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Tamias panamintinus.

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Tamias panamintinus Merriam, 1893

Panamint Chipmunk

Tamias panamintinus Merriam, 1893:134. Type locality "Panamint Mountains [Inyo County—Miller and Rehn, 1901:43], California (between Death Valley and Panamint Valley). Exact locality, Johnson Cañon [near lower edge of piñon belt at about 5,000 feet altitude, in vicinity of Hungry Bill's Ranch—Grinnell, 1933:128]."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae. The genus *Tamias* contains 25 species (Wilson and Reeder, 1993); *T. panamintinus* is in the subgenus *Neotamias* (Levenson et al., 1985). Two subspecies of *T. panamintinus* are recognized (Hall, 1981):

T. p. acrus (Johnson, 1943:94). Type locality "1.4 mi. SE Horse Spring, 5,000 feet altitude, Kingston Range, northeastern San Bernardino County, California."

T. p. panamintinus Merriam, 1893:134, see above (*juniperus* Burt is a synonym).

DIAGNOSIS. *Tamias panamintinus* (Fig. 1) is sympatric or parapatric with *T. amoenus* (Howell, 1929), *T. merriami*, *T. minimus*, *T. palmeri*, *T. umbrinus* (Callahan, 1976), and *T. speciosus* (Hall, 1981). Compared with *T. amoenus*, *T. panamintinus* is about the same size, but differs in having shorter feet and ears, paler coloration, gray rather than brown crown of head, narrower and paler dark facial stripes, less conspicuous dark dorsal stripes (only the median one is black and the outermost pair is barely perceptible), and narrower inner and broader outer pale stripes. The skull of *T. panamintinus* (Fig. 2) is broader with the roof of the braincase more flattened, the braincase is broader, the nasals are less prolonged anteriorly, the incisive foramina are longer, and the upper incisors are less recurved (Johnson, 1943).

Compared with *T. minimus*, *T. panamintinus* from the same geographic area is larger and more reddish, especially in summer pelage, the central area of the underside of the tail is broader and more reddish, the skull is larger, and the braincase is more flattened (Hall, 1946). *T. minimus* has gray shoulders and adjacent part of the back, and the ventral surface of the tail is yellowish (Jameson and Peeters, 1988). Compared with *T. palmeri*, *T. panamintinus* is smaller, the shoulders are less gray, the dorsal stripes are less solidly black and solidly white (Hall, 1946), the ventral surface of the tail is paler (Burt, 1934), the braincase is broader and more-flattened, the upper incisors are shorter, the cheekteeth are smaller, and the zygomatic arches are less parallel (Hall, 1946).

Compared with *T. umbrinus*, *T. panamintinus* is smaller, the shoulders are less gray (Johnson, 1943), the rump and thighs are grayish instead of buffy (Howell, 1929), the dorsal stripes are less contrasting (dark stripes are less solidly black, pale stripes are more reddish), the braincase is broader and more flattened, the upper incisors are shorter, the cheekteeth are smaller, the zygomatic arches are less parallel (Johnson, 1943), and the auditory bullae are relatively larger (Howell, 1929). Compared to *T. speciosus*, *T. panamintinus* is smaller, and has ears that are less pointed, less black in the dark facial and dorsal stripes, less ochraceous wash over the pale stripes and underparts, and a narrower subterminal black band across the underside of the tail. The skull of *T. panamintinus* is relatively broader, but has a narrower and more pointed rostrum. The roof of the braincase is more flattened, the upper rows of cheekteeth diverge less anteriorly (Johnson, 1943), and the auditory bullae are larger in *T. panamintinus* (Merriam, 1893).

Skulls of *T. panamintinus* resemble those of *T. quadrivittatus* from Colorado so closely that the two are hardly distinguishable, although the skull of *T. panamintinus* is slightly smaller and more depressed in the frontonasal region, and has larger auditory bullae (Merriam, 1893). Compared with *T. dorsalis*, *T. panamintinus* has reddish rather than grayish upper parts, reddish and distinct, instead of grayish and indistinct, submedian dark dorsal stripes, more flattened braincase, and parallel, instead of anteriorly convergent, incisive foramina (Hall, 1946). Compared with *T. merriami*, *T. sonomae*, and *T. townsendii*, *T. panamintinus* is smaller, the tail edging is buffy rather than white, the braincase is relatively broader, and the rostrum is narrower. Compared with *T. alpinus*, *T. panamintinus* is larger and, especially in summer pelage, more reddish, with a broader and more flattened braincase. The underside of the tail is more reddish and less yellowish centrally and has a shorter subterminal black area than in *T. alpinus* (Johnson, 1943). Compared with *T. quadrimaculatus* and *T. senex*, *T. panamintinus* can be distinguished by smaller size alone, and the tail has an edging of buff rather than white (Hall, 1946). Also, *T. quadrimaculatus* has long ears and white postauricular ear patches (Jameson and Peeters, 1988).

The baculum of *T. panamintinus* (Fig. 3) differs from *T. bulleri* in having a smaller keel, shorter shaft, and distinct ridges on either side of the tip. Compared with *T. merriami*, the baculum of *T. panamintinus* is distinguished by a base that is widened and not incised dorsally, a thicker shaft, and a tip that is proportionally longer. Compared with *T. minimus*, *T. panamintinus* has a thicker shaft and the base is widened. The baculum of *T. panamintinus* differs from *T. palmeri* and *T. umbrinus* in that the distal 66% (rather than 50%) of the shaft is compressed laterally. Structure of the baculum of *T. panamintinus* is most similar to that of *T. speciosus*, and the geographic ranges of these species are in juxtaposition. However, the baculum of *T. panamintinus* has a proportionally longer base of keel, and the angle formed by tip and shaft is greater (White, 1953).

GENERAL CHARACTERS. The Panamint chipmunk (Fig. 1) is medium-sized (Jameson and Peeters, 1988), and is characterized in summer pelage by bright tawny colors and a conspicuous gray rump, and in winter pelage by duller colors and even more gray on

FIG. 1. A subadult *Tamias p. panamintinus* in the White Mountains, Mono Co., California. Photograph courtesy of H. E. Broadbooks.

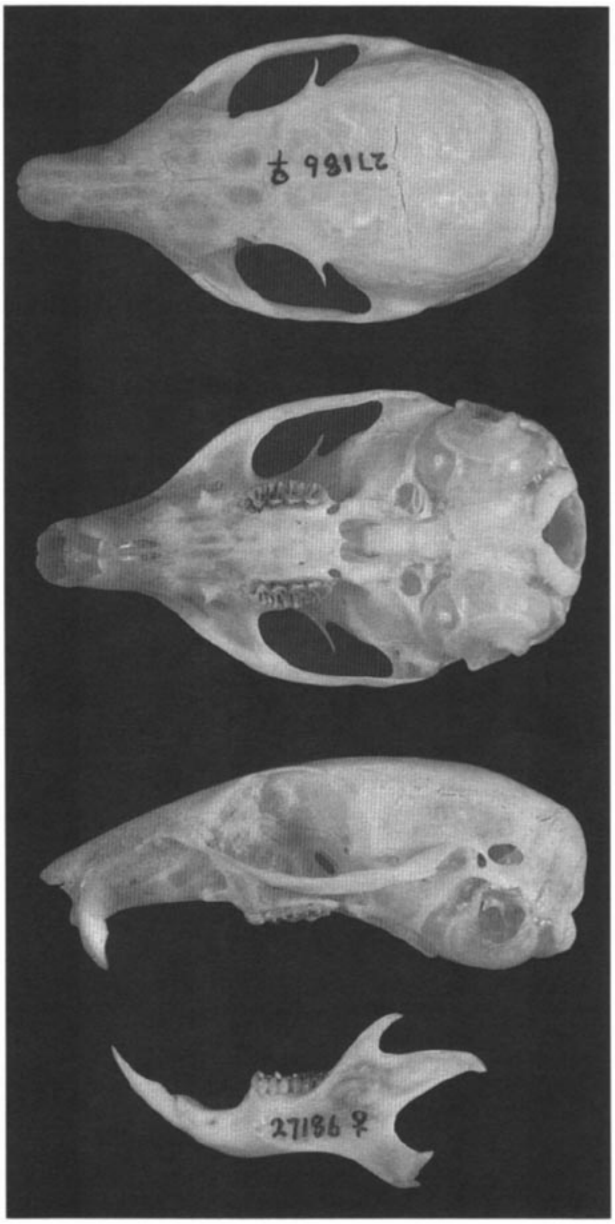

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tamias p. panamintinus* from Hanaupah Canyon, 2,250 m, Panamint Mountains, Inyo Co., California (female, Museum of Vertebrate Zoology, University of California, Berkeley 27186). Greatest length of cranium is 35.3 mm. Photographs by T. H. Henry.

the rump (Howell, 1929). The color is pale buff, with black areas restricted. The crown of the head is pale gray. The dark facial stripes are reduced, the superciliary and ocular stripes are narrow and well defined, and the submalar stripe usually is faintly indicated. The cheeks and pale facial stripes are pale gray, nearly white, and not suffused with ochraceous coloration. The dark dorsal stripes, except the median stripe, usually are brown rather than black; the outermost stripes scarcely are distinguishable from the color of the sides. The inner and outer pale dorsal stripes are about equal in width, and usually are faintly washed with ochraceous coloration. The underside of the tail is paler than the sides in summer pelage, with the subterminal black area extending ca. 12 mm anteroposteriorly. In winter pelage, the fur is long and silky, colors are yellowish, and markings are inconspicuous (Johnson, 1943).

The skull of *T. panamintinus* (Fig. 2) is broad, especially in the posterior part, with zygomatic breadth ca. 62% of condylobasal length. The rostrum is relatively narrow and deep. The braincase is large and square-appearing, the roof is flattened in the vicinity of the frontoparietal suture, and the sides and posterior end are nearly vertical. The zygomatic arches are oppressed to the braincase in the squamosal region, slanting toward the median line anteriorly. The zygomatic processes of the squamosals are more vertical than horizontal when viewed from behind. The teeth are relatively large. The incisors are moderately recurved and the rows of cheekteeth are nearly parallel (Johnson, 1943).

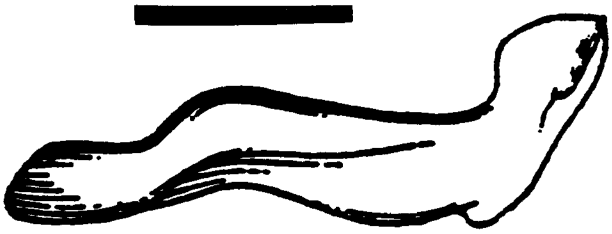

FIG. 3. Lateral view of the right side of the baculum (bar represents 1 mm) of *Tamias p. panamintinus* from Coal Kilns, Panamint Mountains, Inyo Co., California (White, 1953).

Tamias panamintinus exhibits little geographic variation over its range. This condition may result from the restricted habitat it occupies and the consequent uniformity of environmental conditions. Trends of geographic variation in color are slight, but some populations are paler or darker than others. Likewise, cranial characters vary slightly. Compared with *T. p. acrus*, *T. p. panamintinus* is larger, colors are paler, the zygomata are more flaring, and the rostrum is longer and broader (Johnson, 1943).

Average and extreme measurements (in mm) for males and females of *T. p. acrus* (from Kingston Mountains, San Bernardino Co., California) and males and females of *T. p. panamintinus* (from Providence Mountains, San Bernardino Co., California), respectively, are: total length, 202 (192–209), 200 (196–205), 206 (197–211), 209 (200–214); length of head and body, 112 (103–119), 111 (109–112), 117 (109–124), 122 (110–127); length of tail, 90 (88–92), 90 (85–96), 89 (83–95), 87 (84–90); length of hind foot (dry), 28.9 (28.4–29.4), 29.9 (29.0–30.5), 29.7 (28.4–31.1), 30.0 (28.8–30.6); length of ear from crown (dry), 10.7 (9.6–11.3), 10.3 (9.6–11.1), 10.5 (9.6–11.2), 10.8 (10.2–11.2); condylobasal length, 29.6 (29.5–29.7), 29.8 (29.0–30.5), 30.1 (29.7–30.8), 30.2 (29.7–30.8); greatest length of cranium, 33.2 (32.9–33.3), 33.3 (32.5–34.0), 33.8 (33.1–34.4), 33.8 (33.3–34.2); zygomatic breadth, 18.0 (17.7–18.4), 18.3 (17.9–18.5), 18.5 (18.1–19.0), 18.7 (18.4–19.0); breadth of cranium, 15.3 (15.0–15.5), 15.5 (15.0–15.7), 15.8 (15.4–16.2), 15.9 (15.5–16.2); depth of cranium, 11.0 (10.9–11.2), 10.8 (10.5–11.1), 11.0 (10.5–11.4), 10.9 (10.5–11.1); interorbital breadth, 7.0 (6.8–7.1), 7.1 (6.9–7.3), 7.5 (7.1–7.8), 7.2 (6.9–7.5); length of nasals, 10.0 (9.8–10.1), 10.0 (9.4–10.4), 10.1 (9.6–10.8), 10.1 (9.9–10.4); depth of rostrum, 4.7 (4.6–4.9), 4.8 (4.6–5.0), 4.9 (4.8–5.0), 4.9 (4.7–5.1); length of incisive foramina, 2.1 (2.1–2.1), 2.2 (2.2–2.3), 2.3 (2.0–2.6), 2.3 (2.2–2.5); length of lower toothrow, 4.9 (4.9–5.0), 5.1 (5.0–5.2), 5.1 (4.9–5.3), 5.1 (5.1–5.3—Johnson, 1943).

Additional measurements (in mm) or males and females, respectively, are: length of ear (fresh), 18.2, 17.5; length of vibrissae 18.8, 19.2 (Hirshfeld, 1975). For genders combined, mass is 53.3 g (range, 45.5–67.2 g—Howell, 1929). Average mass of females (57.3 g) is greater than that of males (47.3 g—Hirshfeld, 1975; Hirshfeld and Bradley, 1977). Females (118.6 mm) average larger than males (117.9 mm) in length of head and body, but differences are not significant (Levenson, 1990).

DISTRIBUTION. The Panamint chipmunk occurs at 1,230–3,180 m elevation (Bole, 1938; Howell, 1929; Johnson, 1943) in upper Sonoran and lower transition zones of the desert ranges of southeastern California and southwestern Nevada (Fig. 4; Howell, 1929; Johnson, 1943; Merriam, 1893). *T. panamintinus* probably reaches the summits of most of these ranges (Johnson, 1943).

Tamias p. acrus occurs only in the Kingston Mountains of northeastern San Bernardino Co., California. It is isolated from all other populations of *Tamias* by hot, low-lying desert communities. This subspecies is not abundant, and it occupies a potential geographic range of ca. 100 km^2 (Johnson, 1943; D. F. Williams, in litt.).

FOSSIL RECORD. The genus *Tamias* evolved by the early Miocene (Black, 1972). Expansion and contraction of the range of ancestral *T. dorsalis* in the basin and range province of Nevada may have resulted in the peripheral isolation of *T. panamintinus* in Mojave Desert mountain ranges (Levenson et al., 1985). No fossils of *T. panamintinus* are known.

FORM AND FUNCTION. Maximum length of dorsal guard hairs is 13 mm, and pigmentation is absent or slight on the distal pale region (Mayer, 1952). Winter pelage of *T. panamintinus* becomes worn by early summer, so that the dorsal stripes are obliterated (Howell, 1929). Males molt from winter to summer pelage during May and June, and from summer to winter pelage during late August, September, and October. Progression of molt is from anterior to posterior in spring, and the reverse in autumn. Females molt in a similar time frame, but their molt to summer pelage primarily occurs in June and July. Although this 1-month delay may reflect the metabolic burden of pregnancy and lactation, one female that gave birth in the laboratory in June was molting during lactation (Hirshfeld, 1975).

On 9 June, an adult male from the White Mountains, California, and on 14 June, an adult female from the Panamint Mountains, had new summer pelage covering the shoulders and foreback. On 1 June, a male and female from the Providence Mountains, had full, fresh summer pelage, indicating an early molt (Howell, 1929). On 19 June, some Panamint chipmunks from Wheeler Well, Nevada, were completely molted while others on 18 June had not commenced the molt (Burt, 1934). All young-of-the-year in the Providence Mountains had molted completely, or nearly so, into the first summer pelage by 20 May. Most adults on 15 May–11 June were in various stages of spring molt, some with a patch of fresh summer pelage on the nose, others with a remnant of worn winter pelage at the base of the tail. None had molted completely by this time. A male on 11 June had summer pelage on ca. 50% of the body. All chipmunks on 29 December–8 January were in winter pelage (Johnson et al., 1948).

Length of tail is medium for the genus, and averages ca. 77% of length of head and body. The feet are relatively short, and length of hind foot (dry) averages ca. 26% of length of head and body. The ears are short, rounded, and in length average ca. 9% of length of head and body (Johnson, 1943). As in all members of the subgenus *Neotamias*, the dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22 (Howell, 1929; Ingles, 1965; Stephens, 1906).

Average and range of mass of organs (in mass of organ in grams/mass of chipmunk in kilograms) are: brain, 32.9 (23.1–40.4); heart, 4.7 (3.0–6.7); kidney, 8.6 (6.4–10.7); liver, 30.0 (18.4–49.7); lung, 12.9 (9.5–16.3); pancreas, 3.7 (2.2–5.3); adrenals, 0.42 (0.19–0.77); adrenals of breeding males, 0.51 (0.29–0.97); adrenals of non-breeding males, 0.04 (0.03–0.08); testes of breeding males, 7.8 (3.9–14.9); testes of non-breeding males, 0.9 (0.7–1.3); ovaries, 1.4 (0.6–2.3). Because of their larger body mass, females average larger than males in mass of organs. Mass of males and females is greatest in spring, reflecting the breeding cycle. There is a trend toward increases in mass in autumn, but this gain is not statistically different over a 3-month period from September to December (Hirshfeld, 1975).

Energy measurements (kcal/g) of *T. panamintinus* are: biomass, 4.9; ash-free biomass, 5.7; average caloric density, 1.2–1.3 (Kaufman et al., 1975). Chemical composition (in mg/g of dry mass, unless otherwise indicated) of *T. panamintinus* is: average dry mass, 11.6 g; ash, 13.8%; fat, 8.6%; N, 111.4; Ca, 32.6; S, 31.1; P, 22.0; K, 12.2; Na, 4.23; Mg, 1.03; Fe, 310.0; Al, 143.0; Zn, 136.4; Sr, 7.5; Mn, 7.5; Ba, 0.3; B, 5.6; Mo, 3.6 (Wiener et al., 1977).

Non-breeding adults consume 6–8 g of water/day and 4–5.5 g of food/day. They excrete ca. 4 g of urine/day and 0.6 g of feces/day. Breeding females consume more food and water than non-breeding females, but pregnant females consume more than either group. Comparisons of breeding adults and young, based upon consumption/body mass, reveal that young consume relatively greater quantities of food and water (Hirshfeld, 1975).

Tamias panamintinus will not readily accept water from a bottle, but it will consume whole oats and cantaloupes as a source of food and water. Ad lib. consumption of water by *T. panamintinus* is 15% of body mass/day (Hirshfeld, 1975). The daily rate of water exchange is greater for *T. panamintinus* than for the desert kangaroo rat (*Dipodomys deserti*), Merriam kangaroo rat (*D. merriami*), chisel-toothed kangaroo rat (*D. microps*), round-tailed ground squirrel (*Spermophilus tereticaudus*), golden-mantled ground squirrel (*S. lateralis*), white-tailed antelope squirrel (*Ammospermophilus leucurus*), and desert woodrat (*Neotoma lepida*—Yousef et al., 1973).

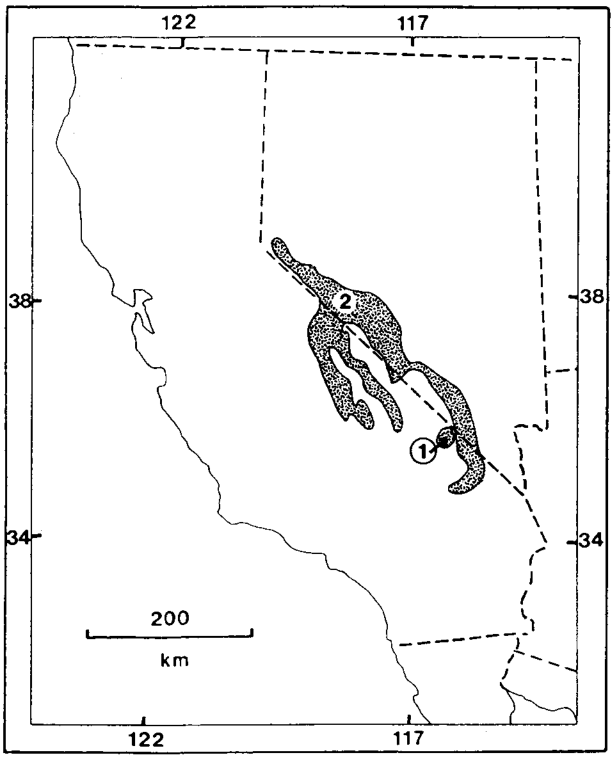

FIG. 4. Distribution of *Tamias panamintinus* in California and Nevada (Hall, 1981): 1, *T. p. acrus*; 2, *T. p. panamintinus.*

When deprived of water (except for whole oats ad lib.) for 10 days, body temperature decreased from an average of 34.6 to 32.8°C. After 1 day without water, *T. panamintinus* reduced food consumption to <50% of that usually consumed. Food consumption progressively declined during the experiment. Chipmunks appeared healthy through the 10 days, but after 5 days they often appeared restless and were quite active when handled. Upon return of the water source, original body mass was reached in 8 days (Hirshfeld, 1975).

When deprived of food (except for cantaloupes ad lib.) for 10 days, mass decreased to 81.4% of the original mass and body temperature dropped to 33.4°C. Test animals appeared normal, but generally increased consumption of water throughout the period. During the experiment, behavior appeared normal for the first 5 days, but in the last 5 days chipmunks appeared less active and usually remained curled up in its nest. However, cantaloupe was consumed at an increasing rate each day they were without food (Hirshfeld, 1975).

Average body temperature of *T. panamintinus* is 34.5°C, and daily rectal temperature is 32.2–35.5°C, with an average of 34.4°C. Body temperature does not appear to be related to ambient temperature or season of the year. When active, body temperature is higher than when inactive (Hirshfeld, 1975). The lower-critical temperature is 29–32°C, and the higher-critical temperature is 34–36°C. *T. panamintinus* is able to maintain a rectal temperature of 34–36°C at ambient temperatures below the lower-critical temperature (Bradley and Yousef, 1974).

Average rate of oxygen consumption is 2.1 ml O_2 g^{-1} h^{-1}. Data on the relationship between ambient temperature (°C) and average frequency of respiration (respirations/min), respectively, are: 5, 100; 10, 149; 15, 173; 20, 185; 25, 186; 30, 144; 35, 204; 40, 304. Thus, average frequency of respiration increases steadily at ambient temperatures of 5–25°C, and then drops at 30°C when the thermoneutral zone is approached, only to rise again until the maximum frequency of respiration is attained at 40°C (Hirshfeld, 1975).

The baculum of *T. panamintinus* (Fig. 3) has a thick shaft and a low keel, which is 33% of the length of tip. The base of the keel is 50% of length of tip, the tip is 52% of length of shaft, the angle formed by the tip and shaft is 110°, the distal 66% of the shaft is compressed laterally, the base is widened, and the shaft is short (2.17 mm—White, 1953).

Average and range of measurements (in mm) of the baubellum of *T. panamintinus* are: length of base, 0.61 (0.39–0.72); length of shaft, 0.69 (0.65–0.72); depth of shaft, 0.38 (0.36–0.39); length of tip, 0.56 (0.52–0.59); length of keel, 0.26 (0.26–0.26); tip-shaft angle, 143° (134–150°). The baubellum is short, with a thick, deep shaft that projects at the base-shaft angle to a straight, tapered, peg-like base. The tip-shaft angle is somewhat rounded, with no obvious heel projection, and the tip is bent to the right ca. 18°. The keel is small, but obvious; the flanges are narrow and curved from the point of the tip to the heel (Sutton, 1982).

ONTOGENY AND REPRODUCTION. In late December, early January (Johnson et al., 1948), and March–August, some male *T. panamintinus* may have enlarged testes, but most are reproductively active April–June. Timing of breeding by females and criteria for reproductive activity are less clear than for males, but copulation probably occurs in April and early May (Hirshfeld, 1975) and parturition occurs in late May and June (Deacon et al., 1964; Hirshfeld, 1975; Johnson et al., 1948). Weaning apparently ends in August, but may carry over into September. Small juveniles first appear above ground in late July and continue to emerge through August (Hirshfeld, 1975). *T. panamintinus* has one litter each year (Jameson and Peeters, 1988), gestation period is ≥36 days (Hirshfeld and Bradley, 1977), average number of embryos is 4.2 (range, three to seven—Hirshfeld, 1975), and average size of litter is 3.8 (range, three to six—Hirshfeld and Bradley, 1977).

In newborn Panamint chipmunks, the skin is pink and semitransparent. Organ movements and white areas containing milk can be seen immediately after nursing, and the posterior portion of the body is darker than the anterior. The body appears hairless, with the exception of the mystacial vibrissae, which are ≤1 mm in length. Eyes of newborn chipmunks bulge and appear dark through the transparent covering of skin. Pinnae of the ears are folded against the sides of the head and are >1 mm in length. Toes, although formed at birth, are united by a membranous covering and have minute claws. About 12–18 h after birth, neonates utter faint squeaks (Hirshfeld and Bradley, 1977).

All hairs and vibrissae grow rapidly, and hair on the head is visible in 8–9 days. It is not until ca. day 20 that individual body hairs can be distinguished by the naked eye, but a few hairs emerge on the side of the body by day 12. A sparse growth of short hairs appears on the venter and legs on day 15. At this time, the tail is still naked, but a few hairs appear proximally by day 17. The tail is the last part of the body to acquire hair, and the four pale and three dark dorsal stripes appear at 12–13 days of age. By the end of week 3, color of adult facial and dorsal body patterns are evident, and by the end of week 4, the hair takes on a sleek, smooth appearance that disappears in weeks 10–11 when young assume the general appearance of young adults (Hirshfeld and Bradley, 1977).

Grooves marking the future eye slits are noticeable within 4 days. The eyes become increasingly prominent and bulging, and open 29–30 days after birth. The pinnae of the ears, which are folded over the ear openings at birth, become erect on day 3 or 4. The external auditory meatus opens at 26–27 days. The toes begin separating at 10 days; their division is complete by day 17. The claws are clear and soft at birth; proximal ends of the claws turn dark first, and by 21 days the claws are completely dark. The lower incisors erupt at 14–16 days, upper incisors at 22–24 days, and cheekteeth at 35–37 days (Hirshfeld, 1975; Hirshfeld and Bradley, 1977).

Growth rate of *T. panamintinus* during the first 50 days after birth is less than that for *T. amoenus*, *T. palmeri*, *T. quadrivitattus*, *T. townsendii*, *Ammospermophilus harrisii*, and 14 species of *Spermophilus* (Levenson, 1979). Average measurements (in mm) of *T. panamintinus* raised in the laboratory at 1, 3, 5, 7, 9, 11, and 13 weeks of age, respectively, are: mass (in g), 5.8, 8.4, 14.8, 23.6, 37.5, 44.3, 47.8; length of head and body, 49.7, 55.3, 66.5, 83.4, 96.2, 110.9, 116.3; length of tail, 20.1, 32.0, 58.2, 72.4, 79.7, 81.2, 81.1; length of hind foot, 10.1, 17.1, 25.9, 30.2, 31.0, 31.1, 31.1; length of ear, 3.6, 6.5, 12.4, 16.2, 17.8, 18.1, 18.2; length of vibrissae, 3.4, 12.4, 14.2, 16.6, 18.4, 19.0, 19.1 (Hirshfeld and Bradley, 1977). Increase in mass is 24.4%/week during weeks 1–6 (O'Farrell, 1980). Body mass at 13 weeks of age is 85–90% of adult mass. All linear measurements attain adult values by ca. 13 weeks of age. Hind foot, tail, ear, and vibrissae reach adult sizes in 9–11 weeks; head and body reach adult lengths in 12 weeks. The hind foot reaches adult size more rapidly than other structures; it attains 50% of adult length in 2.5 weeks and 100% in 9 weeks (Hirshfeld and Bradley, 1977).

In the laboratory, young are well cared for by the mother until they are capable of leading an independent existence. Until the young are weaned, mothers do not leave the nesting cages (Hirshfeld and Bradley, 1977); the mother and nest provide an ambient temperature of ca. 28–29°C (Hirshfeld and Bradley, 1976). Most females appear undisturbed when young are removed from the cages, even when detached from the nipples. No attempt is made by females to carry the young back to the nest, but the young are accepted when replaced (Hirshfeld and Bradley, 1977).

Young Panamint chipmunks squeak, especially when the mother makes sudden movements. If separated from the mother, neonates continue suckling motions for brief periods. Overall activity of neonates increases during the first 48 h after birth. By 12 days, they pull themselves around by their front legs, and by 19 days they are able to hold their body off the ground. At 3 weeks, movements are jerky and uncoordinated, although they have begun to scratch their ears with the hind feet. They became active outside the nest at ca. 5 weeks of age. Young are sensitive to quick movements in their environment. By 6 weeks of age, young eat solid food and may feed as they sit on their haunches; they also clean their faces in an adult manner. When asleep, young sleep with forepaws held over the face, with body and tail curled in a ball. Young raised in captivity never become accustomed to humans or to handling. During the process of catching the young, they buzzed or trilled, tried to bite, and attempted to ward off capture with the forepaws (Hirshfeld, 1975; Hirshfeld and Bradley, 1977).

Average body temperature (°C) and oxygen consumption (ml $O_2\ g^{-1}\ h^{-1}$), respectively, at 1, 3, 5, 7, 9, 11, and 13 weeks of age are: 25.5, 1.01; 29.5, 1.79; 32.0, 2.49; 33.0, 3.01; 33.0, 3.24; 33.0, 2.20; 34.5, 2.29 (Hirshfeld, 1975). Young *T. panamintinus* attain body temperatures approaching that of adults by ca. 10 weeks of age. Rate of oxygen consumption increases until ca. week 10; at 10–13 weeks, rate of oxygen consumption remains about the same. At 13 weeks of age, *T. panamintinus* consumes oxygen at a rate similar to that of adults (Hirshfeld and Bradley, 1976).

Juveniles of both genders can be distinguished from adults by smaller size of body, large head in proportion to body, and soft, fluffy pelage (Hirshfeld, 1975). The rump and hind legs are the last areas to molt from juvenile to adult pelage (Johnson et al., 1948).

ECOLOGY. The Panamint chipmunk inhabits pinyon pine-juniper (*Pinus-Juniperus*) woodland in the southwestern Great Basin region (Cade, 1963; Hall, 1946; Hirshfeld and Bradley, 1977; Howell, 1924; Johnson, 1943). Its range is virtually identical to that of pinyon pine in the region (Johnson et al., 1948), but *T. panamintinus* may occur at the upper limit of creosotebush (*Larrea*) and mesquite (*Prosopis*) vegetation, or it may be found in limber (*Pinus flexilis*) and bristlecone pines (*Pinus aristata*) above the pinyon-juniper belt (Elliot, 1904). On mountain ranges of medium elevation, pinyon forests occupied by *T. panamintinus* cover summits and upper slopes. On the highest ranges, such as the Sierra Nevada and the White and Inyo mountains, California, pinyon forests form a distinct belt above which is sagebrush (*Artemisia*), mountain mahogany (*Cercocarpus*), or coniferous forests inhabited by other species of chipmunks (Johnson, 1943).

Tamias panamintinus primarily is a rock-dweller. In its habitat, soil cover is thin, with fissured granite cliffs and ledges. Logs that could be used as refuges or nesting places are small and quickly disintegrate by weathering (Johnson, 1943). The Panamint chipmunk seems to depend on rocks for shelter. Although it climbs in pinyon pines and probably obtains food from them in the form of seeds in years when good crops are produced, the facts that the crop of pinyon seeds in uncertain and that the trees rarely furnish suitable refuge or nesting sites lead to the conclusion that the close correspondence between local ranges of chipmunks and pinyon pine results from similar tolerance to some environmental factor, probably temperature, rather than dependence of one species on the other. In the Providence Mountains, *T. panamintinus* is abundant on the pinyon-covered plateau and walls of narrow side canyons in January, and again in May and June (Johnson et al., 1948).

In the White Mountains, a ground nest and a tree nest of *T.*

panamintinus were present in July. The tree den was located in a crevice between the divided trunk of a live, 9-m tall single-leaf pinyon (*Pinus monophylla*) 1.5 m above the ground. In the compact debris that had accumulated in the crack, a nest chamber 15 cm in diameter had been hollowed out; dry grass served as bedding (Broadbooks, 1977).

Food of *T. panamintinus* consists of fruits of pinyon pines and junipers (Burt, 1934), spring forbs, and insects (Jameson and Peeters, 1988). During May and June in the Panamint Mountains, *T. panamintinus* was feeding on seeds of juniper; most Panamint chipmunks had their cheekpouches filled with these seeds (Elliot, 1904). In Nevada, seeds, fruits, greens, and flowers are consumed from March through September, with seeds and fruits generally greater in volume and equal in frequency to greens and flowers. Arthropods often are eaten, except in spring months, and small amounts of lichens, bark, and carrion are consumed (Hirshfeld, 1975). One Panamint chipmunk had a willow (*Salix*) catkin in is mouth (Hall, 1946). In the laboratory, *T. panamintinus* will consume a mixed diet of whole oats, peanut butter, bird seed, cantaloupe, apples, lettuce, and celery. This diet provides a variety of food and succulents as a water source (Hirshfeld and Bradley, 1977).

In Nevada, *T. dorsalis* also inhabits areas with pinyon pine, but *T. panamintinus* occurs west of the area occupied by *T. dorsalis* (Hall, 1946). The range of *T. panamintinus* is complementary to that of *T. amoenus*; *T. panamintinus* occupies outlying desert ranges of southeastern California and southwestern Nevada. On eastern slopes of the Sierra Nevada, *T. panamintinus* ranges north to within a short distance of the range of *T. amoenus monoensis* and the two may occur together at some places. *T. panamintinus* occurs to 2,100 m elevation on Bishop Creek, while *T. amoenus monoensis* occurs at 2,520 m elevation near the head of Owens River. In the White and Inyo mountains, *T. panamintinus* occurs with *T. umbrinus inyoensis*; their ranges overlapping at 2,280–2,520 m elevation (Howell, 1929).

In Clark Canyon, Charleston Mountains, Nevada, *T. panamintinus* primarily occurs at lower elevations than *T. palmeri*, but there is broad elevational overlap. Both species occur in the white fir-Ponderosa pine (*Abies concolor-Pinus ponderosa*—2,190–2,670 m in elevation), the ecotone between single-leaf pinyon-Utah juniper (*Pinus monophylla-Juniperus osteosperma*) and white fir-Ponderosa pine (2,460–2,520 m elevation), and the mountain mahogany-manzanita (*Cercocarpus ledifolius-Arctostaphylos pungens*—2,280–2,460 m elevation) communities. *T. panamintinus* is most abundant in lower elevational (2,025–2,160 m) single-leaf pinyon-Utah juniper communities, whereas *T. palmeri* is most abundant in the white fir-Ponderosa pine community and in the ecotone between the single-leaf pinyon-Utah juniper and white fir-Ponderosa pine communities (Deacon et al., 1964).

Tamias panamintinus and *T. minimus* are found at an elevation of 2,100 m, near Crowley Lake Dam, Mono Co., California. This area is on several alluvial fans at the base of the mountains. Slopes above the fans primarily are covered with single-leaf pinyon, while the fans are rocky, and have a thick growth of sagebrush (*Artemisia tridentata*), with scattered single-leaf pinyon, Jeffrey pine (*Pinus jeffreyi*), juniper, and mountain mahogany (Brand, 1970).

In the Grapevine Mountains, Death Valley National Monument, California, *T. panamintinus* occurs in single-leaf pinyon and Utah juniper habitat with characteristic species of birds (e.g., ash-throated flycatcher, *Myiarchus cinerascens*; California jay, *Aphelocoma californica*; pinyon jay *Cyanocephalus cyanocephalus*; bush-tit, *Psaltriparus minimus*; blue-gray gnatcatcher, *Polioptila caerulea*; black-throated gray warbler, *Dendroica nigrescens*) and mammals (e.g., western pipistrelle, *Pipistrellus hesperus*; badger, *Taxidea taxus*; white-tailed antelope squirrel; pocket gopher, *Thomomys*; Great Basin pocket mouse, *Perognathus parvus*; long-tailed pocket mouse, *P. formosus*; western harvest mouse, *Reithrodontomys megalotis*; deer mouse, *Peromyscus maniculatus*; canyon mouse, *P. crinitus*; pinyon mouse, *P. truei*; desert woodrat, *Neotoma lepida*; porcupine, *Erethizon dorsatum*; Nuttall cottontail, *Sylvilagus nuttallii*; desert cottontail, *S. auduboni*; mule deer, *Odocoileus hemionus*; mountain sheep, *Ovis canadensis*—Miller, 1946). At 1,500 m elevation in the Providence Mountains, some low-zone biotic associates of *T. panamintinus* are white-tailed antelope squirrels, desert sparrows (*Amphispiza bilineata*), collared lizards (*Crotaphytus collaris*), spotted toads (*Bufo punctatus*), and Joshua trees (*Yucca brevifolia*—Johnson, 1943). In the Charleston Mountains, Nevada, small mammals occurring with *T. panamintinus* include the white-tailed antelope squirrel, golden-mantled ground squirrel (*Spermophilus lateralis*), Great Basin pocket mouse, western harvest mouse, canyon mouse, brush mouse (*P. boylii*), cactus mouse (*P. eremicus*), deer mouse (*P. maniculatus*), pinyon mouse, bushy tailed woodrat (*Neotoma cinerea*), and desert woodrat (Deacon et al., 1964).

No evidence of plague has been found in *T. panamintinus* in California (Nelson, 1980). Endoparasites of *T. panamintinus* include the nematode *Syphacia eutamii* (Archie et al., 1988), but no ectoparasites are known.

The Panamint chipmunk has been trapped using Museum Special traps, Victor rat traps, and Sherman live traps, baited with a mixture of peanut butter and oatmeal (Archie et al., 1988). Sherman live traps (ca. 8 by 8 by 25 cm), baited with a mixture of peanut butter and whole oats, placed near dead shrubs and fallen or dead trees captured *T. panamintinus* (Hirshfeld, 1975).

In the Kingston Mountains, *T. p. acrus* lives in arid pinyon-juniper woodlands, where it has nests among ledges and cliffs. Mining and cattle grazing are the major land uses in the area and are not considered to be a threat to the population (D. F. Williams, in litt.).

BEHAVIOR. *Tamias panamintinus* primarily is terrestrial (Grinnell, 1933), and rarely ventures from rocks (Johnson et al., 1948); it climbs rock ledges, bushes (Hall, 1946), small trees (Grinnell, 1933), and along lower limbs of pinyon trees (Hall, 1946). In the laboratory, *T. panamintinus* is less prone to climb than *T. palmeri.* The Panamint chipmunk usually remains close to fallen logs and rock piles, and it rarely occurs in open areas away from shelter for any sustained period of time (Hirshfeld, 1975).

When alarmed, *T. panamintinus* seeks refuge in fissures in cliffs and ledges or in spaces under granite boulders. Frequently, it perches on tops of rocks, where it can see ≥100 m in all directions and from which it can retreat into crevices if danger threatens. In such places, it shells seeds it has gathered from the surrounding area, leaving little heaps of broken shells of pinyons and other seeds. *T. panamintinus* uses smaller rocks and crevices than rock squirrels (*Spermophilus variegatus*) in the same area, and it avoids sunny south-facing slopes and adjacent sandy washes that are occupied by white-tailed antelope squirrels (Johnson et al., 1948).

In the drier part of the Panamint Mountains, *T. panamintinus* comes down canyon sides slowly and cautiously in midday to drink from springs, and often stops to utter sharp, chattering call notes (Elliot, 1904). In January, Panamint chipmunks are active and conspicuous on clear days even when cold winds are blowing, but on cloudy and rainy days they keep out of sight. At this season, the period of greatest activity is near midday. In May and June, activity commences at sunrise, peaks at ca. 0900 h, tapers off during the hot part of the day, and is resumed in late afternoon. Usually, chipmunks are not active after sunset, but sometimes they forage in early evening over cliffs that are still warm and that have been heated by the sun during the day (Johnson et al., 1948).

Tamias panamintinus commonly is encountered above ground during milder periods of winter and is considered an occasional hibernator (Hirshfeld, 1975; Hirshfeld and Bradley, 1977), although no data are available to verify this pattern of hibernation (O'Farrell, 1980). In Springdale Canyon, Nevada, *T. panamintinus* was active on 5 April when temperature in the shade was below freezing, and even in the sunshine the temperature was so low as to indicate that this species does not hibernate (Hall, 1946).

Tamias panamintinus appears earlier in spring than *T. palmeri.* However, this difference in time of appearance probably is because of the occurrence of *T. panamintinus* at lower elevations where winters are warmer and shorter. *T. panamintinus* may or may not hibernate, depending upon local weather conditions (Hirshfeld, 1975).

The Panamint chipmunk has an annual rhythm with flexibility in phasing that enables adjustment to environmental variation among years (Heller and Poulson, 1970). It is active at all seasons, except when temperatures are <8–10°C for several days. Activity of males may decrease in late summer and autumn, and activity of females may cease in late winter and early spring (Hirshfeld, 1975; O'Farrell, 1980).

Tamias panamintinus shows intraspecific aggression, especially near baited traps. These aggressive encounters occur during all seasons. Actual physical displays are most prominent in spring (Hirshfeld, 1975).

The Panamint chipmunk utters vocalizations while in trees, and on logs or rocks (Brand, 1970). It may emit a chip, chippering,

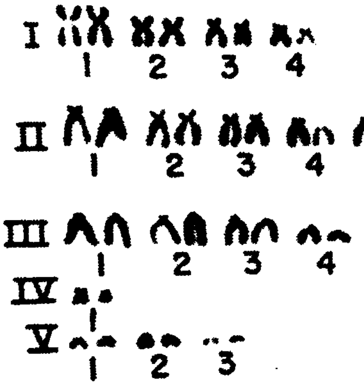

FIG. 5. Karyotype of *Tamias p. panamintinus* from Grandview Campground, Ancient Bristlecone Forest, Inyo Co., California. Roman numerals indicate the type of chromosome: I, large metacentric; II, large submetacentric; III, large acrocentric; IV, small metacentric; V, small acrocentric. The number of chromosomes of each type is noted (modified from Sutton and Nadler, 1969).

chuck, chattering (in courtship), or whistle. Vocalization rates are: chips/min, 25 (range, 10–44); chips/burst, 1.4 (range, 1.0–3.1); bursts/min, 17 (8–44); length of syllable (in s), 0.100 (0.055–0.245); interval between chips within bursts, 0.275 (0.185–0.420). Frequency rates (in kilocycles/s) are: bottom of upsweep, 1.5 (1.0–4.5); top of upsweep, 13.5 (10.5–16.5); bottom of downsweep, 2.0 (1.0–3.5—Brand, 1976). The upsweep is quite consistent; initially it rises slowly, then it sweeps rapidly upward. A downsweep always is present, and the lower one-half of the downsweep often is elongated to a variable degree. Often there also is a terminal pulse of sound, usually coming after the chip. The terminal pulse and elongated syllables give chips of *T. panamintinus* their unique sound (Brand, 1970).

In chips of *T. panamintinus*, *T. merriami*, *T. townsendii*, and *T. umbrinus*, there occasionally is a short break between upsweep and downsweep. The elongated lower parts of the upsweeps of chips of *T. panamintinus* and *T. umbrinus* resemble whistles of *T. amoenus* and *T. speciosus*, and may have arisen from a common ancestral call. *T. panamintinus* calls at a slower rate (average, 25 chips/min) than *T. alpinus*, *T. amoenus*, or *T. minimus*, and its chips are given in bursts rather than in a series. In some sequences, chips are given singly, but at a tempo characteristic of chipping sequences consisting of bursts, rather than a series (Brand, 1970).

When first captured, *T. panamintinus* is aggressive. After some time in captivity, this tendency wanes and handling is easier. However, some males never lose their aggressiveness and continually chatter and protect their cages from outside disturbances. Females are not defensive (Hirshfeld, 1975).

In the White Mountains, a young *T. panamintinus* was observed entering its rock den in a roadbank, then it reappeared at the entrance several times. Finally, the mother, who had been watching 15 m away, came up and nuzzled her young offspring, then ran off with the young following closely behind. The female went in spurts of ca. 3 m, stopping for a few seconds after each run to look back and let her young offspring catch up. Their course was a straight line 82 m across the slope to her den in a pinyon pine. It took them ca. 3 min to reach the tree. The family went in at 2017 h when light intensity at the zenith was 875 footcandles. The next day they retired at 2000 h when the light was 11,000 footcandles. At noon on the day they moved, the mother met one of her young 30 m from the den on the rocks of the roadbank, where she sniffed its nose and anal area. Then she went to the ground den. The female emerged at 1325 h with one of her young, which then tried to suckle. The mother nuzzled it briefly, then ran off along the rocky roadbank for 30 m in the general direction of the tree den, going in spurts, and being followed closely by the young chipmunk. The next morning a total of seven young chipmunks was counted, which was a record number for tree-nesting chipmunks and for *T. panamintinus* (Broadbooks, 1977).

Half-grown young will play around rocks. When alarmed, they will seek refuge beneath rocks, but after a few minutes they may venture into the open again. When a strange object (e.g., a human) is observed, a half-grown young may become immobile for ≥4 min, then it may run away or become very cautious. It may survey the situation carefully, slowly moving the tail from side to side, then hopping a short distance and looking and listening again. Half-grown young may give a vocalization resembling a grunt. Adults are more wary. Young may respond to vocalizations from an adult by going toward the sound (Burt, 1934).

GENETICS. The Panamint chipmunk has karyotype B of *Tamias* (Fig. 5; Nadler et al., 1977). The diploid number of chromosomes is 38, including four pair of large metacentric, six pair of large submetacentric, four pair of large acrocentric, one pair of small metacentric, and three pair of small acrocentric chromosomes. The X chromosome is submetacentric and the Y is a small acrocentric (Sutton and Nadler, 1969).

Among 36 allozymes examined in *T. panamintinus*, nine (25%) were polymorphic (esterase-1 and 2, phosphoglucomutase-2 and 3, glutamate oxalate transaminase-2, hemoglobin-1, postalbumin-1 and 2, plasma protein-A). The number of loci heterozygous per individual averaged 0.061 (range, zero to six—Kaufman et al., 1973). Of 20 allozymes examined in a subsequent study, *T. panamintinus* had an average heterozygosity of 0.022 and one polymorphic locus (red cell phosphoglucomutase—Levenson et al., 1985).

REMARKS. Although *T. panamintinus* is more closely related to *T. amoenus* than to any other species, this relationship is somewhat remote, and morphologic and habitat differences between *T. panamintinus* and *T. amoenus* are sufficiently great to preclude the possibility of intergradation. In its choice of habitats, *T. panamintinus* resembles the much larger *T. dorsalis* and the range of these species are complementary, approaching but not meeting in southern Nevada; they do not seem to be closely related (Johnson, 1943).

The taxonomic relationships of *T. panamintinus* to other species of *Tamias* are not clear. Based upon cranial and external morphology and coloration, *T. panamintinus* has been placed in the *amoenus* group with *T. amoenus* (Howell, 1929). Based upon bacular morphology, *T. panamintinus* has been placed in the *speciosus* group with *T. bulleri*, *T. palmeri*, *T. speciosus*, and *T. umbrinus* (White, 1953). Phenetic analyses of morphologic characters have grouped *T. panamintinus* in clusters with *T. dorsalis*, *T. palmeri*, *T. umbrinus*, and *T. quadrivittatus*. Cladistic analyses of electrophoretic data have placed *T. panamintinus* with *T. dorsalis* (Levenson et al., 1985; Nadler et al., 1985); based upon these analyses of morphology and allozymes, *T. panamintinus* has been placed in the *dorsalis* species group with *T. dorsalis*, *T. quadrivittatus*, and *T. rufus* (Levenson et al., 1985).

Currently, chipmunks previously assigned to the genus *Eutamias* are included in the genus *Tamias* (Levenson et al., 1985; Nadler et al., 1969, 1977; Wilson and Reeder, 1993). However, there are indications that *Eutamias* and *Tamias* may be distinct genera, e.g., divergence in the late Miocene (Ellis and Maxson, 1979; Hafner, 1984), differences in pattern of dorsal stripes, structure of the hyoid, chromosomes, dental formulas, bacula (Hoffmeister, 1986), microcomplement-fixation reactions, and allozymes (Ellis and Maxson, 1979; Hafner, 1984).

Tamias is from the Greek *tamias* meaning a storer or distributor (Jaeger, 1955), and the specific epithet *panamintinus* refers to the Panamint Mountains, California. *T. panamintinus* also has been referred to as the Panamint Mountains chipmunk (Elliot, 1905).

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