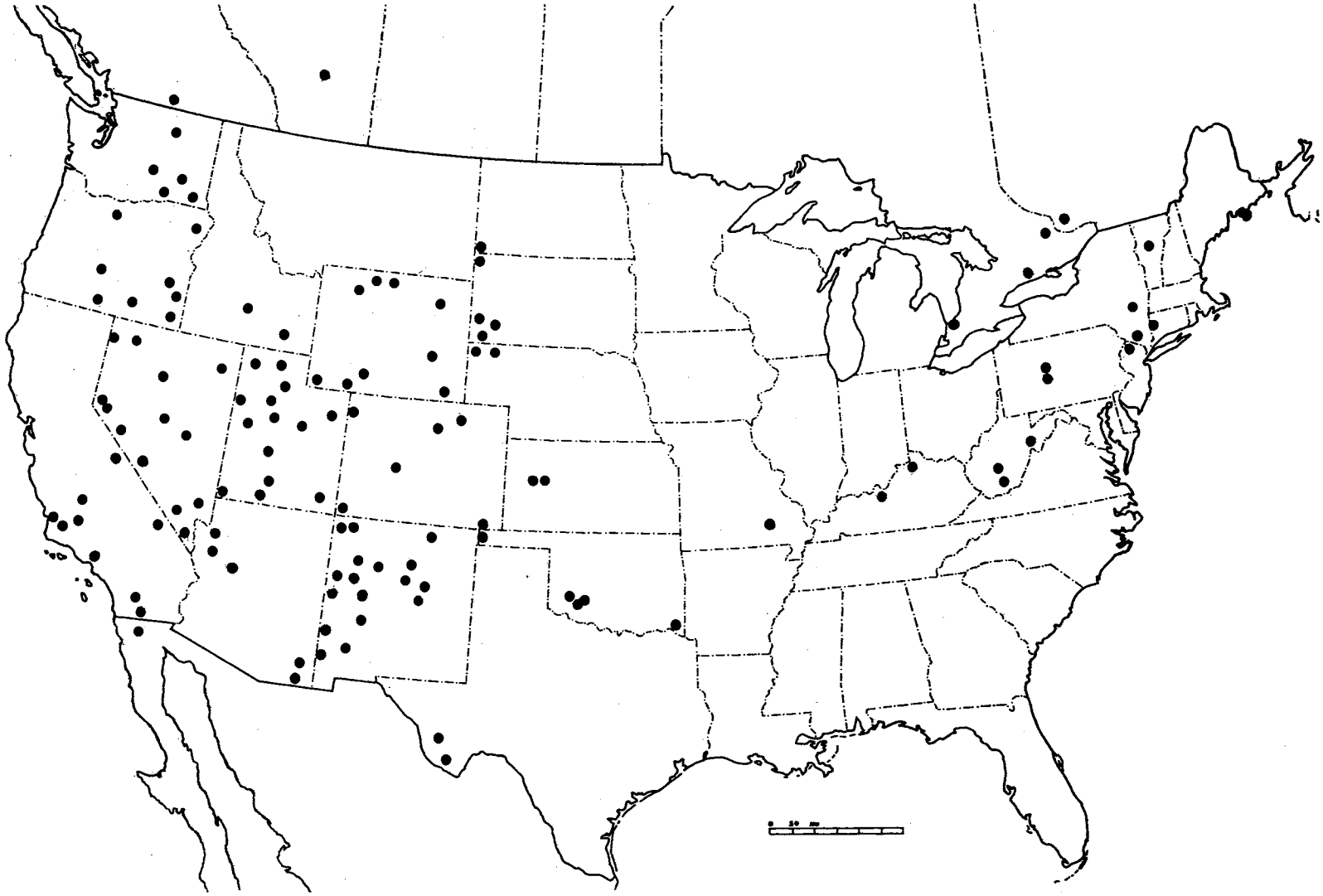

Fig. 2. Geographic distribution of specimens examined in the course of the study.

III. MATERIALS AND METHODS

Collection data for each of the 519 specimens were copied from the accompanying tags. In addition to color analysis, seven measurements were made from each skin and eight from each skull.

Measurements

The body measurements taken were: total length, tail length, hindfoot length, ear length, forearm length, third metacarpal length, and the forearm length minus the third metacarpal length. The first four measurements were taken from the collectors tag, unless obviously in error. The last three measurements were made from the dried skin. Measurements were as follows: Forearm length; from the distal to the proximal end of the forearm. Third metacarpal length; from the proximal end of the forearm to the distal end of third metacarpal. This measurement was substracted from the forearm length to arrive at the seventh measurement. The difference was rarely negative.

Skull measurements taken were: condylobasal length, palatal length, rostral breadth, interorbital breadth, cranial breadth, mastoid breadth, maxillary tooth row length and cranial height. Interorbital breadth, mastoid breadth, condylobasal length and maxillary tooth row length are described in Cockrum (1962) and cranial breadth in Blair (1957). Fine-pointed calipers were needed to measure the maxillary tooth row length to get under the cingula of the canine and last molar.

Palate length: From the anterior midline to the posterior border of the palate left of the median spine. The spine of the posterior border was not measured because it was often broken. Rostral breadth: Shortest width between the infraorbital canals. Cranial height: From the basioccipital to the top of the cranium. All measurements were made by the author with the same pair of dial calipers and recorded in millimeters.

Color

Color observations were made objective by choosing (as color standards) the darkest-colored and lightest-colored specimens, plus a uniformly-graded series representing shades of color between the two extremes. These were selected without regard to the collection site. Each bat was assigned a number ranging from 0 for the lightest to 16 for the darkest. Colors corresponding to the standard specimens were selected from Maerz and Paul (1930). These are designated in the standard chart below.

ASSIGNED NO.	CATALOG NO. & LOCATION	PLATE FROM MAERZ AND PAUL
0	KSTC m-367, Logan Co. Kansas	9 I 4
1	None	
2	None	
3	CAS 9 379, Monterey Co. Cal.	9 J 6
4	VMMC 5888, Rumsey, Alberta, Canada	10 J 5
5	SIU m 781, Weldona, Morgan Co. Col.	13 H 6
6	UNM 1981, Bernalillo Co. N. N.	12 H 7
7	REM 3074, Cochise Co. Ariz.	13 G 8

ASSIGNED NO.	CATALOG NO. & LOCATION	PLATE FROM MAERZ AND PAUL
8	OSU 3983, Kiowa Co. Okla.	14 I 8
9	UA 7464, Kingman, Ariz.	13 I 10
10	None	
11	OSU McCurtain Co. Okla.	14 I 8
12	None	
13	AMNH 14 5068, Monroe, N. Y.	
14	MCZ 42524, Renfrew Co. Ont.	8 J 10
15	None	
16	UMMZ 82878, Otter Point, Maine	3 L 12

Color type for an area was selected from the more recently-collected and typically-colored specimens because older material was obviously faded. No attempt was made to account for fading in older specimens.

This method does not show an important color factor in this species. Pacific Northwest and northern Great Plains bats have tricolored hair resulting from the appearance of a light yellow band between the basal black and the apical brown. This yellowish band is absent in bats from most parts of the southwest and eastern United States.

When specimens from the East and Southwest had the tips of the hair worn, overall color appeared darker. If those from the Pacific Northwest and northern Great Plains had the tips worn, overall appearance was lighter. Specimens with worn hair were not used in color comparisons.

Statistical Analysis of Data

After measuring a specimen, its collection site was recorded by geographical coordinates. Specimens from adjoining localities were assigned the same coordinates to increase sample size. Counties were often used as the basis for grouping, but in some cases specimens were grouped from adjoining counties. The data were analyzed on an IBM 1410 computer for sample size, mean, standard deviation and coefficient of variation of each character from each locality.

Treatment of Data

The coefficient of variation (V) was compared with that found by other workers studying geographic variation in small mammals (Hoffmeister and Lee, 1963), and individual variation appears to be essentially of the same order of magnitude as in other species (see also Hoffmeister, 1951; Lidicker, 1960). Table I shows the coefficient of variation (V), corrected according to Haldane (1955), for three samples of Myotis leibi. Sexes have been combined in the samples. In most samples the females appeared to be slightly larger than males but this difference is not statistically significant at the 75% level. Selected measurements from three samples of different subspecies are given in Table II showing variation between the sexes.

Because of their high coefficient of variation the third metacarpal length, tail length, hindfoot length, total length, and ear length were rejected for taxonomic evaluation. The use of different measuring techniques rather than inherent variability probably accounts for the high V values of these rejected measurements (tail length, total length,

hindfoot length, and ear length). Third metacarpal length variation seems to be inherent. Means of the ten characters which had low V values were plotted on individual maps. Sample size was recorded beside each mean. The importance of each mean value was directly proportional to its sample size. Each map was examined independently and areas of change or homogeneity were noted. A composite map of these changes and similarities was made, with equal weight being given to each character. From this composite a final decision was made concerning the number of subspecies. The exact delineation of subspecies boundaries was made only after evaluation of the distance over which the character shift occurred, number of shifts occurring simultaneously, and magnitude of these shifts.

TABLE I

COEFFICIENTS OF VARIATION IN THREE SAMPLES OF MYOTIS LEIBI
CORRECTED ACCORDING TO HALDANE (1955)

	RENFREW CO. ONTARIO N=45	SOCORRO CO. NEW MEXICO N=18	TREGO CO. KANSAS N=10
TOTAL LENGTH*	4.99	4.98	4.51
TAIL*	6.21	7.73	7.08
HIND FOOT*	12.00	15.35	4.98
EAR*	7.23	11.02	12.45
FOREARM	2.61	3.34	1.74
CONDYLPREMAXILLA	2.17	2.53	2.55
PALATE	3.28	3.52	3.96
ROSTRAL WIDTH	3.75	4.16	4.71
INTERORBITAL WIDTH	3.43	4.04	4.57
CRANIAL BREATH	2.22	2.74	3.74
MASTOID BREATH	2.34	2.65	2.50
MAXILLARY TOOTH ROW	2.64	3.12	3.56
THIRD METACARPAL	3.43	3.66	2.75
FOREARM MINUS THIRD METACARPAL*	60.75	33.86	22.84
CRAINAL HEIGHT	3.09	2.60	3.88
MEAN*	3.09	3.40	3.50

*Samples marked with an asterisk were not used in the study as taxonomic characters nor were they figured in the mean.

TABLE II

SEXUAL VARIATION IN MYOTIS LEIBI

Locality		Total Length	Condylpremaxilla	Forearm	Cranial Breadth	Maxillary Tooth Row	Sample Size
Renfrew Co., Ontario	♂♂	82.1	12.92	31.34	6.75	4.86	19
	♀♀	82.3	13.03	31.81	6.79	4.88	26
San Diego Co., California	♂♂	79.6	13.14	32.08	6.39	5.14	11
	♀♀	84.3	13.21	32.17	6.43	5.14	5
Valencia Co., New Mexico	♂♂	82.4	13.27	32.80	6.52	5.20	8
	♀♀	85.2	13.66	34.29	6.56	5.32	9

IV. ANALYSIS OF DATA

The distribution of averages shown on the maps (Figs. 4-13) for ten meristic characters and color revealed four areas in North America where this species consists of populations that show considerable homogeneity. These four areas are: 1. from southeastern Oklahoma east and northeast including all populations of New England and Northeastern Canada, 2. New Mexico, Arizona, southern 3/4 of Utah, the southwestern half of Colorado, and the Oklahoma Panhandle, 3. Washington, Oregon, British Columbia and northwestern Nevada, and 4. Kansas, Nebraska, eastern South Dakota, southwestern North Dakota and Wyoming. Some appreciation of the degree of homogeneity within these populations and of the magnitude of change from area to area may be seen by examining the accompanying maps (Figs. 3-13). These figures contain only one-third of the population means used in evaluating relationships. The values shown represent the largest sample size available from each vicinity.

All eleven characters used show a shift in their respective characters between the populations of the eastern United States, including the main part of Oklahoma, and the populations in Nebraska, Kansas, the Oklahoma Panhandle and New Mexico.

Six characters (Maxillary tooth row length, condylobasal length, palatal length, rostral breadth, forearm length, length of third metacarpal) as well as color show a character shift between populations of

Kansas, Nebraska, Wyoming, and South Dakota and those of southwestern Colorado, New Mexico and Arizona. All eleven (Figs. 3-13) characters show a shift between the populations of Oregon, Washington and British Columbia and those of Arizona, New Mexico, Utah, Oklahoma Panhandle and Old Mexico. The overall change is considerable but available information indicates a wide area of varying degrees of intergradation between the two stable extremes.

Eight meristic characters, (Maxillary tooth row length, interorbital width, mastoid breadth, condylobasal length, rostral breadth, forearm length, cranial breadth, and cranial height) and color show populations of the Pacific Northwest are demonstrably separable from those of the northern Great Plains, and that intergradation occurs from the vicinity of the Utah-Idaho-Nevada junction north to the Canadian border. The main northern Rocky Mountain ranges probably separate the two populations north of the southern Idaho Snake River basin.

Symbols corresponding to numbers in the color code are plotted on the accompanying map (Fig. 3). Symbols represent average color intensity for local samples, and cannot be interpreted in terms of actual colors, but they do depict relationships.

Darkest individuals occur in the northeastern United States and a gradual lightening occurs from east to southwest. In the Southwest bats are colored with medium intensity. Big Bend specimens from Texas are lighter, which accounts for their assignment to Myotis s. subulatus (Davis, 1944). From Southwest to Northwest the color becomes lighter and tricolored. A light straw color is characteristic of bats in the northern Great Plains and especially Kansas.

Bats of the Northwest are darker than the Kansas, Nebraska, and Wyoming specimens but lighter than bats of the central Southwest.

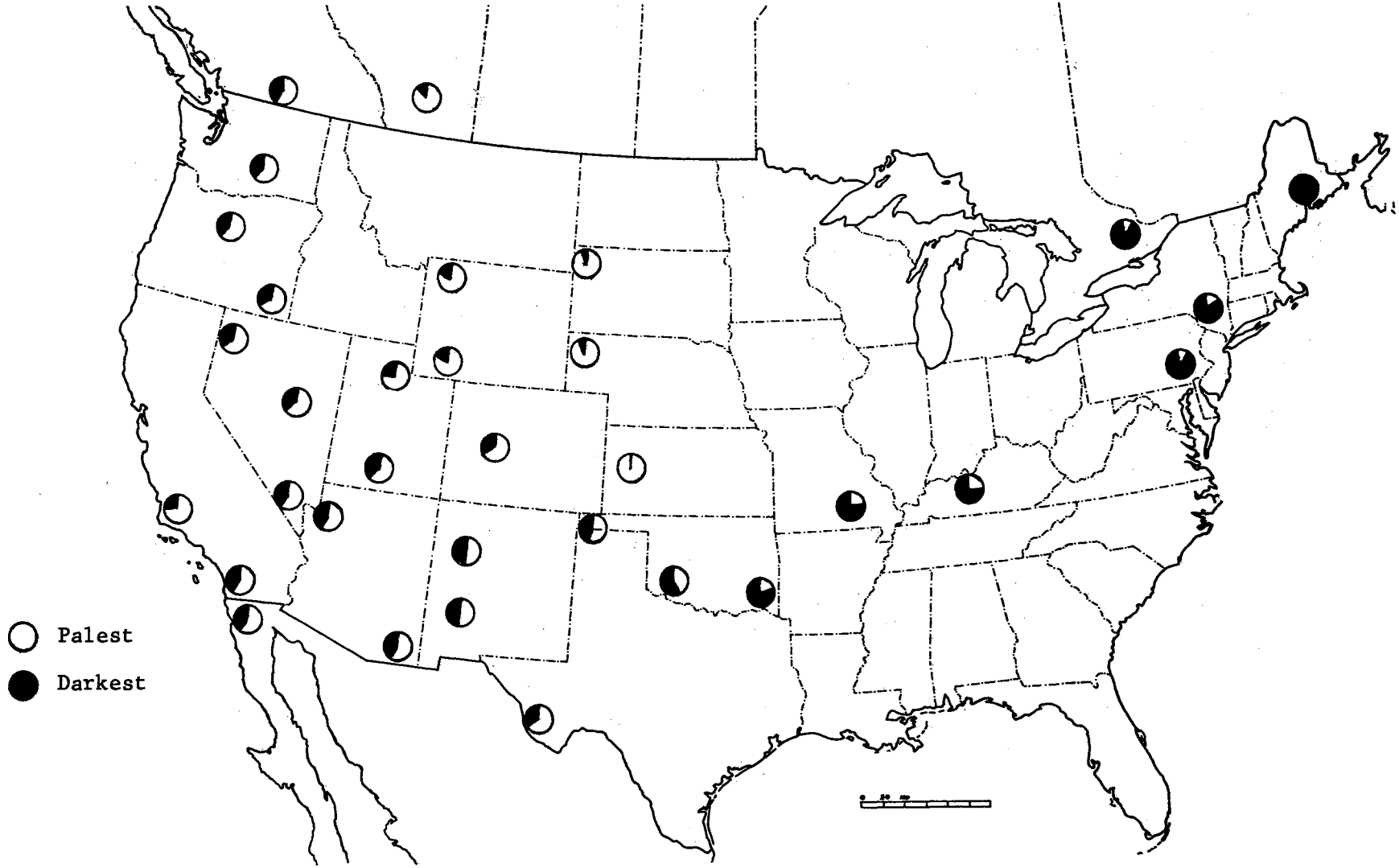

Fig. 3. Geographical variation in the color of Myotis leibi. Open circles indicate palest color; black circles, darkest color.

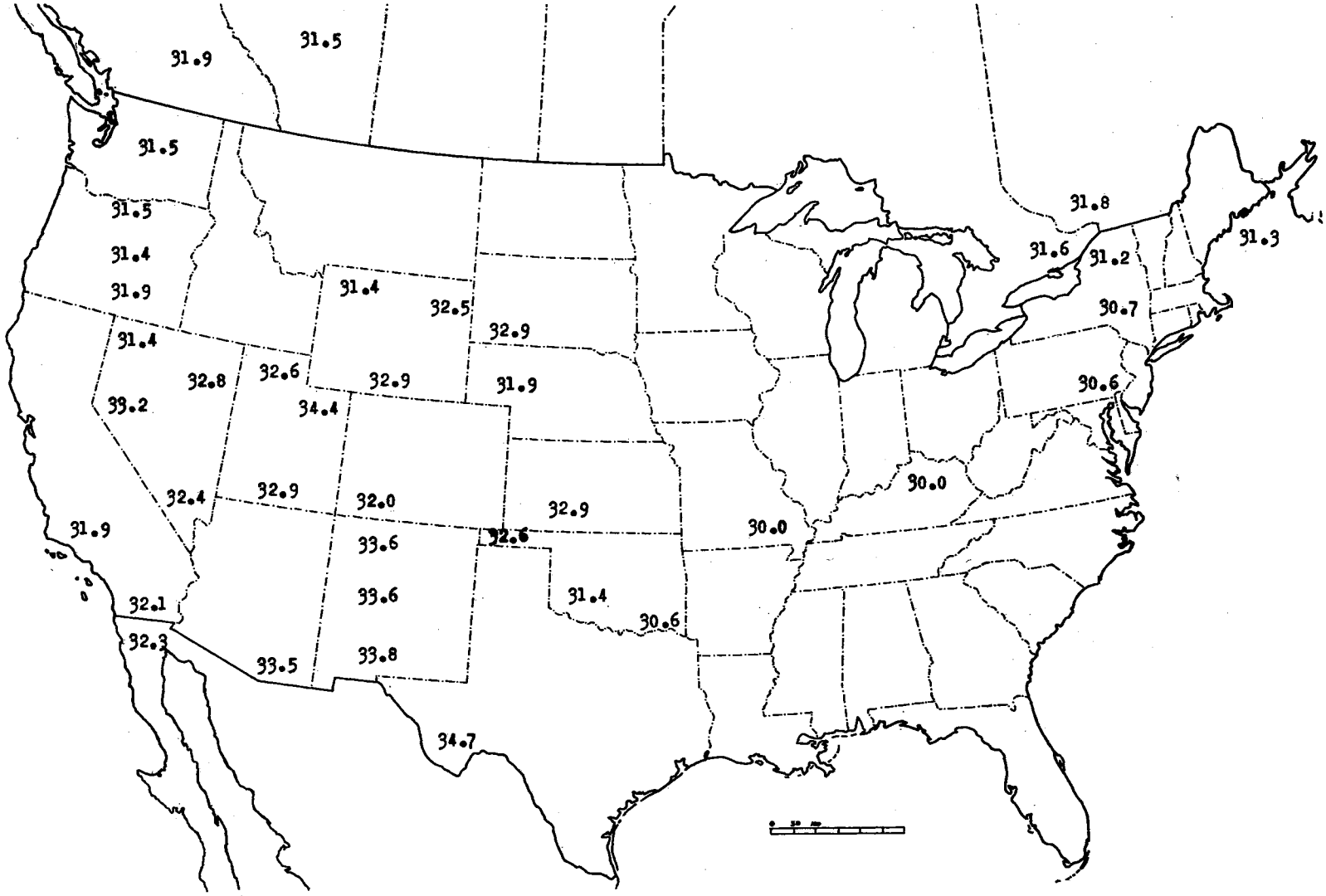

Fig. 4. Geographic distribution of means of forearm length in Myotis leibi.

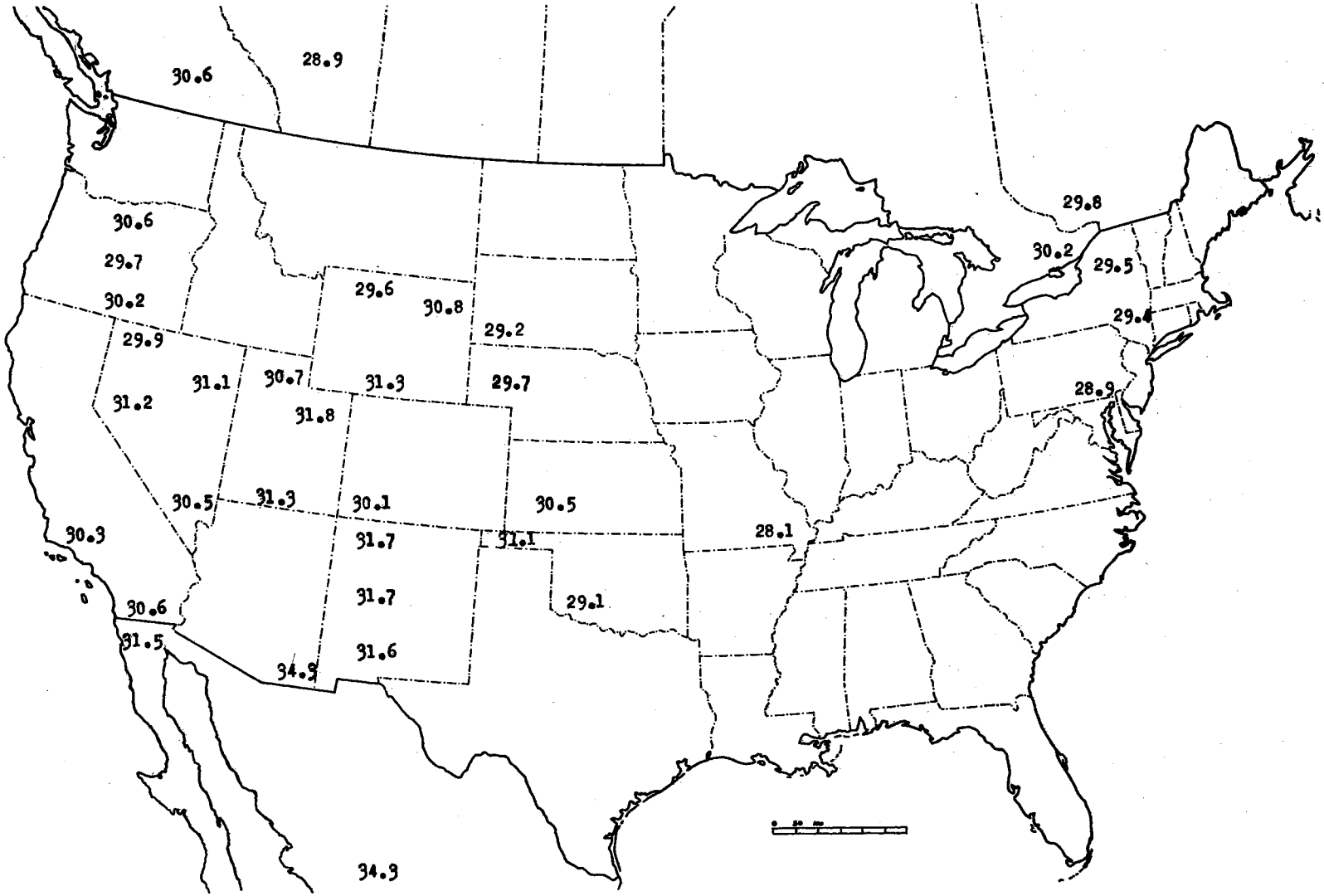

Fig. 5. Geographic distribution of means of third metacarpal length in Myotis leibi.

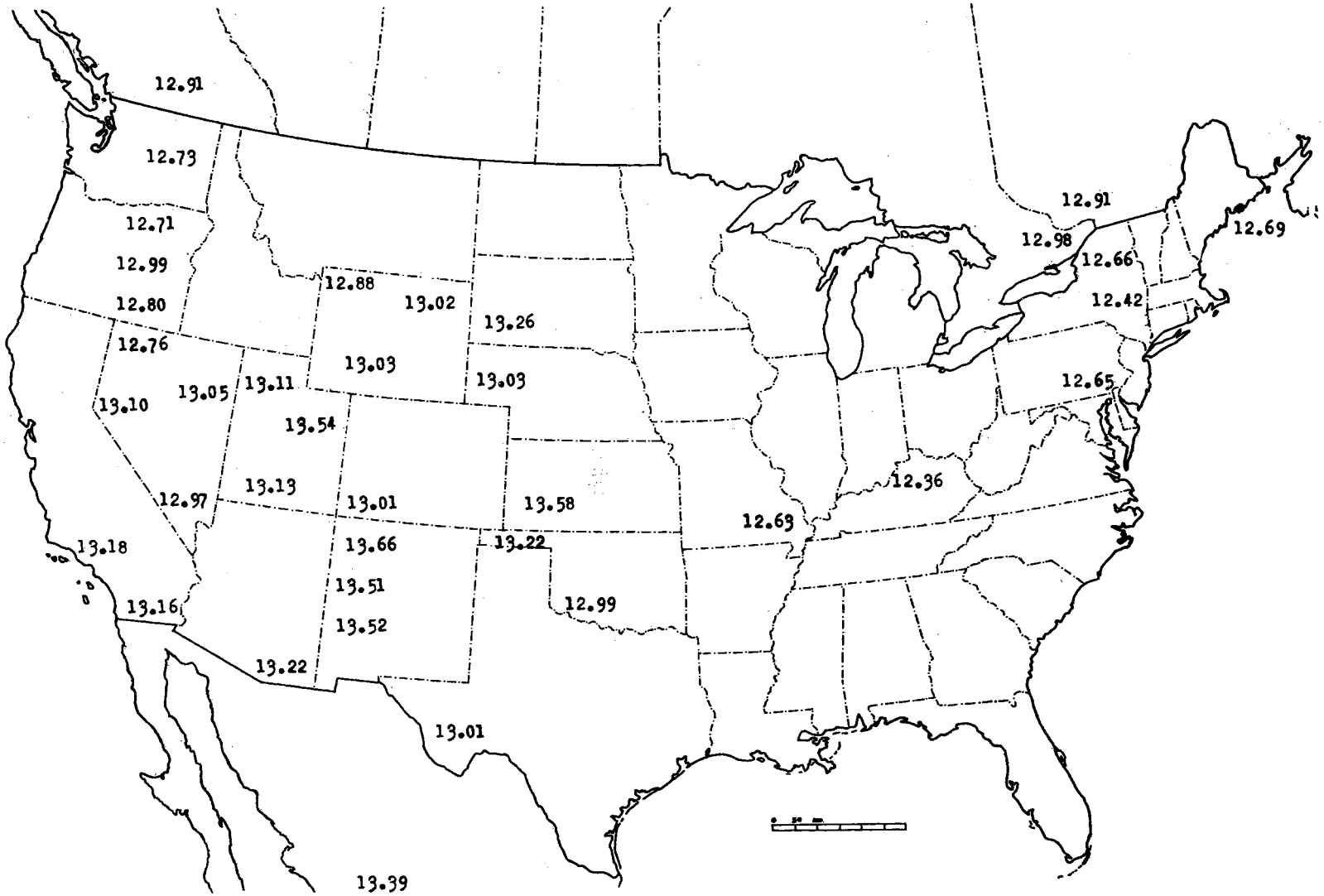

Fig. 6. Geographic distribution of means of condylobasal length in Myotis leibi.

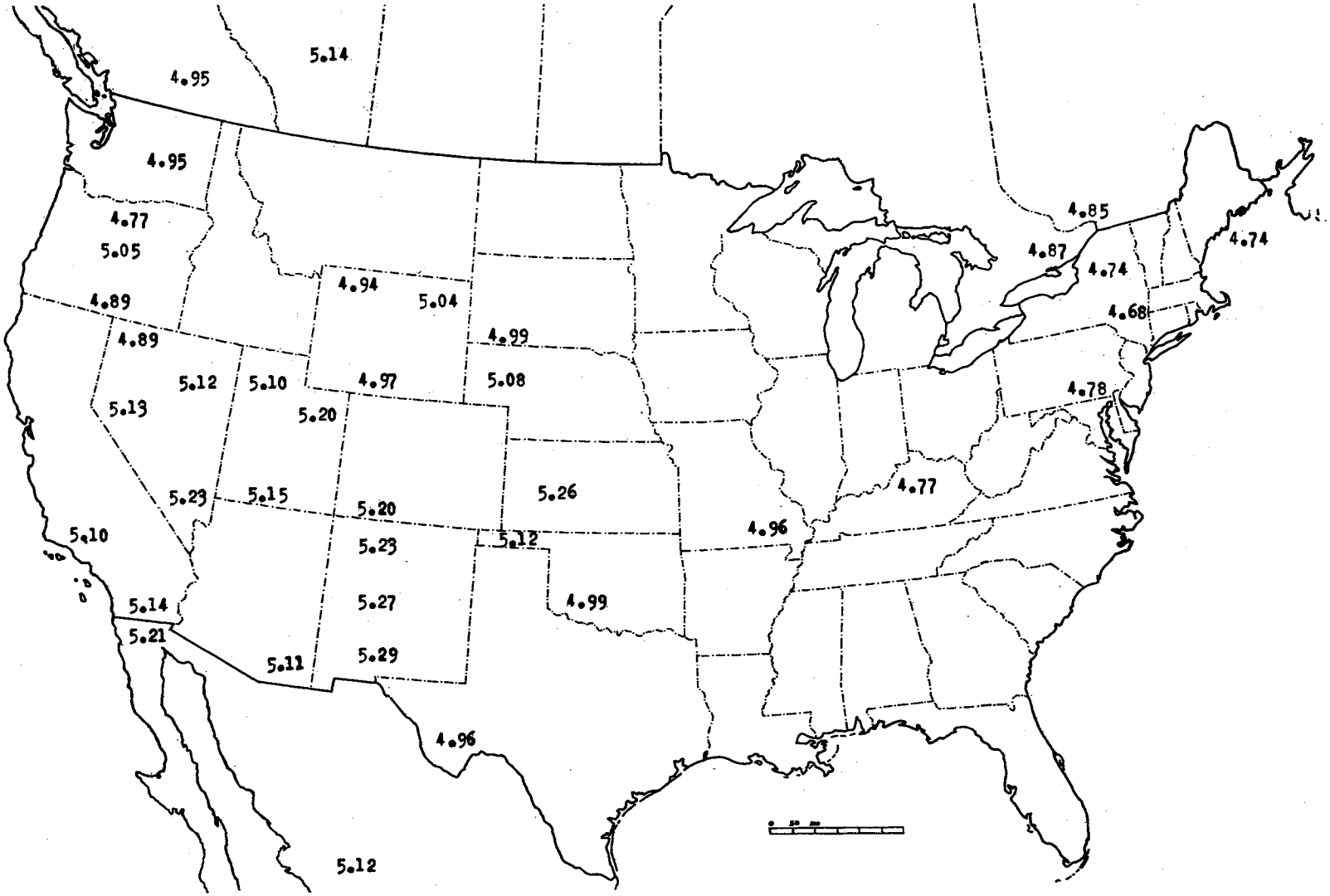

Fig. 7. Geographic distribution of means of maxillary toothrow length in Myotis leibi.

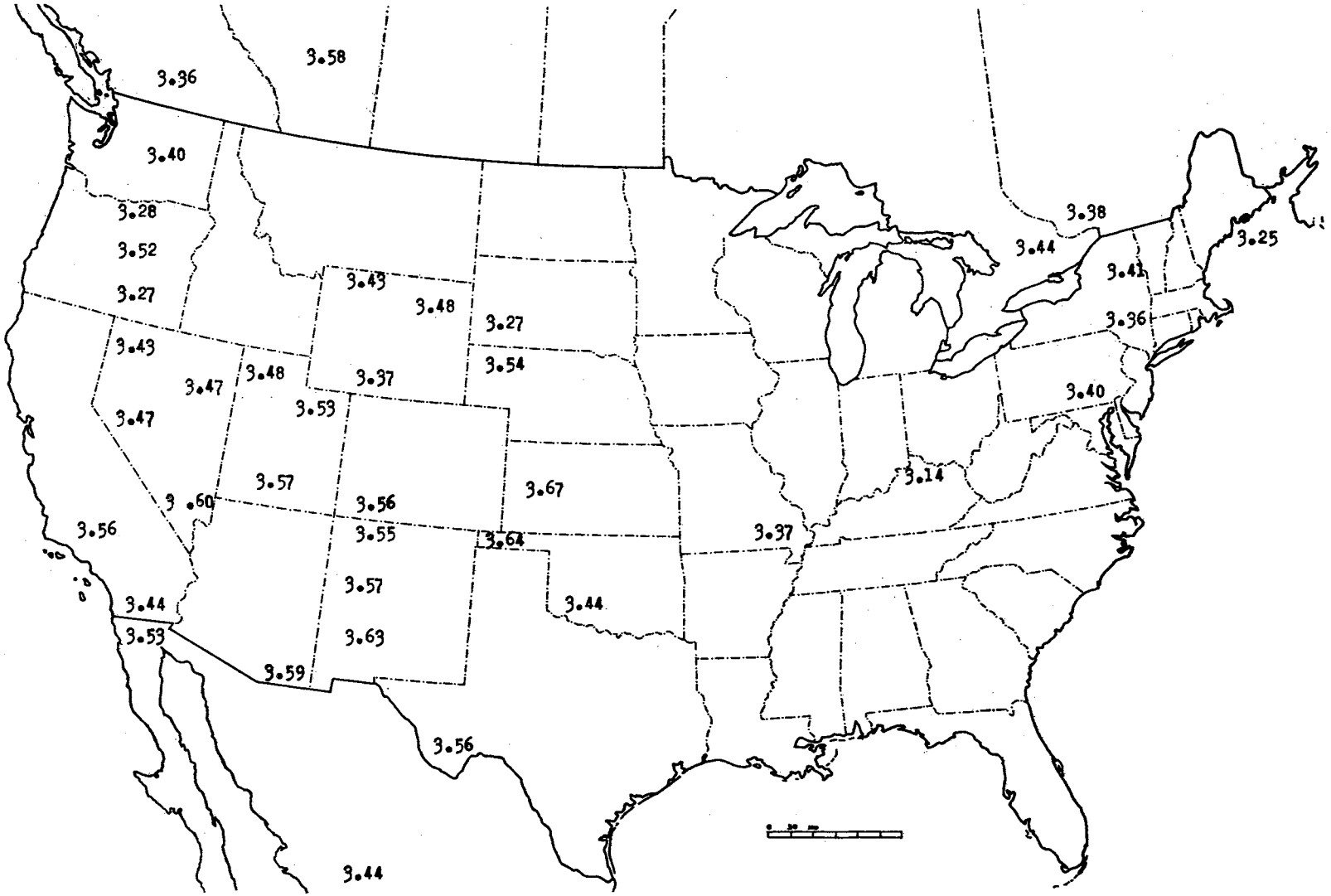

Fig. 8. Geographic distribution of means of rostral width in Myotis leibi.

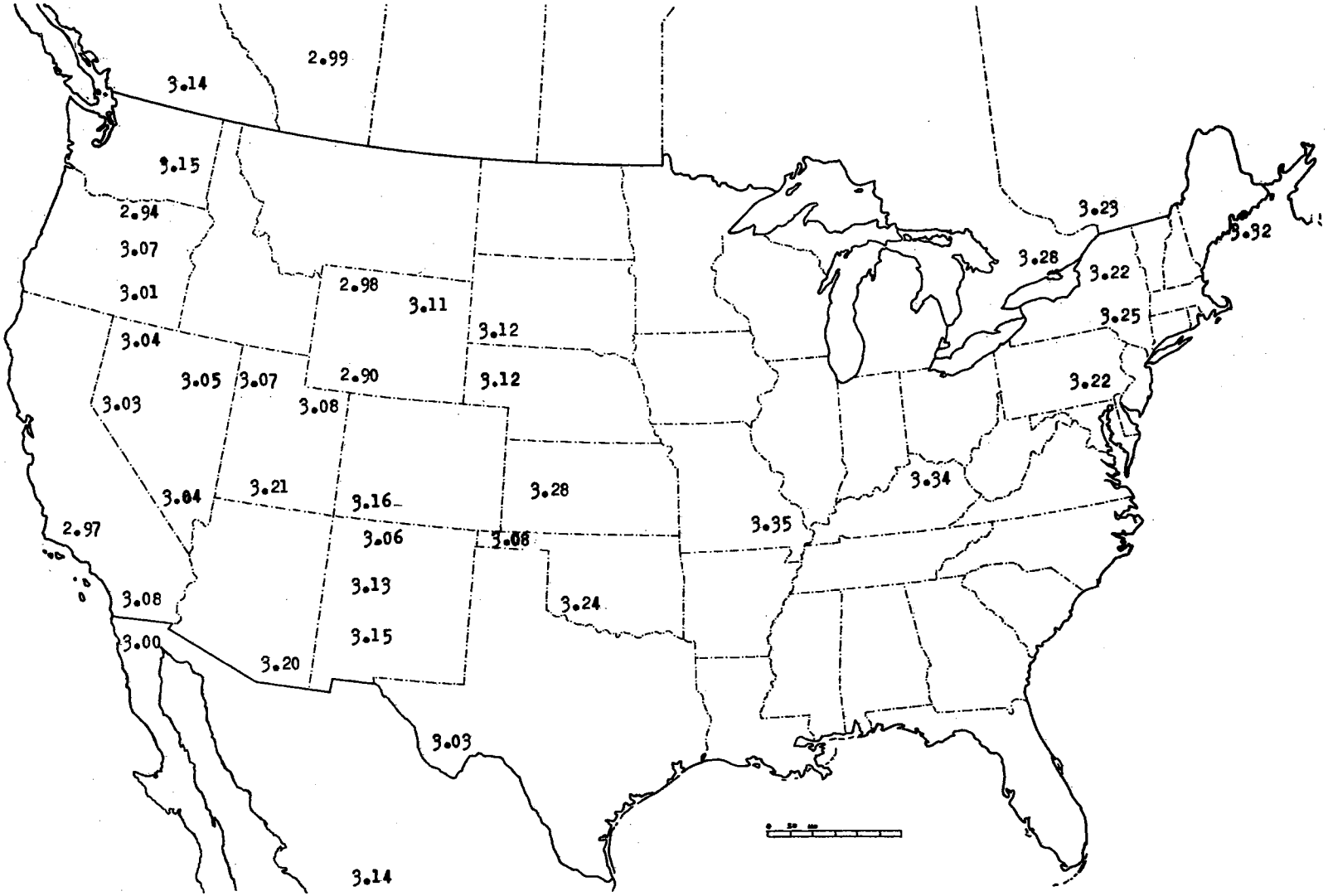

Fig. 9. Geographic distribution of means of interorbital width in Myotis leibi.

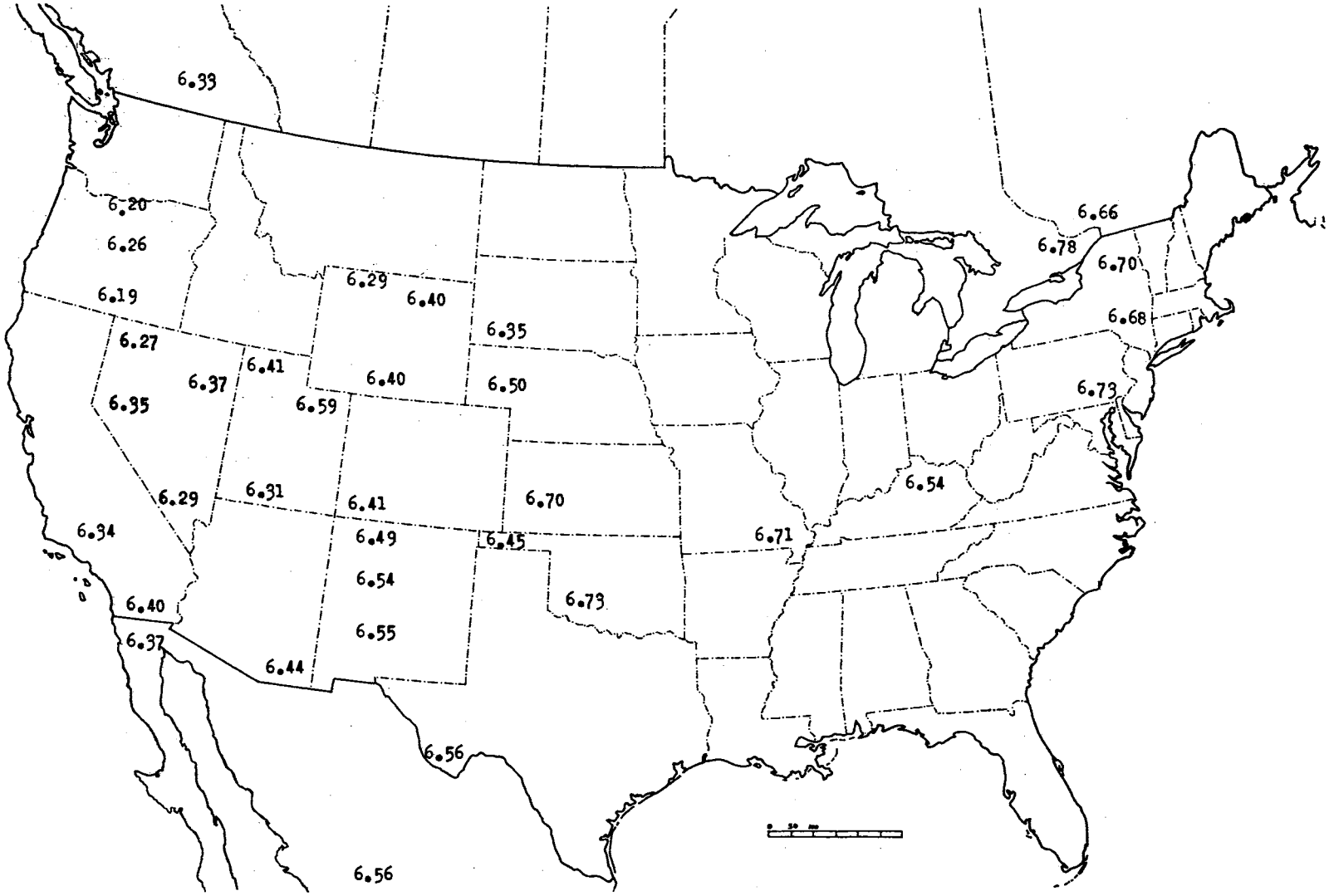

Fig. 10. Geographic distribution of means of cranial breadth in Myotis leibi.

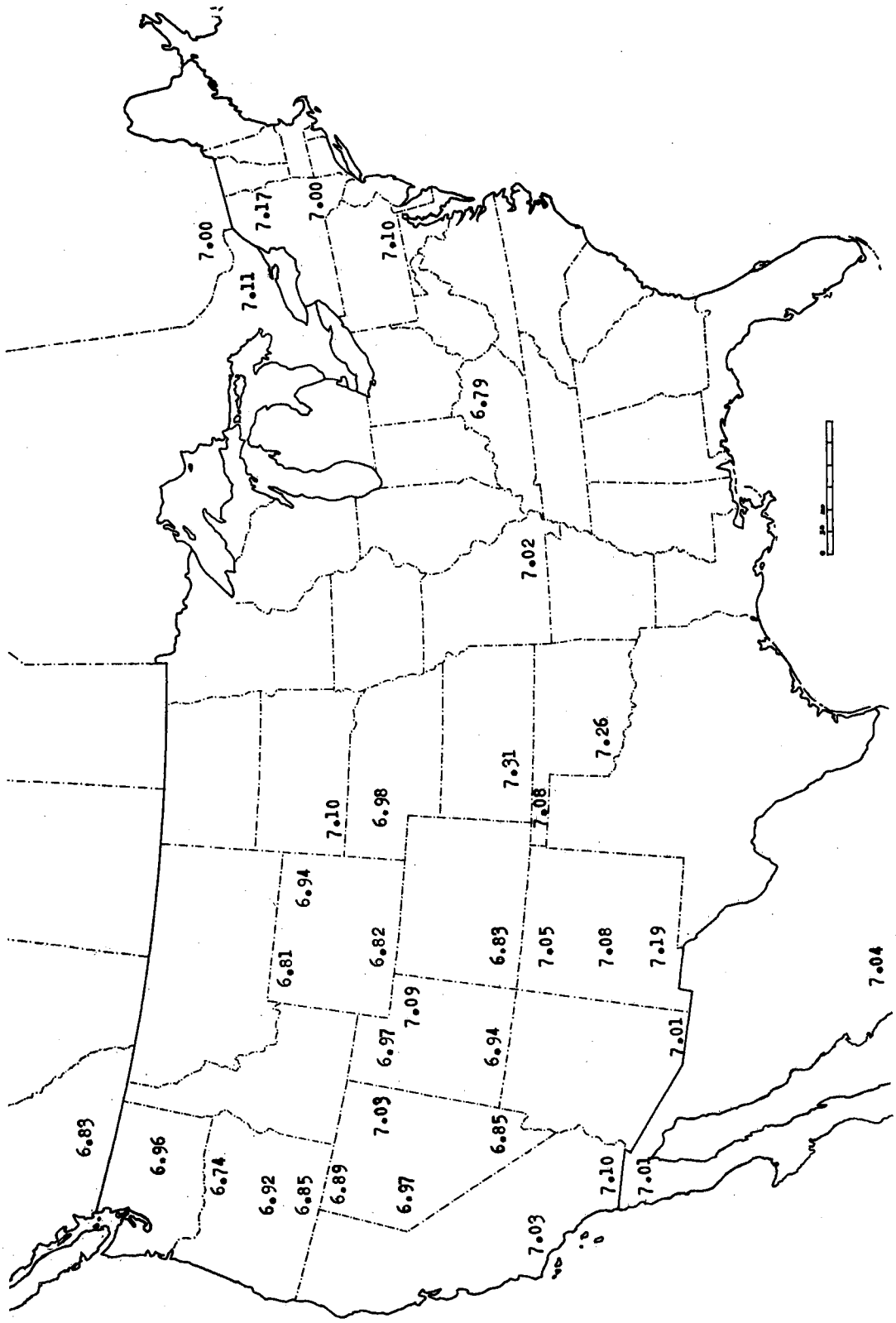

Fig. 11. Geographic distribution of means of mastoid breadth in Myotis leibi.

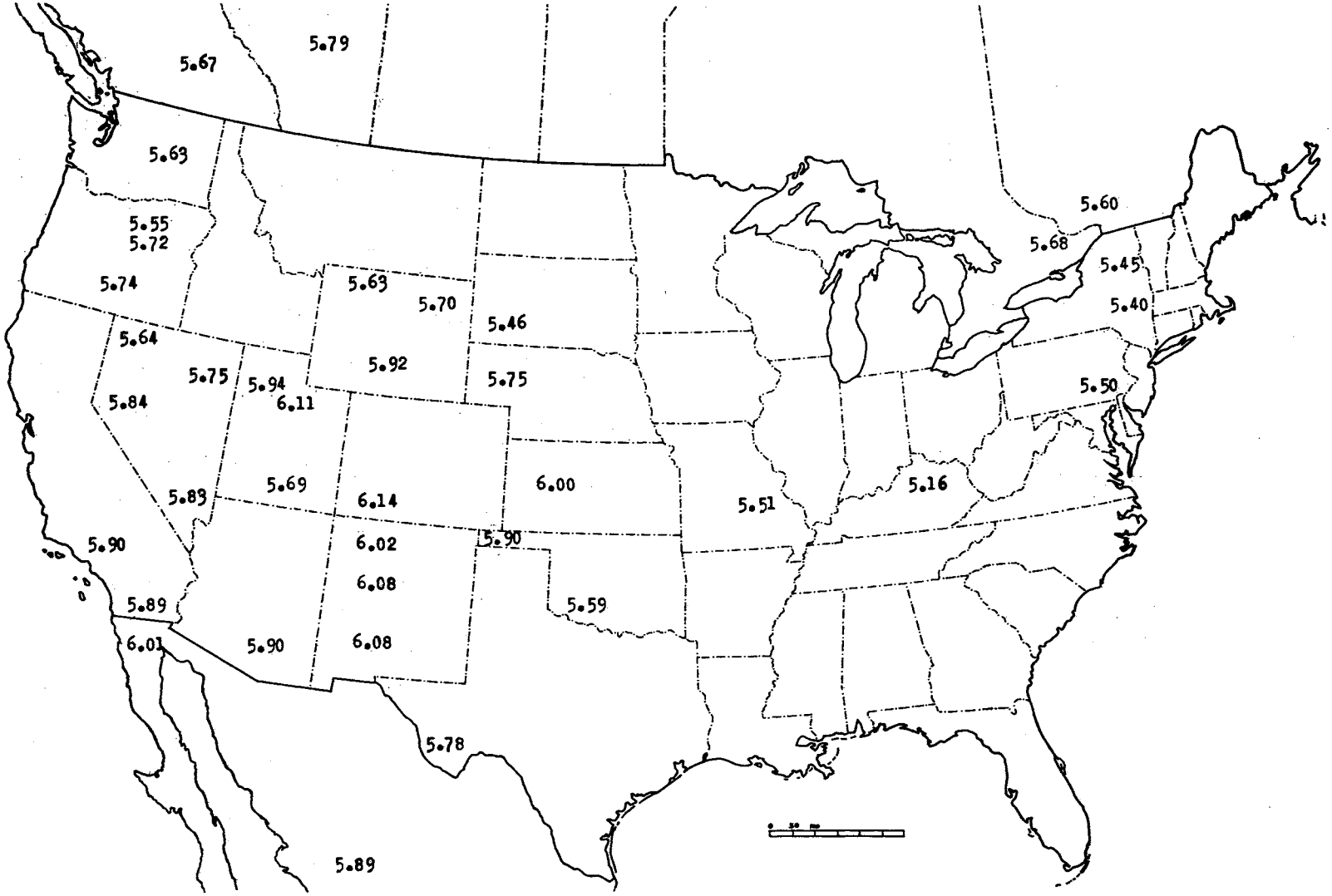

Fig. 12. Geographic distribution of means of length of palate in Myotis leibi.

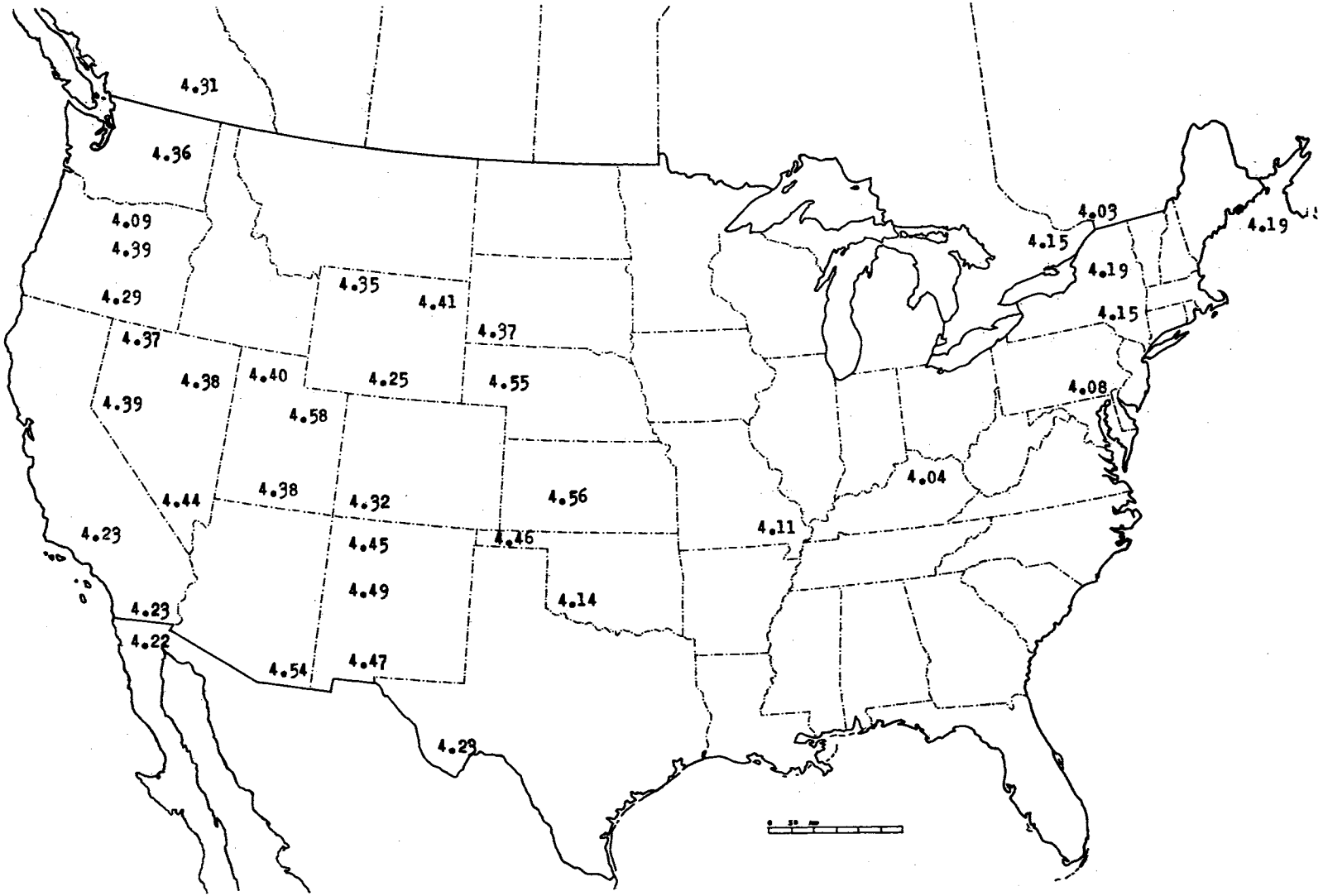

Fig. 13. Geographic distribution of means of cranial height of Myotis leibi.

V. REVISION OF THE SPECIES MYOTIS LEIBI

Myotis leibi is usually collected from mountain ranges, caves, or rock outcroppings. As Cockrum (1960) has shown distribution may not be continuous over an entire subspecies range, although published maps may suggest this. Discontinuous distribution caused by topography probably causes gene exchange to vary between subpopulations.

The geographic distribution of the species (Fig. 2) indicates that the Great Plains divides the species in two. Only across the Southern plains, from the rocky areas of eastern New Mexico to the Ouachita-Ozark Mountains plateau is there a tenuous connection by way of the Wichita Mountains of southwestern Oklahoma. Although bats of the Wichitas closely resemble Northeastern bats they do show some western affinity. However, no New Mexican specimens show eastern affinity.

Eastern Kansas, southeastern Nebraska and Iowa appear to be devoid of this species, as the Iowa record (Scott, 1938) proves to be Myotis keeni. The writer questions the record for northeastern Nebraska (Stevens, 1945), and a diligent search failed to locate the specimen. There is doubt it was preserved (Gunderson per. comm.). No direct relationship is apparent between specimens from Kansas, Nebraska and the Dakotas and those from Missouri, Kentucky and the Northeast.

No direct relationship is apparent between Kansas bats and those of the Oklahoma Panhandle nor between Kansas bats and the Wichita

Mountains population as was indirectly suggested by Davis (1944) when he related Texas Big Bend specimens to those of Kansas. The Texas population and other peripheral populations except for the Kansas one, seem to be directly related to the central Southwestern population.

It might be expected that the Mississippi Valley would act as a barrier between the Ozarks and the Appalachians, but the Missouri specimen and the southeastern Oklahoma specimen are indistinguishable from Appalachian bats.

The Great Basin in Nevada seems to act as a filter barrier between the Southwest and the Pacific Northwest. Numerous character shifts of low magnitude occur at various places. The totality of change is clinal. Probably this is correlated with the Great Basin terrain, which would divide the species into sub-groups of limited distribution.

The northern Rockies in Idaho, British Columbia, and Alberta seem to separate coast and inland populations completely.

Populations of the west-central Kansas chalk bluffs are semi-isolated from those of the Nebraska buttes.

Subspecies range and areas of intergradation as determined in this study are shown in Fig. 14. These data indicate a recognizable unnamed subspecies in the Pacific Northwest that intergrades with the northern plains population near the eastern end of the Snake River basin in Idaho. It intergrades, over most of the Great Basin of Nevada, with the southwestern subspecies found in Arizona, Utah, Colorado, and New Mexico. Southern California specimens seem to be intergrades also. Formal description of the new subspecies, and a summary of the Myotis leibi complex of subspecies follows.

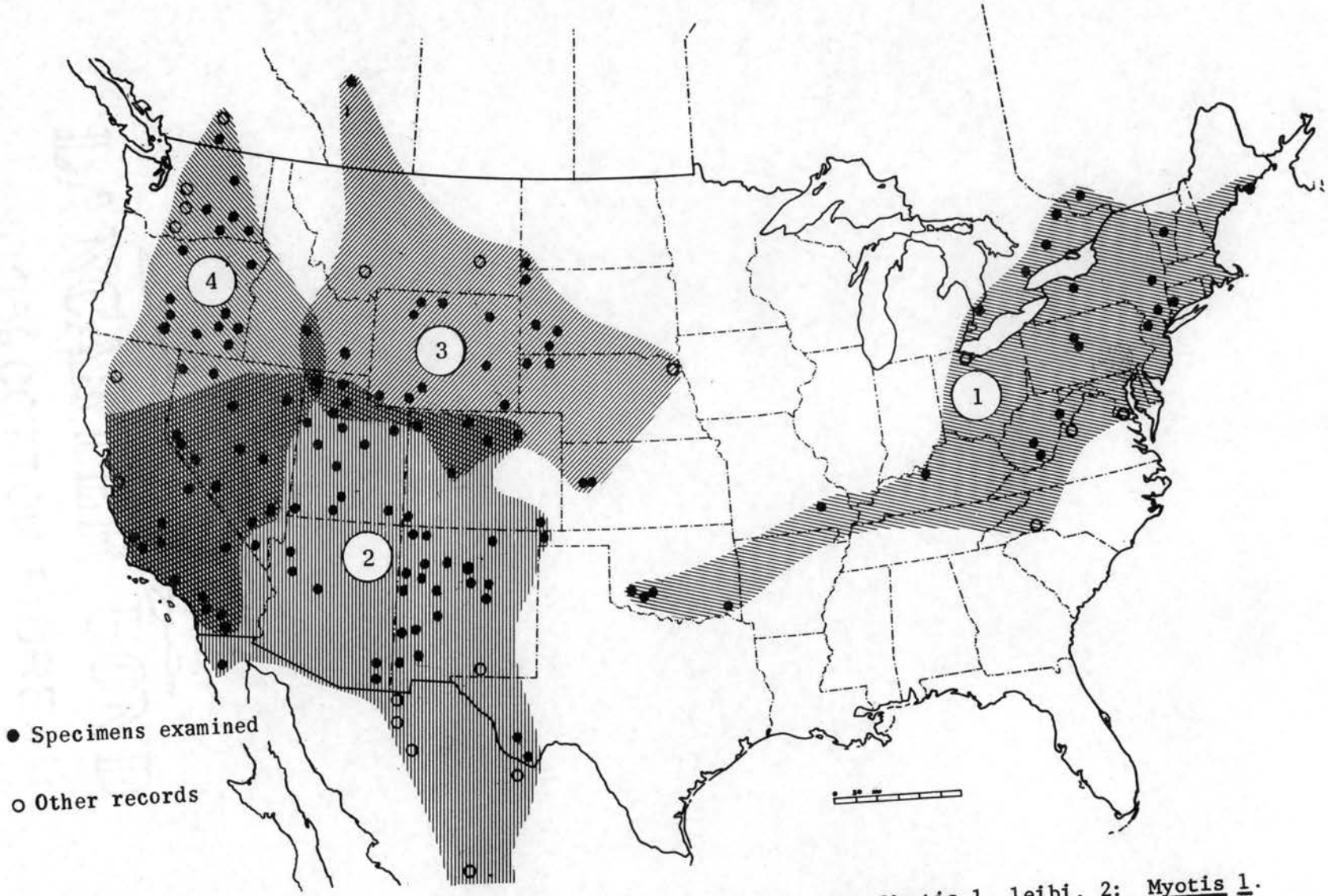

Fig. 14. Geographical distribution of Myotis leibi. 1: Myotis l. leibi, 2: Myotis l. melanorhinus, 3: M. l. ciliolabrum, 4: Myotis l. microcephalus. Cross hatching indicates areas of intergradation.

Myotis leibi microcephalus Ssp. nov.

Type, adult male, skin and skull, No. 18458 San Diego Society of Natural History, from 14 miles S. E. Bend, Skelton Cave, Deschutes County, Oregon. Collected by S. S. Jewett on 24 February 1929.

Distribution. British Columbia, Washington, Oregon and Northwestern Nevada, intergrading with Myotis leibi melanorhinus to the south and M. l. ciliolabrum to the east (Fig. 14).

Diagnosis. Size small for the species. Condylobasal length averaging under 13; maxillary tooth row averaging 5.05 or less, often near 4.75; forearm usually less than 32, often near 30; mastoid breadth less than 7.09; cranial breadth small usually less than 6.35. Color variable but usually darker, more buffy than in M. l. ciliolabrum and appearing more tricolored than in M. l. melanorhinus.

Measurements of Type

Total length, 82; tail length, 42; hindfoot length, 7; forearm length, 31.71; third metacarpal length, 29.59; condylobasal length, 12.83; length of palate, 5.67; rostral width, 3.49; interorbital width, 3.06; cranial breadth, 6.26; mastoid breadth, 6.96; maxillary tooth row length, 4.88; cranial height, 4.42. An appreciation of the difference between M. l. microcephalus and the other subspecies may be seen by examining Figs. 4-13.

This subspecies is compared with M. l. leibi, M. l. melanorhinus, and M. l. ciliolabrum in Table III.

Myotis leibi microcephalus and M. l. leibi are geographically disjunct. They are the smallest of two subspecies. Myotis l. leibi is

darker than M. l. microcephalus which has a light yellow band between apical brown and basal black bands. This band is absent in M. l. leibi. The available material can be separated with 100% accuracy.

M. l. microcephalus is smaller than M. l. melanorhinus (Table III) in forearm length, cranial breadth, and condylobasal length. Color separates the two as M. l. melanorhinus lacks the light yellow band on the hair present in M. l. microcephalus.

M. l. microcephalus is distinguished from M. l. ciliolabrum by its darker warm buffy color and by forearm length, condylobasal length and cranial breadth (see Table III).

Subspecific variation. The smallest size is in Oregon and becomes progressively larger through Washington into British Columbia. The Nevada specimens show intergradation with M. l. melanorhinus in all measurements. No northern California specimens were examined and conclusions of range extent in California cannot be drawn. Southern California specimens appear intergradient between melanorhinus and microcephalus.

Remarks. This subspecies was named microcephalus because of its reduced skull measurements, especially of the braincase.

Specimens examined.--Total 72 from the following localities: BRITISH COLUMBIA: Osoyoos, 3 (UBC). WASHINGTON: Grant County: O'Sullivan Dam, 1 (SCW). Whitman County: Wawawai, 1 (SCW). Franklin County: Cornell, 1 (SCW). Adams County: Macall, 1 (SCW). Chelan County: Shelan, 1 (UW). OREGON: Malheur County: Cow Lakes, 1 (SD); Sheaville, 1 (USNM); Rockville, 1 (USNM); Skullsprings, 1 (USNM); Rome, 1 (USNM); Riverside, 3 (USNM); Lake County: Silver Lake, 1 (SD). Sherman County: Millers, 3 (USNM), 1 (MCZ). Baker County:

Homestead, 1 (USNM). Deschutes County: Sisters, 1 (USNM); 14 mi. SE Bend, 1 (SD); Skeleton Cave, 1 (OS). Harvey County: T 31 S R 32 1/2 E Sec. 33, 1 (OS). County unknown: McDermitt, 3 (USNM); John Day, 1 (USNM); Warren Valley, 1 (USNM); Blue River, 1 (USNM); 12 mi. Creek, 1 (USNM). NEVADA: Washoe County: Little High Rock Canyon, 4 (MVZ); 4 1/2 mi. E Cal. line Smoke Creek, 6 (MVZ); 9 mi. E Cal. line Smoke Creek, 3 (MVZ); 9 1/2 mi. E and 3 mi. N Bidwell, 1 (MVZ). Pershing County: El Dorado Canyon Humboldt Range, 1 (MVZ). Storey County: 6 mi. NE Virginia City, 1 (MVZ). Mineral County: Fletcher, 12 (MVZ); 1 mi. NE Rawhide, 3 (MVZ). Lander County: Peterson Creek Shoshone Mts., 4 (MVZ); Smith Creek, 1 (MVZ). Lyon County: 12 mi. S Yerington Walker River, 1 (MVZ); Ramsey, (MVZ), 2 (UI).

Myotis leibi leibi

1842 Vespertilio leibi, Audubon and Bachman, Jour. Acad. Nat. Sci. Philadelphia, Ser. I, Vol. 8, P. 284, Erie Co. Ohio, then Michigan.

1913 Myotis winnemana Nelson, Proc. Biol. Soc. Washington, Vol. 26, P. 183, Aug. 8. Plummer Island Md.

1928 Myotis subulatus leibi. Miller and G. M. Allen, Bull. U. S. Nat. Museum 144: 171, May 25.

Distribution. Southern Oklahoma, probably northwest Arkansas, northern half of Tennessee and western quarter of North Carolina, north to the coast of Maryland, thence northward to Otter Point Maine, west to Wakefield Quebec, southern Ontario to the type locality Erie Co. Ohio to the northern part of Kentucky and central Missouri (Fig. 14).

Diagnosis. Color, dark brown showing little or no chestnut. Overall size small; interorbital width usually greater than 3.15; forearm usually less than 32; third metacarpal usually less than 31. Braincase flattened with little or no rise in profile between rostrum and braincase.

Comparisons. The meristic characteristics of Myotis l. leibi are compared with those of the other subspecies in Table III. M. l. leibi is darker than M. l. ciliolabrum and specimens examined could be separated by color with 100% accuracy. M. l. leibi is darker than M. l. melanorhinus. Neither subspecies has tricolored hair but melanorhinus has a chestnut color and less sheen than leibi. The Wichita specimens are intermediate in color between the two subspecies. M. l. leibi is compared to M. l. microcephalus under the discussion of M. l. microcephalus°

Subspecific variation. The Myotis leibi leibi of Maine and Canada are largest for the subspecies. From these localities there is a clinal trend to a smaller size to the West and Southwest to Kentucky. From Kentucky to southwestern Oklahoma the trend is toward larger size with bats of the Wichita Mountains almost equal to Ontario bats. Color: Color trends are shown in Fig. 3. Little variation was found between the bats of the Ozark-Ouachita Mountains and Appalachians.

Specimens examined.--Total 119 from the following localities: ONTARIO: Renfrew County: Fourth chute near Douglas, 32, (ONMC), 4 (MCZ), 3 (USNM), 1 (UMMZ), 4 (ROM), 2 (AMNH); Peel County: Terna Cotta, 1 (ROM). Middlesex County: Mt. Brydges, 1 (ROM). Hastings County: Tyendinaya tup, 1 (ROM). QUEBEC: Gatineau County: la. fliche Cave near Wakefield, 2 (ROM), 1 (ONMC). VERMONT: Orange

County: Vershire, Ely Copper Mine, 3 (MCZ). MAINE: Hancock County: Mt. Desert Island, Otter Point, 1 (UMMZ). CONNECTICUT: Litchfield County: Roxbury, 1 (AMNH). NEW YORK: Monroe County: Lake Winape Mines, 3 (AMNH). Albany County: Hailes Cavern, Thatcher Park, 2 (CUM), 7 (MCZ); Albany Filtration Plant Cave, 1 (AMNH). Westchester County: Croton Falls Magnetic Mine, 1 (AMNH). NEW JERSEY: Morris County: Hibernia, Hibernia Mine, 1 (CUM); Andover Iron Mine, 2 (AMNH). Passaic County: Midvale, Roomey Mine, 2 (AMNH). PENNSYLVANIA: Mifflin County: Siglerville, Aitkin Cave, 1 (MCZ), 1 (CUM); 1 mi. NE Siglerville, 2 (CUM), 11 (AMNH); lime sink near Siglerville, 1 (CUM), 4 (AMNH), Centre County: Stover Cave 2 (AMNH). WEST VIRGINIA: Monroe County: Greenville, Saltpeter Cave, 2 (PU). Greenbriar County: Organ Cave, 2 (REM); White Sulpher Springs, 1 (MCZ). Pendleton County: Schoolhouse Cave 4 1/2 mi. NE Riverton, 1 (UI). KENTUCKY: Beckenridge County: Wind Cove, 1 (SIU), 2 (SIU); Mammoth Cave, 2 (USNM). MISSOURI: Iron County: 3 mi. S Graniteville, 1 (UI). OKLAHOMA: McCurtain County: W of Mt. Fork River, 1 (OSU). Greer County: Guster Cave, 2 (OSU); 1 mi. N Granite, 1 (OSU). Kiowa Co.: Suoboda Cave 1 mi. NW Mountain Park, 1 (OSU); Radziminski Mts. Cave, 2 (OSU); Windmill Cave 15 mi. S and 2 mi. W of Carnegie, 1 (OSU). Comanche County: South Refuge Building, 1 (OSU).

M. leibi melanorhinus

1886, Vespertilio ciliolabrum Merriam, Proc. Biol. Soc. Washington, Vol. 4, P. 4, December 17, (Part; specimens from Grant County, N. Mexico).

1911, Myotis californicus ciliolabrum Cary, North Amer. Fauna, No. 33, P. 209, Aug. 17, (Part; specimen from Snake River, Routt County, Colo.).

1890, Vespertilio melanorhinus Merriam, North Amer. Fauna No. 3, P. 46, Sept. 11. A Synonym of californicus Lyon and Osgood, Catal. Type sp. Mamm. U. S. Nat. Mus., Bull. U. S. Nat. Mus., No. 62, P. 271, Jan. 28, 1909.

1893, Vespertilio albescens melanorhinus H. Allen, Monogr. Bats North Amer., Bull. U. S. Nat. Mus., No. 43 P. 91, March 14, 1894.

1893, Vespertilio nitidus henshawii. H. Allen, Monogr. Bats North Amer. Bull. U. S. Nat. Mus., No. 43, P. 103.

1903, Myotis orinomus Elliot, Field Columbian Mus., Publ. 79, Zool. ser., Vol. 3, P. 228, June, (La Grulla, San Pedro Martir Mountains, Lower California, Mexico.)

1908, Myotis lucifugus longicrus J. Grinnell, Univ. California Publ. Zool., Vol. 5, P. 158, October 31, (Part).

1928, Myotis subulatus melanorhinus Miller and Allen, U. S. Nat. Mus. Bull. 144, P. 169, April 18.

Type locality. San Francisco Mountain, Coconino Co. Arizona near Little Spring. The type specimen is No. 18684 in United States National Museum.

Distribution. Oklahoma Panhandle, eastern New Mexico south to Texas Big Bend country, south through Chihuahua, Durango, and Michiocon, north to lower California, Arizona, southern Nevada, Utah and Colorado.

Diagnosis. The largest subspecies of M. leibi. Maxillary tooth row length over 5.10, forearm greater than 32.00. Cranial height over 5.30; braincase rounder and a greater rise in transition between

rostrum and braincase. Color is bright chestnut to light reddish brown, much paler on West Coast.

Comparisons. M. l. melanorhinus is darker than M. l. ciliolabrum. Melanorhinus does not have tricolored hair as does ciliolabrum. Melanorhinus is larger than ciliolabrum as is shown in Table III. The overlap in measurements between the two subspecies is usually caused by the large size of the Kansas ciliolabrum. However, the color of the Kansas specimens observed is so distinct from melanorhinus that they can be separated with 100% accuracy. Melanorhinus is compared to M. l. leibi and M. l. microcephalus under their respective heading.

Subspecific variation. The largest members of this subspecies are found in New Mexico. The Oklahoma Panhandle specimens are also large. Toward the west specimens are more variable and show morphological difference. Colorado specimens are often undefinable to subspecies as are some Nevada, Utah, and California specimens. Because this subspecies intergrades with all other subspecies, it exhibits high variability.

Specimens examined.--Total 258 from the following localities: NEW MEXICO: Bernalillo County: 14 (UNM); Sandia Park 3 (UNM); Isleta, 2 (UNM); Till N, R. 4E Sec. 3, 1 (UNM). Sandoval County: 4 (UNM). Valencia County: 2 (UNM); Canyon Lobo Ranger Station, 2 (UMMZ); 8 mi. SE Paxton, 9 (UMMZ); 1 1/2 mi. SW San Mateo, 1 (UMMZ). Socorro County: Magdalena, 14 (UNM); Socorro, 1 (USNM). Valencia County: 2 (UNM). Sierra County: Winston 2 (UNM). Catron County: Glenwood, 6 (UNM), 1 (AMNH). San Juan County: 3 (UU), 5 (UNM), Farmington, 1 (UNM). McKinley County: Crownpoint, 4 (UNM), Zuni, 1 (USNM); Ft. Wingate, 2 (USNM); Thoreau, 2 (AMNH). Taos County:

4 (UNM); Tres Piedros, 1 (USNM); Sheep Springs, 1 (UNM); Contonment, 1 (USNM). San Miguel County: Pecos, 1 (USNM); Las Vegas 1 (USNM). Grant County: Silver City, 2 (USNM), 1/2 mi. E Vanadium, 1 (UA); Bridge #7 Coolidge Dam Road, 1 (NM). Guadalupe County: Santa Rosa, 2 (USNM). Santa Fe County: Santa Fe, 1 (JMM). Rio Arriba County: 167 mi. above mouth of San Juan, 5 (UU). COLORADO: Baca County: Skull Canon, 1 (CU). Gunnison County: Red Creek, 1 (UU), Dry Gulch and Gunnison River, 1 (UU). Rio Blanco County: 1 (AMNH). Montezuma County: Mesa Verde Natl. Park, 5 (KU). OKLAHOMA: Cimarron County Mouth N Carizzo Creek, 5 (OSU). TEXAS: Culberson County: 2 (TCWC). Brewster County: W. T. Burhom Ranch, 1 (AMNH); 3 mi. S Government Springs, 1 (AMNH). ARIZONA: Cochise County: 3.5 mi. SW Portal, 4 (UA); SW Research Station, Portal, 1 (UA); 1.5 mi. S Portal, 1 (UA); South Fork Cave Creek, 1 (PU); Chiricahua Mountains, 1 (OSU). Mohave County: Glag Mine Hualapai Mts., 3 (UA); 4.5 mi. SE of Kingman, 2 (UA). Yavapai County: Prescott, 1 (AMNH). NEVADA: Clark County: Sheep Mts., 1 (DRD), 1 (RH), Potosi Mts., 1 (MVZ). Nye County: 7 mi. W Tyho, 1 (ROM), 2 1/2 mi. E, 1 mi. S Grape Vine Peak, 2 (MVZ); 2 mi. S Oak Creek, 1 (MVZ), 1/2 mi. S Oak Springs, 1 (MVZ); 7 mi. N Tyho, 12 (MVZ); Wisconsin Creek, 1 (MVZ); Ouinn Canyon Mts., 8 (MVZ). White Pine County: Lehman Cave, 3 (MVZ); Mt. Moriah, 2 (MVZ). Esmeralda County: Cave Spring, 7 (MVZ). Lincoln County: Irish Mts., 4 (MVZ). UTAH: Carbon County: Soldier Canyon, 2 (RH). Kane County: 4 mi. N Kaneh, 2 (RH). Garfield County: Star Springs, 1 (UU); 5 mi. N Boulder, 1 (UU); Posey Lake, Aquarius Plateau, 1 (BYU). Utah County: Goshen Dam, 1 (UU). Tooele County: 1 mi. E of Ibapah, 5 (UU); 5 mi. N of Ibapah, 4 (UU). Sanpete County: 3 1/2 mi. E Sterling, 1 (UU).

San Juan County: Abajo Mts., 1 (UU). Millard County: 1/2 mi. NE Maple Grove Camp, 4 (UU); 4 mi. E Oak City, 1 (UU). Unitah County: 1/2 mi. SW Dragon, 1 (UU); Leroy, 1 (UU). Box Elder County: 5 mi. SW Nafton, 1 (UU). Washington County: Valcanic Cave at Dameron Valley, 1 (UU); Santa Clara, 1 (UU); Upper Sand Cave Reservoir, 1 (UU). CALIFORNIA: Monterey County: 1 (CAS). Inyo County: Argus Mts., Darwin Canyon Falls, 1 (UMMZ). San Diego County: 5 mi. E Pine Valley on Highway 80, 6 (SD); 1 (RH); Jaumba, 1 (DRD); 1 (AMNH); Vallecito Stge, 1 (CN); Olianis H Marsh, 2 (AMNH); Santa Ysabel, 1 (SD); Santerae Canyon Bridge, 1 (SD). Riverside County: 5 mi. E Aquanga, 1 (RH); Snow Creek Canyon, 1 (ON). Tulare County: 4 mi. SE Porterville, 1 (AMNH). Los Angeles County: 7 mi. N Azura, 1 (MH). Mono County: 2 mi. S Benton Station, 1 (DRD); White Mts., 1 (DRD). Kern County: Carneros Springs, Temblor Range, 1 (CAS); Walker Basin, 1 (DRD). San Luis Obispo County: 5 mi. NE Shandon, 3 (CAS); 9 mi. W Simmler, 1 (CAS); 1 mi. SW Cholame, 1 (CAS). BAJA CALIFORNIA MEXICO: La Grulla, 5 (USNM), 1 (MCZ), 2 (SD); Santa Eulalia, 1 (SD); Valle de la Trinidad, 4 (SD); Sierra Juarez, 1 (SD); Sanjri de Cristo, 3 (SD). MICHOACON: San Jaun, 2 (WNMZ).

M. leibi cilioliabrum

Vespertilio ciliolabrum 1886, Merriam Proc. Biol. Suc. Washington, Vol. 5, p. 2. December 17 Banner, Trego Co. Kansas.

Vespertilio nididus ciliolabrum 1894, H. Allen Monogr. Bats North Amer., Bull. U. S. Nat. Mus., No. 43 (1893), p. 101, March 14.

Myotis californicus ciliolabrum 1897, Miller North Amer. Fauna, No. 13, p. 72, Oct. 16.

TABLE III

MEASUREMENTS OF MYOTIS LEIBI

Locality	Forearm Length	Third Metacarpal Length	Condylobasal Length	Length of Palate	Rostral Width	Interorbital Width	Cranial Breadth	Mastoid Breadth	Maxillary Tooth Row	Cranial Height	Sample Size
					leibi						
1.	31.61	30.18	12.98	5.68	3.43	3.28	6.77	7.11	4.86	4.14	46
2.	30.61	28.85	12.64	5.59	3.40	3.22	6.73	7.10	4.78	4.08	11
3.	31.40	29.17	12.97	5.59	3.44	3.23	6.72	7.26	4.98	4.14	6
4.	30.67	29.39	12.41	5.40	3.35	3.24	6.68	7.00	4.69	4.14	8
					melanorhinus						
5.	32.60	31.10	13.22	5.90	3.64	3.08	6.45	7.08	5.12	4.46	5
6.	33.56	31.73	13.34	6.01	3.54	3.06	6.47	7.05	5.23	4.44	6
7.	33.83	31.63	13.52	6.07	3.62	3.15	6.55	7.18	5.29	4.47	18
8.	33.59	31.73	13.51	6.07	3.55	3.13	6.54	7.08	5.26	4.49	16
9.	32.31	31.57	13.38	6.01	3.52	3.00	6.37	7.01	5.21	4.22	17
					ciliolabrum						
10.	32.88	30.49	13.57	6.00	3.66	3.28	6.69	7.30	5.26	4.55	10
11.	32.53	30.75	13.02	5.70	3.45	3.11	6.40	6.94	5.04	4.41	5
12.	31.44	29.58	12.88	5.63	3.42	2.97	6.29	6.81	4.94	4.34	6
13.	31.90	29.70	13.03	5.75	3.54	3.12	6.50	6.98	5.08	4.55	7
					microcephalus						
14.	31.97	30.20	12.79	5.73	3.27	3.00	6.19	6.85	4.89	4.29	4
15.	31.92	30.55	12.91	5.66	3.36	3.14	6.33	6.82	4.95	4.31	9
16.	31.35	29.85	12.76	5.64	3.43	3.04	6.27	6.87	4.89	4.37	11
17.	31.49	30.57	12.71	5.55	3.28	2.93	6.20	6.74	4.77	4.09	3

Locality: 1. Renfrew County, Ontario; 2. Mifflin County, Pennsylvania; 3. Wichita Mountains, Oklahoma; 4. Albany County, New York; 5. Cimarron County, Oklahoma; 6. San Juan, New Mexico; 7. Socorro County, New Mexico; 8. Bernalillo County, New Mexico; 9. Baja, California; 10. Trego County, Kansas; 11. Campbell County, Wyoming; 12. Greybull, Wyoming; 13. Davis County, Nebraska; 14. Malheur County, Oregon; 15. Osoyoos, British Columbia; 16. Washoe County, Nevada; 17. Miller, Oregon.

Myotis subulatus Warren 1910, Mammals of Colorado p. 275. (Not of subsequent writers).

Myotis subulatus subulatus Say, 1928, Miller and Allen. The American Bats of the Genera Myotis and Pizonyx. U. S. Nat. Mus. Bull. 144, p. 168, May 25.

Type locality. Near Banner, Trego Co. Kansas in bluff on Hackberry Creek, about one mile from Castle Rock. Type specimen is in National Museum.

Distribution. Kansas northeast to the northern border of Nebraska north to southwest North Dakota, Montana, southern Alberta, south to Wyoming and Idaho.

Diagnosis. Color; lightest subspecies of M. leibi with tricolored hair of straw or very light orange color. Intermediate in size between melanorhinus and microcephalus (see Table III).

Comparisons of M. l. ciliolabrum to the other subspecies is discussed under their respective subspecies account and in Table III.

Subspecific variation. The Kansas population attains the greatest overall size. It is possible that sub-groups of this subspecies are semi-isolated. M. l. ciliolabrum intergrades with microcephalus to the west and melanorhinus to the south. Color variation is shown in Fig. 3.

Specimens examined--Total 70 from the following localities: KANSAS: Logan County: 2 (KU), Elkader Chalk Bluffs, 1 (KT). Trego County: 3 (KU); Banner, 8 (USNM), 4 (KU). NEBRASKA: Sheridan County: 4 (KU). Sioux County: SE Sugar Loaf twp Sand Cr., 1 (UMMZ); Antelope twp, 1 (UMMZ). NORTH DAKOTA: Slope County: Amidon, 1 (KU). SOUTH DAKOTA: Shannon County: Corral Draw, 6 (AMNH), 1 (UMMZ). Jackson County: Kadoka, 1 (UMMZ). Pennington County: Diamond S Ranch, 1 (UMMZ);

8 mi. ENE Rapid City, 1 (UMMZ). Harding County: 8 (KU). IDAHO: Blaine County: Carey, 2 (UMMZ). Bannock County: Pocatello, 1 (ROM). WYOMING: Rattlesnake, 1 (USNM); Greybull, 2 (USNM), 1 (MCZ); Bull Lake, 1 (USNM). Campbell County: 6 (KU). Park County: 1 (KU); Cody, 1 (USNM). Converse County: 1 (KU). Laramie County: 1 (KU). Sweetwater County: Bitter Creek, 1 (AMNH); 339 Ri. mi. N Green River, 1 (UU). Uinta County: Mountain View, 1 (ROM). Bighorn County: Otto, 2 (AMNH). ALBERTA: Red Deer River near Rumsey, 1 (UAC), 2 (HMC). COLORADO: Morgan County: 7 mi. N and 2 mi. E Weldona, 1 (SIU).

VI. SUMMARY

This study was undertaken to examine, critically, intraspecific variation in the bat Myotis subulatus (Say).

The validity of subulatus as the specific name for the species is discussed and it is concluded that Say's specimen was Myotis yumanensis, not the species is leibi (Audubon and Bachman).

Seven skin measurements, eight skull measurements and color analyses were made of 519 specimens.

In most characters individual variation is found to be average and secondary sexual variation probably unimportant.

The geographic variation of ten meristic characters and color indicate four areas of character homogeneity separated by areas of change in character values. The concordancy of these areas form a basis for determining the number of subspecies and the range of each subspecies.

Four subspecies of Myotis leibi are recognized. Three subspecies, leibi, melanorhinus and ciliolabrum have available names but an undescribed form microcephalus is formally described.

The geographic distribution of each subspecies was shown.

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Biographical:

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Education: Graduated from Warren High School, Warren, Arkansas, in 1960; attended Ouachita Baptist College in 1960-61; attended Arkansas Agricultural and Mechanical College, 1961-63 and received the Bachelor of Science degree from Arkansas A. & M. College in May, 1965. Completed the requirements for the Master of Science degree from Oklahoma State University in May, 1965.

Professional Experience: Fellow, Oklahoma State University Cooperative Wildlife Research Unit, 1964; Graduate Teaching Assistant, Oklahoma State University, 1964-65.

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