MAMMALIAN SPECIES No. 742, pp. 1–14, 3 figs.

Thomomys bottae.

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Published 13 July 2004 by the American Society of Mammalogists

Thomomys Wied-Neuwied, 1839

Diplostoma Richardson, 1829:206. Type species *Diplostoma bulbivorum* Richardson, 1829:206.
Oryctomys Eydoux and Gervais, 1836:20. Type species *Oryctomys* (*Saccophorus*) *bottae* Eydoux and Gervais, 1836:23.
Thomomys Wied-Neuwied, 1839:377. Type species *Thomomys rufescens* Wied-Neuwied, 1839:378.
Megascapheus, Elliot, 1903a:190. Type species *Diplostoma bulbivorum* Richardson, 1829:206.

CONTEXT AND CONTENT. Order Rodentia, suborder Sciurognathi, superfamily Geomyoidea, family Geomyidae, subfamily Geomyinae, tribe Thomomyini, genus *Thomomys*. *Thomomys* is distinguished as follows: anterior surface of upper incisors smooth, occasionally with fine, indistinct groove near medial edge; M3 elliptical; small, narrow forefoot with small claws (Bailey 1915; Hall 1981). A key to the 9 extant species of *Thomomys* follows (Bailey 1915; Clark and Stromberg 1987; Elliot 1903a; Goldman 1947; Hall 1981; Patton 1999b; Thaeler 1968a, 1980):

1 Root of I1 above P4; angular process continuous with well-developed flange along ventral side of ramus; open sphenoidal fissure; diploid numbers, 40–60 2
Root of I1 above and between P4 and M1; angular process not continuous with weakly-developed flange along ventral side of ramus; closed sphenoidal fissure; diploid numbers, 74–82. 6
2 Height of ear from notch, <6.9 mm 3
Height of ear from notch, >6.9 mm 5
3 Length of hind foot, 25–38 mm ..... *T. talpoides*
Length of hind foot, <25 mm 4
4 Pale tan pelage; length of hind foot, 20–22 mm; total length, 161–184 mm; only from Sweetwater and Carbon counties, Wyoming ..... *T. clusius*
Yellowish to dark brown pelage; length of hind foot, 21–22 mm; total length, 167–303 mm; from southwestern Wyoming, central Idaho, and parts of Montana and Utah ..... *T. idahoensis*
5 Reddish brown to black pelage; height of ear from notch, 7–8.5 mm; premaxillae extending 1.5–2.5 mm behind nasals; nasals truncate or rounded posteriorly; length of baculum, 22–31 mm; from Washington, Oregon, and California. ..... *T. mazama*
Dark brown pelage; height of ear from notch, 8–9 mm; premaxillae short of nasals or extending at most 0.5 mm behind nasals; nasals V-shaped posteriorly; length of baculum, <22 mm; from California and western Nevada ..... *T. monticola*
6 Pterygoids concave on inner surface and convex on outer surface; groove on exoccipital; length of hind foot, ≥40 mm (adult males), ≥38 (adult females); only from Willamette River and adjacent tributaries in Oregon ..... *T. bulbivorus*
Pterygoids flat and straight or nearly so; no groove on exoccipital; length of hind foot, <40 mm (adult males), <38 mm (adult females) 7
7 Skull not conspicuously short and wide; nasals wedge-shaped and narrowing posteriorly; zygomata slender and nearly parallel; post-auricular spots usually large, confluent with black dorsum in some individuals; overall pelage gray, black, or umber, often with dorsal black stripe; generally 3 pairs of mammae; typically from oak woodlands and pine forests; only from 4 mountain ranges in southern Arizona, Animas Mountains of New Mexico, and western Mexico ..... *T. umbrinus*
Skull short and wide; nasals slightly tapered and gradually narrowed posteriorly; zygomata heavy with maxillary arm expanded to form external angle near its contact with jugal; postauricular spots small; overall pelage gray, black, or ochraceous, lacking prominent dorsal black stripe; generally 4 pairs of mammae; not distributed as above 8
8 Dorsum grayish washed with buff, or black; white patch on chin; typically in shadscale and sagebrush in disjunct patches in California, Idaho, Nevada, and Oregon ..... *T. townsendii*
Dorsum pale gray to ochraceous to dark blackish-brown; white patches often on throat, chest, and/or abdomen; occupies wide variety of vegetation types from southern Oregon to northern Mexico ..... *T. bottae*

Thomomys bottae (Eydoux and Gervais, 1836)

Botta's Pocket Gopher

Oryctomys bottae Eydoux and Gervais, 1836:23. Type locality "Californie," restricted to the vicinity of Monterey by Baird (1856:335).
Thomomys bottae: Baird, 1856:335. First use of current name combination.
Thomomys aureus Allen, 1893:50. Type locality "Bluff City, Utah."
Thomomys toltecus Allen, 1893:52. Type locality "Juarez, northern Chihauhau" (= Chihuahua), Mexico.
Thomomys angularis Merriam, 1897:214. Type locality "Los Baños, Merced Co., California."
Thomomys leucodon Merriam, 1897:215. Type locality "Grant Pass, Rogue River Valley, Oregon."
Thomomys operarius Merriam, 1897:215. Type locality "Keeler, Owens Lake, Inyo Co., California."
Thomomys latirostris Merriam, 1901:107. Type locality "Little Colorado River, Painted Desert, Arizona."
Thomomys baileyi Merriam, 1901:109. Type locality "Sierra Blanca, Texas."
Thomomys sinaloae Merriam, 1901:108. Type locality "Altata, Sinaloa, Mexico."
Thomomys cabezonae Merriam, 1901:110. Type locality "Cabezon, San Gorgonio Pass, California."
Thomomys desertorum Merriam, 1901:114. Type locality "Mud Spring, Detrital Valley, Arizona."
Thomomys mewa Merriam, 1908:146. Type locality "Raymond, Madera County, California."

FIG. 1. Photograph of *Thomomys bottae*. Photograph courtesy of R. R. Hollander.

Thomomys magdalenae Nelson and Goldman, 1909:24. Type locality "Magdalena Island, Lower California, Mexico," Baja California Sur.

Thomomys canus Bailey, 1910:79. Type locality "Deep Hole, at north end of Smoke Creek Desert, Nevada."

Thomomys diaboli Grinnell, 1914:313. Type locality "Sweeney's Ranch, in hills of Diablo Range twenty-two miles south of Los Baños, Merced County, California."

Thomomys infrapallidus Grinnell, 1914:314. Type locality "seven miles southeast of Simmler, Carrizo Plain, San Luis Obispo County, California."

Thomomys oreoecus Burt, 1932:154. Type locality "Greenwater [Black Mountains, eight miles southwest of Ryan], Inyo County, California; altitude 4,300 feet."

Thomomys phelleoecus Burt, 1933:56. Type locality "Hidden Forest, Sheep Mountains, Clark County, Nevada; altitude 8,500 feet."

Thomomys simulus Nelson and Goldman, 1934:120. Type locality "Alamos, southern Sonora, Mexico (altitude 1,200 feet)."

Thomomys sturgisi Goldman, 1938a:56. Type locality "Carmen Mountains, Coahuila, Mexico (altitude 6,000 feet)."

CONTEXT AND CONTENT. Context as for genus, subgenus *Megascapheus* (Patton 1993a). One of 4 species in the subgenus (Patton 1993a). Species boundaries within *Thomomys* are complex; *T. bottae* was 1 of 3 species (with *townsendii* and *umbrinus*) combined within *T. umbrinus* by Hall and Kelson (1959) and Hall (1981), leading to use of *T. umbrinus* for this taxon until the 1980s. Confusion regarding species boundaries was addressed by Patton (1973), Patton and Dingman (1970), and Patton and Smith (1981, 1990, 1994). Almost 50% of the 195, formally recognized subspecies are from Baja California, Arizona, and Nevada (Goldman 1947; Hall and Davis 1935; Huey 1964; Patton 1999a). Parenthetical numbers refer to distribution map.

T. b. abbotti Huey, 1928:89. Type locality "1 mile east of El Rosario, Lower California, Mexico (river-bottom association), lat. 30°03′north, long. 115°48′W," Baja California." (1)

T. b. absonus Goldman, 1931:425. Type locality "Jacob's Pools, Houserock Valley, Coconino County, northern Arizona (altitude 4,000 feet)." (2)

T. b. abstrusus Hall and Davis, 1935:391. Type locality "Fish Spring Valley, 2 mi. SE Tulle Peak, 7,000 ft., Nye County, Nevada." (3)

T. b. acrirostratus Grinnell, 1935:408. Type locality "valley of Mad River at 2,700 feet altitude, 7 miles above Ruth, Trinity County, California." (4)

T. b. actuosus Kelson, 1951:67. Type locality "Corona, Lincoln County, New Mexico." (5)

T. b. aderrans Huey, 1939:71. Type locality "Carrizo Creek, San Diego County, California." (6)

T. b. affinis Huey, 1945:254. Type locality "Jacumba, San Diego County, California." (7)

T. b. agricolaris Grinnell, 1935:409. Type locality "Stralock Farm, 3 miles west of Davis, Yolo County, California." (8)

T. b. albatus Grinnell, 1912:172. Type locality "California side of the lower Colorado River at the old Hanlon Ranch, near Pilot Knob, Imperial County." (9)

T. b. albicaudatus Hall, 1930:444. Type locality "Provo, 4,510 feet altitude, Utah County, Utah." (10)

T. b. alexandrae Goldman, 1933b:464. Type locality "plain 5 miles southeast of Rainbow Lodge, near Navajo Mountain, Coconino County, Arizona (altitude 6,200 feet)." (11)

T. b. alienus Goldman, 1938b:338. Type locality "Mammoth, San Pedro River, Pinal County, Arizona (altitude 2,400 feet)." (12)

T. b. alpinus Merriam, 1897:216. Type locality "Mt. Whitney, High Sierra, California. Exact locality, Big Cottonwood Meadows (altitude, 10,000 feet, 8 miles SE. of Mt. Whitney peak." (13)

T. b. alticolus Allen, 1899:14. Type locality "Sierra Laguna (altitude 7,000 feet), Lower California," Baja California Sur. (14)

T. b. altivallis Rhoads, 1895:34. Type locality "San Bernardino Mts., California (alt. 5,000 ft.)." (15)

T. b. amargosae Grinnell, 1921:239. Type locality "Shoshone, 1560 feet altitude on the Amargosa "River," Inyo County, California." (16)

T. b. analogus Goldman, 1938a:59. Type locality "Sierra Guadalupe, southeastern Coahuila, Mexico." (17)

T. b. angularis Merriam, 1897:214, see above. (18)

T. b. angustidens Baker, 1953:508. Type locality "Sierra del Pino, 5,250 ft., 6 mi. N and 6 mi. W Acebuches, Coahuila." (19)

T. b. anitae Allen, 1898:146. Type locality "Santa Anita, Lower California," Baja California Sur. (20)

T. b. apache Bailey, 1910:79. Type locality "Lake La Jara (7,500 feet altitude), on the Jicarilla Apache Indian Reservation, New Mexico." (21)

T. b. aphrastus Elliot, 1903b:219. Type locality "San Tomás, Lower California, Mexico," Baja California. (22)

T. b. aridicola Huey, 1937:354. Type locality "10 miles south of Gila Bend (or, exactly, on Ajo railroad right of way, about 2 miles north of Black Gap), Maricopa County, Arizona." (23)

T. b. argusensis Huey, 1931:43. Type locality "Junction Ranch, Argus Mountains, Inyo County, California." (24)

T. b. aureiventris Hall, 1930:444. Type locality "Kelton, 4225 feet altitude, Box Elder County, Utah." (25)

T. b. aureus Allen, 1893:50, see above. (26)

T. b. awahnee Merriam, 1908:145. Type locality "Yosemite Valley, California." (27)

T. b. baileyi Merriam, 1901:109, see above. (28)

T. b. basilicae Benson and Tillotson, 1940:93. Type locality "La Misión, 2 miles west of Magdalena, Sonora, Mexico" (*occipitalis* Benson and Tillotson is a synonym). (29)

T. b. birdseyei Goldman, 1937a:134. Type locality "Pine Valley Mountains, five miles east of Pine valley, Washington County, Utah (altitude 8,300 feet)." (30)

T. b. bonnevillei Durrant, 1946:41. Type locality "Fish Springs, 4,400 ft., Juab County, Utah." (31)

T. b. boregoensis Huey, 1939:70. Type locality "Beatty Ranch, Borego Valley, San Diego County, California." (32)

T. b. boreorarius Durham, 1952:498. Type locality "Swamp Point, 7522 ft. alt., 18 1/2 mi northwestward of Bright Angel Point, North Rim of the Grand Canyon, Coconino County, Arizona." (33)

T. b. borjasensis Huey, 1945:262. Type locality "San Borjas Mission, Baja California, Mexico, lat. 28°52′N, long. 113°53′W." (34)

T. b. bottae Eydoux and Gervais, 1836:20, see above. (35)

T. b. brazierhowelli Huey, 1960:407. Type locality "San Fernando Mission, Baja California, Mexico, lat. 30°." (36)

T. b. brevidens Hall, 1932a:330. Type locality "Breen Creek, 7000 feet altitude, Kawich Range, Nye County, Nevada." (37)

T. b. cabezonae Merriam, 1901:110, see above. (38)

T. b. cactophilus Huey, 1929:241. Type locality "Punta Prieta, Lower California, Mexico, lat. 28°56′north, long. 114°12′ west," Baja California.(39)

T. b. camargensis Anderson, 1972:288. Type locality "1 mi. S Camargo, 3950 ft., Chihuahua," Mexico. (40)

T. b. camoae Burt, 1937:1. Type locality "Camoa, [Río Mayo], Sonora, Mexico." (41)

T. b. caneloensis Lange, 1959:131. Type locality "Huachuca Mountains, west foothills, Canelo, 10 miles south of Elgin, 5,100 ft., Santa Cruz County, Arizona." (42)

T. b. canus Bailey, 1910:79, see above. (43)

T. b. carri Lange, 1959:130. Type locality "Huachuca Mountains, northwest slope, Carr Peak, 8,400 feet, Cochise County, Arizona." (44)

T. b. catalinae Goldman, 1931:419. Type locality "Summerhaven, Santa Catalina Mountains, Pima County, Arizona (altitude 7,500 feet)." (45)

T. b. catavinensis Huey, 1931:45. Type locality "Cataviña, Lower California, Mexico, lat 29°54′north, long. 114°57′ west," Baja California. (46)

T. b. cedrinus Huey, 1955:100. Type locality "summit of Crossman Peak, (Juniper-Piñon Belt), Chemehuevis Mountains, Mohave County, Arizona." (47)

T. b. centralis Hall, 1930:445. Type locality "2 1/2 miles east of Baker (1 1/4 miles west of Nevada-Utah boundary on 39th parallel), 5700 feet altitude, White Pine County, Nevada." (48)

T. b. cervinus Allen, 1895:203. Type locality "Phoenix, Arizona." (49)

T. b. chiricahuae Nelson and Goldman, 1934:117. Type locality "Pinery Canyon, west slope of Chiricahua Mountains, Arizona (altitude 7,500 feet)." (50)

T. b. chrysonotus Grinnell, 1912:174. Type locality, "Ehrenberg, Yuma County, Arizona." (51)

T. b. cinereus Hall, 1932a:327. Type locality "West Walker River, Smiths Valley, 4700 feet altitude, Lyon County, Nevada." (52)
T. b. collinus Goldman, 1931:421. Type locality "Fly Park, Chiricahua Mountains, Cochise County, Arizona (altitude 9,000 feet)." (53)
T. b. collis Hooper, 1940:7. Type locality "New Mexico, Valencia County, thirty miles south of Grants, Shuman's Ranch, township 6 north, range 10 west, section 30." (54)
T. b. comobabiensis Huey, 1937:354. Type locality "5 miles northwest of Sells, Pima County, Arizona (elevation, approximately 2400 feet)." (55)
T. b. concisor Hall and Davis, 1935:390. Type locality "Potts Ranch, 6900 ft., Monitor Valley, Nye County, Nevada." (56)
T. b. confinalis Goldman, 1936:119. Type locality "35 miles east of Rock Springs, Texas (altitude 2,450 feet)." (57)
T. b. connectens Hall, 1936:296. Type locality "Clawson Dairy, 5 miles north of Albuquerque, 4,943 feet elevation, Bernalillo County, New Mexico." (58)
T. b. contractus Durrant, 1946:50. Type locality "Scipio, 5,315 ft., Millard County, Utah." (59)
T. b. convergens Nelson and Goldman, 1934:123. Type locality "Costa Rica Ranch, delta of Sonora River, southwest of Hermosillo, Sonora, Mexico." (60)
T. b. convexus Durrant, 1939:159. Type locality "E. side Clear Lake, 4,600 ft., Millard County, Utah." (61)
T. b. crassus Chattin, 1941:274. Type locality "180 ft., 1 ½ mi. W Niland, Imperial County, California." (62)
T. b. cultellus Kelson, 1951:64. Type locality "Halls Peak, Mora County, New Mexico." (63)
T. b. cunicularis Huey, 1945:252. Type locality "Los Palmitos (western end of Pattie Basin), on the southeastern base of the Sierra Juárez (desert slope), latitude 31°44′N., longitude 115°36′W., Baja California, Mexico." (64)
T. b. curtatus Hall, 1932a:329. Type locality "San Antonio, 5400 feet altitude, Nye County, Nevada." (65)
T. b. depauperatus Grinnell and Hill, 1936a:4. Type locality "east base Tinajas Atlas Mountains, 7 miles south of Raven Butte, 1150 feet altitude, Yuma County, Arizona." (66)
T. b. depressus Hall, 1932a:326. Type locality "Dixie Meadows [at south end of Humboldt Salt Marsh], 3,500 feet altitude, Churchill County, Nevada." (67)
T. b. desertorum Merriam, 1901:114, see above. (68)
T. b. desitus Goldman, 1936:113. Type locality "Big Sandy River, near Owen, Mohave County, Arizona (altitude 2,000 feet)." (69)
T. b. detumidus Grinnell, 1935:405. Type locality "open grassy hillside, 250 feet altitude, 1½ miles south of (town of) Pistol River, Curry County, Oregon." (70)
T. b. diaboli Grinnell, 1914:313, see above. (71)
T. b. dissimilis Goldman, 1931:425. Type locality "east slope of Mount Ellen, Henry Mountains, Garfield County, Utah (altitude 8,000 feet)." (72)
T. b. divergens Nelson and Goldman, 1934:122. Type locality "four miles west of Huachinera, Bavispe River, northeastern Sonora, Mexico (altitude about 4,000 feet)." (73)
T. b. estanciae Benson and Tillotson, 1939:152. Type locality "La Estancia, 6 miles north of Nacori, Sonora." (74)
T. b. extenuatus Goldman, 1935:149. Type locality "Willcox, Cochise County, Arizona (altitude 4,000 feet)." (75)
T. b. flavidus Goldman, 1931:417. Type locality "Parker, Yuma County, Arizona (altitude 350 feet)." (76)
T. b. fulvus Woodhouse, 1852:201. Type locality "near the San Francisco Mountain, New Mexico." (77)
T. b. fumosus Hall, 1932a:329. Type locality "Milman Ranch, Moores Creek, 19 miles southeast of Millett P.O., Nye County, Nevada." (78)
T. b. grahamensis Goldman, 1931:420. Type locality "Graham Mountains (Pinaleno Mountains on some maps) Graham County, Arizona (altitude 9,200 feet)." (79)
T. b. growlerensis Huey, 1937:353. Type locality "7 miles east of Papago Well, Pima County, Arizona (or, exactly, along a well wooded desert wash on the southwestern side of a range of hills in the southern end of Growler Valley; the Agua Dulce Mountains form the southern boundary of this locality and are not far distant)." (80)
T. b. guadalupensis Goldman, 1936:117. Type locality "McKittrick Canyon, Guadalupe Mountains, Texas (altitude 7,800 feet)." (81)
T. b. harquahalae Grinnell and Hill, 1936a:7. Type locality "Ranegras Plain, 10 miles west of Hope, Yuma County, Arizona; altitude approximately 950 ft." (82)
T. b. homorus Huey, 1949:55. Type locality "1 mile east of Rancho Lagunitas, Baja California, Mexico, lat. 28°20′N., long. 113°15′W." (83)
T. b. howelli Goldman, 1936:116. Type locality, "Grand Junction, Mesa County, Colorado (altitude 4,600 feet)." (84)
T. b. hualpaiensis Goldman, 1936:114. Type locality "Hualpai Peak, Hualpai Mountains, Mohave County, Arizona (altitude 7,000 feet)." (85)
T. b. hueyi Goldman, 1938b:340. Type locality "Spud Rock Ranger Station, Rincon Mountains, Pima County, Arizona (altitude 7,400 feet)." (86)
T. b. humulis Baker, 1953:503. Type locality "3 mi. W Had. [Hacienda] San Miguel, 2,200 ft., Coahuila." (87)
T. b. imitabilis Goldman, 1939:30. Type locality "La Paz, southern Lower California, Mexico," Baja California Sur. (88)
T. b. incomptus Goldman, 1939:29. Type locality "San Jorge, near Pacific coast west of Pozo Grande and about 25 miles southwest of Comondú, southern Lower California, Mexico (altitude 50 feet)." (89)
T. b. infrapallidus Grinnell, 1914:314, see above. (90)
T. b. ingens Grinnell, 1932:405. Type locality "east side levee, 290 feet altitude (2 miles due west of Millux, as shown on U.S.G.S. "Buena Vista Lake Quadrangle"), Buena Vista Lake, Kern County, California." (91)
T. b. internatus Goldman, 1936:115. Type locality "Salida, Chaffee County, Colorado (altitude 7,000 feet)." (92)
T. b. jacinteus Grinnell and Swarth, 1914:154. Type locality "Round Valley, 9000 feet altitude, San Jacinto Mountains, Riverside County, California." (93)
T. b. jojobae Huey, 1945:256. Type locality "Sangre de Cristo, Baja California, Mexico, lat. 31°51′N.; long. 116°06′W." (94)
T. b. juarezensis Huey, 1945:255. Type locality "Laguna Hanson, Sierra Juárez, Baja California, Mexico." (95)
T. b. lachuguilla Bailey, 1902:120. Type locality "arid foothills near El Paso, Texas." (96)
T. b. lacrymalis Hall, 1932a:328. Type locality "Arlemont [= Chiatovich Ranch, Fish Lake Valley], 4900 feet altitude, Esmeralda County, Nevada." (97)
T. b. laticeps Baird, 1856:335. Type locality "Humboldt Bay" California. (98)
T. b. latirostris Merriam, 1901:107, see above. (99)
T. b. latus Hall and Davis, 1935:393. Type locality "Cherry Creek, 6500 ft., White Pine County, Nevada." (100)
T. b. lenis Goldman, 1942:75. Type locality "Richfield, Sevier County, Utah." (101)
T. b. leucodon Merriam, 1897:215, see above. (102)
T. b. levidensis Goldman, 1942:76. Type locality "Manti, Sanpete County, Utah (altitude about 5,500 feet)." (103)
T. b. limitaris Goldman, 1936:118. Type locality "four miles west of Boquillas, Brewster County, Texas." (104)
T. b. limpiae Blair, 1939:2. Type locality "Limpia Canyon, about one mile north of Fort Davis, Jeff Davis County, Texas; altitude, 4,700 feet." (105)
T. b. litoris Burt, 1940:1. Type locality "Stearns Point, Magalena Bay (west side), Lower California, Mexico," Baja California Sur. (106)
T. b. lorenzi Huey, 1940:219. Type locality "7 miles north of Boulder Creek, Santa Cruz County, California." (107)
T. b. lucidus Hall, 1932c:67. Type locality "Las Palmas Cañon, 200 feet altitude, west side of Laguna Salada (north of 32°N. latitude), Lower California, Mexico," = 2 miles east of Gaskill's Tanks, Baja California (Patton 1999a). (108)
T. b. lucrificus Hall and Durham, 1938:15. Type locality "Eastgate, Churchill County, Nevada." (109)
T. b. magdalenae Nelson and Goldman, 1909:24, see above. (110)
T. b. martirensis Allen, 1898:147. Type locality "San Pedro Martir Mountains (alt. 8200 feet), Lower California," = La Grulla Meadow, Sierra San Pedro Martir, 7400 feet, Baja California (Patton 1999a). (111)
T. b. mearnsi Bailey, 1914:117. Type locality "Gray's Ranch in Animas Valley, southwest corner of New Mexico." (112)
T. b. melanotis Grinnell, 1918:425. Type locality "10,500 feet al-

titude on Big Prospector Meadow, White Mountains, Mono County, California." (113)
T. b. mewa Merriam, 1908:146, see above. (114)
T. b. minimus Durrant, 1939:161. Type locality "Stansbury Island, Great Salt Lake, Tooele County, Utah." (115)
T. b. minor Bailey, 1914:116. Type locality "Ft. Bragg, Mendocino Co., California." (116)
T. b. modicus Goldman, 1931:418. Type locality "La Osa (near Mexican Boundary), southern end of Altar Valley, Pima County, Arizona." (117)
T. b. mohavensis Grinnell, 1918:427. Type locality "Mohave River bottom, 2700 feet altitude, near Victorville, San Bernardino County, California." (118)
T. b. morulus Hooper, 1940:9. Type locality "New Mexico, Valencia County, eight miles southeast of Paxton, Bill Porter's Ranch." (119)
T. b. muralis Goldman, 1936:112. Type locality "From lower end of Prospect Valley, Grand Canyon, Hualpai Indian Reservation, Arizona (altitude 4,500 feet)." (120)
T. b. mutabilis Goldman, 1933a:75. Type locality "Camp Verde, Yavapai County, Arizona (altitude 3,200 feet)." (121)
T. b. nanus Hall, 1932a:331. Type locality "south end of Belted Range, five and one-half miles northwest of Whiterock Spring, 7,200 feet altitude, Nye County, Nevada." (122)
T. b. nasutus Hall, 1932d:96. Type locality "west fork of Black River, 7550 feet altitude, Apache County, Arizona." (123)
T. b. navus Merriam, 1901:112. Type locality "Red Bluff, California." (124)
T. b. neglectus Bailey, 1914:117. Type locality "San Antonio Peak (Bear Flat Meadows at 6400 feet altitude) in the San Gabriel Mountains, California." (125)
T. b. nesophilus Durrant, 1936:2. Type locality "Antelope Island, Great Salt Lake, Davis County, Utah." (126)
T. b. nicholi Goldman, 1938b:337. Type locality "from 20 miles south of Wolf Hole (road to Parashouts), Shivwits Plateau, Mohave County, Arizona (altitude 5,000 feet.)" (127)
T. b. nigricans Rhoads, 1895:36. Type locality "Witch Creek, San Diego Co., California." (128)
T. b. operarius Merriam, 1897:215, see above. (129)
T. b. operosus Hatfield, 1942:151. Type locality "6 mi. N. Yarnell (Peeples Valley), Yavapai Co., Arizona." (130)
T. b. optabilis Goldman, 1936:116. Type locality "Coventry, Naturita Creek Valley, Montrose County, Colorado (altitude 6,500 feet)." (131)
T. b. opulentus Goldman, 1935:150. Type locality "Las Palomas, on the Rio Grande, Sierra County, New Mexico." (132)
T. b. oreoecus Burt, 1932:154, see above. (133)
T. b. osgoodi Goldman, 1931:424. Type locality "Hanksville, Wayne County, Utah." (134)
T. b. paguatae Hooper, 1940:4. Type locality "New Mexico, Valencia County, one-half mile north of Cebolleta [Seboyeta Post Office]." (135)
T. b. pallescens Rhoads, 1895:36. Type locality "Grapelands, San Bernardino Valley, California." (136)
T. b. parvulus Goldman, 1938b:339. Type locality "pass between Santa Catalina and Rincon Mountains, Pima County, Arizona (altitude 4,500 feet)." (137)
T. b. pascalis Merriam, 1901:111. Type locality "Fresno, San Joaquin Valley, California." (138)
T. b. patulus Goldman, 1938b:341. Type locality "bottomland along Hassayampa River, two miles below Wickenburg, Maricopa County, Arizona (altitude, 2,000 feet)." (139)
T. b. pectoralis Goldman, 1936:120. Type locality "from vicinity of Carlsbad Cave, Carlsbad Cave National Monument, Eddy County, New Mexico." (140)
T. b. peramplus Goldman, 1931:423. Type locality "Wheatfield Creek, west slope of Tunicha Mountains, Apache County, northwestern Arizona (altitude 7,000 feet)." (141)
T. b. perpallidus Merriam, 1886:588. Type locality "the arid Colorado desert, in southern California." Reported as "Palm Springs [formerly Agua Caliente, Riverside County, Calif.]" by Miller and Kellogg (1955:284). (142)
T. b. perpes Merriam, 1901:111. Type locality "Lone Pine, Owens Valley, California." (143)
T. b. pervagus Merriam, 1901:110. Type locality "Espaniola, New Mexico." (144)
T. b. pervarius Goldman, 1938a:57. Type locality "Lloyd Ranch, 35 miles south of Marfa, Presidio County, Texas (altitude 4,200 feet)." (145)
T. b. phasma Goldman, 1933a:72. Type locality "two miles south of Tule Tank, Tule Desert, near Mexican boundary, Yuma County, Arizona." (146)
T. b. phelleoecus Burt, 1933:56, see above. (147)
T. b. pinalensis Goldman, 1938b:342. Type locality "Oak Flat, 5 miles east of Superior, Pinal Mountains, Arizona." (148)
T. b. piutensis Grinnell and Hill, 1936b:103. Type locality "French Gulch, Piute Mountains, altitude 6700 feet, 2 ½ miles northwest Claraville, Kern County, California." (149)
T. b. planirostris Burt, 1931:38. Type locality "Zion National Park, Washington County, Utah." (150)
T. b. planorum Hooper, 1940:5. Type locality "New Mexico, Valencia County, one and one-half miles southwest of San Mateo." (151)
T. b. powelli Durrant, 1955:79. Type locality "Hall Ranch, Salt Gulch, 8 miles west of Boulder, 6,000 feet, Garfield County, Utah." (152)
T. b. providentialis Grinnell, 1931:1. Type locality "Purdy, 4,500 feet altitude, 6 miles southeast of New York Mountain, Providence Range, San Bernardino County, California." (153)
T. b. proximarinus Huey, 1945:261. Type locality "Boca la Playa, 16 miles west of Santo Tomás, Baja California, Mexico (mesa bordering the sea), lat. 31°32′N, long. 116°38′W." (154)
T. b. proximus Burt and Campbell, 1934:151. Type locality "Old Parker Ranch (Picketts Ranch on U.S. Geological Survey topographic map, Patagonia Quadrangle, edition of August, 1905), altitude 4800 feet, west slope of Santa Rita Mountains, Pima County, Arizona." (155)
T. b. puertae Grinnell, 1914:315. Type locality "La Puerta (Mason's Ranch), eastern San Diego County, California." (156)
T. b. pusillus Goldman, 1931:422. Type locality "Coyote Mountains, Pima County, Arizona (altitude 3,000 feet)." (157)
T. b. retractus Baker, 1953:507. Type locality "Fortín, 3,300 ft., 33 mi. N and 1 mi. E San Gerónimo, Coahuila." (158)
T. b. rhizophagus Huey, 1949:54. Type locality "Las Flores, 7 miles south of Bahía de Los Angeles, Baja California, Mexico, lat. 28°50′N., long. 113°32′W." (159)
T. b. riparius Grinnell and Hill, 1936a:4. Type locality "Blythe, Riverside County, California." (160)
T. b. robustus Durrant, 1946:30. Type locality "Orr's Ranch, Skull Valley, 4,300 ft., Tooele County, Utah." (161)
T. b. rubidus Youngman, 1958:376. Type locality "2 9/10 miles east of Cañon City, 5344 feet, Fremont County, Colorado." (162)
T. b. rufidulus Hoffmeister, 1955:126. Type locality "2 miles east of Joseph City, Navajo County, Ariz." (163)
T. b. ruidosae Hall, 1932d:96. Type locality "Ruidoso, 6700 feet altitude, Lincoln County, New Mexico." (164)
T. b. rupestris Chattin, 1941:272. Type locality "1,131 ft., 2 mi. E Clemens Well, Riverside County, California." (165)
T. b. ruricola Huey, 1949:53. Type locality "4 miles north of Santa Catarina Landing, Baja California, Mexico, lat. 29°35′N, long. 115°17′W." (166)
T. b. russeolus Nelson and Goldman, 1909:25. Type locality "San Angel, 30 miles west of San Ignacio, Lower California, Mexico," Baja California Sur. (167)
T. b. sanctidiegi Huey, 1945:258. Type locality Balboa Park, San Diego, California. (168)
T. b. saxatilis Grinnell, 1934:193. Type locality "open, rocky, uncultivated ground, one mile north of Susanville, at 4400 feet altitude, Lassen County, California." (169)
T. b. scapterus Elliot, 1903b:224. Type locality "Lone Pine, Owens Valley, Inyo County, California." (170)
T. b. scotophilus Davis, 1940:204. Type locality "one and one-half miles west of Bat Cave, Sierra Diablo, Hudspeth County, Texas." (171)
T. b. sevieri Durrant, 1946:45. Type locality "Swasey Spring, House Mountains, 6,500 ft., Millard County, Utah." (172)
T. b. siccovallis Huey, 1945:258. Type locality "El Cajón Canyon, 3,200 feet altitude, east base of Sierra San Pedro Mártir, Baja California, Mexico, lat. 30°54′N; long. 115°10′W." (173)
T. b. silvifugus Grinnell, 1935:406. Type locality "near Coyote Peak, at 3000 feet altitude, Humboldt County, California." (174)
T. b. simulus Nelson and Goldman, 1934:120, see above. (175)
T. b. sinaloae Merriam, 1901:108, see above. (176)

T. b. solitarius Grinnell, 1926:177. Type locality "Finger-rock Wash, Stewart Valley, 5400 feet altitude, Mineral County, Nevada." (177)
T. b. spatiosus Goldman, 1938a:58. Type locality "Alpine, Brewster County, Texas (altitude about 4,500 feet)." (178)
T. b. stansburyi Durrant, 1946:36. Type locality "South Willow Creek, Stansbury Mountains, 7,500 ft., Tooele County, Utah." (179)
T. b. sturgisi Goldman, 1938a:56, see above. (180)
T. b. suboles Goldman, 1928:203. Type locality "from alluvial bottom at Old Searchlight Ferry, Colorado River (northwest of Kingman), Arizona (altitude 1,000 feet)." (181)
T. b. subsimilis Goldman, 1933a:74. Type locality "Harquahala Mountains, Yuma County, Arizona (altitude 3,000 feet)." (182)
T. b. texensis Bailey, 1902:119. Type locality "the head of Limpia Creek at 5,500 feet altitude in the Davis Mts., Texas." (183)
T. b. tivius Durrant, 1937:5. Type locality "Oak Creek Canyon, 6 miles east Oak City, 6,000 feet, Millard County, Utah." (184)
T. b. toltecus Allen, 1893:52, see above. (185)
T. b. trumbullensis Hall and Davis, 1934:51. Type locality "three miles south of Nixon Spring, Mt. Trumbull, Mohave Co., Arizona." (186)
T. b. tularosae Hall, 1932b:411. Type locality "Cook Ranch, ½ mile west of Tularosa, Otero County, New Mexico." (187)
T. b. vanrossemi Huey, 1934:1. Type locality "Punta Peñascosa, Sonora, Mexico." (188)
T. b. varus Hall and Long, 1960:35. Type locality "1 mi. S El Dorado, Sinaloa, México." (189)
T. b. vescus Hall and Davis, 1935:389. Type locality "Toquima Range, S slope Mount Jefferson, 9,000 ft. altitude, Nye County, Nevada." (190)
T. b. villai Baker, 1953:505. Type locality "7 mi. S and 2 mi. E Boquillas, 1800 ft., Coahuila." (191)
T. b. virgineus Goldman, 1937a:133. Type locality "Beaverdam Creek, near confluence with Virgin River, at Littlefield, northwestern Arizona (altitude 1,500 feet)." (192)
T. b. wahwahensis Durrant, 1937:3. Type locality "Wah Wah Springs, 30 miles west of Milford, 6500 feet, Beaver County, Utah." (193)
T. b. winthropi Nelson and Goldman, 1934:122. Type locality "Hermosillo, Sonora, Mexico." (194)
T. b. xerophilus Huey, 1945:257. Type locality "near Diablito Spring, summit of San Matias Pass (between Sierra Juárez and Sierra San Pedro Mártir), Baja California, Mexico." (195)

DIAGNOSIS. Characteristics of the subgenus *Megascapheus* (containing *T. bottae*) that separate it from the subgenus *Thomomys* include a heavy rostrum; base of P4 inclined anteriorly, base of incisor between bases of P4 and M1; infraorbital canals opening anterior to incisive foramina; open sphenoid fissure; anterior enamel plate of p4 narrow and not recurved (Thaeler 1980). Separation of *T. bottae* from *T. townsendii* and from *T. umbrinus* is problematic. Botta's pocket gopher is best distinguished near zones of contact by a combination of characters, including color (generally lacking a prominent medial black stripe); moderately procumbent incisors; slightly tapering nasals with gradually narrowing posterior ends; straight pterygoid processes; concave maxillofrontal suture articulating near center of lacrimal; 2 pairs of pectoral mammae; long, straight shape of baculum (averaging >10.5 mm); and fewer acrocentric autosomes in the karyotype (Dunnigan 1967; Hoffmeister 1986; Patton 1973, 1999a; Patton et al. 1984; Thaeler 1968b).

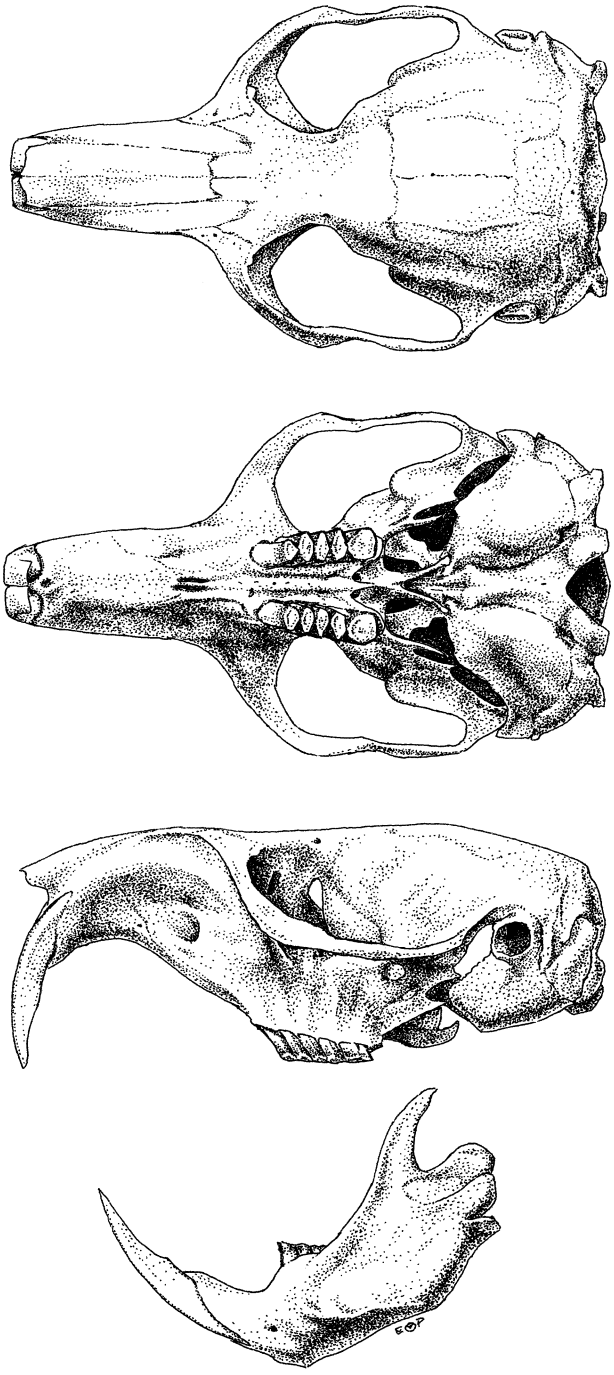

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Thomomys bottae* (adult female, Denver Museum of Nature and Science, DMNH 8528) from Las Animas County, Colorado. Greatest length of cranium is 37.9 mm. By Eric Parrish.

GENERAL CHARACTERS. *Thomomys bottae* has a fusiform body, large head, robust claws, and loose skin (Fig. 1). Pelage consists of fine, moderately-long hairs with scattered guard hairs (Hill 1937). Pelage color relates to soil color and moisture gradients (Benson 1933; Getz 1957; Goldman 1947; Ingles 1950; Patton 1973; Patton and Smith 1990). Hair follicles grow through dermis and contact underlying paniculus carnosus muscles. Hair length and density of follicles is greater in winter than in summer and might be greater in females (Morejohn and Howard 1956).

Dorsal pelage color is extremely variable geographically; color (especially brightness) is 1 characteristic used to recognize subspecies (Patton and Smith 1990). In some populations hair color changes seasonally (Morejohn and Howard 1956).

Cranial features (Fig. 2) include a presphenoid foramen, separation of optic foramen and sphenoidal fissure, confluence of foramina ovale and lacerum, vestigial vascular canal, and absence of stapedial foramen (Hill 1935). Skull has a broad rostrum with slightly tapered nasals narrowing posteriorly; heavy zygomata with prominent external angles near sutures with jugal; interparietals not extending posteriorly beyond plane of sutures between parietals and supraoccipital; and broad, decurved, upper incisors (Goldman 1947).

Sexual dimorphism varies geographically and is primarily associated with sizes of males. Males continue to grow with age, whereas growth of females ends as they become reproductive (Howard and Childs 1959; Patton 1993c; Patton and Smith 1990). Growth rates are related closely to nutrition (Patton and Brlylski 1987; Patton and Smith 1990). Cranial shape is probably more

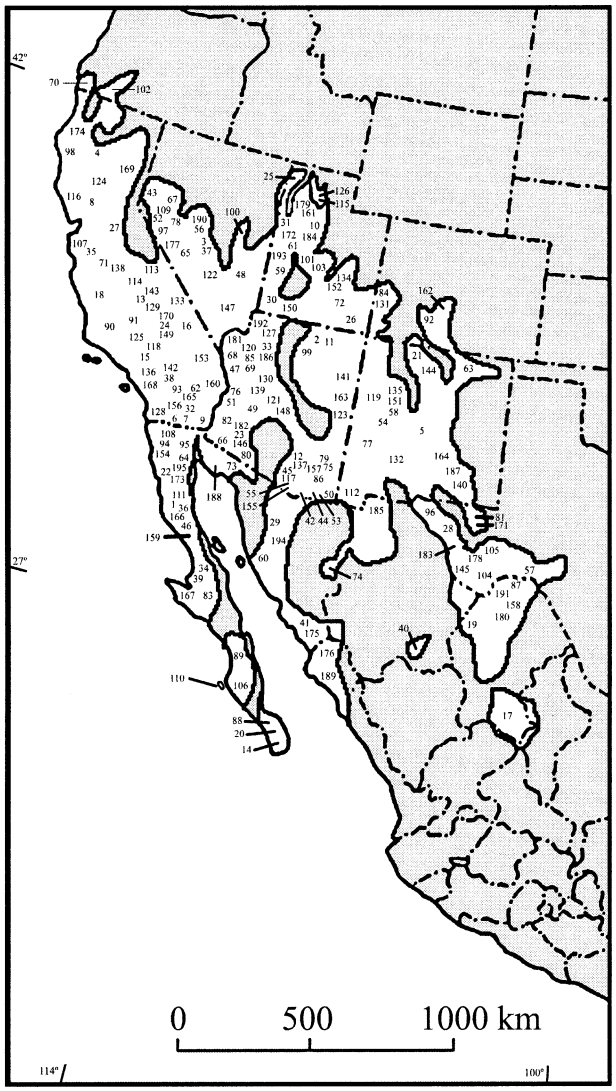

FIG. 3. Distribution of *Thomomys bottae*. Numbers correspond to subspecies in Context and Content. Type localities after Hall 1981.

important than size "in recognizing evolutionarily significant geographic units of pocket gopher species" (Patton and Brlylski 1987: 504).

Reported means and ranges of total length, length of tail, and length of hind foot (in mm, with parenthetical *n* and *SD*, respectively), include: 205.2, 177–225 (13, 15.2); 57.9, 48–64 (13, 4.8); 28.6, 25–33 (12, 2.3) for animals from southern Texas (Yancey 1997). Means and ranges of 18 *T. b. altivallis* and *T. b. jacinteus* (subspecies and sexes combined, *SD* not reported) from San Jacinto, California are: total length 230, 203–267; length of tail 75, 62–85; and length of hindfoot 31, 28–36 (Grinnell and Swarth 1914). Mean measurements for females and males respectively from *T. b navus* in California (with parenthetical *n* and *SE* are: total length, 206.3 (1267, 0.42), 227.2 (985, 0.71); length of tail, 58.2 (1267, 0.18), 65.3 (985, 0.27); and length of hind foot, 25.2 (168, 0.13), 27.1 (137, 0.20—Miller 1952). External and cranial measurements are available for topotypes of 23 taxa from Utah (Durrant 1952), for subspecies from Nevada (Hall 1995), and for 38 subspecies in Mexico (Patton 1999a).

DISTRIBUTION. The distribution of *T. bottae* ranges from southern Oregon south into Coahuila, Chihuahua, Nuevo Leon, Sinaloa, Sonora, and Baja California (Patton 1999a, 1999b). Elevational records include a report of *T. b. melanotis* up to at least 4,200 m (14,000 feet—Bole 1938). The large number of subspecies makes geographic delineation on a single figure difficult; instead, type localities for all subspecies are indicated (Fig. 3). Partial geographic distributions for some subspecies are available (Patton 1999a; Patton and Smith 1990).

FOSSIL RECORD. Fossils from Rancholabrean deposits occur in California, Nevada, New Mexico, Texas, and Mexico (Harris 1988; Jakway 1958). The oldest record is 103,000 years ago from Newport Bay Mesa, California (Kurtén and Anderson 1980). Late Rancholabrean and Holocene sites from the Southwest and Great Basin all fell within or very close to the present range (Faunmap Working Group 1994). Fossils (>15,000 years ago) have been recovered from the Hueco Mountains in the Burnet, Muscox, Upper Sloth, and Fowlkes caves in Texas and New Mexico (Van Devender et al. 1987). Extralimital records are from Cimarron County, Oklahoma (31,000 years ago) and Union County, New Mexico (500 years ago—Dalquest et al. 1990).

FORM. Dental formula is 1/1, 0/0, 1/1, 3/3 = 20. Morphology was described by Gunther (1956), Hill (1935, 1937), Holliger (1916), Lessa and Thaeler (1989), and Stein (1993, 2000).

Mean endocranial volume was 1.48 ± 0.04 (cc ± *SD*) for 7 individuals with mean body mass of 185.2 ± 27.6 (g ± *SD*). The encephalization quotient was 0.56 and total dorsal surface area of the brain was 188.3 mm^2 (Hafner and Hafner 1984).

Anomalies among 132 specimens from Mesa Verde included a female with malocclusion of lower premolars, a male with a deformed coronoid process, and a male with several cranial anomalies (Douglas 1969). Both albinism and melanism occur (Bailey 1915). Unusual color morphs from California include partly-white individuals representing *T. b. mewa*, *T. b. pascalis*, *T. b. perpallidus*, and *T. b. puertae*; white individuals of *T. b. bottae* and *T. b. navus*; black individuals of *T. b. bottae*, *T. b. navus*, and *T. b. pallescens*; and red representatives of *T. b. navus* (Storer and Gregory 1934).

FUNCTION. Animals weighing 111, 143, 143, and 262 g had resting metabolic rates of 0.97, 0.84, 0.85, and 0.61 ml O_2/gh, respectively (Contreras and McNab 1990). Botta's pocket gophers maintain a body temperature of 36 ± 0.3°C (*SD*) at ambient temperatures of 5–25°C (Vleck 1979).

Mean rates of O_2 consumption while burrowing vary from 2.8 to 7.1 cm^3 O_2/gh, averaging 4 times resting metabolic rate at the same temperature (Gettinger 1984b; Vleck 1979). Tolerance of hypoxia in burrows and at high elevations is correlated with high hematocrit, O_2 capacity, alveolar exchange area, and concentrations of hemoglobin, acid-soluble phosphates, and skeletal myoglobin (Lechner 1976, 1977). Efficiency of energy assimilation (54%) does not change seasonally (Gettinger 1984b). *T. bottae* is relatively insensitive to CO_2, but individual sensitivity varies (Darden 1972). A mathematical model describing energy cost and/or benefits for pocket gophers predicts that burrows are as small in diameter as possible, but that they are longer than need be, possibly related to quality and quantity of aboveground foods (Andersen 1982). Burrow length reflects minimized energetic costs of burrowing (Vleck 1981).

T. bottae is a tooth-limb digger or chisel-tooth digger (Hildebrand 1982; Nevo 1979; Stein 2000). Limbs are shorter, incisors and jaw muscles are larger, tooth enamel is thicker, and skull is more procumbent than for geomyids who dig primarily with their limbs (Hildebrand 1982; Lessa 1990; Lessa and Patton 1989; Lessa and Thaeler 1989). Incisors, manipulated by massive jaw and neck muscles, loosen dirt, which is moved rearwards by the head and/or feet. The use of teeth to dig allows a broad use of soils because enamel in teeth is much harder than keratin in claws (Lessa 1990; Lessa and Thaeler 1989). Wear on incisors can be asymmetrical (Stangl et al. 1989). Extrusive growth rate of upper incisors of 2 *T. bottae* averaged 0.62 (range, 0.54–0.68) mm/day; growth of lower incisors was 0.99 (range, 0.89–1.05) mm/day (Howard and Smith 1952).

Claw growth among 5 *T. b. navus* varied widely. Mean growth of the center nail on manus was 0.25 ± 0.02 *SE* mm/day. Growth rate of the 3 center nails on manus was 0.23 ± 0.02 mm/day and growth of remaining nails on fore- and hind feet was 0.13 ± 0.00 (Howard 1953).

Nutritional values of local foods strongly influence rates of growth; cranial dimensions of *T. bottae* in desert-scrub were smaller than those of individuals in alfalfa fields (Patton and Brlylski 1987). Mass of females and mass changes in young from desert-scrub were smaller that those of animals in the same age classes from alfalfa fields.

The first silky hairs of young are replaced simultaneously, followed by acquisition of the gray juvenile coat, first on head and then spreading posteriorly (Morejohn and Howard 1956). Adult molt generally commences on head near eyes and ears (spreading posteriorly), on tip of tail (spreading anteriorly), and on feet (expanding dorsally). Spot molting occurs on abdomen (Morejohn and Howard 1956). Females might start summer coats sooner but complete them more slowly than males (Howard and Childs 1959; Morejohn and Howard 1956).

ONTOGENY AND REPRODUCTION. In agricultural fields and other habitats with abundant food, the breeding season can be year-round (Loeb 1990; Patton and Smith 1990). Populations in Orange County, California breed throughout the year, with activity peaking in early November and late March (Bond 1946; Miller 1946). In northern and/or higher elevation regions, breeding is restricted to spring (Miller 1946). Reproductive activity in southern Colorado started in March or late February, with no lactating females or scrotal males taken August–September (Douglas 1969). In Arizona, males were scrotal in February and lactating females were caught in May (Bandoli 1981). In alfalfa fields, up to 4 litters can be produced in 1 year (Dixon 1929; Loeb 1990).

Females can breed in the season of their birth in areas with plentiful food, whereas males do not (Patton 1993c). In desert scrub, no females bred in the season of their birth, in contrast to 46% of the females in a population in alfalfa fields (Patton 1993c, Patton and Brlylski 1987). Body size does not predict reproductive condition accurately (Daly and Patton 1986; Gunther 1956; Reichman et al. 1982). Nonjuvenile females are potentially reproductive at all body masses.

Birth occurred at 18 days after copulation of 2 pairs of *T. bottae* in the lab (Schramm 1961). Litter sizes were 1 and 4, with parturition lasting ca. 30 min and 4 h, respectively. Labor movements in the female producing 1 young consisted of bulging of abdominal walls, accompanied by a slight forward movement of the body. No other assistance in the birth was provided.

Mean litter sizes in 6 populations in California ranged from 4.1–5.6 (Patton and Smith 1990). Litter sizes ranged from 1–12 (n = 46) in irrigated alfalfa fields in California (Loeb 1990). Litter sizes of 3 and 3.2 were reported from Colorado and Arizona respectively (Bandoli 1981; Douglas 1969). Females collected in Nevada carried 1–10 embryos (Lay 1978).

Four juvenile *T. b. pallescens* of indeterminate age were partially naked, blind, ca. 87 mm, and lacked pouches (Anthony 1923). Juveniles described by Hill (1934) had umbilical cords attached and were naked, blind, and ca. 50 mm.

ECOLOGY. *Thomomys bottae* occupies valleys, desert ranges, and mountain slopes to above timberline (Patton 1999b). Distribution appears to be limited by suitable soils, climate, competition, and vegetative structure. Hard soils can limit distribution (Davis and Robertson 1944; Howard and Childs 1959).

Barriers to dispersal include unsuitable soils, rivers, rock formations, and deserts and other inhospitable environments (Best 1973; Douglas 1969; Goldman 1937b, 1947; Grinnell 1918; Miller 1964; Reichman and Baker 1972). Dispersal occurs on the surface and under soil or snow; the longest move recorded was 300 m (Daly and Patton 1990; Vaughan 1963; Vaughan and Hansen 1964). Average distances (m) moved within 24 h were 31.83 m by 11 adult males, 28.36 by 29 adult females, 8.32 by 4 subadult males, and 20.56 by 9 subadult females (Williams and Baker 1976).

Agricultural areas occupied by *T. bottae* include alfalfa fields (Goldman 1947; Long 1940; Marshall 1940; Miller 1952, 1964; Patton and Brlylski 1987), hay fields (Jewett 1929), orange groves (Howell 1922), pine plantations (Dingle 1956), shortgrass range and cultivated fields (Moulton et al. 1983), and both dry and irrigated pastures (Howard 1961; Ingles and Biglione 1952). Forests and woodlands used by *T. bottae* include stands dominated by aspen (*Populus tremuloides*—Cantor and Whitham 1989), incense cedar (*Libocedrus decurrens*) and white fir (*Abies concolor*—Holdenried 1940), Engleman spruce (*Picea engelmannii*) and corkbark fir (*A. lasiocarpa*—Stromberg and Patten 1991), ponderosa pine (*Pinus ponderosa*—Goldman 1947; Miller 1964; Youngman 1958), and mixed ponderosa and scrub oak (*Quercus*) at elevations of ca. 2,100–2,700 m (Hill 1942). Woodlands dominated by blue oak (*Q. douglasii*), interior live oak (*Q. wislizenii*), digger pine (*P. sabiniana*), and wedgeleaf ceanothus (*Ceanothus cuneatus*); meadows including mountain meadows bounded by fir, spruce, and aspen; salt grass (*Distichlis*) swales; and riparian communities with plants such as arrowweed (*Pluchea sericea*) also are used (Banks 1967; Goldman 1947; Howard and Childs 1959; Patton and Brlylski 1987). Drier habitats occupied by *T. bottae* include piñon-juniper and shortgrass (Bandoli 1981; Douglas 1969; Miller 1964; Youngman 1958); chaparral (Gettinger 1984a); communities dominated by sagebrush (*Artemisia tridentata*), *Atriplex*, and *Coleogyne ramossissima*; deserts with giant cactus (*Carnegiea gigantea*) and other cactuses; and communities with mesquite (*Prosopis juliflora*), paloverde (*Cercidium torreyanum*), creosotebush (*Covillea tridentata*), catsclaw (*Acacia greggii*), and ironwood (*Olneya tesota*—Douglas 1969; Goldman 1947; Patton and Brlylski 1987). Burrows may be closely associated with prickly pear (*Opuntia*—Douglas 1969; Miller 1964).

Burrows tend to be more plentiful in alluvial areas and along highways than in pastures (Best 1973; Goldman 1947; Miller 1964). Populations in the Davis Mountains, Texas are more concentrated near creeks during seasonal dry periods (Reichman and Baker 1972). When ranges overlap with those of *Pappogeomys* and *Geomys*, burrows of *T. bottae* generally occur in harder soils and higher ground (Best 1973; Miller 1964; Southern 1979). *Thomomys b. limpiae*, *T. b. texensis*, and *P. castanops* occur sympatrically in the Davis Mountains (Riechman and Baker 1972).

The typical burrow consists of 1 or more fan-shaped, surface mounds where excavated dirt has been deposited, sometimes with other debris retrieved from burrow. Entries through mounds can be open, but usually are plugged with soil. The system includes downshafts, ramps, areas for defecation, and chambers for nests and food storage. Feeding tunnels parallel the surface, allowing access to the surface and to underground plant parts, whereas deeper tunnels house nests lined with dried grass and/or fur. Side tunnels off feeding tunnels allow disposal of excavated soil (Gettinger 1984a; Hickman 1990; Vleck 1981). Frequently foods are stored in chambers, or sometimes in sides of burrows (Douglas 1969; Long 1940; Miller 1957). Burrows are illustrated by Miller (1957). In excavated burrows of *T. b. fulvus* and *T. b. mutabalis* in Arizona, reproductive males had significantly longer burrows, more linear burrows (thus, more adjacent neighbors), and larger perimeters and home ranges than did females and nonreproductive males (Reichman et al. 1982). Burrows are shorter in more productive areas (Gettinger 1984a; Reichman et al. 1982). Where *T. bottae* is sympatric with *Pappogeomys castanops* on the Mesa de Maya in Colorado, feeding burrows occurred in the same types of soil and vegetation but at significantly different average depths (Moulton et al. 1983). Burrows off the mesa were allopatric; sympatry on the mesa represented an intermediate stage in competitive exclusion. In northeastern New Mexico, 41 burrows of *T. bottae* averaged 131.954 mm in depth and 70.460 mm in diameter (Best 1973).

Thomomys bottae takes a variety of acorns, bulbs, forage, seeds, and tubers. Fifteen plant species eaten by captives from Mesa Verde, Colorado, included roots and stems of *Artemisia frigida*, *A. ludoviciana*, *Chrysothamnus nauseosus*, and *Penstemon linariodes*. *T. bottae* also fed on *Opuntia* in the field (Douglas 1969). In fecal samples from Arizona, bitterweed (*Hymenoxys richardsonii*), blue grama (*Bouteloua gracilis*), Fendler three-awn (*Aristida fendleriana*), forget-me-not (*Cryptantha jamesii*), and snakeweed (*Gutierrezia sarothrae*) were consistently important, with *Bouteloua* comprising 24.4% of the average diet (Bandoli 1981). Seasonally, cholla (*Opuntia macrorhiza* and *O. fragilis*), paperflower (*Psilostrophe sparsiflora*), and rabbit brush (*C. nauseosus*) were used; winter diets of females included more *C. nauseosus* that those of males (Bandoli 1981). Stomach contents of *T. bottae* from California chaparral were primarily of annuals such as *Stephanomeria virgata* (49% of total dry mass), with grasses (*Bromus*) and leaves of *Rhamnus californica* in summer, whereas grasses, leaves, and bark comprised the winter diet (Gettinger 1984b). *T. bottae* harvested at a rate of >10 kg/gopher and consumed at a rate of ca. 5 kg/gopher or 95 MJ. *T. b. sanctidiegi* had significant seasonal changes in diet, with shoots of forbs and grasses comprising major foods (Hunt 1992). Corms and roots are used more heavily during periods of plant dormancy (Bandoli 1981; Douglas 1969; Howard and Childs 1959).

Other foods include parts of aspen (*Populus tremuloides*), broadleaf filaree (*Erodium botrys*), cacti of the genus *Opuntia*, fig trees (species not identified), iris (species not identified), Jeffrey pine (*P. jeffreyi*), lodgepole pine (*P. contorta*), lupines (*Lupinus*

kingii), ocotillo (*Fouqueria splendens*), ponderosa pine (*P. ponderosa*), pumpkins and squashes (species not identified), sagebrush (*A. carruthii* and *A. dracunculoides*), and scotch pine (species not identified—Bandoli 1981; Cahalane 1939; Cantor and Whitham 1989; Cox and Hunt 1994; Crouch 1971; Dingle 1956; Douglas 1969; Fitch and Bentley 1949; Gettinger 1984b; Hall 1995; Howell 1922; Linsdale 1938). Cones and nuts of piñon pine (*P. edulis*) were found in subterranean caches, and coprophagy occurs in captive animals (Douglas 1969). Methods used for studying diet quality were compared by Loeb and Schwab (1989).

American marten (*Martes americana*), badgers (*Taxidea taxus*), barn owls (*Tyto alba*), coyotes (*Canis latrans*), gopher snakes (*Pituophis catenifer*), great blue herons (*Ardea herodias*), great horned owls (*Bubo virginianus*), long-eared owls (*Asio otus*), rattlesnakes (*Crotalis viridis*), red-tailed hawks (*Buteo jamaicensis*), San Joaquin kit foxes (*Vulpes macrotis mutica*), and weasels (*Mustela*) are known predators (Cypher et al., 1994; Douglas 1969; Evans and Emlen 1947; Howard and Childs 1959; Lantz 1910; Marti et al. 1986; Ports and McAdoo 1986; Presnall 1948; Tappe 1941; Von Bloeker 1937; White et al. 1995). Increased gopher activity in autumn corresponds with more remains in owl pellets (Evans and Emlen 1947). *T. bottae* made up 71.4%, by weight, of barn owls' diet, although owls were rare on the site (Howard and Childs 1959).

Botflies (species not identified), fleas (*Foxella ignota*, *Thrassis petiolatus*), lice (*Geomydoecus californicus*, *G. minor*, *G. thomyus*, *Trichodectes geomydis*), mites (*Haemogamasus ambulans*, *Haemolaelaps geomys*, *Hirstionyssus geomydis*, *Ischryopoda armatus*, *Trobicyla californica*), nematodes (*Heligmosomoides thomomyos*), tapeworms (*Hymenolepis horrida*), and ticks (*Dermacentor*, *Ixodes sculptus*, *I. kingi*) are among reported parasites (Douglas 1969; Gardner and Jasmer 1983; Howard and Childs 1959; Linsdale 1938; Miller and Ward 1960). The 102 species and subspecies of chewing lice of the genus *Geomydoecus* (Mallophaga: Trichodectidae) are exclusive and obligatory parasites of *T. bottae* and other pocket gophers, with varying degrees of host specificity (Emerson and Price 1985; Hafner et al. 1998; Kim and Adler 1985; Nadler et al. 1990; Price 1972). Identification of lice has assisted in determination of a genetic hybrid zone between *T. bottae* and *T. townsendii* (Patton et al. 1984). *Thomomys bottae* is not a reservoir for human diseases (Cockrum 1997; J. Pape, pers. comm.). Burying beetles (*Nicrophorus investigator*) feed on carcasses (Smith and Heese 1995).

Densities of 10–62/acre occur in alfalfa fields (Howard 1961; Howard and Childs 1959; Miller 1957; Miller 1964). A density of 29.6/acre was estimated in Californian, foothill rangeland (Fitch and Bentley 1949). In *T. bottae* and other species of pocket gophers, scale-defined density declined with increasing female body mass (Smallwood and Morrison 1999). A population crash was reported (Howard 1961). Livestock grazing reduced abundance of *T. bottae* on annual grasslands in Tehama County, California (Hunter 1991).

Adult sex ratios vary from equality to nearly 4 females/male (Howard and Childs 1959; Lay 1978; Patton and Feder 1981; Patton and Smith 1990). Populations in better habitats have greater sexual dimorphism and greater skew in sex ratio (Patton and Smith 1990).

Thomomys bottae mixes soil to depths of 20 cm (Cox 1990; Grinnell 1923; Hobbs and Hobbs 1987; Mielke 1977). Experiments with soil plugs and metal markers suggest that Mima mounds result from soil movement by *T. bottae* (Cox 1990; Cox and Allen 1987).

T. bottae affects plant communities through herbivory and changes in soil. Successional species such as *Sphaeralcea coccinea* replaced clumps of cacti (*Opuntia*) preyed upon by *T. b. aureus* (Douglas 1969). Density of *T. bottae* correlates with mortality of aspen in northern Arizona (Cantor and Whitham 1989), and increased activity occurs in fertilized areas (Hobbs et al. 1988).

Patches of bare ground created by *T. bottae* can affect seedling establishment (Stromberg and Patten 1991). Significant areas (up to 25–30% of the soil surface) can be covered by gopher mounds (Koide et al. 1987); 1 mound measured ca. 2.1 m long and over 0.9 m wide in the Toyabe Mountains of Nevada (Linsdale 1938). Creation of mounds can cover plants in the immediate vicinity, and mounds themselves are colonized differentially (Douglas 1969; Hobbs and Hobbs 1987; Hobbs and Mooney 1985; Koide et al. 1987).

Hickman (1977b) discussed interactions of *T. bottae* with various invertebrates and vertebrates. Golden-mantled ground squirrels (*Spermophilus lateralis*) and tiger salamanders (*Ambystoma tigrinum*) used burrows of *T. bottae* in Colorado (Vaughan 1961).

Major economic impacts result from effects on archaeological sites, soil erosion, water diversion, management of hazardous wastes, spreading of weeds, and altered vegetation (Dice 1939; Dingle 1956; Douglas 1969; Howard and Childs 1959; Smallwood and Morrison 1999). Because of these negative effects, the purpose of many publications is to describe the use of strychnine baits, traps, and other control methods (Dingle 1956; Miller 1953).

Hanley (1944) offered recommendations regarding keeping *T. b. pascalis* in captivity.

BEHAVIOR. *T. bottae* primarily feeds underground, but many instances of aboveground foraging have been reported (Douglas 1969; Grinnell 1923; Howard and Childs 1959; Howell 1922; Huntly and Inouye 1988; Linsdale 1938). Incisors are used to cut both above- and belowground foods. Forbs "were cut off about an inch above the ground, and the rasping sound of the gophers' teeth shearing through the plant fibers was audible in the still air for twenty to thirty feet" (Cahalane 1939:430). Pine seedlings can be pulled into burrows (Crouch 1971; Dingle 1956).

Captive *T. bottae* selected flowers and buds over woody portions of *Stephanomeria virgata* and other annuals; grasses were consumed entirely (Gettinger 1984b). Food handling by 2 captives was as follows: pieces of carrot and lab chow were carried by the teeth or rolled to a digging site; there, soil was loosened with teeth and foreclaws while "tumbling the food item against the loosening soil" (Katz 1980:270). Then soil was pushed out of the tunnel with the manus, face, and food item. The same food item was retrieved from cast soil, returned to the digging site, and used again in excavation (Katz 1980).

Adults maintain exclusive territories throughout the year and juveniles of both sexes disperse after weaning (Lidicker and Patton 1987; Miller 1964). Mean territory sizes were 390 m^2 (1,300 $feet^2$) for 60 females and 810 m^2 (2,700 $feet^2$) for 36 males (Howard and Childs 1959). Territories do not increase when population density decreases, and individuals that have established a territory rarely move to a new one (Howard and Childs 1959). Surface areas of burrow systems in New Mexico averaged 286.4 ± 59.4 *SD* m^2 for females and 474.7 ± 148.2 *SD* m^2 for males (n = 14—Bandoli 1987). Natal movements were 7.5–141 m ($\bar{X}$, 56.7 m; n and *SD* not specified—Vaughan 1963). Short longevity results in an estimated genetically effective population size of >110 individuals, larger than predicted (Lidicker and Patton 1987).

Use of burrows by >1 adult is limited to the breeding season, when several individuals can be observed in or near burrows (Howard and Childs 1959). In 4 cases nests 1.6 m deep were shared by 1 female and 1 male (Reichman et al. 1982). In 3 cases males were captured in female burrows during the reproductive season (Bandoli 1981).

Burrowing activity correlates positively with greater soil moisture in spring, fall, and winter and is correlated negatively with dry, hot summers (Cox and Allen 1987; Cox and Hunt 1992; Howard and Childs 1959; Miller 1948). Trapping success and clearing of tunnels (i.e., burrow maintenance) correlated negatively with time since last rainfall and with air temperature; moisture makes digging easier and enhances growth of herbaceous plants (Cox and Hunt 1992). High burrowing activity in fall has been associated with foraging, but may be climate-related (Bandoli 1981; Cox 1990). *Thomomys bottae* moves deeper into burrows to avoid high temperatures; it lacks cooling mechanisms (such as panting and salivating) common to nonfossorial mammals (Vleck 1979).

Travel on the surface has been noted many times (Howell 1922). In 1 case, >50 males, females, and young *T. b. bottae* became stuck in oil remaining from street repairs (Bryant 1913).

Burrows are actively defended (Vleck 1979). Aggressive behaviors include attacks and standing ground while being attacked (Baker 1974). Aggression between *G. bursarius*, *P. castanops*, and *T. bottae* occurs (Hickman 1977b). In the laboratory, *T. talpoides* dominated *T. bottae*. Numbers of attacks did not differ between sexes (Baker 1974). Aggressive encounters with other individuals can result in bite wounds on the forepaws (Baker 1974). Pouches can be everted in aggressive encounters (Howard and Childs 1959).

Stalking and other behaviors are associated with prospecting and excavating burrows (Hickman 1984). Incisors loosen soil and remove rocks (Grinnell 1923). Mound production and burrow ex-

tension are correlated in both sexes (Bandoli 1981). Males are more active than females during winter.

Adults and subadults of both sexes can return home when released at distances ≤90 m from their territories (Howard and Childs 1959). Dispersal occurs aboveground (Howard and Childs 1959). Sometimes juveniles occupy territories that have been vacated, but only outside their original home ranges. Dispersal was 30–60 m (n = 5), 60–90 m (n = 3), and 90–120 m (n = 5, of which 2 were captured later off the study plot—Howard and Childs 1959). *T. bottae* can swim (Hickman 1977a).

Botta's pocket gophers are active night and day (Bandoli 1987; Best 1973; Gettinger 1984a; Reichman et al. 1982). In Riverside County, California, 6 individuals were active 8.7 ± 0.7 *SE* h/day (mostly in shallow feeding burrows) and were most active during 1600–2000 h (Gettinger 1984a). In Bernalillo County, New Mexico, gophers were most active between 1500–1800 h (Bandoli 1987).

Vocalizations are limited to clicking of teeth and to soft sounds described as hisses, murmurs, purrs, or squeaks (Francescoli 2000; Hill 1937; Howard and Childs 1959; Schramm 1961).

Copulatory episodes of 2 pairs of wild-caught *T. bottae* brought into captivity lasted 25 and 54 min with multiple intromissions (Schramm 1961). Copulatory behavior of the 2 females included vocalizations, upright posture, and closed eyes. Males mounted from the rear, on the female's sides, or on the female's back, grasping the female's neck and shoulders with the front paws. One male switched to different sides of the female's tail after withdrawing and resuming intromission. In 80 breeding trials, 2 breedings were successful and fighting was uncommon.

Maternal behavior includes bringing foods to the nest. Green grass was found in stomachs of young pups whose eyes were not yet open (Dixon 1929).

GENETICS. Diploid numbers range from 74–88, with most populations 2n = 76 (Hafner et al. 1983; Patton and Dingman 1970; Patton and Smith 1990; Thaeler 1980). Karyotype varies geographically from an all-biarmed autosomal complement (in the west) to 1 with more than half the complement comprised of uniarmed elements (in the east—Patton and Smith 1990). Hybridization between *T. bottae* and *T. townsendii*, *T. bottae* and *T. umbrinus*, and among subspecies of *T. bottae* occurs (Hoffmeister 1969; Patton 1973; Patton and Dingman 1968; Patton et al., 1979, 1984; Thaeler 1968a, 1968b). Hybrid formation with *T. townsendii* and *T. umbrinus* is limited largely to the F1 generation, indicating that genetic isolation is complete or nearly so. Hybrid males between *bottae* and *umbrinus* are sterile, and hybrid females show 50% reduction in fertility (Patton 1973). Studies of hybrid zones were reviewed by Patton (1993b).

Karyotype varies over a large number of populations throughout the range of *T. bottae* (Patton 1972; Patton and Dingman 1968; Patton and Smith 1990; Patton and Yang 1977; Thaeler 1980). Extensive differentiation in gene markers such as protein allozymes also occurs among populations. Geographically distant populations can differ by >30% (Patton and Yang 1977), and intrapopulation variation can equal 6% (Patton and Feder 1981). Karyotypic and genic diversity have been related to environmental gradients (Patton 1970), the physical and biotic properties of the subterranean niche (Nevo et al. 1984), biogeographic events (Patton 1972), demographic properties of local populations (Lidicker and Patton 1987; Patton and Feder 1981), and degree of gene flow between populations (Daly and Patton 1990; Patton and Yang 1977). Diploid number for 903 individuals representing 56 subspecies is 2n = 76 (Thaeler, 1980), but varies; 2n = 74 for *T. b. simulus*, 2n = 74–76 for *T. b. opulentus* from New Mexico, 2n = 75–76 for *T. b. mearnsi* from New Mexico, 2n = 76–78 for *T. bottae* from western Texas, and 2n = 82 for *T. b. pervagus* from Colorado (Berry and Baker 1971; Patton and Dingman 1970; Thaeler 1980). Genic variation and chromosomal disparity do not hinder formation of hybrid zones between many subspecies (Daly and Patton 1990; Ingles and Biglione 1952; Patton 1972; Patton and Yang 1977; Patton et al. 1979; Thaeler 1968b).

Skin-graft experiments were performed on Botta's pocket gophers from 1 population with high variation in mean heterozygosity and from 2 that had low variation (Sanjayan and Crooks 1996). Individuals from the low-variation population accepted within-population grafts, whereas those from the more variable population did not; all tested individuals rejected grafts from outside their own population.

REMARKS. The generic name *Thomomys* was derived from the Greek terms *thomos* and *mys*, meaning a heap and a mouse, respectively. The specific name honors Dr. Paolo Emilio Botta (1802–1870), a collector for the Museum of Natural History of Paris and 1 of the first naturalists to collect specimens in California (Jaeger 1955). Five subspecies of *T. bottae* (*T. b. guadalupensis*, *T. b. limpiae*, *T. b. mearnsi*, *T. b. paguatae*, and *T. b. texensis*) bear a federal status of C2 (Yenson et al. 1998).

We thank K. Gully, L. Hetterson, K. Honda, and N. Kall of the Denver Museum of Nature and Science for assistance with literature; R. Hollander for the photo; and E. Parrish for the illustration. Special thanks are due L. L. Choate and J. L. Patton for careful reviews of our manuscript.

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Associate Editors of this account were LUI MARINELLI and ELAINE ANDERSON. Editor was VIRGINIA HAYSSEN.

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