

Thomomys townsendii. By B. J. Verts and Leslie N. Carraway

Published 30 July 2003 by the American Society of Mammalogists

Thomomys Wied-Neuwied, 1839

- Geomys* Rafinesque, 1817:45 (in part). Type species *Geomys pinetis* Rafinesque (= *Mus tuza* Barton).
- Pseudostoma* Say, 1823:406. Type species *Pseudostoma talpoides*. A renaming of *Geomys borealis*.
- Cricetus* Richardson, 1828:518 (in part). Type species *Cricetus talpoides*.
- Diplostoma* Richardson, 1829:206. Type species *Diplostoma? bulbivorum*.
- Oryctomys* Eydoux and Gervais, 1836:20 (in part). Type species *Oryctomys (Saccophorus) bottae*.
- Thomomys* Wied-Neuwied, 1839:377. Type species *Thomomys rufescens*.
- Megascapheus* Elliot, 1903:190. Type species *Diplostoma bulbivorum* Richardson.
- Pleiothomomys* Gidley and Gazin, 1933:354. Type species *Pleiothomomys potomacensis*.

CONTEXT AND CONTENT. Order Rodentia, family Geomyidae, genus *Thomomys*, which includes subgenera *Thomomys* and *Megascapheus*. Distinguished from other Geomyidae by ≤ 1 faint lingual sulcus on I1s; elliptical M3s; basitemporal fossa absent; and small, narrow forefeet with strong claws (Akersten 1973; Hall 1981). Also, enamel on both upper and lower molariform teeth is arranged in 10 vertical plates, 4 (1 each anterior, posterior, labial, and lingual) on both P4 and p4 and 2 (1 each anterior and posterior) on each M1–M3 and m1–m3 (Merriam 1895). A key to species (modified from Hall 1981; Jameson and Peeters 1988; and Verts and Carraway 1998, with characters from Hoffmeister 1986; Thaeler 1972, 1980; and Thaeler and Hinesley 1979) follows:

- 1 Sphenoidal fissure present 2
Sphenoidal fissure absent 5
- 2 Hind foot ≤ 33 mm 3
Hind foot ≥ 34 mm 4
- 3 Maxillo-frontal suture concave and abuts lacrimal near center; 0–18 acrocentric chromosomes; usually 4 pairs mammae, 2 pairs pectoral and 2 pairs inguinal
..... *Thomomys bottae*
- Maxillo-frontal suture convex and abuts lacrimal in medial half; 54–56 acrocentric chromosomes; usually 3 pairs mammae, 1 pair pectoral and 2 pairs inguinal
..... *Thomomys umbrinus*
- 4 Length of hind foot usually >40 mm in males, >38 mm in females; pterygoids concave on inner surface, convex on outer surface; exoccipital with 2 grooves; pelage dark sooty brown dorsally, lead colored ventrally; irregular white throat patch present *Thomomys bulbivorus*
Length of hind foot usually <40 mm in males, <38 mm in females; pterygoids straight; exoccipital lacking grooves; pelage usually grayish or light grayish brown dorsally, slightly lighter ventrally; white throat patch absent; pelage of some individuals black with white feet and chin
..... *Thomomys townsendii*
- 5 Length of ear from notch 8–9 mm; nasals extend posteriorly as far as premaxilla; pelage dark brown dorsally; feet white *Thomomys monticola*
Length of ear from notch usually <8 mm; premaxilla extend posteriorly beyond nasals; feet gray 6
- 6 Mandible with wide (≥ 1.5 mm) flange on posteriolateral edge; length of baculum 22–31 mm in adult males; pelage black, blackish with reddish dorsal stripe, or reddish brown *Thomomys mazama*
Mandible with narrow (≤ 1 mm) flange on posteriolateral

- edge; length of baculum 10.5–23.4 mm in adult males; pelage yellowish gray to yellowish brown 7
- 7 Karyotype diploid number (2n) = 40, 42, 44, 46, 48, 52, 54, 56, or 60 and broadly distributed from Cascade and Sierra Nevada ranges of British Columbia, Oregon, Washington, and California; east to Alberta and western Nebraska; and south to central New Mexico
..... *Thomomys talpoides*
Karyotype 2n = 46, 56, or 58 and restricted to small areas in Montana, Idaho, Utah, and Wyoming 8
- 8 Karyotype 2n = 46 and restricted to extreme southern Wyoming *Thomomys clusius*
Karyotype 2n = 56 and restricted to small areas in southern Montana and northeastern Idaho, or karyotype 2n = 58 and restricted to extreme southeastern Idaho, northern Utah, and western Wyoming *Thomomys idahoensis*

Thomomys townsendii (Bachman, 1839)

Townsend's Pocket Gopher

- Geomys Townsendii* Bachman, 1839:105. Type locality "Columbia River." Locality erroneous; type probably collected near Nampa, Canyon Co., Idaho (Bailey 1915:42, 1933:242).
 - Thomomys townsendii*: Allen, 1893:61. First use of name combination.
 - Thomomys nevadensis* Merriam, 1897:213. Type locality "Austin, [Lander Co.] Nevada."
 - Thomomys relictus* Grinnell, 1926:2. Type locality "valley of Susan River two miles south of Susanville, Lassen County, California."
 - Thomomys umbrinus* Hall, 1981:469 (in part). Based on hybridization (intergradation presumed) with *T. bottae*.
- CONTEXT AND CONTENT.** Context as above. Subgenus *Megascapheus* (Thaeler 1980). Two subspecies are recognized currently (Rogers 1991b):

- T. t. nevadensis* Merriam, 1897:213, see above (*bachmani*, *elkensis*, and *relictus* are synonyms).
- T. t. townsendii* (Bachman, 1839:105), see above (*atrogriseus*, *owhensis*, and *similis* are synonyms).

DIAGNOSIS. *Thomomys townsendii* (Fig. 1) can be distinguished from congeners by a combination of large size (exceeded only by *T. bulbivorus*), presence of a sphenoidal fissure, and straight pterygoids. It also has light grayish or light brownish pelage with dark gray ears or black pelage with white patches on chin or feet (Hall 1981; Jameson and Peeters 1988; Thaeler 1968a; Verts and Carraway 1998).



FIG. 1. Photograph of a *Thomomys townsendii*. Used with permission of photographer Mary-Anne Rogers.

GENERAL CHARACTERS. *Thomomys townsendii*, as other geomyids, is highly adapted for fossorial life. Head is large. Neck is truncate and essentially continuous with forelimbs; both head and neck are heavily muscled. Forefeet are large with fimbriated toes and long, heavy claws. Body tapers posteriorly to relatively narrow hips, short legs, and stout plantigrade hind feet. Eyes and pinnae are small. Fur-lined cheek pouches open external to mouth. Upper incisors are asuculate or unisuculate, slightly procumbent, and protrude through lips. In comparison with other *Thomomys*, degree of procumbency in *T. townsendii* is related entirely to its greater overall size. Vibrissae extend beyond width of head. Tail stubby, slightly tapered, and nearly naked (Akersten 1973; Bailey 1915; Lessa and Patton 1989; Merriam 1895). Females possess 8 mammae, 2 pairs pectoral and 2 pairs inguinal (Hall 1946). Baculum is short (10.7–13.9 mm in northern California), curved, and compressed proximally; most have a longitudinal groove and a ventral keel (Thaeler 1968a).

Skull (Fig. 2) is relatively large, flattened dorsally, with wide-spreading zygomata, narrow rostrum and nasals, large angular auditory bullae depressed to level of basioccipital, and short braincase with well-developed sagittal and occipital crests in older individuals (Bailey 1915). Basioccipital is heavy, thick, and narrow. Pterygoids are straight, and exoccipitals lack grooves. Anterior opening of infraorbital canal even with or anterior to anterior palatine foramina (Hall 1946). Mandibles are heavy, each with an articular process narrowly connected with flange along posteriolateral ramus (Thaeler 1980). Base (root) of somewhat procumbent I1 extends posterior to base of P4; base of M1 produces a bony protuberance in orbital region (Thaeler 1968a, 1980). The anterior ethmoid foramen, the opening that permits passage of anterior ethmoid nerve through frontal, is confluent with large sphenoidal fissure (Hill 1935).

Pelage of *T. townsendii* is buffy gray to sooty gray dorsally and a rich buff ventrally. Nose, face, and ear patch are dark gray. Feet and tail are a soiled gray. Chin is white (Bailey 1915), and many individuals in some regions have white marks on top of head (Thaeler 1968a). Melanism occurs in a small proportion of individuals in some regions (Rogers 1991a). Those with black pelage often have white spots on chin or feet (Jameson and Peeters 1988). Tonal intermediates between melanistic and typically colored individuals were recorded (Bailey 1915). Pelage is molted in late spring–early summer and in autumn (Bailey 1915); many specimens exhibit 1 or more molt lines.

Averages ($\pm SE$) and ranges for body dimensions (in mm) for 18 females and 24 males (in parentheses) from Harney and southern Malheur counties, Oregon (*T. t. nevadensis*), were (Verts and Carraway 1998): total length, 246 ± 3.7 , 222–289 (261 ± 3.3 , 235–288); length of tail, 72 ± 1.8 , 62–90 (76 ± 1.5 , 63–95); and length of hind foot, 34 ± 0.6 , 27–39 (36 ± 0.4 , 32–42). Values for same dimensions for 17–18 females and 19 males (in parentheses) from northern Malheur Co., Oregon (*T. t. townsendii*), were: 271 ± 2.9 , 248–288 (291 ± 3.9 , 258–340); 86 ± 1.2 , 75–98 (92 ± 2.2 , 78–113); and 37 ± 0.7 , 33–47 (38 ± 0.4 , 36–42). Averages and ranges for same dimensions for 21 female and 24 male (in parentheses) *T. t. nevadensis* (current classification) from Nevada (Hall 1946) were: 247, 232–264 (267, 239–290); 71, 53–86 (77, 60–95); and 35, 33–37 (37, 34–41). Averages for same dimensions for 13 female and 15 male (in parentheses) *T. t. townsendii* (current classification) from Idaho (Davis 1939) were: 254 (285), 77 (88), and 34 (38). Ranges (*n* not provided) for same dimensions for female and male (in parentheses) *T. t. nevadensis* (current classification) from California (Thaeler 1968a) were: 225–273 (252–301), 65–90 (73–101), and 30–39 (34–40). Averages and ranges for same dimensions for 87 females and 58 males (in parentheses) from 9–14 populations throughout the range of *T. t. townsendii* were: 251.5, 213–288 (279.0, 231–315); 75.5, 60–96 (85.9, 65–110); and 35.1, 32–39 (38.1, 33–41), and for 177–178 females and 152 males (in parentheses) from 15–17 populations of *T. t. nevadensis*, they were: 257.2, 140–289 (276.0, 232–318); 76.4, 38–90 (83.2, 59–108); and 35.6, 20–45 (37.5, 32–45—Rogers 1983).

Averages ($\pm SE$) and ranges for cranial dimensions (in mm) for 18 females and 24 males (in parentheses) from Harney and southern Malheur counties, Oregon (*T. t. nevadensis*), were (Verts and Carraway 1998): basilar length, 38.72 ± 0.54 , 36.05–45.61 (40.8 ± 0.44 , 36.58–44.92); zygomatic breadth, 29.11 ± 0.33 , 26.89–33.57 (30.49 ± 0.26 , 27.90–32.95); mastoid breadth, 24.38 ± 0.34 , 22.78–29.24 (25.67 ± 0.28 , 23.42–28.93); least interor-

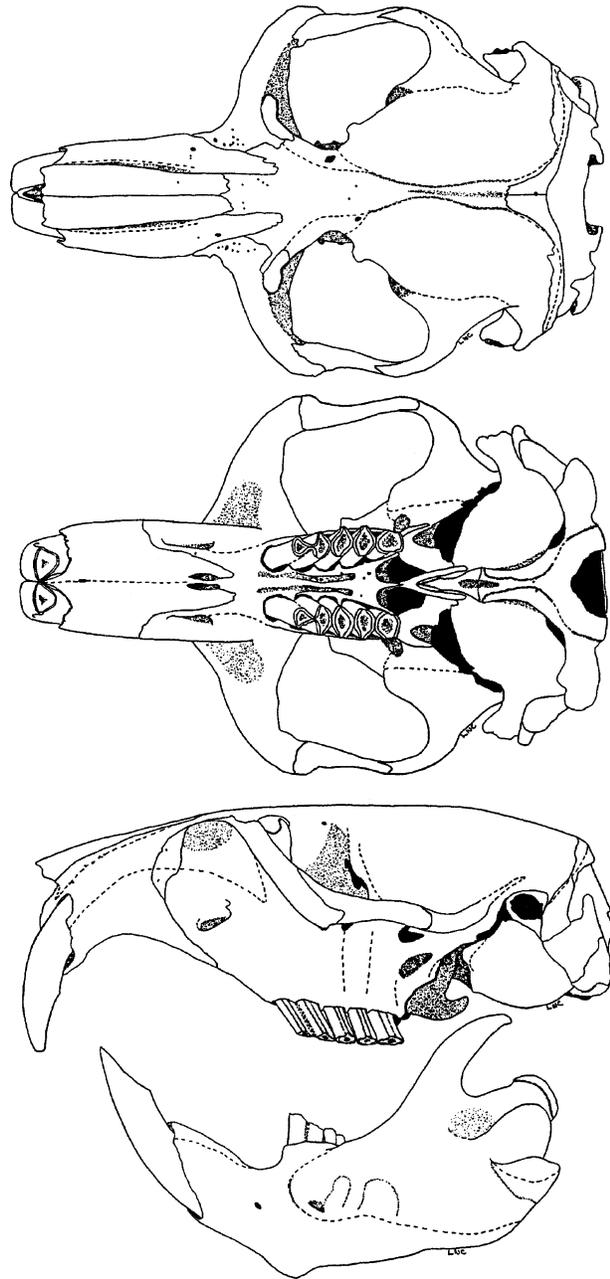


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Thomomys townsendii* (OSUFW [Oregon State University Department of Fisheries and Wildlife] 1646; from 28 mi S, 3 mi W Burns, Harney Co., Oregon). Greatest length of skull is 44.62 mm. Skull plate reprinted from Verts and Carraway (1998) with permission of the University of California Press.

bital breadth, 7.02 ± 0.08 , 6.46–7.62 (7.02 ± 0.09 , 6.11–7.95); skull depth, 17.54 (incorrectly reported as 15.54) ± 0.17 , 16.55–19.90 (18.21 ± 0.16 , 16.74–19.85); length of mandible, 28.48 ± 0.48 , 26.03–34.09 (30.03 ± 0.38 , 26.54–33.61); and length of mandibular toothrow, 9.87 ± 0.09 , 9.00–10.36 (10.00 ± 0.08 , 9.37–10.85). Values for same dimensions for 18 females and 19 males (in parentheses) from northern Malheur Co., Oregon (*T. t. townsendii*), were: 42.40 ± 0.27 , 39.63–43.71 (45.21 ± 0.53 , 41.20–50.16); 31.22 ± 0.25 , 28.93–32.54 (33.21 ± 0.42 , 30.32–36.92); 25.49 ± 0.23 , 23.90–26.61 (27.28 ± 0.36 , 24.69–30.33); 7.41 ± 0.06 , 6.94–7.81 (7.37 ± 0.05 , 6.77–7.83); 9.89 ± 0.16 , 8.52–10.93 (10.07 ± 0.12 , 9.29–10.92); 18.29 ± 0.17 , 16.35–19.86 (19.36 ± 0.23 , 17.95–21.55); 30.31 ± 0.31 , 27.71–32.39 (32.83 ± 0.45 , 29.14–36.39); and 10.30 ± 0.11 , 9.42–11.08

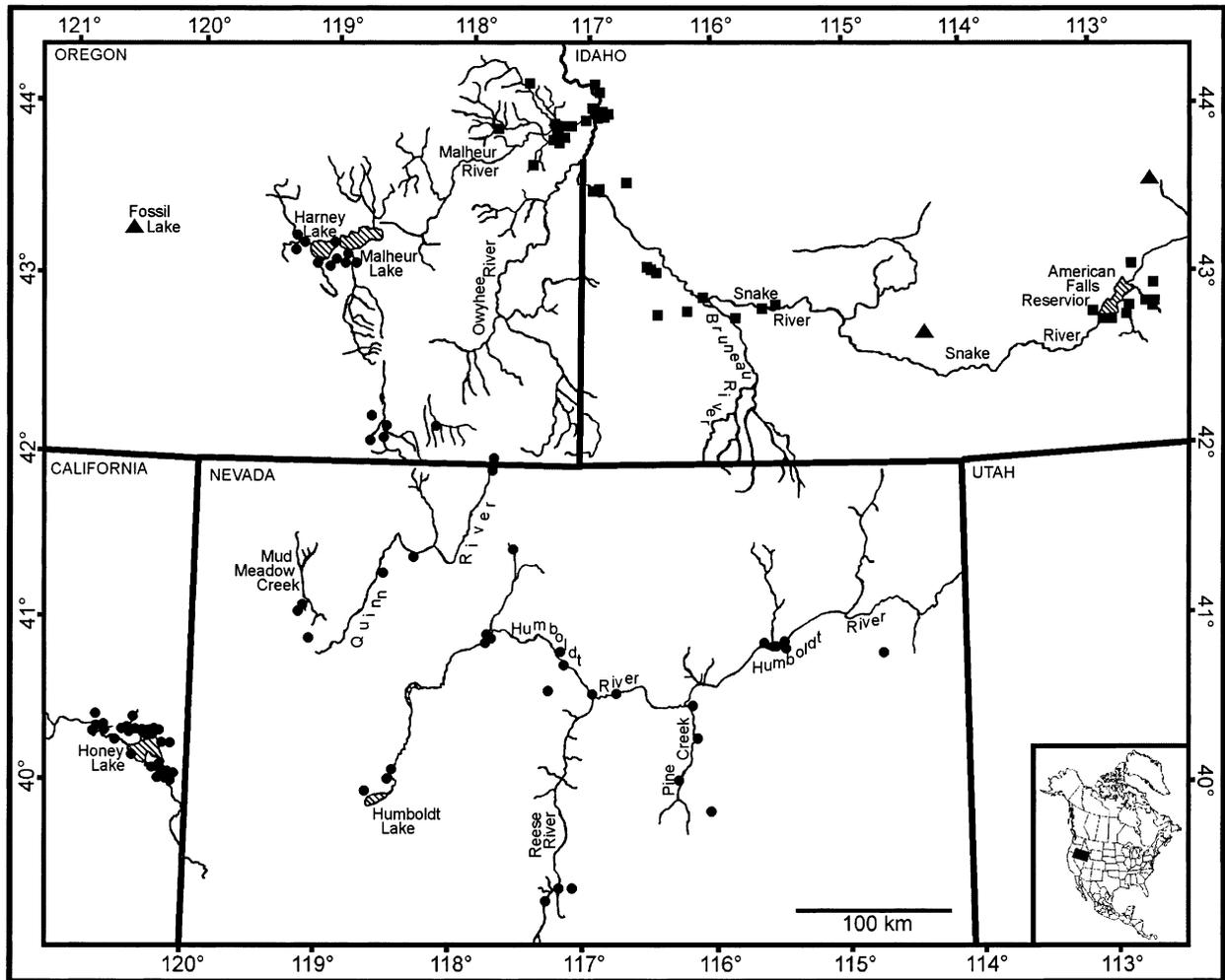


FIG. 3. Distribution of localities at which specimens of *Thomomys townsendii* were collected (Bailey 1915; Davis 1939; Hall 1946; Rogers 1991a; Thaeler 1968a; Verts and Carraway 1998). Subspecies are *T. t. nevadensis* (closed circles) and *T. t. townsendii* (closed squares). Triangles indicate sites at which fossils of *T. townsendii* were collected (Allison 1966; Elfman 1931; Gazin 1935; Gruhn 1961; Guilday 1969; Hopkins et al. 1969; McDonald and Anderson 1975).

(10.37 ± 0.08 , 9.73–10.88). Averages and ranges for cranial dimensions (in mm) for 9 female and 9 male (in parentheses) *T. t. townsendii* (current classification) from Idaho (Davis 1937) were: basilar length, 38.5, 36.7–41.0 (45.1, 42.8–47.7); zygomatic breadth, 28.2, 27.1–29.9 (33.0, 31.9–34.6); least interorbital breadth, 7.6, 7.2–8.1 (7.4, 7.0–7.9); mastoid breadth, 22.7, 21.9–24.5 (27.0, 25.4–29.2); length of nasals, 14.9, 14.0–16.4 (18.9, 17.4–20.2); rostral breadth, 8.7, 8.2–9.6 (10.2, 9.5–11.2); rostral length, 17.8, 17.1–19.0 (22.1, 20.5–23.4); length of maxillary toothrow, 9.7, 9.3–9.9 (10.5, 9.7–11.0); and palatofrontal depth, 16.9, 16.1–18.3 (19.9, 18.2–20.6). Ranges for condylo-nasal length and zygomatic breadth (in mm) for female and male (in parentheses) *T. t. nevadensis* (current classification) from northern California (*n* not provided) were: 41.5–48.9 (46.1–53.8) and 25.9–31.0 (28.1–33.8), respectively (Thaeler 1968a). Averages and ranges for cranial dimensions (in mm) for 82–87 females and 57–58 males (in parentheses) from 9–16 populations throughout the range of *T. t. townsendii* were: basilar length, 39.15, 34.5–45.0 (44.89, 37.5–49.6); zygomatic breadth, 30.80, 25.0–32.2 (32.18, 26.5–36.4); mastoid breadth, 23.74, 21.2–26.5 (25.13, 23.2–30.0); skull depth, 13.56, 12.2–15.1 (14.75, 13.2–16.5); least interorbital breadth, 7.24, 6.8–7.9 (7.20, 6.6–7.7); and length of maxillary toothrow, 9.73, 8.1–11.1 (9.89, 8.7–11.5—Rogers 1983). Same dimensions for 176–189 females and 150–160 males (in parentheses) from 9–10 populations from throughout the range of *T. t. nevadensis* were: 39.28, 36.1–46.3 (48.77, 39.6–50.2); 29.65, 26.8–34.5 (29.75, 27.6–36.6); 24.73, 21.9–29.3 (29.23, 23.2–30.6); 14.19, 13.0–16.4 (15.04, 13.3–16.9); 6.99, 6.0–7.9 (6.94, 6.1–7.9); and 9.65, 8.6–10.9 (9.99, 8.7–11.3—Rogers 1983).

Of 28 dimensions measured on skulls of 144 *T. t. nevadensis* from California (values presented in Rogers 1983), only 2 (length of maxillary toothrow and length of anterior edge of jugal) were related significantly with age (3 age classes based on fusion of cranial sutures), but all except 3 (interorbital constriction, height of foramen magnum, and width of premaxillary tongue) differed significantly between sexes (Rogers 1991a). Only 1 (length of toothrow) exhibited a significant sex–age interaction.

Body mass (in g) for 7 female and 9 male *T. t. nevadensis* from Oregon averaged (ranges in parentheses) 245.1 (190–356.3) and 281.6 (203–378), respectively (Verts and Carraway 1998); averages and ranges for 5 females and 5 males of same subspecies from Nevada were: 230.2 (211.8–244.3) and 270.9 (242.2–288.5), respectively (Hall 1946). Averages and ranges for 5 female and 8 male *T. t. townsendii* from Oregon were: 277.2 (265–288) and 346.6 (291–380), respectively (Verts and Carraway 1998). Ranges in body mass of female and male *T. t. nevadensis* (*n* not provided) from California were: 174.5–251.2 and 183.1–376.0, respectively (Thaeler 1968a).

DISTRIBUTION. Disjunct populations of *T. townsendii* reflect boundaries of historical drainages in northern Great Basin region of northeastern California, southern Idaho, northern Nevada, and southeastern Oregon (Fig. 3). Apparent maximum elevation recorded for a specimen was 1,980 m at Stergen Meadows, Pueblo Mountains, Oregon (Verts and Carraway 1998).

FOSSIL RECORD. Fossil material assignable to *T. townsendii* was collected at Fossil Lake, Oregon (Wisconsinan—Allison

1966; Elftman 1931; Grayson 1982) and along the Snake River, Idaho, at American Falls (Sangamonian—Gazin 1935); Rainbow Beach (Wisconsinan—McDonald and Anderson 1975); Wasden Site (Wisconsinan—Recent—Guilday 1969); and Wilson Butte Cave (Wisconsinan—Recent—Gruhn 1961). Fossil Lake and the latter 2 sites are extralimital (Fig. 3). Material described as *T. vetus* (Davis 1937) from Fossil Lake was considered conspecific or closely related with *T. townsendii* (Rogers 1991a). *T. scuderi* from the same locality was allocated to *T. townsendii* by Elftman (1931), but the describer (Hay 1921) and Davis (1937) considered it allied with *T. bottae*.

FORM AND FUNCTION. Statistical analyses of pelage-color characters (brightness, wavelength, and purity) from 31 localities indicated “a substantial degree of overlap in coloration across the range of *Thomomys townsendii*” (Rogers 1991a:116). Brightness exhibited the greatest variation among characters examined. Nevertheless, discriminating power based on color characters at sub-specific or broader geographic levels was $\leq 50\%$ (Rogers 1991a).

Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20. Premolars are 8-shaped in cross section (Bailey 1915). Anterior enamel plate on p4 is flat, narrow, and broadly separated from lingual plate (Thaeler 1980). All 6 *T. townsendii* examined were classified as possessing a lingual groove on I1s, but grooves were represented by “color traces only” in 5 individuals (Akersten 1973:350, table 1). None possessed a medial groove.

Of 9 species of *Thomomys*, *T. townsendii* ($n = 20$) possessed the lowest mean ($\pm SD$) ratio (0.771 ± 0.02) of skull flattening (skull depth/mastoid width), the 2nd greatest mean relative zygomatic breadth ratio (zygomatic breadth/least interorbital breadth, 4.215 ± 0.33), and next to lowest relative length of maxillary tooth-row ratio (alveolar length of maxillary tooththrow/greatest length of skull, 0.191 ± 0.01). Skull-flattening ratio varied significantly with age, and zygomatic breadth and maxillary tooththrow ratios varied significantly with sex (Wilkins 1988).

Average ($\pm SD$) orientation of enamel bands on upper molariform teeth ranged from $78.5 \pm 5.2^\circ$ to $98.3 \pm 8.6^\circ$; orientation on all teeth in both left and right maxilla differed significantly from 90° . Enamel-band orientation did not differ between sexes (Wilkins 1988). Average ($\pm SD$) direction of scars (scratches) on dentin and enamel of occlusal surfaces of upper molariform teeth resulting from chewing ranged from $-1.0 \pm 2.6^\circ$ to $0.1 \pm 3.2^\circ$ on left and $-1.3 \pm 2.2^\circ$ to $-2.1 \pm 2.7^\circ$ on right. Scars on right, but not on left, deviated significantly from 0° (Wilkins 1988). Nevertheless, differences in both orientation of enamel bands and direction of scars were not considered biologically meaningful; therefore, *T. townsendii* was deemed to chew propalinally.

ONTOGENY AND REPRODUCTION. In northern Malheur Co., Oregon, a pregnant and lactating female *T. townsendii* was taken on 27 March, and other pregnant individuals were taken during 29 March to 1 April (Horn 1923). The pregnant and lactating female contained 6 embryos. On 27–28 March, 5 young were taken from the same hole from which the lactating female was collected; 1 of these, a young male, weighed 180 g (Horn 1923). Based on reported periods of gestation and lactation for other species of *Thomomys*, Verts and Carraway (1998) estimated date of breeding for these Townsend’s pocket gophers as 7 February or earlier. Average number of embryos in 12 gravida was 6.8 (range, 3–10). Nine of 12 pregnant females exhibited evidence of having suckled young, adding to evidence that >1 litter is produced annually (Horn 1923). In Idaho, 2 females collected on 23 February each contained five 10-mm-long embryos; none of 29 specimens collected during May–August was pregnant, although “most of those taken in May and June showed evidence of having had young” (Davis 1939:247). Young-of-the-year were two-thirds grown by 1 June (Davis 1939).

ECOLOGY. Populations of *T. townsendii* tend to be allopatric or parapatric with those of other geomyids (Patton and Smith 1993; Thaeler 1968a; Verts and Carraway 1998). In northeastern California, range of *T. townsendii* contacts or interdigitates with those of *T. bottae*, *T. monticola*, and *T. talpoides*, but not with that of *T. mazama*. In a timbered area where mountain slopes flatten at the edge of a valley, *T. townsendii* and *T. monticola* were captured within 12 m of each other (Thaeler 1968a).

Townsend’s pocket gophers are restricted to fluvial and lacustrine habitats with deep, relatively moist, loamy, alkaline soils (Davis 1937, 1939; Rogers 1991a; Thaeler 1968a). They do not

range “into the dry sagebrush country beyond the moist and fertile bottomlands” (Bailey 1936:251; Thaeler 1968a). They may be abundant in irrigated fields (Jameson and Peeters 1988). Nevertheless, in some regions, their distribution may be limited by absence of saltgrass (*Distichlis spicata*), rootstalks of which *T. townsendii* purportedly feeds upon (Bailey 1936; Grinnell 1926; Thaeler 1968a). Also, in northeastern California, *T. townsendii* may be excluded from otherwise seemingly appropriate regions by competition with *T. bottae* (Thaeler 1968a).

In addition to saltgrass, *T. townsendii* consumes other grasses, legumes, especially alfalfa, and other cultivated crops such as grains, potatoes, and other large-rooted vegetables (Bailey 1936). Although not quantified, populations in cultivated fields may become sufficiently dense that crops become severely damaged unless pocket gophers are controlled by trapping or poisoning or driven out by flood irrigation. Those driven out of their tunnels by flooding commonly move to edges of fields or to adjacent fields, then gradually return when the soil dries adequately. These gophers sometimes burrow through banks of irrigation ditches causing loss of water and leading to extensive damage to crops by flooding (Bailey 1936).

In Malheur Co., Oregon, 438 pellets regurgitated by a pair of barn owls (*Tyto alba*) occupying a lacustrine cliff contained remains of 59 Townsend’s pocket gophers constituting 5.3% of 1,112 prey items identified. Most of the Townsend’s pocket gopher remains were those of subadults (criteria of age not provided), suggesting that most dispersal is age-related and on the surface. Other prey of the pair of barn owls included *Dipodomys ordii*, *Microtus montanus*, *Mus musculus*, *Neotoma cinerea*, *Peromyscus maniculatus*, *Perognathus parvus*, *Reithrodontomys megalotis*, *Sorex vagrans*, *Spermophilus canus*, and *Sylvilagus nuttallii*, suggesting possible mammalian associates of *T. townsendii* (Maser et al. 1980).

Fleas (Siphonaptera) reported from *T. townsendii* are *Foxella ignota* and *Orchopeas sexdentatus*. *T. townsendii* is considered an accidental host for both species (Lewis et al. 1988). *T. townsendii* is the primary host of the chewing louse (Mallophaga) *Geomydoecus idahoensis*; however, in the Honey Lake, California region, this louse occasionally parasitizes *T. townsendii*–*T. bottae* hybrids (Patton et al. 1984). *G. shastensis*, usually hosted by *T. bottae*, occasionally occurs on *T. townsendii*, on F₁ hybrids, and on backcrosses of hybrids with *T. bottae*. *G. idahoensis* was the only species of louse found on backcrosses of hybrids and *T. townsendii*. In another area in northeastern California, hybrids were hosts to *G. centralis* (Patton et al. 1984).

BEHAVIOR. *Thomomys townsendii* is largely fossorial, excavating tunnels and pushing spoil therefrom into large mounds on the surface. In Nevada, a 0.9- by 0.6-m mound contained a newly excavated stone ca. 7.6 cm long by 5.1 cm in diameter (Taylor 1911). In California, mounds with diameters and heights (in cm) of 120 by 14, 114 by 18, and 105 by 21 had burrow diameters (in cm) of 6.5, 7.5, and 7.5, respectively (Grinnell 1926). In fields supporting large populations of these gophers, “nearly half the surface of the ground” may be covered by mounds of earth (Bailey 1936:251). Mounds are constructed by pushing soil “through an inclined tunnel rather than a vertical shaft” (Hall 1981:454). In northeastern California, diameters of burrows constructed by female ($n = 16$) *T. townsendii* averaged ($\pm SE$) 9.72 ± 1.87 cm, whereas those dug by males ($n = 17$) averaged 11.58 ± 1.21 cm (Patton and Smith 1993).

Thomomys townsendii tends to be solitary and asocial. It exhibits agonistic behavior except during mating and when a female rears its young. Individuals rarely leave their tunnel systems and usually plug all entrances to the system with earth to exclude potential predators. Removal of a plug stimulates the occupant to replug the entrance quickly, a behavior capitalized upon by collectors (Hall 1981).

Occurrence of a molecular marker (length variant in mitochondrial D-loop) in pocket gophers in a hybrid zone between *T. townsendii* and *T. bottae* in northeastern California indicated that all hybrids were the result of mating of a *T. bottae* female and a *T. townsendii* male. *T. bottae* females whose body mass averages ca. one-third that of male *T. townsendii* must have actively sought larger males because tunnels of female *T. bottae* were too small for male *T. townsendii* to enter (Patton and Smith 1993). From this evidence, combined with knowledge of asocial behavior, territori-

ality, burrow diameter, sexual size dimorphism, and differential breeding success among male *Thomomys*, Patton and Smith (1993) concluded that the mating system in these gophers was promiscuous based on female choice.

GENETICS. Initially, Wentworth and Sutton (1969) reported that 6 of the 7 nominal subspecies of *T. townsendii* had $2n = 76$ and a fundamental number (FN) of 142, but *T. t. similis* had $2n = 40$ and FN = 68. Karyotypes with $2n = 76$ had 12 pairs of large to small metacentric (group I), 22 pairs of large to medium submetacentric (group II), and 3 pairs of medium-large to small acrocentric (group III) chromosomes. Subsequently, Thaeler (1973) found $2n = 76$ for *T. t. similis* and suggested that Wentworth and Sutton (1969) had inadvertently reported the karyotype for *T. talpoides bridgeri* collected concurrently with *T. t. similis*. He illustrated the same chromosomal complement (p. 329, figure 1) for *T. t. similis*, as described by Wentworth and Sutton (1969) for the other 6 nominal races of *T. townsendii*. Rogers (1991b) also determined $2n = 76$ for all 7 races, but reported FN = 146 for *T. t. bachmani* and *T. t. relictus* and FN = 148 for the remaining races. All 7 nominal races had 16 pairs of large to small submetacentric or metacentric chromosomes. The 2 deviant races had 20 pairs of large to small subtelocentric and 1 pair of medium acrocentric chromosomes, whereas all the remaining 21 pairs of chromosomes in the other 5 nominal races were large to small subtelocentrics (Rogers 1991b). The X chromosome is a large submetacentric, and the Y chromosome is a small to minute acrocentric (Rogers 1991b; Thaeler 1973; Wentworth and Sutton 1969).

Thomomys t. bachmani has 2 transferrin bands identical with those of 4 races of *T. umbrinus* (= *T. bottae*) in California, but the bands migrate more slowly than those of *T. bulbivorus* (Bongardt et al. 1968). Based on Rogers' Genetic Distance ($D \pm SD$) values, *T. townsendii* was most similar to *T. bottae* ($D = 0.214 \pm 0.033$; $n = 18$ populations) and in order of increasing dissimilarity to *T. umbrinus* ($D = 0.264 \pm 0.043$; $n = 11$ populations), *T. bulbivorus* ($D = 0.428$), *T. monticola* ($D = 0.596$), and *T. talpoides* ($D = 0.651 \pm 0.051$; $n = 3$ populations). *T. townsendii* was considered to have been derived from the western unit ($2n = 76$) of *T. bottae* (Patton and Smith 1981).

Genic heterozygosity (H) ranged from 0.000 to 0.028 ($\bar{H} = 0.012$ in 16 populations) representing all 7 nominal races of *T. townsendii*; thus, the species is the least variable within the genus *Thomomys* (Rogers 1991b). Among these populations, genetic differentiation (S) also was low ($\bar{S} = 0.956$; range, 0.896–0.998). Of proteins encoded by 27 presumptive loci, 17 were monomorphic: ACON, ALB, α GPD, GPI, GOT-2, ICD-1, ICD-2, LAP, LDH-1, LDH-2, MDH-1, MDH-2, NP, PEP-C, PGD, SOD, and SORDH. ADA, ADH, EST-4, GAPDH, GOT-1, MPI, PEP-B, PGM, PREALB, and TRF were polymorphic (Rogers 1991b). Populations from Honey Lake Valley, California, and Humboldt River, Nevada, drainage systems are monomorphic for the "a" allele of GOT-1, and those of the Snake River, Idaho and Oregon, system are monomorphic for the "b" allele. Rogers' Genetic Distance for populations in these 2 geographic regions was 0.089. These 2 features were considered sufficient for combining the 7 nominal races into the 2 currently recognized subspecies: *T. t. townsendii* and *T. t. nevadensis* (Rogers 1991b).

Cellular DNA content (2 C-value) varied from 10.40 pg DNA in 1 population of *T. t. nevadensis* to 10.76–11.12 pg DNA in 2 populations of *T. t. townsendii* (Sherwood and Patton 1982). Analysis of a 399-base pair (bp) section of the mitochondrial DNA (mtDNA) cytochrome-*b* (*cyt-b*) and a 126-bp section of intron-1 of the nuclear β -globin genes in individuals from 9 populations of *T. townsendii*, representing both currently recognized subspecies, revealed the latter was identical for all individuals tested (Patton and Smith 1994).

CONSERVATION STATUS. Within the state Heritage Status Rankings, *T. townsendii* is listed as S? in California, S4? in Idaho, S4S5 in Nevada, and S4 in Oregon; thus, it is considered an "unprotected nongame species" throughout its distribution as of 2001 (NatureServe 2001; L. Alexander, in litt.; L. Cooper, pers. comm.; G. Gould, pers. comm.; C. Harris, pers. comm.).

REMARKS. The generic name *Thomomys* was derived from the Greek *thomos* meaning a heap (probably in reference to the mounds of earth produced in tunneling) and the Greek *mys* meaning mouse (probably in reference to the somewhat mouse-like body

shape—Jaeger 1978). The specific name *townsendii* is a patronymic in honor of J. K. Townsend who collected the 1st specimen.

Mitochondrial DNA *cyt-b* divergence values for samples of *T. t. nevadensis* from Honey Lake Valley, California, and from Oregon and Nevada were bimodal, ranging from ca. 2% to 8%, whereas samples of *T. t. townsendii* from Oregon and Idaho were unimodal and ranged from ca. 1% to 6%. Divergence values between *T. t. nevadensis* and *T. t. townsendii* ranged from ca. 9% to 12% (Patton and Smith 1994).

Analyses of mtDNA *cyt-b* sequences suggest that *T. townsendii* is polyphyletic and is believed to have evolved from a branch of *T. bottae* (Patton and Smith 1989). Along narrow (<1 km wide) zones of contact in the Honey Lake, Lassen Co., California region, *T. townsendii* hybridizes with "strongly differentiated geographic units" (Smith 1998:1) of *T. bottae*: *T. b. canus* at Garnier Ranch southeast of the lake and *T. b. saxatilis* along Gold Run Creek to the west of the lake (Patton and Smith 1994; Thaeler 1968b). Hybrids comprise <20% of samples; most hybrid individuals are F_1 s, suggesting "that hybrids suffer a substantial degree of infertility and/or inviability" (Patton and Smith 1994:12). Based on an mtDNA sequence divergence of only 0.008% (Patton and Smith 1994), resulting from asymmetric reproduction (Patton and Smith 1993), the initial hybridization event with introgression of genetic material occurred between *T. b. canus* and *T. townsendii*. Subsequent to this fixation event, a hybrid zone developed between *T. b. saxatilis* and *T. townsendii*. Only within this 1-km-wide zone, mtDNA of *T. townsendii* is fixed for that of *T. b. saxatilis*. *T. townsendii* in the Honey Lake, California region, where it hybridizes with *T. bottae*, is more closely related both genetically and morphologically with races of *T. bottae* in central and southern California (Patton and Smith 1989).

Sequences of intron-1 of the nuclear β -globin gene support "monophyly of *T. townsendii* with paraphyly of *T. bottae*" (Patton and Smith 1994:21, figure 6a). Despite lack of evidence of introgression of genetic material beyond the hybrid zones, Hall (1981) "included . . . these taxa within his concept of [*Thomomys*] *umbrinus*" (Patton 1993:474). However, the opposing genealogical findings, in addition to gross morphological differences, make application of either phyletic or evolutionary species concepts to these pocket gophers a dilemma (Patton and Smith 1994).

We thank M. A. Rogers and J. L. Patton for commenting on an earlier draft of the manuscript.

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Associate editors for this account were ELAINE ANDERSON and LUI MARINELLI. Editor was VIRGINIA HAYSSEN.

B. J. VERTS AND LESLIE N. CARRAWAY, DEPARTMENT OF FISHERIES AND WILDLIFE, NASH HALL 104, OREGON STATE UNIVERSITY, CORVALLIS, OREGON 97331-3803.