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SYSTEMATICS AND BIOGEOGRAPHY OF *ONYCHOMYS LEUCOGASTER* IN WESTERN NORTH AMERICA

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ABSTRACT.—Systematic and biogeographic relationships of *Onychomys leucogaster* in western North America were assessed using morphometric, karyotypic, and fossil data. The names *O. l. utahensis* and *O. l. fuscogriseus* are relegated to synonymy with *O. l. brevicaudus*. Populations in northeastern Oregon and eastern Washington are named and described as a new subspecies. Populations in the Wyoming Basin are referred to the Northern Plains subspecies, *O. l. missouriensis*. We hypothesize that *O. leucogaster* inhabited a "cold" desert refugium in the location of the present Mohave "hot" desert during the last glacial episode. The species colonized the Great Basin during late glacial time and the Wyoming Basin and northern Columbia Plateau during early Holocene time. Populations of *O. leucogaster* on the Colorado Plateau phenetically are more like those on the Central Great Plains than those in the Great Basin or Wyoming Basin.

The northern grasshopper mouse, *Onychomys leucogaster*, inhabits shrub steppe, desert shrub, and grassland habitats in western North America. Hall (1981) listed 13 subspecies, of which three—*O. l. brevicaudus* Merriam, *O. l. fuscogriseus* Anthony, and *O. l. utahensis* Goldman—occur primarily in the Great Basin and on the Columbia Plateau (capitalized names of biogeographic provinces follow Hunt, 1974). *O. l. brevicaudus* reportedly also ranges into the southwestern corner of the Bridger Basin in Wyoming (Hall, 1981; Hollister, 1914; Long, 1965) and intergrades with *O. l. arcticeps* Rhoads, the subspecies that inhabits the remainder of the Wyoming Basin and the Central Great Plains. *O. l. missouriensis* (Audubon and Bachman) is known from north and east of the Wyoming Basin on the Northern Great Plains. The Colorado Plateau is occupied by two subspecies, *O. l. melanophrys* Merriam west of the Colorado and Green rivers and *O. l. pallescens* Merriam to the east (Fig. 1).

Systematic relationships of these taxa have not been analyzed since Hollister's (1914) generic revision. Carleton and Eshelman (1979) indicated the need for reanalysis, pointing out that populations of *O. leucogaster* in the Great Basin are distinct phenetically from populations elsewhere. Conversely, Engstrom and Choate (1979) opined that populations in the Wyoming Basin in Colorado more nearly resemble populations in the Great Basin than populations on the Central Great Plains. The objectives of this study were: 1) to analyze patterns of variation among the subspecies *O. l. brevicaudus*, *O. l. fuscogriseus*, and *O. l. utahensis* of the Great Basin/Columbia Plateau; 2) to evaluate the relationship between *O. l. brevicaudus* of the Great Basin, *O. l. arcticeps* of the Central Great Plains, and *O. l. missouriensis* of the Northern Great Plains; 3) to propose a model, based in part on *O. leucogaster*, to explain mammalian colonization of the cold deserts of the Great Basin, Wyoming Basin, Columbia Plateau, and Colorado Plateau (Fig. 1) in the period after the Wisconsin pluvial.

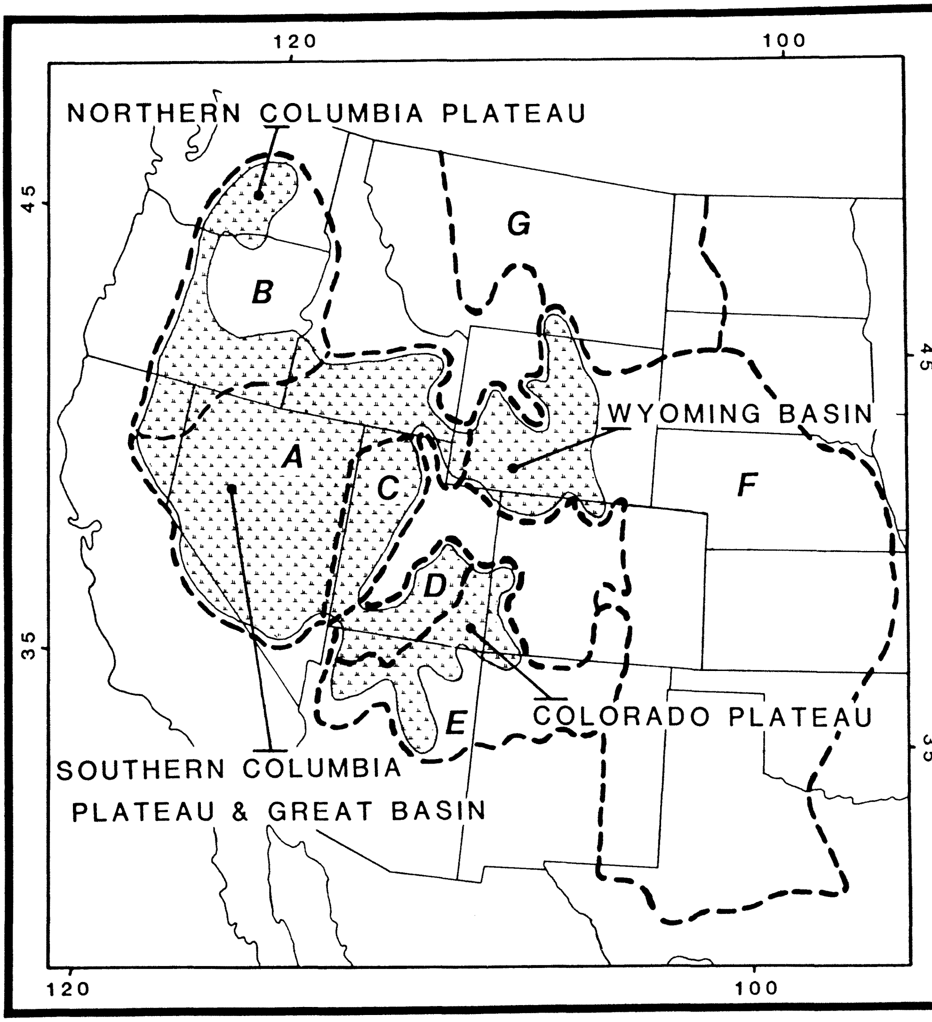

FIG. 1.—Approximate geographic distribution of "cold" desert habitats in western North America (stippled—after Shelford, 1963), and ranges of subspecies addressed in this study (Engstrom and Choate, 1979; Hall, 1981). A, *Onychomys leucogaster brevicaudus*; B, *O. l. fuscogriseus*; C, *O. l. utahensis*; D, *O. l. melanophrys*; E, *O. l. pallescens*; F, *O. l. arcticeps*; G, *O. l. missouriensis*.

MATERIALS AND METHODS

We initially assigned specimens to six age classes based on wear to the lower molars, generally as described by Engstrom and Choate (1979) except that we subdivided their "old adult" age class into two categories, one in which the teeth were not worn below the cingulum (age class 5) and the other in which they were (age class 6). We recorded pelages as juvenile, molting to subadult, subadult, molting to adult, adult, or worn adult (Engstrom and Choate, 1979) and noted that the squamosal component of the zygomatic arch expands laterally as the skull enlarges with age. We based final recognition of age classes primarily on tooth wear but made adjustments when obvious inconsistencies existed between tooth wear, pelage, and development of the zygomatic arches.

We recorded four external and 13 cranial (to the nearest 0.1 mm) measurements for each specimen. Total length (TL), length of tail (LT), length of hind foot (LHF), and length of ear (LE) were taken from museum specimen labels. Greatest length of skull (GLS), breadth of braincase (BB), zygomatic breadth (ZB), interorbital constriction (IC), rostral breadth (RB), and cranial depth (CD) were taken as described by Choate (1973) and Engstrom and Choate (1979). Length of nasals (LN) (described by Genoways, 1973), alveolar length of maxillary toothrow (ALMX), and length of interparietal (LIP) were measured with dial calipers and a dissecting microscope. Coronoid-angular height (HCA), measured from the angular process to the top of the coronoid process, and capsular-angular height (CAH), from the angular process to the top of the capsular process, were measured with the ramus set on the lower arm of a dial caliper. Length of mandibular toothrow (LM) and depth of ramus (DR, taken below the midpoint of ml on the labial side), were measured with an ocular micrometer mounted in a dissecting microscope.

Dorsal pelage color is not an especially useful taxonomic character for analysis of systematic relationships among populations of *O. leucogaster* (Dice and Blossom, 1937; Engstrom and Choate, 1979; Van Cura and Hoffmeister, 1966). Accordingly, we discuss patterns of pelage coloration herein but did not assess geographic trends thereof. We scored three states for the color of the hair tufts in front of the pinnae: 1—tuft composed of no or few white hairs; 2—tuft with few but conspicuous white hairs (generally comprising the lateral portion of the ear tuft); 3—tuft composed primarily of white hairs contrasting markedly with brown and gray shades of the dorsum. Scoring was done with the aid of a dissecting microscope so that even worn pelages could be evaluated.

We analyzed two components of nongeographic variation for all cranial characters using procedures of the SAS computer programs (Helwig and Council, 1979). Sexual dimorphism was assessed using age classes 2, 3, and 4 of sample WB-21, and variation among age classes 2, 3, and 4 was determined for samples WB-21, GB-9, GP-33, CP-14, and CP-17. These data were subjected to a single classification analysis of variance (GLM) and an a posteriori contrast analysis (Duncan multiple range test; DUNCAN option of GLM) to identify nonsignificant subsets for each variable.

We calculated standard univariate statistics (mean, range, standard deviation, standard error, and coefficient of variation) for each character in each sample using the UNIVARIATE procedure of SAS. Geographic variation was assessed for each cranial character except ZB using the ANOVA and DUNCAN options of GLM.

Multivariate analyses excluded external measurements because of their high variability and ZB because of a large number of missing values. A correlation matrix was generated from standardized character means for each sample and then subjected to principal components analysis (PCA) using NT-SYS (Rohlf et al., 1974). A cluster analysis (procedure UPGMA of NT-SYS) subsequently was performed on a distance matrix derived from standardized sample means.

Statistical analyses were applied to a total of 34 geographic samples (Fig. 2), each designated below by a number and code letters that identify the physiographic region and accompanied by the multivariate sample size (in parentheses). GB-1 (46).—OREGON: Gilliam, Jefferson, Morrow, Sherman, Umatilla, and Wheeler counties; WASHINGTON: Adams, Asotin, Benton, Douglas, Franklin, Garfield, Grant, Lincoln, Walla Walla, and Yakima counties. GB-2 (20).—CALIFORNIA: Modoc and Siskiyou counties; NEVADA: northern Humboldt and Washoe counties; OREGON: Klamath and Lake counties. GB-3 (13).—IDAHO: Ada, Canyon, Elmore, Owyhee, and Washington counties; OREGON: Harney and Malheur counties. GB-4 (9).—IDAHO: Bingham, Butte, and Minidoka counties. GB-5 (21).—UTAH: Box Elder, Salt Lake, and Tooele counties. GB-6 (21).—UTAH: Beaver, Juab, and Millard counties. GB-7 (12).—NEVADA: Nye County. GB-8 (6).—NEVADA: Eureka and White Pine counties. GB-9 (36).—NEVADA: Elko County. GB-10 (45).—NEVADA: southern Humboldt County. GB-11 (21).—CALIFORNIA: Lassen and Plumas counties; NEVADA: southern Washoe County. GB-12 (24).—NEVADA: Churchill, Lander, and Pershing counties. GB-13 (13).—CALIFORNIA: Alpine and Mono counties; NEVADA: Lyon and Mineral counties. CP-14 (40).—ARIZONA: Coconino County west of the Colorado River; UTAH: Kane County. CP-15 (15).—UTAH: Carbon, Emery, Garfield, and Wayne counties. CP-16 (14).—COLORADO: Mesa County; UTAH: Grand County. CP-17 (27).—UTAH: San Juan County. CP-18 (24).—ARIZONA: Coconino County east of the Colorado River. WB-19 (19).—IDAHO: Bear Lake County; UTAH: Daggett, Rich, and Uintah counties; WYOMING: Lincoln County, Uinta County, and Sweetwater County west of the Green River. WB-20 (10).—WYOMING: Sublette County. WB-21 (56).—WYOMING: Sweetwater County east of the Green River. WB-22 (16).—COLORADO: Moffat County. WB-23 (31).—COLORADO: Jackson County; WYOMING: Albany and Carbon counties. GP-24 (11).—WYOMING: Big Horn, Hot Springs, and Park counties. GP-25 (5).—WYOMING: Fremont County. GP-26 (10).—WYOMING: Natrona County. GP-27 (21).—NEBRASKA: Cherry, Dawes, and Sheridan counties; SOUTH DAKOTA: Bennett County. GP-28 (21).—MONTANA: Big Horn, Carter, Powder River, and Rosebud counties; SOUTH DAKOTA: Harding County; WYOMING: Campbell, Crook, Sheridan, and Weston counties. GP-29 (14).—NORTH DAKOTA: Billings, Bowman, Morton, Oliver, Sioux, and Stark counties. GP-30 (9).—MONTANA: Dawson, Richland, and Roosevelt counties; NORTH

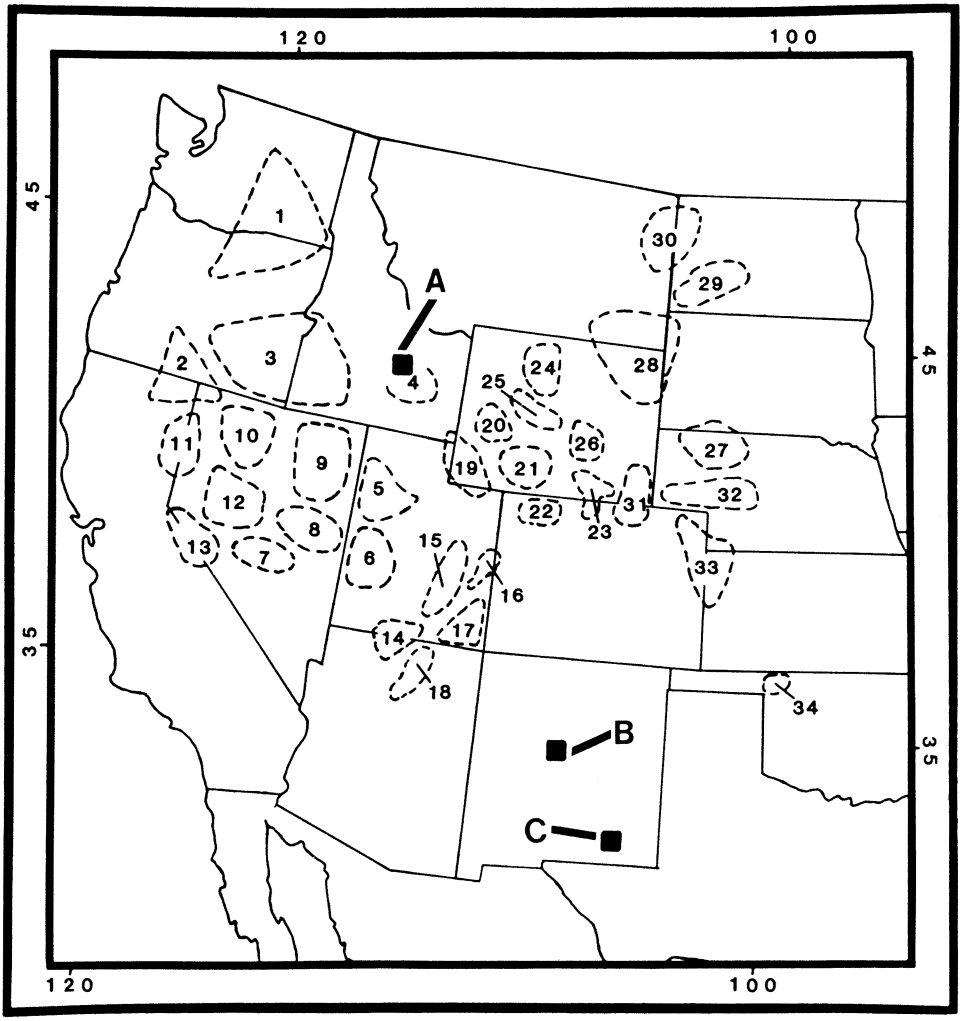

FIG. 2.—Locations of samples of *Onychomys leucogaster* used in this study. Numbers correspond to samples identified in text. Letters refer to fossil faunas identified in text: A, Owl Cave; B, Isleta Caves; C, Dry Cave.

DAKOTA: Williams County. GP-31 (27).—COLORADO: Larimer and Weld counties; WYOMING: Goshen, Laramie, and Platte counties. GP-32 (26).—NEBRASKA: Cheyenne, Custer, Garden, Keith, Kimball, Lincoln, Logan, and Thomas counties. GP-33 (48).—COLORADO: Logan and Yuma counties; KANSAS: Wallace County; NEBRASKA: Dundy and Hitchcock counties. GP-34 (17).—OKLAHOMA: Harper County.

Non-differentially stained karyotypes of *O. leucogaster* were prepared using the in vivo bone-marrow technique described by Patton (1967) as modified by Baker et al. (1982). Diploid and fundamental numbers were determined from photomicrographs. Karyotypes were examined from the following localities (number of specimens, all housed at MHP, and sex are indicated in parentheses). COLORADO. *Jackson Co.*: Arapahoe National Wildlife Refuge, 8,100 ft., T8N, R79W, NW ¼ Sec. 5 (1F). KANSAS. *Rawlins Co.*: 4 mi. S, 5 mi. E Atwood, T4S, R32W, NW ¼ Sec. 6 (1F). NEVADA. *Elko Co.*: 4 mi. SW Deeth, exit 328 off hwy. I-80, River Ranch rd. (1M, 1F). OREGON. *Morrow Co.*: 4 mi. S Boardman (1M, 2F). UTAH. *Emery Co.*: 8 mi. S, 11 mi. W Green River, San Rafael Desert, T22S, R14E, Sec. 23 (1M). *Wayne Co.*: 8 mi. N, 10 mi. E Mt. Ellen, Burr Desert, 4,800 ft., T30S, R12E, Sec. 6 (1M, 1F). WYOMING. *Lincoln Co.*: 10¾ mi. E Sage, T21N, R117W, SW ¼ Sec. 7 (3F).

We examined *O. leucogaster* from three late Pleistocene/early Holocene cave faunas (Fig. 2). Because

TABLE 1.—*Variation among age classes 2, 3, and 4 for 13 cranial measurements (identified in text) of* Onychomys leucogaster. *Horizontal lines represent nonsignificant subsets as determined by Duncan's multiple range tests.*

	GB-9			WB-21			GP-33			CP-14			CP-17		
Character	2	3	4	2	3	4	2	3	4	2	3	4	2	3	4
GLS															
BB															
ZB															
IC															
RB															
LN															
ALMX															
CD															
LM															
LIP															
DR															
HCA															
CAH															

most specimens consist of edentulous mandibles, alveolar length of the mandibular toothrow (ALMN) was recorded for each fossil mandible and for representative extant specimens, as follows (sample size is listed in parentheses): Wasden site (117), Owl Cave, Bonneville County, Idaho—10,500–8,000 BP (Guilday, 1969); Owl Cave (93)—8,000–3,400 BP; Dry Cave (15), Bernalillo County, New Mexico—mostly 15,000–10,000 BP, all post full-glacial (Harris, 1970, 1980); Isleta Caves (13), Eddy County, New Mexico—suggested date near 11,000 BP (Harris, 1970), described by Harris and Findley (1964). Samples of Recent northern grasshopper mice used for comparison were: COLORADO PLATEAU (13)—Mesa County, Colorado; Grand, Kane, San Juan, and Wayne counties, Utah. GREAT BASIN (82)—Mono County, California; Bingham, Butte, and Minidoka counties, Idaho; Elko and Humboldt counties, Nevada; Millard County, Utah. GREAT PLAINS (30)—Logan County, Colorado. WYOMING BASIN (47)—Jackson and Moffat counties, Colorado; Carbon, Sweetwater, and Sublette counties, Wyoming.

RESULTS

Nongeographic variation.—We found no significant mensural differences between sexes in age classes 2, 3, or 4. Carleton and Eshelman (1979), Engstrom and Choate (1979), and Van Cura and Hoffmeister (1966) likewise found little consistent sexual dimorphism in *O. leucogaster*. Therefore, sexes were pooled for subsequent analyses. Based on results of analyses of variation among age groups (Table 1), age classes 3 and 4 were pooled for all measurements except ALMX and LM, for which age classes 2, 3, and 4 were pooled.

Geographic variation.—Univariate statistics for representative geographic samples of *O. leucogaster* are presented in Table 2. Complete statistics are available from the authors upon request. Analyses of variance revealed significant ($P < 0.001$) differences among samples for all characters. In general, grasshopper mice from the Great Basin and Columbia Plateau were smallest, mice from the Wyoming Basin and the Northern Great Plains were intermediate, and specimens from the Colorado Plateau and the Central Great Plains were largest. LM and ALMX exhibited the most pronounced differences between mice from the Great Basin and all other samples. GLS was large in samples from the Central Great Plains and the Colorado Plateau. LIP consistently was large in specimens from the Colorado Plateau. Unlike other measurements, IC and RB were not smallest in mice from the Great Basin/Columbia Plateau except in sample GB-1.

Dice-Leraas diagrams for LN and ALMX (Fig. 3) illustrate the small size of grasshopper mice

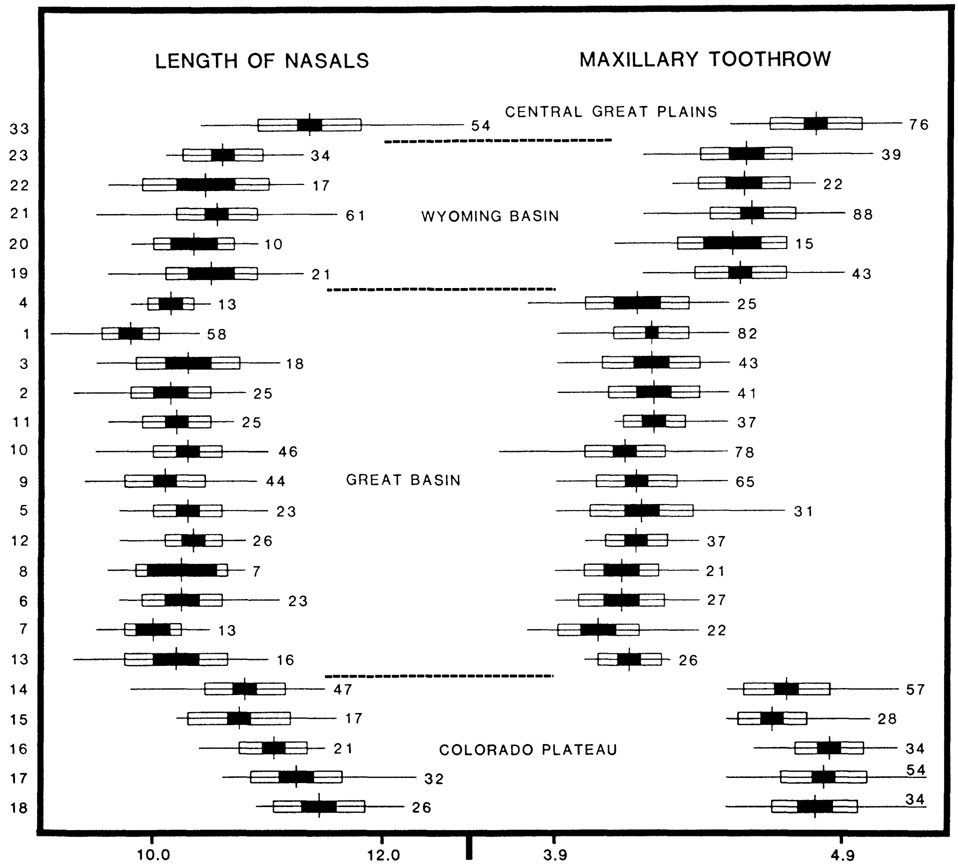

FIG. 3.—Geographic variation in length of nasals and alveolar length of maxillary toothrow in *Onychomys leucogaster*. The vertical line represents the mean, the horizontal line represents the range, the open box encompasses ±1 SD, and the closed box encompasses ±2 SE of the mean. Numbers along the left margin are sample numbers (identified in text), and numbers to the right of the horizontal lines are sample sizes.

in the Great Basin and on the Columbia Plateau. In particular, molar size is smaller in samples from the Great Basin and Columbia Plateau than from other regions based on ALMX and LM and by additional variables analyzed by Carleton and Eshelman (1979). Sample GB-1 averaged appreciably smaller than samples from farther south (Table 2). This sample was smallest within the Great Basin/Columbia Plateau for six of 12 characters (Riddle, 1984) and larger than only one other sample for two of the remainder. Specimens from the Wyoming Basin generally are intermediate in size between those from the Great Basin/Columbia Plateau and those from the Central Great Plains. Samples from the Colorado Plateau consistently average larger than those from the Great Basin, Columbia Plateau, or Wyoming Basin. On the Colorado Plateau, samples from west of the Colorado and Green rivers average smaller than those from farther east.

Analysis of variance among samples from the Great Basin/Columbia Plateau (Riddle, 1984) revealed little consistent north-to-south or east-to-west variation. One exception pertained to LM, which appeared to decrease in size clinally from north to south. LN was essentially invariant throughout the Great Basin, but sample GB-1 formed a unique, non-overlapping subset with short nasals. Furthermore, this sample formed a subset with only one other sample (GB-6) for RB, indicating a short, delicate rostrum in grasshopper mice from the northern Columbia Plateau as compared with *O. leucogaster* from the Great Basin and southern Columbia Plateau.

As in the univariate analyses, coherent regional groups were found in the principal component

TABLE 2.—*Descriptive statistics for 4 external and 13 cranial measurements for 7 representative samples of* Onychomys leucogaster. *The top number is the mean, the middle number is the standard error, and the number in parentheses is the sample size. Sample codes are identified in text.*

Sample	TL	LT	LHF	LE	GLS	BB	ZB	IC	RB	LN	ALMX	CD	LM	LIP	DR	HCA	CAH
GB-1	132.35	36.33	18.98	16.83	26.02	12.09	13.62	4.64	5.15	9.81	4.23	9.43	3.88	2.67	3.14	6.52	4.64
	0.80	0.43	0.11	0.21	0.06	0.03	0.08	0.02	0.02	0.04	0.01	0.03	0.01	0.03	0.02	0.03	0.03
	(55)	(55)	(55)	(23)	(46)	(55)	(29)	(56)	(58)	(58)	(82)	(51)	(83)	(54)	(59)	(59)	(59)
GB-9	136.12	37.50	19.74	17.36	26.40	12.17	13.93	4.76	5.38	10.08	4.18	9.60	3.79	2.75	3.20	6.70	4.67
	0.94	0.55	0.11	0.36	0.08	0.04	0.07	0.02	0.02	0.05	0.02	0.03	0.02	0.05	0.02	0.04	0.03
	(46)	(46)	(46)	(25)	(38)	(41)	(35)	(45)	(46)	(44)	(65)	(41)	(63)	(42)	(46)	(46)	(46)
CP-14	146.76	43.11	21.21	18.03	27.82	12.38	14.89	4.85	5.43	10.79	4.71	9.87	4.19	3.39	3.37	6.92	4.88
	1.13	0.58	0.14	0.26	0.07	0.05	0.08	0.02	0.02	0.05	0.02	0.04	0.02	0.04	0.04	0.04	0.04
	(46)	(46)	(38)	(32)	(44)	(44)	(37)	(47)	(47)	(47)	(57)	(44)	(55)	(44)	(46)	(46)	(46)
CP-17	150.70	45.88	22.18	18.76	28.42	12.60	14.59	5.02	5.53	11.27	4.84	10.15	4.36	3.28	3.38	7.07	4.84
	1.31	0.90	0.13	0.31	0.10	0.05	0.12	0.03	0.03	0.07	0.02	0.04	0.02	0.05	0.03	0.06	0.06
	(33)	(33)	(33)	(29)	(29)	(28)	(15)	(33)	(33)	(32)	(54)	(29)	(52)	(32)	(33)	(32)	(32)
WB-21	132.82	37.43	20.10	17.74	26.87	12.33	14.80	4.74	5.44	10.53	4.58	9.78	4.11	2.57	3.33	6.95	4.93
	0.92	0.52	0.15	0.14	0.07	0.03	0.08	0.02	0.02	0.05	0.02	0.03	0.01	0.04	0.02	0.04	0.04
	(60)	(61)	(59)	(53)	(57)	(60)	(51)	(60)	(61)	(61)	(88)	(59)	(89)	(62)	(62)	(62)	(62)
GP-28	140.65	36.96	20.00	17.00	26.89	12.33	14.74	4.57	5.24	10.76	4.62	9.85	4.15	2.46	3.45	7.04	5.02
	1.65	0.84	0.17	0.63	0.13	0.06	0.10	0.04	0.04	0.09	0.02	0.05	0.03	0.07	0.04	0.06	0.06
	(23)	(23)	(23)	(8)	(21)	(23)	(21)	(23)	(23)	(22)	(33)	(23)	(32)	(23)	(23)	(23)	(23)
GP-33	150.84	41.98	22.19	17.04	28.34	12.43	15.21	4.71	5.56	11.33	4.80	10.19	4.31	2.84	3.50	7.36	5.12
	0.97	0.64	0.13	0.23	0.07	0.04	0.09	0.02	0.03	0.06	0.02	0.03	0.02	0.05	0.02	0.04	0.04
	(55)	(55)	(54)	(47)	(52)	(54)	(51)	(55)	(55)	(54)	(76)	(54)	(74)	(55)	(54)	(53)	(54)

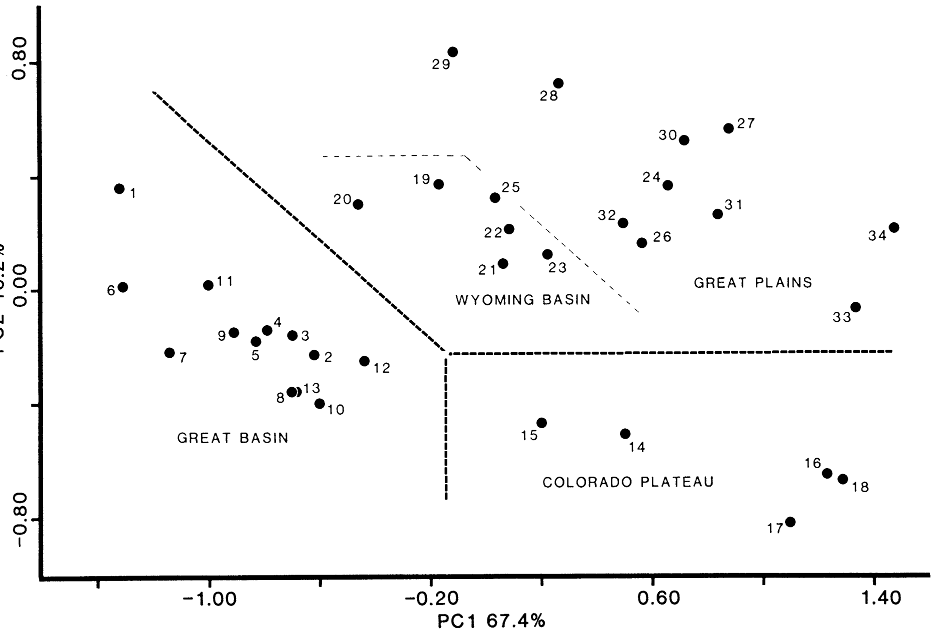

FIG. 4.—Scatter diagram of principal components I and II generated from the matrix of correlation of 12 cranial measurements using 13 samples of *Onychomys leucogaster* from the Great Basin/Columbia Plateau (1–13), 5 samples from the Colorado Plateau (14–18), 5 samples from the Wyoming Basin (19–23), and 11 samples from the Great Plains (24–34).

analysis (Fig. 4). Sample GB-1, for example, separated from other samples from the Great Basin/Columbia Plateau. The first axis separated samples from the Colorado Plateau east (CP-16, CP-17, and CP-18) and west (CP-14 and CP-15) of the Colorado and Green rivers. Samples from the Great Basin/Columbia Plateau again resembled those from the Wyoming Basin more than those from the Colorado Plateau. Most characters were highly correlated with PC1, reflecting

TABLE 3.—*Character loadings on the first three principal components for 12 cranial measurements (identified in text) for 34 samples of* O. leucogaster.

	I	II	III
Eigenvalue	8.085	1.944	0.845
% total variance	67.4	16.2	7.0
Cumulative % variance	67.4	83.6	90.6
Characters			
Greatest length of skull	0.922	−0.281	−0.109
Breadth of braincase	0.852	0.011	0.085
Interorbital constriction	−0.091	−0.925	0.135
Rostral breadth	0.433	−0.700	0.500
Length of nasals	0.953	−0.010	−0.116
Alveolar length of maxillary toothrow	0.929	0.104	−0.156
Cranial depth	0.973	0.010	−0.021
Length of mandibular toothrow	0.929	0.175	−0.154
Length of interparietal	0.444	−0.616	−0.619
Depth of ramus	0.916	0.135	0.120
Coronoid-angular height	0.942	0.149	0.215
Capsular-angular height	0.898	0.242	0.229

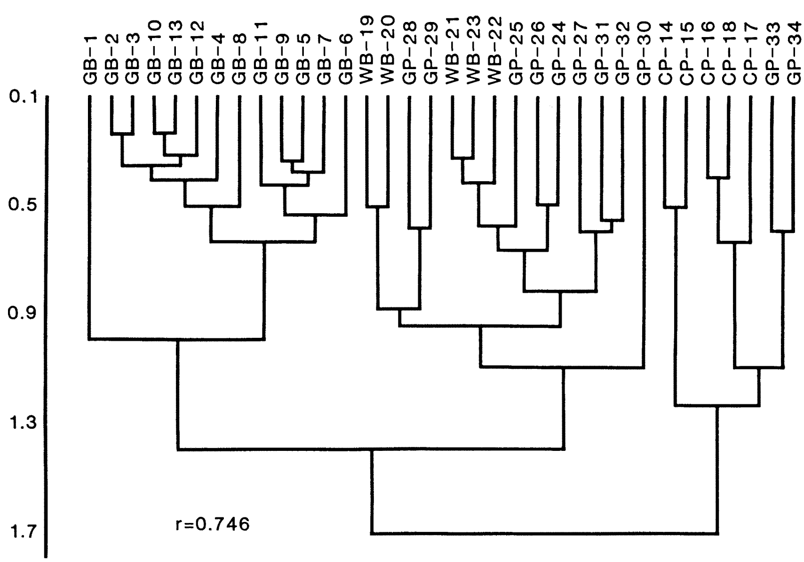

FIG. 5.—Cluster analysis (UPGMA) of 34 samples of *Onychomys leucogaster* generated from the distance matrix. The coefficient of cophenetic correlation is 0.746.

size-related differences among samples (Table 3). IC, RB, and LIP correlated highly with PC2. IC and RB reflect the anterior width of the skull; both are relatively large in the short but stout skulls of mice from the Great Basin/Columbia Plateau (with the previously noted exception of RB in GB-1). RB and IC are broad in specimens from the Colorado Plateau, particularly in samples CP-16, CP-17, and CP-18 from east of the Colorado and Green rivers.

A UPGMA cluster generally grouped samples within physiographic regions (Fig. 5). Samples from the Great Basin/Columbia Plateau, excepting GB-1, form a tight cluster. Another cluster joins samples from the Wyoming Basin and the Northern Great Plains. Finally, samples from the Central Great Plains and the Colorado Plateau cluster together, with differentiation apparent on the Colorado Plateau across the Colorado and Green rivers.

In general, ear tufts are white in mice from the Great Basin, the Columbia Plateau, the Wyoming Basin, and the Northern Great Plains (Fig. 6). Few mice from the Colorado Plateau have completely white ear tufts, although mice from west of the Colorado and Green rivers frequently have a small, lateral patch of white hairs. A transition to non-white ear tufts occurs in east-central Wyoming and the Nebraska Panhandle, and white ear tufts are practically nonexistent on the Central Great Plains. Coloration of ear tufts apparently is not related to overall coloration of the dorsum.

Karyotypes of northern grasshopper mice from the Great Basin, Columbia Plateau, Wyoming Basin, Central Great Plains, and Colorado Plateau apparently are invariant in diploid and fundamental numbers ($2n = 48$; $FN = 96$). This karyotype has been reported elsewhere for specimens from southern Kansas, Texas, and New Mexico (Baker et al., 1979).

Our three temporally successive Great Basin/Columbia Plateau samples, beginning about 10,500 years BP, correspond closely in ALMN (Fig. 7). Samples from Dry Cave and Isleta Caves are small; nevertheless, the specimens from Isleta Caves fall within the size range for extant *O. leucogaster* from the Great Plains and Colorado Plateau, and no overlap exists with fossil or extant material from the Great Basin/Columbia Plateau. The sample from Dry Cave varies more than that from the Isleta Caves; possibly the smallest of these specimens represent *O. arenicola* (Hinesley, 1979) or *O. torridus*. Nevertheless, specimens from Dry Cave clearly are larger than specimens from the Great Basin/Columbia Plateau.

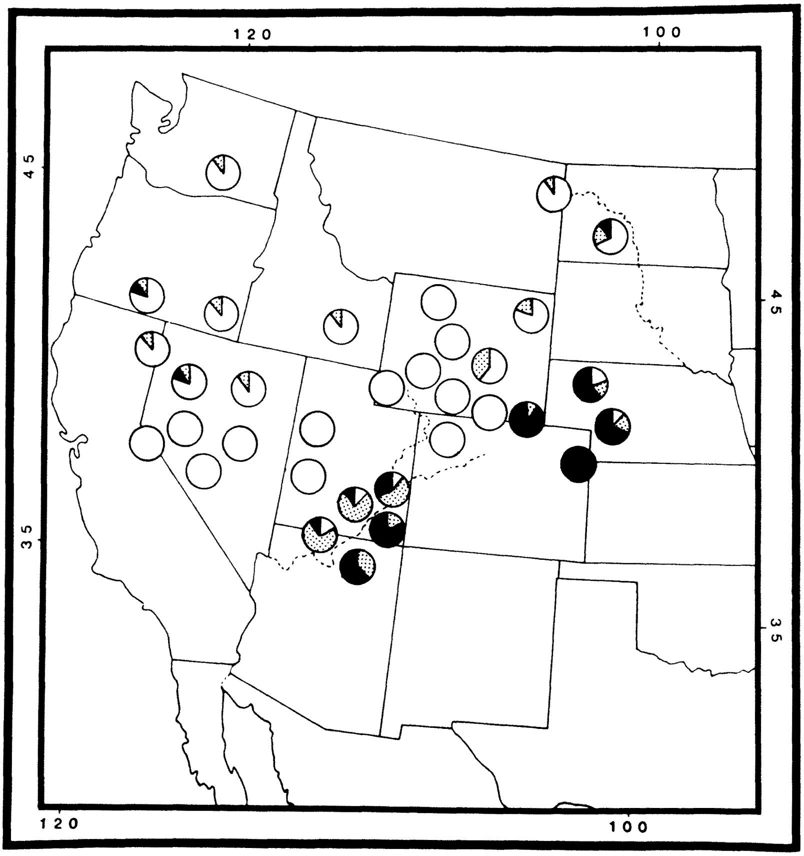

FIG. 6.—Geographic variation in frequency of character states for color of the ear tuft in *Onychomys leucogaster*: 1 (white), unshaded; 2 (partially white), stippled; 3 (non-white), darkly shaded. Samples are those illustrated in Fig. 2.

DISCUSSION

Great Basin/Columbia Plateau

Merriam (1891) described *O. l. brevicaudus* based on specimens from Blackfoot, Idaho. This new subspecies was said to differ from typical *O. leucogaster* (type locality, near Fort Clark, South Dakota—Merriam, 1889) in being smaller and having a shorter tail, larger ears, smaller skull, shorter rostrum, and shorter zygomatic arches. Subsequently, Anthony (1913) described *O. l. fuscogriseus* based on specimens collected at Ironside, Malheur Co., Oregon; he said (p. 11) that this subspecies differed from *O. l. brevicaudus* in color, although "cranial characters [are] as in *brevicauda* [sic]." Hollister (1914:441, 443) considered both subspecies valid, with *brevicaudus* occurring in "southern Idaho, extreme southwestern Wyoming, northwestern Utah, and west across the northern half of Nevada into Lassen, Plumas, and Mono Counties, California" and *fuscogriseus* occurring in "eastern Washington and Oregon, western Idaho, and northeastern California . . . South to Klamath Lake and the Madeline Plains." Hollister (1914) and Hall (1946) considered these two subspecies poorly differentiated and distinguishable only by color. Bailey (1936), Dalquest (1948), and Davis (1939) recognized both subspecies without comment. Subsequently, Goldman named two additional subspecies from eastern Utah—*O. l. utahensis* (Goldman, 1939) from Stansbury Island, Great Salt Lake, Tooele Co., and *O. l. aldousi* (Goldman, 1942) from the Desert Range Experiment Station, 50 miles west of Milford, Millard

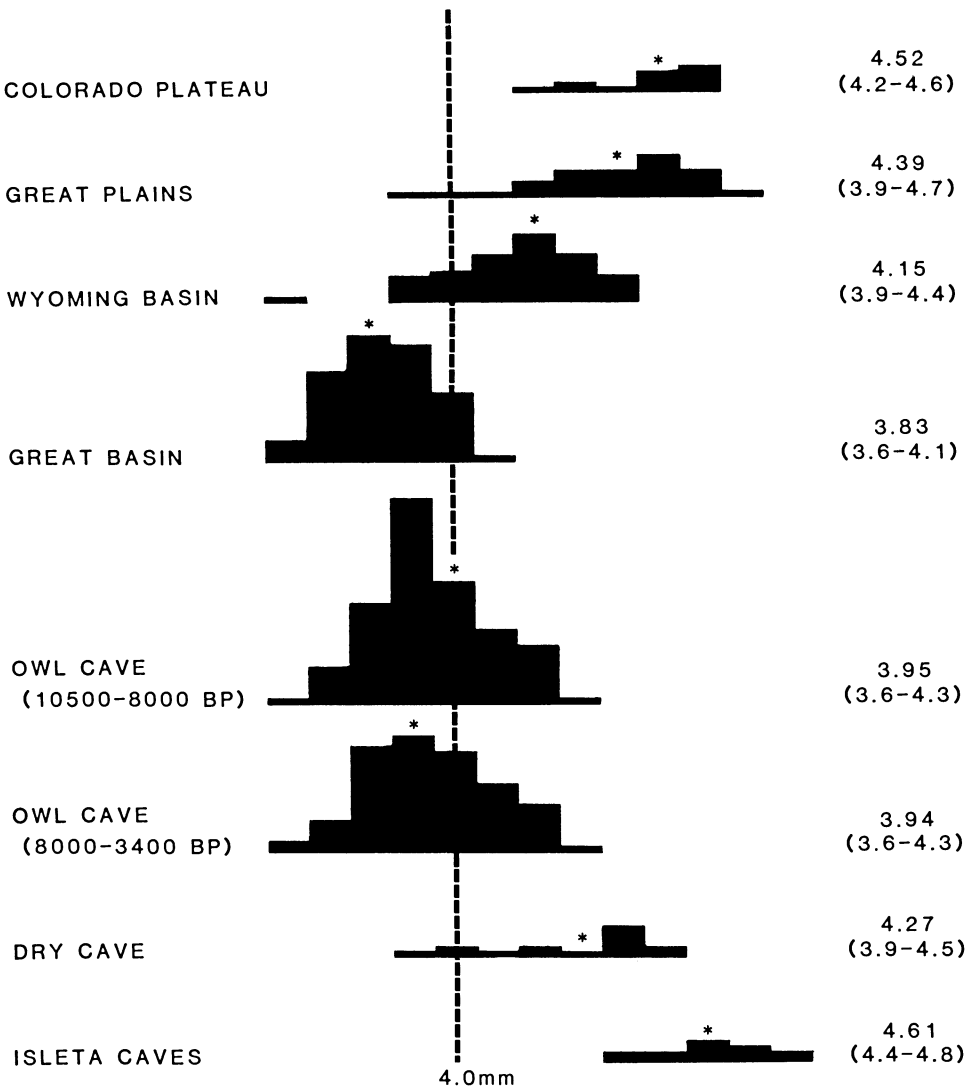

FIG. 7.—Histograms of alveolar length of the mandibular toothrow for fossil (bottom four) and extant (top four) samples of *Onychomys leucogaster*. The mean for each sample is indicated by an asterisk and is given (with the range in parentheses) at the right of the histogram.

Co. Durrant (1952) could not distinguish *aldousi* from *utahensis* and relegated the former as a junior synonym of the latter. He (p. 324) differentiated *utahensis* from *brevicaudus* "by its lighter color . . . and uniformly more convex skull in dorsal outline," but presented no distinguishing measurements. Durrant (1952:324) described the range of *utahensis* as "Western Utah, approximately the area formerly occupied by the Pleistocene Lake Bonneville."

The results of this investigation indicate that, with the exception of sample GB-1, samples of *O. leucogaster* from the Great Basin and Columbia Plateau are nearly uniform. Clinal variation across the Great Basin is suggested only by LM. Ecophenotypic variation might be expected because of the range in latitude (37°N to 44°N); plant communities change across this latitudinal range from open desert in the south in which *Artemisia* and *Atriplex* predominate to shrub steppe in the north in which *Artemisia* and *Agropyron* predominate (Küchler, 1964). These two associations are nearly continuous (Thompson and Mead, 1982; Wells, 1983).

An array of biological attributes (reviewed by McCarty, 1978) suggests that gene flow may occur at a high frequency among contiguous populations of *O. leucogaster*; these attributes include occupation of a wide variety of habitats, a tendency toward carnivory (therefore reduced dependence on specific kinds of vegetation for food), a large home range and propensity toward nomadism, and a vocal repertoire suggesting long range intraspecific communication. The existence of a distinct morphological shift among populations of *O. leucogaster*, therefore, suggests the presence of a substantial barrier to dispersal. Such a barrier presumably exists between populations represented by sample GB-1 (in northeastern Oregon and eastern Washington) and those to the south in the remainder of the Columbia Plateau and Great Basin. The extensively forested Ochoco, Blue, and Wallowa mountains and a broad tract of *Juniperus-Artemisia* steppe between the Ochoco and Cascade mountains (Daubenmire, 1975; Küchler, 1964) may constitute such a barrier.

According to current taxonomy (Hall, 1981), samples GB-1, GB-2, and GB-3 represent the subspecies *O. l. fuscogriseus*. However, unlike sample GB-1, samples GB-2 and GB-3 do not differ morphometrically from samples of *O. l. brevicaudus* (GB-4 and GB-7 through GB-13). Anthony (1913) and Hollister (1914) correctly identified a change in dorsal pelage color near the boundary between *brevicaudus* and *fuscogriseus*, the latter being darker than the former, but this change is not definitive. Certain specimens from south of the subspecies boundary (e.g., AMNH 122158 from the western shore of Pyramid Lake) are indistinguishable in color from adult *fuscogriseus* sampled near Vale, Malheur Co., Oregon. Additionally, mice from south-central Idaho (e.g., specimen BYU 4975 from Butte County, Idaho) often are nearly as dark as specimens from Oregon. The distribution of dark *O. leucogaster* corresponds to the distribution of lava beds and volcanic soils of the Columbia Plateau in Washington, Oregon, the Snake River Plains of Idaho, and parts of northern California (Dalquest, 1948; Hall, 1946; Hunt, 1974). The relationship between color of dorsum in terrestrial, nocturnal small mammals and shades of the substrate on which they dwell has been described (Benson, 1933; Dice and Blossom, 1937) and documented experimentally (Dice, 1945, 1947; Kaufman, 1974, 1975). Kaufman (1974) suggested that matching of pelage and brightness of background is as adaptive as matching of pelage and color of background. The darker pelages of *O. leucogaster* from this region probably are not as bright as the paler brown pelages of mice from farther south, and thus better match the grayish volcanic soils.

We examined five of the ten paratypes of *fuscogriseus* collected by Anthony at Ironside, Malheur Co., Oregon. Anthony apparently misinterpreted the developmental sequence of pelages in grasshopper mice and thereby incorrectly aged these specimens. For example, Anthony (1913) described specimen AMNH 33538 as being in transition from immature to adult based on condition of the pelage. Based on tooth wear, this specimen clearly represents category 2; moreover, based on development of tail hair and presence of old juvenile pelage under fresh pelage, this animal clearly is a subadult. Anthony thus probably included subadult pelages, which are darker than adult pelages, in his description of the subspecies *fuscogriseus*, thereby accentuating its difference from *brevicaudus*. In color of the ear tuft, *fuscogriseus* differs little from *brevicaudus*.

Samples GB-5 and GB-6 represent the subspecies *O. l. utahensis* in western Utah. Again, no morphometric differences exist between these samples and samples (listed above) of *brevicaudus*. As Durrant (1952) noted, *O. leucogaster* is particularly pale in western Utah, where the species inhabits the Bonneville Basin, a region of pale, alkaline soils (Cronquist et al., 1972) left by the recession of Pleistocene Lake Bonneville. However, specimens from within the range of *brevicaudus* (e.g., MVZ 41851 and 41852 from White Pine County, Nevada) that occur in the Bonneville Basin are indistinguishable in color from specimens (e.g., USNM 2783 from Tooele County, Utah) from within the range of *utahensis*. Accordingly, populations assigned to the subspecies *utahensis* are merely local color variants that otherwise do not differ from the subspecies *brevicaudus*.

Wyoming Basin

Long (1965) included within the range of *O. l. brevicaudus* an area "along Bear River in Lincoln County," which is in southwestern Wyoming west of the Bear River Divide. ALMX in a sample of 15 specimens from southwestern Wyoming (west of the Bear River Divide) and adjacent areas of Utah and Idaho (Riddle, 1984) averaged 4.49 (range, 4.3–4.7), well within the range of variation found in populations in the Wyoming Basin but near the upper extreme for populations in the Great Basin/Columbia Plateau region (Fig. 3). Because ALMX consistently separates the latter populations from the former, and because no available evidence otherwise aligns them, we restrict the range of *brevicaudus* to areas west of the eastern margin of the Snake River Plain in Idaho.

Discovery of an abrupt morphometric discontinuity between populations of *O. leucogaster* on either side of the Middle Rocky Mountains was unexpected. A corridor (as low as 1,830 m between Blackfoot Reservoir and Bear Lake, but rising to 2,134 m along a series of north-south ridges east of Bear Lake) between the Snake River Plain near Blackfoot, Idaho, and the Bridger Basin near Cokeville, Wyoming, presently consists of shrub steppe slopes and cultivated lowlands. This corridor appears to be suitable for habitation by *O. leucogaster*, although trapping near Soda Springs in 1983 yielded no *Onychomys*. Dispersal through this corridor might occur, but the abrupt shift there between small and medium-sized mice suggests that populations of *O. leucogaster* in the Wyoming Basin are effectively isolated from those in the Great Basin/Columbia Plateau region.

Although morphometric data suggest the existence of a barrier at the east end of the Snake River Plain, dispersal between the Great Basin/Columbia Plateau and Wyoming Basin likely occurred in the recent past. Specimens in samples WB-19 and WB-20 are slightly smaller than specimens in samples from farther east in the Wyoming Basin. This pattern, and the high frequency of white ear tufts in specimens from the Wyoming Basin, suggest gene exchange with populations in the Great Basin/Columbia Plateau region. We note in this regard that two small mammals associated with *O. leucogaster* in the Great Basin and on the Columbia Plateau, *Brachylagus idahoensis* and *Perognathus parvus*, occur eastward into the Wyoming Basin as far as Kemmerer and the Green River, respectively (Campbell et al., 1982; Kirkland, 1981), suggesting a recent intrusion of sagebrush steppe species from the Great Basin/Columbia Plateau into southwestern Wyoming. Also, one of us (BRR) recently (5 August 1983) trapped *P. parvus* near Soda Springs, Idaho, at an elevation of 1,830 m, thus verifying the presence of Great Basin pocket mice along this corridor.

Grasshopper mice in the Wyoming Basin are relatively uniform in cranial and external morphology. Size increases gradually east of the Wyoming Basin, near Casper, onto the Northern Great Plains. The gradual change in phenetic attributes between populations of the Wyoming Basin and the Northern Great Plains corresponds to a transition from sagebrush steppe to grama-needlegrass-wheatgrass prairie (Küchler, 1964). Conversely, size increases abruptly between the Wyoming Basin and the Central Great Plains; grasshopper mice in the latter region (represented by samples GP-33 and GP-34), are larger than those in the Wyoming Basin and the Northern Great Plains. Dispersal between the Wyoming Basin and Central Great Plains is restricted south of Casper by the Laramie Mountains.

Colorado Plateau

Northern grasshopper mice on the Colorado Plateau probably have been isolated from those in both the Great Basin/Columbia Plateau and Wyoming Basin for a relatively long time. The abrupt contrast in morphology of grasshopper mice on either side of the Wasatch Mountains and southern high plateaus that separate the Great Basin from the Colorado Plateau was not emphasized by Durrant (1952), but Armstrong (1977) commented on the apparent effectiveness of this barrier throughout the Holocene with respect to small mammals. Farther south, sample

CP-14 from northern Arizona and southern Utah does not include specimens from the Arizona Strip region north of the Colorado River in Mohave County, Arizona, and we have not examined *O. leucogaster* from that area; however, external and cranial measurements of grasshopper mice from Mohave County reported by Van Cura and Hoffmeister (1966) do not differ appreciably from those of *O. l. melanophrys* from farther east in northern Coconino County, Arizona (included in sample CP-14). Moreover, measurements of specimens from Mohave County, Arizona, clearly are larger than those in any Great Basin sample (Van Cura and Hoffmeister, 1966; Table 2). Current evidence indicates that there is no intergradation in the Arizona Strip between populations of *O. leucogaster* in the Great Basin and on the Colorado Plateau.

In the north, Kirkland (1981) considered the Uinta Mountains to be an effective barrier to species of non-boreal small mammals, or a boundary marking the limit of subspecies to the north (in the Bridger Basin) and to the south (in the Uinta Basin). *O. leucogaster* may have been prevented from dispersing between the Wyoming Basin and Colorado Plateau by this barrier and by the Tavaputs Plateau south of the Uinta Basin. The apparent effectiveness of barriers separating the Great Basin and Wyoming Basin from the Colorado Plateau is further demonstrated by the fact that northern grasshopper mice from the Colorado Plateau resemble those from the Central Great Plains more than those from the Great Basin and Wyoming Basin.

The Colorado and Green rivers evidently are effective barriers to gene flow among populations of *O. leucogaster* on the Colorado Plateau. The results of this investigation indicate that the subspecies *O. l. melanophrys* and *O. l. pallescens* are well differentiated.

Paleobiogeography

Carleton and Eshelman (1979) presented measurements for samples of *O. leucogaster* from two late Pleistocene or early Holocene localities (Schulze Cave and Friesenhahn Cave) on the Edwards Plateau in south-central Texas. With ages estimated at about 9,680 and 9,200 years BP, respectively (Lundelius et al., 1983), these faunas are approximately contemporaneous with the earliest samples from Owl Cave, Idaho, and with samples from Isleta Caves and Dry Cave, New Mexico. Most molar dimensions of grasshopper mice from Schulze and Friesenhahn caves are larger than in extant samples of *O. leucogaster* from North Dakota, Nebraska, Oklahoma, and Texas (Carleton and Eshelman, 1979). Conversely, fossil specimens from Owl Cave and extant specimens from the Great Basin are smaller than specimens from those states. Carleton and Eshelman (1979:30) referred to the fossil species *O. pedroensis*, which ranged in time from the late Blancan Borchers local fauna to the late Pleistocene (late Sangamon or early Wisconsin) Jinglebob local fauna, as "the antecedent of Recent *leucogaster*." Molar dimensions of that extinct species are larger than those of *O. leucogaster* from Schulze Cave and Friesenhahn Cave. *O. pedroensis* is known from Kansas and southern Arizona but not from the Great Basin. In fact, no specimens of *Onychomys* are known from the Great Basin or Columbia Plateau before the end of the Pleistocene (Lundelius et al., 1983). The presence of small *O. leucogaster* in the Great Basin/Columbia Plateau region (Owl Cave) documents the existence of two discrete size classes of northern grasshopper mice since latest Pleistocene time.

The late Quaternary vegetational history of portions of western North America, as inferred from pollen and macrofossil records, suggests that habitats suitable for arid-adapted mammals did not exist north or east of the present Mohave Desert region during full-glacial time (Table 4). We hypothesize that *O. leucogaster* was a component of the fauna in a "cold" desert refuge in the location of the present Mohave "hot" desert during that time. This would place geographic isolation of populations of northern grasshopper mice in the Great Basin from the remainder of the species sometime prior to 20,000 years BP, and would account for the existence at the close of the Pleistocene of size differences among populations of *O. leucogaster* comparable to those among extant populations. Existence of the Mohave refuge is further supported by the occurrence of *Brachylagus idahoensis* in Clark County, Nevada (Tule Springs), and San Bernadino County, California (Kokoweef Cave), during late Wisconsin time (Lundelius et al., 1983). Moreover, tabulation of small mammals known to have occurred farther south and east in the Sonoran

TABLE 4.—*Late Quaternary vegetational history for selected basins, deserts, and plateaus in western North America as inferred from pollen and macrofossil data.*

Time interval	Region	Inferred vegetational patterns	References
Full glacial (about 25000–15000 ybp)	Columbia Plateau	"quasi-arctic" (north), subalpine forest (Snake River Plain)	Wells, 1983
	Great Basin	montane and boreal forest, possible shrub-steppe on valley floors	Thompson and Mead, 1982 Wells, 1983
	Mohave Desrt	pinon-juniper woodland, semi-desert shrubs below 1,500 m	Spaulding et al., 1983
	Colorado Plateau	extralocal and elevationally depressed montane conifers (Grand Canyon and southeastern Utah), possible shrub-steppe	Spaulding et al., 1983
Late glacial/early holocene (about 15000–7000 ybp)	Columbia Plateau	shift to *Artemisia* steppe about 10300 ybp, highest frequency of *Atriplex* about 7000 ybp (eastern Snake River Plain)	Bright, 1966 Bright and Davis, 1982
	Great Basin	upward shift in forests, invasion of lowlands by semi-desert shrubs beginning about 12500 ybp	Wells, 1983
	Mohave Desert	mosaic of woodland and desert-scrub below 1,000 m	Spaulding, 1983
	Colorado Plateau	change to modern conditions beginning about 12000 ybp, montane forest at 1,710 m (southeastern Utah) about 11810 ybp	Cole, 1981 Spaulding and Van Devender, 1977
Early–mid holocene (about 7000–4000 ybp)	western North America	Altithermal Interval (climatic warming and drying): upward shift in vegetation	Richmond, 1965
Mid–late holocene (after about 4000 ybp)	western North America	Neoglaciation: downward shift in vegetation	Bright and Davis, 1982 Hansen, 1947 Madsen and Currey, 1979 Richmond, 1965

Desert during late Wisconsin time (Mead et al., 1983) did not include any species characteristic of Great Basin steppe (e.g., *Brachylagus idahoensis, Spermophilus townsendii, Perognathus parvus, Dipodomys microps, Onychomys leucogaster*, or *Lemmiscus curtatus*).

Northern grasshopper mice hypothetically dispersed northward into the Great Basin during late glacial time and occurred at least as far north as Owl Cave on the Snake River Plain in southeastern Idaho by 10,500 years BP. Morphometric differentiation suggests that *O. leucogaster* has had limited access to the Colorado Plateau from the Great Basin throughout the Holocene. Such access most likely was near the Utah-Arizona border, through the Arizona Strip region. Although much of this area consists of sagebrush steppe and shortgrass rangeland, several mammals characteristic of Great Basin steppe are conspicuously absent (Hoffmeister and Durham, 1971). These include *Brachylagus idahoensis, Sylvilagus nuttallii, Lepus townsendii, Spermophilus townsendii, Microdipodops megacephalus*, and *Lemmiscus curtatus*, all of which occur in the Great Basin of western Utah (Armstrong, 1977). The current transition from northern "cold" desert to southern "hot" desert at 37°N occurs at a pronounced elevational gradient (Meyer, 1978).

To the north, continuity probably existed between the steppes of the Great Basin/Columbia Plateau and Wyoming Basin during the early Holocene. Whereas warming and drying in the Arizona Strip and adjacent southern Utah would have increased the extent of "hot" desert and thereby would have decreased continuity between the "cold" deserts of the Great Basin and Colorado Plateau, a similar climatic trend farther north would have increased "cold" desert connections between the Great Basin and Wyoming Basin and between the former and the northern Columbia Plateau. These connections likely again became constricted with the onset of Neoglaciation (Table 4).

Late-glacial and early Holocene fossil faunas (Anderson, 1974; Lundelius et al., 1983; Walker, 1982) indicate little mingling of Great Basin steppe and Great Plains grassland biota. Notably, Great Basin species such as *Brachylagus idahoensis, Sylvilagus nuttallii, Spermophilus townsendii, Spermophilus beldingi,* and *Perognathus parvus* are not known from Great Plains faunas and Great Plains species such as *Spermophilus tridecemlineatus, Cynomys ludovicianus, Geomys bursarius, Perognathus hispidus,* and *Microtus ochrogaster* are absent from Great Basin and Columbia Plateau faunas. We hypothesize that the Wyoming Basin has served as a filter barrier between the Great Basin and the Great Plains since the Wisconsin pluvial.

Quaternary vegetational history (Table 4) and phenetic similarities among populations of *O. leucogaster* (Fig. 5) thus can be incorporated into a model for late Quaternary affinities among regional components of the "cold" desert steppe fauna in western North America (Fig. 8). Additional knowledge of late-glacial/Holocene faunas and study of systematic relationships of steppe species are needed to test this model.

Taxonomic Conclusions

Based on the results of this study, we propose four changes in taxonomic arrangement. First, the name *O. l. utahensis* is relegated to synonymy with *O. l. brevicaudus*. Second, the name *O. l. fuscogriseus* is relegated to synonymy with *O. l. brevicaudus*. Third, populations north of the Ochoco, Blue, and Wallowa mountains in northeastern Oregon and eastern Washington that formerly were assigned to *O. l. fuscogriseus* warrant recognition as a separate subspecies. No name is available for these populations, and a new subspecies therefore is named and described below. Fourth, populations in the Wyoming Basin that formerly were assigned to *O. l. arcticeps* are reassigned to *O. l. missouriensis*, and the range of *O. l. arcticeps* in Wyoming is restricted to areas of the Central Great Plains east of the Laramie Mountains.

Onychomys leucogaster durranti, new subspecies

Holotype.—Adult female (age class 3), skin (adult pelage) and skull, University of California Museum of Vertebrate Zoology no. 87519, obtained on 22 July 1939 by L. Tevis, original number 157; type locality, 4 mi. E Burbank, 500 feet, Walla Walla Co., Washington.

Distribution.—Shrub steppe of northeastern Oregon and eastern Washington, north of the Ochoco, Blue, and Wallowa mountains, west to Jefferson County in Oregon and Yakima County in Washington, north to Douglas County and east to Asotin County in Washington.

Measurements of holotype.—Total length, 122; length of tail, 34; length of hind foot, 20; length of ear, 16; greatest length of skull, 25.5; breadth of braincase, 11.6; zygomatic breadth, 13.5; interorbital constriction, 4.6; rostral breadth, 5.3; length of nasals, 9.5; alveolar length of maxillary toothrow, 4.2; cranial depth, 9.3; length of mandibular toothrow, 3.8; length of interparietal, 3.1; depth of ramus, 3.2; coronoid-angular height, 6.8; capsular-angular height, 4.9.

Diagnosis.—Size small for the species (Table 2); skull short with small nasals, delicate rostrum, small dentary, and particularly narrow zygomatic and interorbital breadths; basal ear tufts usually white; dorso-lateral pelage a mixture of pale and dark brown hairs resulting in pale or dark grayish-brown appearance; mid-dorsal stripe darker; ventral hairs with prominent gray bases except fully white on chin and throat.

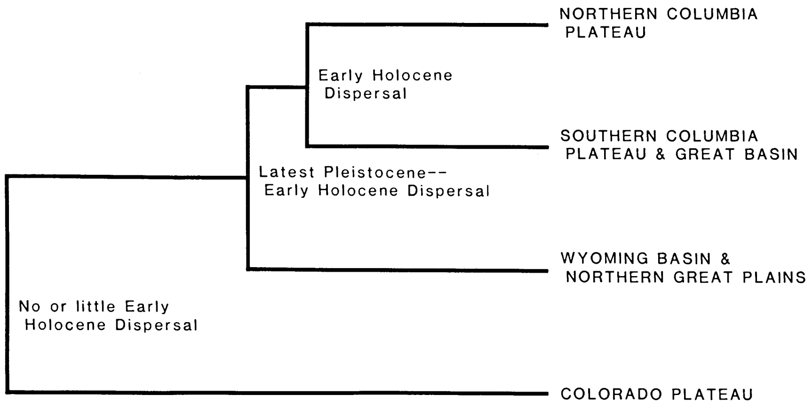

FIG. 8.—A model of North American shrub steppe faunal affinities based on phenetic similarities among populations of *Onychomys leucogaster* and inferred late Quaternary vegetational history (see Table 4). Inferred dispersal barriers and corridors are described in text.

Comparisons.—From *O. l. brevicaudus*, *O. l. durranti* differs in being conspicuously smaller in most measurements. From other subspecies of *O. leucogaster*, *O. l. durranti* differs in being much smaller, generally darker, and in having especially smaller molar teeth and rostrum (Table 2).

Etymology.—Named in honor of Stephen D. Durrant (1902–1975), whose studies in Utah have whetted interest in biogeography of the intermontane plateaus and basins of western North America.

Remarks.—*O. l. durranti* occupies xeric steppe habitats (Lyman and Livingston, 1983) in northeastern Oregon and in the Columbia Plateau, southeastern Washington, and Yakima Valley faunal regions (Dalquest, 1948) in Washington.

SPECIMENS EXAMINED

This list includes all specimens examined for the new subspecies *O. l. durranti* and for the revised subspecies *O. l. brevicaudus* and *O. l. missouriensis*. Specimens examined for other subspecies studied in this investigation (*O. l. arcticeps*, *O. l. leucogaster*, *O. l. melanophrys*, and *O. l. pallescens*) are listed in the thesis by Riddle (1984).

Onychomys leucogaster durranti, new subspecies

OREGON. *Gilliam Co.*: Arlington, 225 ft., 1 (MVZ); Willows, 2 (USNM); Willows Junction, 1 (USNM). *Jefferson Co.*: Gateway, 2 (USNM). Morrow Co.: 4 mi. S Boardman, 5 (MHP); Heppner, 2 (USNM); 2½ mi. SW Irrigon, 300 ft., 4 (MVZ). *Sherman Co.*: Columbia River, 300 ft., at mouth of John Day River, 1 (MVZ). *Umatilla Co.*: Umatilla, 5 (USNM); Umatilla, 298 ft., 2 (MVZ). *Wheeler Co.*: Twickenham, 1 (USNM).

WASHINGTON. Adams Co.: Lind, 5 (USNM). *Asotin Co.*: Asotin, 1 (USNM). *Benton Co.*: 5 mi. W Kennewick, 1 (MVZ); Paterson, 250 ft., 1 (MVZ); Umatilla National Wildlife Refuge, 1 mi. N, 6 mi. W Plymouth, 1 (OSMNH); Plymouth, 1 (MVZ). *Douglas Co.*: 3 mi. NW Baird, 3 (USNM); Douglas, 1 (USNM). *Franklin Co.*: 8 mi. ENE Pasco, 650 ft., 2 (MVZ); Pasco, 4 (USNM). *Garfield Co.*: Pomeroy, 1,900 ft., 1 (USNM). *Grant Co.*: Coulee City, 7 (USNM); north shore Moses Lake, 1 (USNM). *Lincoln Co.*: Odessa, 6 mi. E Sylvan Lake, 1 (USNM). *Walla Walla Co.*: 4 mi E Burbank, 500 ft., 8 (MVZ); 2 mi. SSE Burbank, 350 ft., 7 (MVZ); Touchet River, 1 mi. W. Lamar, 850 ft., 2 (MVZ); Touchet, 2 (USNM); Wallula, 6 (1 MVZ, 5 USNM). *Yakima Co.*: Ahtanum Ridge, Yakima, 2 (MVZ); Mabton, 4 (USNM); White Swan, Yakima Indian Res., 1,000 ft., 2 (USNM); 10 mi. W Yakima at Wiley City, 2,000 ft., 1 (USNM); Rattle Snake Hills, 30 mi. E. Yakima, 1 (USNM).

Onychomys leucogaster brevicaudus Merriam, 1891

CALIFORNIA. *Alpine Co.*: 2 mi. NE Woodfords, 5,700 ft., 1 (MVZ). *Lassen Co.*: Amedee, 6 (USNM); Warm Spring, 9 mi. E Amedee, 4,000 ft., 1 (MVZ); 2.3 mi. S, 0.6 mi. W Herlong, 4,160 ft., T26N, R16E, Sec. 14, 1 (MVZ); 5 mi. E Litchfield, 4,600 ft., 1 (MVZ); Long Valley, Willow Ranch, 4 (USNM); Madelin Plains, 3 (USNM); 7 mi N. Observation Peak, 5,300 ft., 1 (MVZ); Observation Peak, 1 (MVZ); 1 mi. SW Warm Spring, 4,000 ft., 7 (MVZ). *Modoc Co.*: Dry Creek, Warner Mtns., 9 (MVZ); Steele Meadow, 4,700 ft., 2 (MVZ); Sugar Hill, 2 (MVZ). *Mono Co.*: Pelliser Ranch, 5 mi. N Benton, 5,600 ft., 6 (MVZ); Benton, 5,639 ft., 1 (MVZ); McKeevers' Ranch, 2 mi. S Benton Station, 5,200 ft., 1 (MVZ); Taylors Ranch, 2 mi. S Benton Station, 5,300 ft., 7 (MVZ); 1 mi. S hwy. 167, 6 mi. W state line NE of Mono Lake, 6,780 ft., 1 (MVZ); 1¼ mi. ESE Lee Vining, 1 (MVZ); 1 mi. S Williams Butte, 6,900 ft., 1 (MVZ). *Plumas Co.*: Sierra Valley, Vinton, 4 (USNM); 1 mi. E Vinton, 4,900 ft., 1 (MVZ). *Siskiyou Co.*: Picard, 1 (USNM); Tule Lake, 1 (USNM); Lava Bed National Monument, Whitney Butte, 1 (MVZ).

IDAHO. *Ada Co.*: Nampa, 3 (USNM); *Bingham Co.*: 2.8 mi. S Atomic City, T1N, R31E, 3 (MHP); Blackfoot, 5 (USNM). *Butte Co.*: Big Lost River, 1 (USNM); Nuclear Reactor Test Site, 9 (BYU). *Canyon Co.*: Bowmont, 1 (USNM). *Elmore Co.*: Glenns Ferry, 5 (USNM). *Minidoka Co.*: Snake River Desert, 23 mi. N Minidoka, Sparks Well, 4 (USNM); Snake River Desert, 20 mi. N. Minidoka, Twin Lakes, 3 (USNM); Snake River Desert, 20 mi. N Minidoka, Twin Springs, 3 (USNM); Minidoka, 5 (USNM). *Owyhee Co.*: Grasmere, 5,200 ft., 1 (UPS); Murphy, 1 (USNM). *Washington Co.*: Weiser, 1 (USNM). *County unknown*: Deer Flats, 1 (USNM).

NEVADA. *Churchill Co.*: 7½ mi. NW Fallon, 1 (USNM); 4 mi. NW Fallon, 1 (USNM); 1 mi. NW Mountain Well, 5,350 ft., 1 (MVZ); Osobb Valley, 2 (USNM); 9 mi. E Stillwater, 1 (USNM); 1½ mi. N Timber Lake, Carson Sink, 1 (USNM). *Elko Co.*: Bull Run Mtns., 1 (USNM); Carlin, 1 (USNM); Cobre, 6,100 ft., 1 (MVZ); 2 mi. SW Cobre, 2 (MVZ); 4 mi. SW Deeth, exit 328 off hwy. I-80, River Ranch rd., 2 (MHP); Elko, 5 (USNM); 10 mi. W Elko, 4 (USNM); 10 mi. SW Elko, 1 (MVZ); 2 mi. NW Halleck, 5,200 ft., 6 (KU); 5 mi. W Halleck, 5,200 ft., 1 (MVZ); 3 mi. W Halleck, 5,200 ft., 5 (KU); 3 mi. W Halleck, 5,300 ft., 4 (MVZ); Halleck, 5,200 ft., 1 (KU); Halleck, 16 (USNM); 3 mi. SW Halleck, 3 (USNM); Elburg, 3 mi. S Halleck, 4 (KU); 4 mi. S Halleck, 6 (USNM); 5 mi. SW Halleck, 1 (USNM); 6 mi. SW Halleck, 1 (USNM); 6 mi. S Halleck, 2 (USNM); Humboldt National Forest, 3 mi. S Lamolle, 2 (MVZ); 13 mi. N Montello, 5,000 ft., 2 (MVZ); Mountain City, 4 (USNM); 9 mi. NE San Jacinto, 5,300 ft., 1 (MVZ); Ruby Mtns., Summit Secret Pass, 6,200 ft., 1 (KU); 1½ mi. N Tecoma, 4,900 ft., 2 (MVZ); 1½ mi. NE Tecoma, 4,900 ft., 2 (MVZ); Tecoma, 4,900 ft., 3 (MVZ); Goose Creek, 2 mi. W Utah Line, 5,000 ft., 1 (MVZ); Wells, 1 (USNM); no particular locality, 1 (KU). *Eureka Co.*: 5 mi. N Beawawe, 1 (MVZ); ½ mi. S Beawawe, 3 (MVZ); 8 mi. W Eureka, 1 (MVZ); Evans, 3 (MVZ); Diamond Valley, 4 mi. SE Romano, 1 (MVZ); Winzell, 3 (MVZ). *Humboldt Co.*: 23 mi. NW Battle Mountain, 2 (MVZ); Base of Pine Forest Mtns., Big Creek Ranch, 1 (MVZ); Cottonwood Range, 1 (USNM); 1 mi. S Denio, Oregon, 4,200 ft., 1 (MVZ); 2½ mi. E Flanigan, 4,200 ft., 8 (MVZ); 3½ mi. E Flanigan, 4,200 ft., 3 (MVZ); Flowing Springs, 1 (USNM); Golconda, 3 (USNM); Hot Spring, Thousand Creek, 4,300 ft., 5 (MVZ); 16 mi. NE Iron Point, 4,500 ft., 15 (MVZ); 18 mi. NE Iron Point, 4,600 ft., 16 (MVZ); 36 mi. NE Paradise Valley, 5,500 ft., 1 (MVZ); 1½ mi. N Quinn River Crossing, 4,100 ft., 2 (MVZ); 2½ mi. SW Quinn River Crossing, 4,100 ft., 1 (MVZ); 17½ mi. S, 5 mi. W Quinn River Crossing, Jackson Creek Ranch, 4,000 ft., 2 (MVZ); Sheldon Antelope Range, 1 (USNM); Catnip Meadow, Sheldon Antelope Range, 1 (BS/FC); 5 mi. N Summit Lake, 5,900 ft., 1 (MVZ); 7 mi. N Winnemucca, 4,400 ft., 1 (MVZ); 1½ mi. NW Winnemucca, 4,900 ft., 1 (MVZ); 1 mi. N Winnemucca, 4,600 ft., 6 (MVZ); Winnemucca, 2 (USNM); 3 mi. SW Winnemucca, 4,500 ft., 2 (MVZ); 4 mi. SW Winnemucca, 4,500 ft., 3 (MVZ); 5 mi. SW Winnemucca, 4,500 ft., 3 (MVZ); 10 mi. SW Winnemucca, 4,500 ft., 11 (MVZ). *Lander Co.*: Reese River Valley, 7 mi. N Austin, 5 (MVZ); Malloy Ranch, 5 mi. W Austin, Reese River, 1 (MVZ); Austin, 3 (USNM); Reese River Valley, 34 mi. SW Austin, 1 (USNM); 35 mi. SW Austin, 4 (USNM); Battle Mtn., 1 (USNM); 1 mi. E Battle Mtn., 7 (MVZ); Birch Creek, 7,000 ft., 1 (MVZ); Kingston R.S., 7,500 ft., 1 (MVZ); Izenhood, 3 (MVZ); 3 mi. S Izenhood, 1

(MVZ); Silver Creek, 1 (USNM); 6 mi. ENE Smiths Creek Ranch, 5,550 ft., 1 (MVZ). *Lyon Co.*: 1 mi. SE Wadsworth, 4,200 ft., 1 (MVZ); West Walker River, Smiths Valley, 4,700 ft., 1 (MVZ). *Mineral Co.*: Fingerock Wash, Stewart Valley, 5,400 ft., 2 (MVZ); Fletcher, 6,098 ft., 1 (MVZ); 7 mi. NW Shurz, 4,500 ft., 1 (MVZ); E Walker River, 2 mi. NW Morgans Ranch, 5,100 ft., 1 (MVZ). *Nye Co.*: Monitor Valley, 30 mi. N Belmont, 1 (USNM); Hot Creek Valley, 3½ mi. E Hot Creek, 5,650 ft., 1 (MVZ); Gold Flat, 5.5 mi. W Kawich P.O., 5,150 ft., 2 (MVZ); 5 mi. S Millett, 5,500 ft., 2 (MVZ); Reese River, 3 (USNM); N end of Reveille Valley, Old Mill, 6,200 ft., 1 (MVZ); Round Mtn., 1 (USNM); 11½ mi. NE San Antonio, 5,700 ft., 1 (MVZ); San Antonio, 5,400 ft., 1 (MVZ); Garden Valley, 8½ mi. NE Sharp, 1 (MVZ); 17 mi. W Sunnyside, White River Valley, 2 (MVZ); Ralston Valley, 15½ mi. NE Tonopah, 5,800 ft., 2 (MVZ); Ralston Valley, 1 mi. N, 34 mi. E Tonopah, 5,650 ft., 3 (MVZ); 3 mi. S, 9 mi. W Tybo, 6,200 ft., 1 (MVZ). *Pershing Co.*: El Dorado Can., Humboldt Range, 6,000 ft., 1 (MVZ); Buena Vista Valley, 9 mi. E Fanning, 4,100 ft., 1 (MVZ); Rabbit Hole Mtns., 2 (USNM); 3 mi. NNE Toulon, 3,900 ft., 1 (MVZ); 1½ mi. NE Toulon, 3,900 ft., 1 (MVZ); 15 mi. SW Winnemucca, 1 (MVZ). *Washoe Co.*: 1 mi. W Hausen, 4,650 ft., 2 (MVZ); 2½ mi. SE Hausen, 5,200 ft., 1 (MVZ); 10 mi. SE Hausen, 4,675 ft., 2 (MVZ); Junction House, 4,500 ft., 1 (MVZ); 3 mi. E Painted Point, 5850 ft., 1 (MVZ); 2¾ mi. SW Pyramid, 4,300 ft., 1 (MVZ); Pyramid Lake, 3 (USNM); Pyramid Lake, 1 mi. SW Suteliffe Station, 4,100 ft., 2 (USNM); Pyramid Lake, 4.5 mi. S Suteliffe Station, 4,200 ft., 7 (USNM); 8½ mi. E Vya, 5,900 ft., 1 (MVZ); Wadsworth, 2 (USNM). *White Pine Co.*: 1 mi. N Baker, 6 (MVZ); 5½ mi. SE Ely, 6,500 ft., 3 (MVZ); Steptoe Creek, 5½ mi. SE Ely, 6,400 ft., 2 (MVZ); Spring Valley, 7 mi. SW Osceola, 6,275 ft., 1 (MVZ); Mt. Moriah, 3 mi. E Smith Creek Cave, 5,500 ft., 1 (MVZ).

OREGON. *Harney Co.*: Alvord Valley, 1 (USNM); 5 mi. NNE Burns, 4,200 ft., 1 (MVZ); Burns, 1 (USNM); 23 mi. S, 2.3 mi. W Burns, 4 (OSMNH); 1½ mi. E Denio, 4,200 ft., 1 (MVZ); Harney, 2 (USNM); Alvord Desert, Lake Alvord, 1 (MVZ); Narrows, 2 (USNM); 1 mi. S Narrows, 4,200 ft., 6 (MVZ); Steens Mtns., T31S, R32 E½, Sec. 5, 1 (OSMNH); Steens Mtns., T31S, R32 E½, Sec. 4, 3 (OSMNH); Steens Mtns., T31S, R32 E½, Sec. 3, 3 (OSMNH); Alvord Desert, Steens Mtns., T33S, R35E, Sec. 21, 1 (OSMNH). *Klamath Co.*: Klamath Basin, Lost River, 2 (USNM); Klamath Falls, 3 (USNM); Swan Lake Valley, 2 (USNM); Tule Lake, 1 (USNM). *Lake Co.*: 8 mi. N Alkali Lake, 1 (USNM); NE edge Alkali Lake, 4,200 ft., 1 (MVZ); Buck Creek, 1 (USNM); Fremont, 1 (USNM); Goose Lake Valley, 8 mi. N Lake View, 1 (USNM); Warner Lake, Plush, 1 (USNM); Rock Creek, 1 (USNM); Silver Lake, 1 (USNM). *Malheur Co.*: Brogan, 2 (OSMNH); Head of Crooked Creek, Owyhee Desert, 4,000 ft., 1 (USNM); Ironside, 4,000 ft., 5 (AMNH); 8 mi. W Jordan Valley, 4,500 ft., 1 (MVZ); 21 mi. N McDermitt, Nevada, 5,300 ft., 2 (MVZ); Rockville, 1 (USNM); Owyhee River, Rome, 4 (USNM); ½ mi. S Rome, 3,600 ft., 4 (MVZ); 3 mi. N Vale, 2,600 ft., 3 (MVZ); near Vale, 5 (AMNH). *County unknown*: Squaw Butte, 1 (USNM), White Horse Sink, 1 (USNM).

UTAH. *Beaver Co.*: Desert Range, Milford, 2 (BYU). *Box Elder Co.*: 3 mi. up Clear Creek Canyon, Raft River Mtns., 6,700 ft., 1 (UU); Kelton, 1 (USNM); 7 mi. WNW Lucin, 1 (UU); Lucin, 1 (BYU); NE end New Foundland Mtns., 1 (UU). *Juab Co.*: 7 mi. S. Fish Springs, 4,400 ft., 1 (UU); Nephi, 7 (USNM); Trout Creek, 4,600 ft., 1 (UU); *Millard Co.*: White Valley, 60 mi. SW Delta, 1 (UU); Desert Range Experiment Station, 12 (BS/FC), 2 (BYU); Desert Range Experiment Station, White Sage Valley, 2 (FMNH); Warm Cove, 55 mi. W Milford, 5,500 ft., 1 (UU); Tule Springs, White Valley, 2 (FMNH). *Salt Lake Co.*: Wasatch foothills, 24 mi. E Salt Lake City, 6,500 ft., 3 (MVZ). *Tooele Co.*: Dugway Proving Grounds, 5 (UPS); Ibapah, 5,000 ft., 10 (UU); N base Little Granite Mtn., 4,700 ft., 16 (UU); Stansbury Island, Great Salt Lake, 1 (USNM); 11 mi. W Vernon, 2 (BS/FC).

Onychomys leucogaster missouriensis (Audubon and Bachman, 1851)

COLORADO. *Jackson Co.*: Arapahoe National Wildlife Refuge, 8,100 ft., T8N, R79W, NW ¼ Sec. 5, 1 (MHP); Arapahoe National Wildlife Refuge, 8,100 ft., T7N, R79W, NW ¼ Sec. 20, 6 (MHP); Canadian Creek, 2 (USNM); Canadian Creek, 8,000 ft., 2 (USNM); 5 mi. E Canadian

Creek, 1 (USNM). *Moffat Co.*: Craig, 6,100 ft., 1 (UCM); 6.5 mi. N, 3.5 mi. W Irish Lakes, 7,160 ft., T11N, R101W, NW ¼ Sec. 7, 13 (MHP); 2.5 mi. N, 0.5 mi. W Irish Lakes, 6,720 ft., T11N, R101W, Sec. 35, 1 (MHP); Lay, Bear River, 1 (USNM); 37 mi. NW Maybell, 3 mi. S Irish Canyon, 6,200 ft., T10N, R101W, 1 (BS/FC); Snake River, Lower Bridge, 5,860 ft., 1 (UCM); Snake River, S Sunny Peak, 2 (USNM); Two Bar Spring, 2 (DMNHC).

MONTANA. *Big Horn Co.*: Fort Custer, 8 (USNM). *Carter Co.*: Medicine Rocks, 15 mi. N Ekalaka, 3 (USNM); 11.5 mi. N, 3 mi. E Ekalaka, 1 (KU). *Dawson Co.*: Mt. Sheep Buttes, 1 (USNM). *Powder River Co.*: Powderville, 2 (USNM); Powderville, 2,900 ft., 5 (KU). *Richland Co.*: Tilyous Ranch, 3 (USNM). *Roosevelt Co.*: Johnson Lake, 2 (USNM). *Rosebud Co.*: 1 mi. S, 2 mi. E Forsyth, 2,600 ft., 1 (KU).

NORTH DAKOTA. *Billings Co.*: 1 mi. S, 1 mi. W Medora, 2,300 ft., 1 (KU). *Bowman Co.*: 11 mi. S, 26 mi. W Bowman, 2,900 ft., 1 (KU); 13 mi. S, 26 mi. W Bowman, 3,000 ft., 2 (KU). *Morton Co.*: Glenullin, 1 (USNM). *Sioux Co.*: Cannon Ball, 21 (USNM). *Stark Co.*: 1 mi. N, 1 mi. W Dickinson, 2,700 ft., 3 (KU); Dickinson, 2 (USNM). *Williams Co.*: Buford, 8 (USNM); Ft. Buford, 12 (USNM).

SOUTH DAKOTA. *Harding Co.*: 2 mi. N, 5 mi. W Ludlow, 1 (KU); 14 mi. S, 4 mi. W Reva, 1 (KU); T22N, R1E, NE ¼ Sec. 22, 2 (KU).

UTAH. *Daggett Co.*: Bridgeport, 2 (BYU); 0.5 mi. SW Clay Basin Camp, 6,300 ft., 2 (UU); Martin Draw, 6,800 ft., 1 (UU); Birch Creek, 2 mi. S Utah-Wyoming state line, 7,700 ft., 2 (UU); Browns Park, 2 mi. W Willow Creek, 5700 ft., 1 (UU). *Rich Co.*: South Eden Canyon, 4 mi. E Bear Lake 6,400 ft., 2 (UU); Birch Creek, 6,650 ft., 1 (UU). *Uintah Co.*: 1.5 mi. S Ouray, 4,800 ft., 2 (UU).

WYOMING. *Albany Co.*: 12 mi. S Bosler, 7,110 ft., T17N, R73W, N ½ Sec. 31, 6 (MHP); Flagg Ranch, T17N, R73W, SW ¼ Sec. 21, 1 (UWYO); 3.8 mi. N Laramie, 7,250 ft., 3 (KU); 2 mi. N Laramie, 7,250 ft., 1 (KU); rt. 130, 10 mi. W Laramie, 1 (UWYO); Laramie city landfill, 5 (UWYO); hwy. 30, outskirts of Laramie, 2 (UWYO); 2 mi. E Laramie, 2 (UWYO); 2 mi. E Laramie, 7,300 ft., 1 (KU). *Big Horn Co.*: 7 mi. S Basin, 3,900 ft., 2 (KU); 6 mi. NW Greybull, 3,800 ft., 4 (KU); Greybull, 1 (USNM); 9 mi. N, 5 mi. E Lovell, 1 (KU). *Campbell Co.*: Little Powder River, 2 (USNM); 2 mi. S, 1.5 mi. W Rockypoint, 2 (KU). *Crook Co.*: Moorcroft, 5 (USNM). *Fremont Co.*: Bull Lake, 7,700 ft., 1 (USNM); 2 mi. N, 6 mi. W Burris, 6,450 ft., 2 (KU); Mount Crooks, 8,600 ft., 2 (KU); Nilsons' Ranch on Sheep Creek, S base Owl Creek Mtns., 6,000 ft., 1 (USNM); 5 mi. N, 1 mi. W Shoshoni, 4,700 ft., 3 (KU). *Hot Springs Co.*: Murphy Gulch rd., 9 mi. S, 17.5 mi. E Meeteetse, T47N, R97W, Sec. 21, 4 (MHP); 10 mi. S, 18 mi. E Meeteetse, T47N, R97W, Sec. 28, 2 (MHP). *Laramie Co.*: 10 mi. N Albin, 1 (UWYO); 5.5 mi. S Glenys, 5,200 ft., 2 (KU); Horse Creek, 6.5 mi. W Meriden, 5,200 ft., 2 (KU); Horse Creek, 6 mi. W Meriden, 5,200 ft., 6 (KU); Horse Creek, 4 mi. W Meriden, 5,200 ft., 2 (KU); 1 mi. S Pine Bluffs, 1 (KU); 2 mi. S Pine Bluffs, 5,200 ft., 6 (KU). *Lincoln Co.*: Cokeville, 1 (USNM); Cumberland, 8 (2 BYU, 5 MVZ, 1 USNM); Fontanelle, 6,500 ft., 4 (USNM); head of Bridger Creek, 6,500 ft., 1 (USNM); Kemmerer, 3 (USNM); 10.75 mi. E Sage, T21N, R117W, SW ¼ Sec. 7, 3 (MHP). *Natrona Co.*: 1 mi. NE Casper, 5,150 ft., 14 (KU); Casper, 5 (USNM); 1 mi. N, 9 mi. W Independence Rock, 1 (KU); Dry Creek, 12 mi. W Sun, 6,400 ft., 1 (USNM); Sun, 2 (USNM); Pathfinder Dam, Sun, 2 (USNM); Devils Gate, Sun Ranch, Sweetwater River, 2 (MVZ); 16 mi. S, 11 mi. W Waltman, 6,950 ft., 2 (KU). *Park Co.*: 13 mi. N, 1 mi. E Cody, 5,200 ft., 1 (KU); Pitchfork Ranch, 1 (MHP). *Sheridan Co.*: Arvada, 4 (USNM); 5 mi. NE Clearmont, 3,900 ft., 1 (KU). *Sweetwater Co.*: Bittercreek, 3 (MSB); Bittercreek, K(inney) Ranch, 10 (8 AMNH, 2 FMNH); 18 mi. S Bittercreek, 6,800 ft., 8 (KU); Kinney Ranch, 21 mi. S Bittercreek, 13 (KU); Kinney Ranch, 21 mi. S Bittercreek, 7,100 ft., 9 (MVZ); 22 mi. SSW Bittercreek, 1 (KU); Kinney Ranch, about 23 mi. SW Bittercreek, T15N, R98W, Sec. 8, 2 (MVZ); 30 mi. S Bittercreek, 9 (KU); 33 mi. S Bittercreek, 14 (KU); 33 mi. S Bittercreek, 6,900 ft., 8 (KU); W of Green River, Bryan, 1 (UWYO); 7 mi. E Farson, 7,200 ft., 3 (MVZ); Green River, 1 (USNM); Currant Creek, 352 mi. N Green River, Utah, on Green River, 5,920 ft., 1 (UU); 366 mi. N Green River, Utah, 6,000 ft., 1 (UU); opposite mouth of Sage Creek, 360 mi. N Green

River, Utah, 5,970 ft., 5 (UU); Kinney Ranch, 1 (USNM); Kinney Ranch, 6,800 ft., 3 (KU); 27.5 mi. N, 38 mi. E Rock Springs, 6,735 ft., 1 (UWYO); 27 mi. N, 37 mi. E Rock Springs, 6,700 ft., 1 (KU); 25 mi. N, 38 mi. E Rock Springs, 6,700 ft., 1 (KU); 24 mi. N, 22 mi. E Rock Springs, 6,700 ft., T23N, R100W, NE ¼ Sec. 28, 1 (UWYO); Rock Springs, T22N, R103W, Sec. 1, 2 (UWYO); 26 mi. S, 21 mi. W Rock Springs, 4 (KU); 32 mi. S, 22 mi. W Rock Springs, 2 (KU); 32 mi. S, 22 mi. W Rock Springs, 7,025 ft., 1 (KU); Steamboat Mtn. N of Superior, 1 (USNM); 2.5 mi. N Wamsutter, 1 (KU). *Sublette Co.*: Big Sandy, 7 (3 MHP, 4 USNM); 15 mi. NW Pindale, 7,600 ft., 10 (MVZ). *Uinta Co.*: 14 mi. N Evanston, Bear River, 6,600 ft., 3 (USNM); Evanston, 6 (USNM); Ft. Bridger, 1 (USNM); 10 mi. SW Granger, 1 (USNM); Mountainview, 4 (USNM). *Weston Co.*: Newcastle, 1 (USNM); 23 mi. SW Newcastle, 4,500 ft., 4 (KU).

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