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Tamias amoenus.

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Tamias Bachman, 1839

Tamias Illiger, 1811:83. Type species *Sciurus striatus* Linnaeus.
Eutamias Trouessart, 1880:86. Type species *Sciurus striatus asiaticus* (Gmelin).
Neotamias Howell, 1929:26. Type species *Tamias asiaticus merriami* Allen.

CONTEXT AND CONTENT. Chipmunks are small squirrels classified in Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Tribe Tamiini, and either Subfamily Sciurinae (Black, 1963) or Marmotinae (Gromov et al., 1965). There is no agreement over whether all chipmunks in North America should be included in the genus *Tamias* or whether the eastern chipmunk should be *Tamias* and the western forms *Eutamias*. The following key is adapted from distribution, measurements (mm), color, and baculum characteristics (Fig. 1) taken from Hall (1981), Honacki et al. (1982), Howell (1929), Patterson (1984), Patterson and Heaney (1987), Sutton (1987), and White (1953*a*):

Key to Species of *Tamias*

1 Occurring in northern European Russia, Siberia, China, Korea, Sakhalin, S Kurile Islands, and Japan (Fig. 1-R) ... *T. sibericus*
Occurring in North America ... 2
2 Occurring in North America E of meridian 95 (Fig. 1-V) ... *T. striatus*
Occurring in the United States W of meridian 105, N and W of Lake Michigan, and throughout southern Canada 3
3 Dorsal dark stripes (except median one) indistinct ... 4
Dorsal dark stripes all distinct ... 6
4 Occurring E of California and Baja California; length of baculum 3.8 (*T. d. dorsalis*), shaft slender 0.4, depth of keel 0.5; color gray; average tail length 115; no notch between anterior nasals; greatest length of skull 36–40 (Fig. 1-F) ... *T. dorsalis*
Occurring in California and/or Baja California ... 5
5 Length of baculum 4.3 mm (for *T. o. obscurus*), dorsoventral shaft thick, depth of keel 2.1; average tail length 98; dark stripes reddish; greatest length of skull 33–40 (Fig. 1-I) ... *T. obscurus*
Length of baculum 5.2 (*T. m. merriami*), shaft slender, depth of keel 0.3; average tail length 112 (84–140); color grayish to ochraceus, dark stripes gray or brown; small notch between anterior nasals; greatest length of skull 36–40 (Fig. 1-G) ... *T. merriami*
6 Average greatest length of skull >36.5 ... 7
Average greatest length of skull <36.5 ... 15
7 Occurring only in Mexico (but not in Baja California); length of baculum 4.1, depth of keel 0.8; ventral tail reddish; greatest length of skull 36–40 (Fig. 1-C) ... *T. bulleri*
Occurring in western United States or Canada ... 8
8 Occurring in Arizona, New Mexico, or Texas ... 9
Occurring in other areas of United States and Canada ... 10
9 Length of baculum <4; angle of tip/shaft about 120°; hind foot grayish; average head-body length 143 (136–149); greatest length of skull 36–39 (Fig. 1-D) ... *T. canipes*
Length of baculum >4; angle of tip/shaft about 140°; hind foot buff to cinnamon; average head-body length 127 (118–135); greatest length of skull 35–38 (Fig. 1-E) ... *T. cinereicollis*
10 Back of ears not distinctly bicolored in summer pelage; tips of nasal bones separated by a small median notch; length of baculum 3.7 (*T. s. sonomae*), shaft slender; greatest length of skull 37–40 (Fig. 1-T) ... *T. sonomae*
Back of ears distinctly bicolored in summer pelage; tips of nasals not separated by a median notch ... 11
11 Ears relatively long, notch average 18.8, pointed; submalar dark stripe expands to conspicuous black area below ear; baculum 5.0, shaft somewhat thick, depth of keel 0.4; greatest length of skull 36–39 (Fig. 1-M) ... *T. quadrimaculatus*
Ears shorter, notch average 16.8, rounded; no conspicuous black area below ear ... 12
12 Baculum tip 1.7, longer than shaft, 1.4, shaft dorsoventrally thick, 0.7; greatest length of skull 39–41 (Fig. 1-S) ... *T. siskiyou*
Baculum tip shorter than the shaft ... 13
13 Baculum keel depth <25% of tip length, length of shaft 2.8, moderately thick; upper body dark tawny olive; greatest length of skull 39–41 (Fig. 1-J) ... *T. ochrogenys*
Baculum keel depth >25% of tip length ... 14
14 Baculum length 3.9, shaft dorsoventrally thick, keel depth 0.4; color ochraceous, washed with gray on shoulders and rump; hind feet clay color; greatest length of skull 37–40 (Fig. 1-Q) ... *T. senex*
Baculum length 2.7 (*T. t. cooperi*), shaft slender, keel depth 0.2; color cinnamon buff to tawny, not gray; hind feet buff to brown; greatest length of skull 37–40 (Fig. 1-W) ... *T. townsendii*
15 Baculum shaft thick (shaft depth/shaft length >20%) ... 16
Baculum shaft relatively thin (depth <18% of shaft) ... 17
Baculum shaft very thin (depth <13% of shaft) ... 21
16 Submalar dark stripe obsolete anteriorly; baculum 2.8; occurring in a wide band along the central California–Nevada border; color somewhat grayish; greatest length of skull 33–35 (Fig. 1-L) ... *T. panamintinus*
Submalar dark stripe complete anteriorly; baculum 2.4; occurring only in California, except for a small area in Nevada E of Lake Tahoe; colors bright, with light and dark elements contrasting strongly; baculum 2.4; greatest length of skull 33–36 (Fig. 1-U) ... *T. speciosus*
17 Occurring only on Charleston Peak and Potosi Mts., Nevada; greatest length of skull 35–37 (Fig. 1-K) . *T. palmeri*
Occurring elsewhere ... 18
18 Occurring in northern Idaho, western Montana, and southeastern British Columbia; baculum 4.1 and tip >40% of shaft length in *T. r. simulans*, but 5.2 and the tip <35% of shaft length in *T. r. ruficaudus*; greatest length of skull 34–36 (Fig. 1-O) ... *T. ruficaudus*
Occurring in Arizona, Colorado, New Mexico, or Utah ... 19
19 Occurring in eastern Utah, western Colorado, and northeastern Arizona; baculum 3.5, tip <40% of shaft; greatest length of skull 34–36 (Fig. 1-P) ... *T. rufus*
Occurring in southern Colorado, northeastern Arizona and northern New Mexico ... 20
20 Baculum 4.4, tip length 31% of shaft length; greatest length of skull 33–37 (Fig. 1-N) ... *T. quadrivittatus*
Baculum 2.0 in *T. u. montanus* and 3.3 in *T. u. umbrinus*, tip 41% of shaft length; color generally pale with black areas restricted, but well defined; greatest length of skull 34–37 (Fig. 1-X) ... *T. umbrinus*
21 Occurring only in the Sierra Nevada Range of California; baculum 2.6; underside of tail bright orange-yellow; greatest length of skull 29–32 (Fig. 1-A) ... *T. alpinus*
Occurring from California N to British Columbia and/or E to the Rocky Mountains ... 22
22 Ratio of baculum tip/shaft <28; baculum length 3.3; greatest skull length 29–34 (Fig. 1-H) ... *T. minimus*
Ratio of baculum tip/shaft >28; baculum length 3.0; greatest skull length 31–36 (Fig. 1-B) ... *T. amoenus*

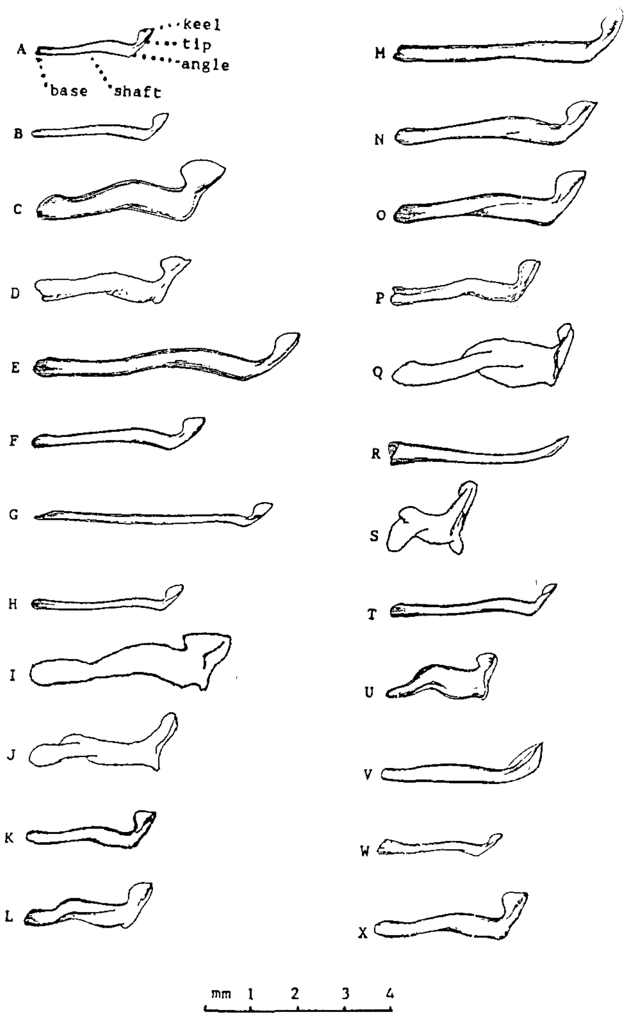

FIG. 1. Bacula (male genital bones) of species in the Genus *Tamias*, (Subgenus *Neotamias*): A, *alpinus*; B, *amoenus*; C, *bulleri*; D, *canipes*; E, *cinereicollis*; F, *dorsalis*; G, *merriami*; H, *minimus*; I, *obscurus*; J, *ochrogenys*; K, *palmeri*; L, *panamintinus*; M, *quadrimaculatus*; N, *quadrivittatus*; O, *ruficaudus*; P, *rufus*; Q, *senex*; R, *sibericus*; S, *siskiyou*; T, *sonomae*; U, *speciosus*; V, *striatus*; W, *townsendii*; X, *umbrinus*.

Tamias amoenus Allen, 1890

Yellow-pine Chipmunk

Tamias amoenus Allen, 1890:90. Type locality "Fort Klamath, Oregon."

Eutamias caurinus Merriam, 1898:352. Type locality "Olympic Mountains, Washington, timberline near head of Soleduck River."

Eutamias canicaudus Merriam, 1903:77. Type locality "Spokane, Washington."

Eutamias ludibundus Hollister, 1911:1. Type locality "Yellowhead Lake, British Columbia."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Subfamily Sciurinae (or Marmotinae), Tribe Tamiini, Genus *Tamias*, and Subgenus *Neotamias*. Fourteen subspecies of *Tamias amoenus* are recognized as follows (Hall, 1981; Howell, 1929):

T. a. affinis J. A. Allen, 1890:103. Type from "Ashcroft, British Columbia."

T. a. albiventris (Booth, 1947:7). Type from "Wickiup Spring, 23 mi. W Anatone, Asotin-Garfield County boundary, Washington."

T. a. amoenus Allen, 1890:90, see above (*propinquus* Anthony is a synonym).

T. a. canicaudus (Merriam, 1903:77), see above.

T. a. caurinus (Merriam, 1898:352), see above.

T. a. celeris (Hall and Johnson, 1940:155). Type locality "near head of Big Creek, 8,000 ft. Pine Forest Mts., Humboldt Co., Nevada."

T. a. cratericus (Blossom, 1937:1). Type locality "Grassy Cone, Craters of the Moon National Monument, 6000 ft. 26 mi. SW Arco, Butte Co., Idaho."

T. a. felix Rhoads, 1895:941. Type locality "Church Mountain, New Westminster district, British Columbia, near international boundary."

T. a. ludibundus (Hollister, 1911:1), see above.

T. a. luteiventris Allen, 1890:101. Type locality "Chief Mountain Lake [=Waterton Lake], Alberta (3½ mi. N United States-Canada boundary)."

T. a. monoensis (Grinnell and Storer, 1916:3). Type from "Warren Fork of Leevining Creek, 9,200 ft., Mono Co., California."

T. a. ochraceus (Howell, 1925:54). Type from "Studhorse Canyon, 6,500 ft., Siskiyou Mts., California."

T. a. septentrionalis (Cowan, 1946:110). Type from "Ootsa Lake Post Office on N shore Ootsa Lake, British Columbia."

T. a. vallicola (Howell, 1922:179). Type from "Bass Creek, 3,725 ft., near Stevensville, Montana."

DIAGNOSIS. Like all chipmunks in western North America the skull of the yellow-pine chipmunk is narrow and lightly built, the postorbital process is slender and fragile, the infraorbital foramen is relatively larger than in most sciurids and lacks a canal, the head of the malleus is not elongated, the plane of the manubrium of the malleus is 90° to the plane of the lamina, the adult hyoid apparatus has fused hypohyal and ceratohyal bones, the tip of the baculum is upturned and has a dorsal keel, and the tail is >40% of total length. The color pattern includes five longitudinal dark stripes that are evenly spaced and subequal in width. The three dorsal stripes extend to rump and shoulder and the two lateral ones extend only along mid-body, whereas in the eastern chipmunk (*T. striatus*), all the lateral, dark stripes are short (White, 1953*a*).

The dental formula is 1/1, 0/0, 2/1, 3/3, total 22. The peglike upper premolar (P3) is present and distinguishes the western and Asiatic chipmunks from *T. striatus* of eastern North America. This tooth is considered by Hall (1981) and White (1953*a*) to be of generic significance; however, Bryant (1945) and Ellerman (1940) considered it to be vestigial and of little taxonomic value.

Average length of head and body of *T. amoenus* is about 15% more than that of the two smallest western chipmunks, *T. alpinus* and *T. minimus*. Average length of skull is about 8% more than that of the other two, and the average length of tail is about 14% greater than that of *T. alpinus* and equal to that of *T. minimus* (Hall, 1981). *T. amoenus* is more reddish than *T. minimus*; length of tail is about 74% of length of head and body compared with 88% for *T. minimus*; ratio of length of baculum tip to length of shaft is 30–35% in *T. amoenus* and 18–28% for *T. minimus* (White, 1953*b*). The baubella (female genital bones) of the two species are so similar that a clear distinction cannot be drawn (Sutton, 1982). Certain subspecies of these two species so closely resemble each other that no specific diagnosis has been framed that will distinguish them in all parts of their geographic range. At any one place, however, the two are distinguishable, with *T. minimus* smaller, paler, underside of tail yellowish instead of reddish, the braincase less flattened, zygomatic arches less flattened, the rostrum shorter, and upper incisors less recurved (Hall, 1981).

The only other species with which *T. amoenus* is likely to be confused is *T. speciosus*. *T. amoenus* is smaller, has shorter and broader-appearing ears, less sharply contrasting pale and dark stripes, with the inner pair of pale dorsal stripes broader and the outer pair usually narrower and less conspicuous. The dark facial stripes are less blackish, light facial stripes more washed with ochraceous, the skull less massive, rostrum more pointed, and the incisive foramina are smaller. These characters are quantitative and not specifically distinctive (Hall, 1981). The genital bones of both sexes, however, provide a clear and unique differentiation, with long, slender bones in both sexes of *T. amoenus* and short, thick bones in both sexes of *T. speciosus*. In a similar way, characteristics of the genital bone distinguish *T. amoenus* from *T. panamintinus* and *T. umbrinus*,

FIG. 2. *Tamias amoenus* female from Davis Lake, 13 km N Portola, Plumas County, California.

with which it is sympatric in some areas of the Sierra Nevada of California (Sutton, 1982; White, 1953*b*).

Characteristics of the baculum provide powerful diagnostic criteria among sciurids in general and among chipmunks in particular. Forms with markedly different bacula represent distinct species and, by critical examination of the genital bones, parapatric forms may be distinguished with confidence (Patterson, 1984; Patterson and Heaney, 1987; White, 1951).

GENERAL CHARACTERS. *Tamias amoenus* (Fig. 2) is a small chipmunk. Average and range for measurements (in mm) for 48 males and 49 females, respectively, from a series including all 14 subspecies are: length of head and body, 116.7 (108–123), 121.3 (115–129); length of tail, 91.9 (78–108), 91.5 (72–109); length of hind foot, 31.9 (29–35), 32.3 (30.0–35.0), and length of ear from notch, 20.8 (18–24), 20.52 (18.0–22.0). Average and range of cranial measurements are: greatest length of cranium, 32.6 (29.9–34.5), 33.4 (31.5–36.3); condylobasal width, 29.0 (27.5–32.5), 29.9 (28.1–32.9); zygomatic width, 17.9 (17.2–18.9), 18.6 (17.3–21.5); cranial width, 15.5 (14.7–16.4), 15.8 (14.9–17.1); interorbital width, 7.4 (6.6–8.5), 7.8 (6.7–9.7); length of nasal bone, 9.9 (9.0–11.0), 10.5 (8.6–12); and length of lower tooth row, 5.2 (4.6–5.7), 5.2 (4.5–5.8). Females are slightly larger than males in all measurements except length of tail, length of lower tooth row, and length of ear from notch, which are essentially equal. Factors implicated in larger female size in chipmunks include hibernation and the timing of resource accumulation (Levenson, 1990).

The narrow braincase (Fig. 3) is evenly rounded and rather deep (not flattened). The zygomatic arches have little flare and often are nearly parallel with the axis of the skull. The rostrum is short and abruptly constricted near the base, the temporal region is flattened, the lambdoidal crest is barely discernable, and the supraorbital notches are even with, or posterior to, the posterior notch of the zygomatic plate (White, 1953*a*).

Color of the body is dark and reddish, with the crown of the head black to smoke gray, mixed with cinnamon. Color differences among the subspecies are: sides of the body range from pinkish cinnamon (*T. a. affinis*) or cinnamon buff (*T. a. monoensis*) through sayal brown to tawny and ochraceous tawny (*T. a. luteiventris*, *T. a. ludibundus*, and *T. a. felix*). Rump and thighs are cinnamon, pinkish cinnamon, cinnamon buff, or ochraceous tawny, mixed in each case with smoke gray; hind feet vary from pale-pinkish cinnamon through cinnamon buff to sayal brown. The under surface of the tail is pinkish cinnamon, clay color, cinnamon, sayal brown, tawny, or ochraceous tawny. The ears are fuscus black, broadly margined posteriorly with buffy (Howell, 1929).

Five longitudinal stripes on the body are separated by four subequal light stripes. Three dark stripes, separated by two light stripes, are on each side of the head. The dark, dorsal stripes are black or fuscous black, often shaded or mixed with tawny, ochraceous tawny or cinnamon. The median pair of pale dorsal stripes is smoke gray or pale smoke gray, usually mixed with cinnamon or tawny. The outer pair of pale stripes is clear, creamy white, narrower, and less conspicuous than the inner, and in *T. a. felix* is mixed with ochraceous tawny. In locomotion away from an observer, the stripe pattern has an effacing effect in the eyes of a pursuer above the level of the chipmunk. Cheek pouches are internal. Body mass varies considerably with the average (and range) of 10 largest males, from a series collected in September when young of the year appear to be grown, 49.7 g (30.0–57.5) and the average of 10 largest females 53.5 g (29.0–58.5; Grinnell et al., 1930).

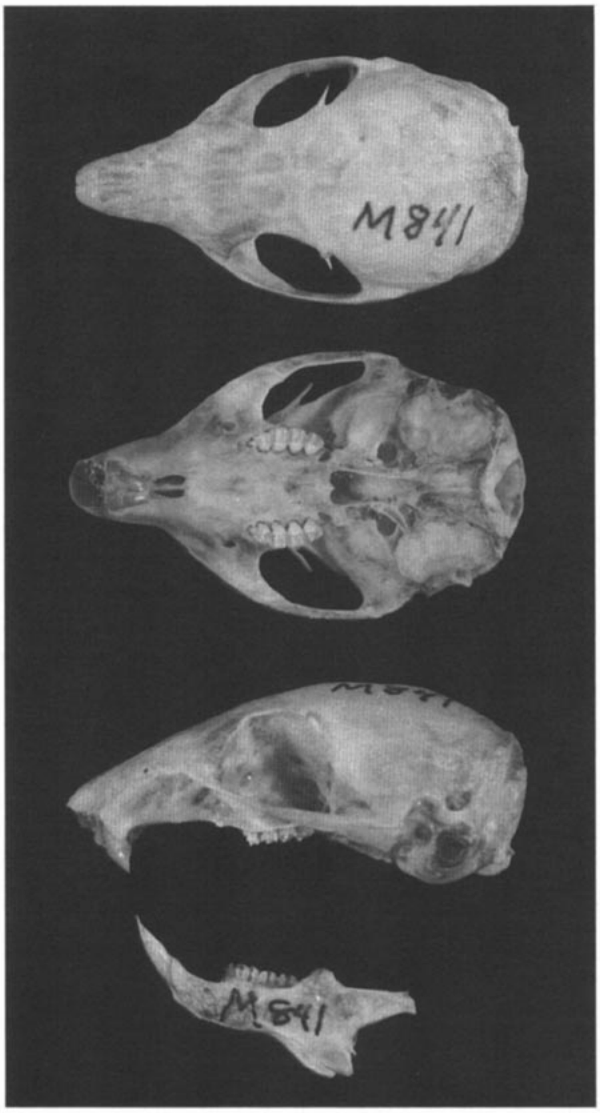

FIG. 3. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tamias amoenus* (male, California State University, Chico, M841, Manzanita Lake, Lassen Volcanic National Park, Shasta County, California). Length of skull is 31.99 mm.

DISTRIBUTION. The yellow-pine chipmunk is found in mountain areas of California northward from Mammoth Pass and the Yolla Bolly Range; northward from northern Nevada and northwestern Utah, and from western Wyoming and western Montana westward throughout Oregon and Washington (Fig. 4). In Canada it is found from the mountains of southwestern Alberta through most of southern British Columbia (Hall, 1981). It usually is found in the Transition Zone, extending its range into the Canadian Zone in some areas where conditions are favorable. The altitudinal range in California extends from about 975 m to timberline at about 2,900 m (Johnson, 1943).

FOSSIL RECORD. North American chipmunks first appear in Miocene deposits, having diverged from tree squirrels about 3.8 × 10^6 years ago during the Oligocene (Ellis and Maxson, 1979). Some time shortly after first appearing on this continent, a tree squirrel or chipmunk-like animal appears to have migrated into Eurasia and spread rather rapidly during the Pliocene into western Europe (Black, 1972). The Pleistocene history of *Tamias* is unclear, with records from North America as well as from Poland and China. Evidence from karyotypes (Nadler et al., 1977) suggests that Nearctic species evolved from Palearctic immigrants of *T. sibericus*. The species *T. amoenus* has not been identified specifically in any fossil fauna.

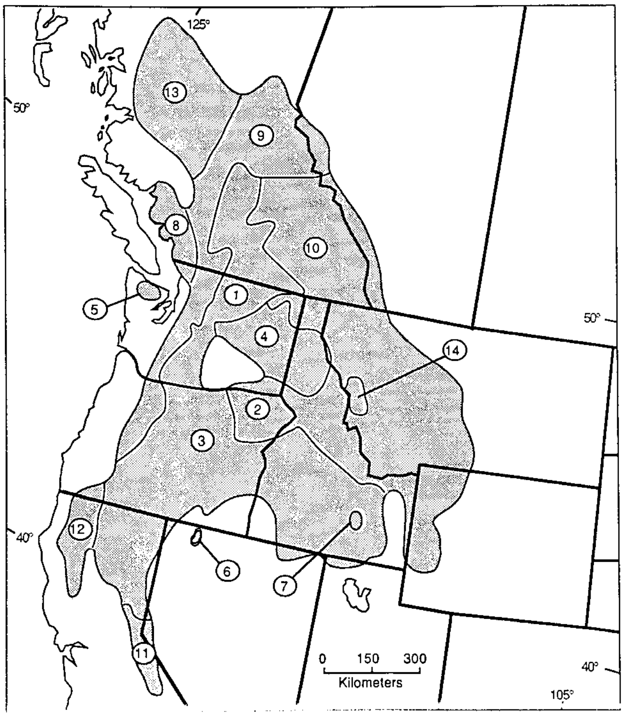

FIG. 4. Distribution of *Tamias amoenus* in western North America (Hall, 1981): 1. *T. a. affinis*; 2. *T. a. albiventris*; 3. *T. a. amoenus*; 4. *T. a. canicaudus*; 5. *T. a. caurinus*; 6. *T. a. celeris*; 7. *T. a. cratericus*; 8. *T. a. felix*; 9. *T. a. ludibundus*; 10. *T. a. luteiventris*; 11. *T. a. monoensis*; 12. *T. a. ochraceus*; 13. *T. a. septentrionalis*; 14. *T. a. vallicola*.

FORM AND FUNCTION. The baculum (os penis or male genital bone) of *T. amoenus* has a thin shaft, a low keel with a height 20% of the length of the tip, and a tip 30–35% of the length of the shaft. The angle formed by the tip and shaft is about 130°; the distal 20% of the shaft is slightly compressed laterally and the length of the shaft is 2.37–2.96 mm (White, 1953*b*).

The baubellum (os clitoris or female genital bone) has a rounded proximal end (base) and bends gradually into the shaft without a definite base-shaft angle apex. The bone is tapered toward the proximal end and the rounded base-shaft angle averages about 90°. The tip is slightly longer than the shaft, with which it makes an abrupt angle, and it is bent from the shaft to the right about 7°. The keel is thin and stands out clearly from the tip. The flat flanges on each side of the tip are about 0.2 mm wide, making the tip in some specimens as wide as it is deep. The baubella of five subspecies of *T. amoenus* are all similar in form and size, but that of *T. a. cratericus* is thicker and much larger (Sutton, 1982).

An autumn molt begins in September or October, with the winter pelage similar to that of the summer, except of a duller tone, with the median pair of pale stripes darker and the sides slightly paler, about sayal brown. A spring molt begins near 1 June, with irregular patches of new pelage appearing in the mid-back and progressive replacement proceeds forward from mid-back and anterior areas, then posteriorly and ventrally. Both melanistic and albino variants are believed to occur although none are known (Broadbooks, 1968; Howell, 1929).

The estimated basal metabolic rate of *T. amoenus luteiventris* is 628 ml O_2 $kg^{-0.75}$ h^{-1}, somewhat lower than that of three subspecies of *T. minimus*. Between ambient temperatures of 3–32°C the body temperature ranged from 36–38°C. The estimated basal heart rate is 264 beats/min. Cardiovascular modifications provide extra reserves when demand for aerobic metabolism rises during bursts of activity (Jones and Wang, 1976).

Tamias amoenus and *T. speciosus* have high thermosensitivity. When the hypothalamus was cooled to 35.2°C, metabolic rate increased immediately. For three *Tamias* species, response by *T. amoenus* was intermediate and it always assumed a prone, sprawling posture as the critical upper temperature was reached. *T. amoenus* has well-developed passive heat-loss mechanisms. Predictions are made that *T. amoenus* can remain exposed to severe heat loads about half as long as the other *Tamias* species. These findings have implications for the distributions of *T. amoenus*, which is typically found in open forest areas with patches of shade and elevated perches out of the hot boundary layer (Chappell et al., 1978). *T. amoenus*, living in open forest with low ground cover, has a brain size that is intermediate for the genus. Males and females have similar brain size (Budeau and Verts, 1986).

ONTOGENY AND REPRODUCTION. Yellow-pine chipmunks emerge from hibernation dens in late March or April and mate in late April or early May, the only mating for each breeding female for the year. Testes are greatly enlarged at this time. Testicular growth is promoted by warm temperature (23°C) and retarded by cold (5°C). It appears likely that temperature, seasonal biotic productivity, and social interactions, along with the more dominant length of day, all act in maintaining the synchrony of the internal program with the external environment (Broadbooks, 1970*a*).

All males were reproductively active during the mating season and all females showed signs of breeding. Ovaries and corpora lutea enlarge at emergence from hibernation, peak in mass during pregnancy, and become small in late summer and autumn. The uteri also enlarge after emergence from hibernation. Body mass of females, field-caught while pregnant, increased steadily for 40 days following parturition, then declined until weaning. Daily food consumption increased about 2.5 fold over the 40 days while mass-specific food consumption only doubled. Following a linear growth phase over the first 40 days, the young attained homeothermy and the capability to use solid food, after which their growth rate increased 2.5 fold for 40–60 days. Young in the smallest litters apparently cannot accelerate development above the normal, while in a large litter of six, the growth rate was below normal, suggesting limitation by the mother's performance (Kenagy et al., 1981; Kenagy and Barnes, 1988).

An average litter of four or five is born in late May or early June and appears outside the den in late June. Lactation lasts through July and August and, by early September, all members of the population are of similar size (Broadbooks, 1970*a*).

ECOLOGY. The yellow-pine chipmunk occupies a much broader range of habitat types than *T. senex*, *T. speciosus*, or *T. quadrimaculatus*, with which it is sympatric; populations in breeding condition exist within the cruising range of individuals of each of the other species (Sharples, 1983). *T. amoenus* usually is found in brush-covered areas where snowberry (*Symphoricarpos*), chinquapin (*Castanopsis*), mountain mahogany (*Cercocarpus*), service berry (*Amelanchier*), antelope brush (*Purshia*), currant (*Ribes*), and buckbrush (*Ceanothus*) are found, providing abundant fruits seasonally. Such shrub areas are interspersed with a variety of grasses and herbs as well as open conifer stands, all producing favored food seeds.

The yellow-pine chipmunk is mainly omnivorous, consuming a wide variety of food items, including seeds, fruits, bulbs or tubers, insects, bird eggs, berries, flowers, green foliage, roots, small animals, and buds of woody plants (Bailey, 1936; Gordon, 1943). Seeds of most conifers are frequently found in the cheek pouches (Tevis, 1952, 1953). Merriam (1891) found 332 seeds of the lodgepole pine (*Pinus Murrayana*) in the pouches of one *T. amoenus* in Idaho. The fungus *Rhizopogon* was present in 90% of the stomachs of *T. amoenus* in Oregon. Winter food stores contained 14,000–68,000 corms and seeds weighing 70–190 g in a subterranean nest chamber. At least 59 species of plants, fruits, seeds, corms, fungi, and several kinds of insects were eaten through the year by yellow-pine chipmunks in central Washington (Maser and Maser, 1987).

Over a three year study there was little fluctuation in population density (1.25/ha). The home ranges were stable with few transients. About 90% of the animals captured in May and early June had been marked by toe clipping the previous year. Young-of-the-year accounted for about 50% of the animals caught from June through late October. Thus, the safest time of the year is the winter hibernation period, with almost 97% of the animals trapped in October recaptured 6 months later. Summer survival from July to October ranged from 33–88% (Broadbooks, 1958, 1970*a*).

Dens are maintained within or beneath stumps or logs, especially where these are overgrown with bushes. In Alberta, rocky areas provided the best concealment cover and nest sites, especially when food plants and scattered trees were near (Meredith, 1972, 1976). Underground dens have a coconut-shaped room 80–90 cm long, 16 cm in diameter, and 0.7–1.5 m underground, reached by a tunnel 2–3 m long. One was filled with dry grasses and thistledown. These dens were similar to those of *T. sibericus*, except that food was kept in a separate chamber (Anthony, 1924). In Montana, a nest of *T. amoenus* was nearly 3 m above the ground in a willow thicket. It was made of dry grasses, was 30–35 cm wide and 15 cm deep, and had an entrance 4 cm wide on the flattened top. A male and four young used a ground nest nearby. There also were tree nests made of dry grass as much as 18 m high in Engleman spruce trees (*Picea Engelmannii*). These nests were about 36 cm in diameter and over twice as large as chambers of ground nests examined. Nests may be placed in trees for several reasons: the ground nest is crowded with young; young explore and feed above ground; parasites and debris are reduced in a new nest; trees are a better refuge from predators (but not from hawks and owls); play and socializing is safer; a more favorable microclimate is provided in summer; there is a better view of surroundings; and conifer twigs and seeds are available for food. Tree nests resemble bird nests and there is the possibility that a bird nest has, at least at times, been taken over and modified for use by the yellow pin chipmunk (Broadbooks, 1974).

Routes of travel between retreats are maintained along fallen logs or branches rather than over open spaces. Where chaparral grows on the edges of talus slopes or over rock outcrops, the crevices among the rocks are used for refuge and dens. *T. amoenus* occupies new territory as it searches for sources of food (Grinnell et al., 1930).

The summer home range of most yellow-pine chipmunks remains the same from one summer to the next, indicating strong attachment to a discrete area which varies from 2 to 2.4 acres. A female yellow-pine chipmunk used in sequence four main areas which comprised her home range for two summers. The smallest area was occupied from 14 June to 18 July while she was nursing young in a burrow. The home range then increased by 24% to include a portion of a cutover plot that was used intensively until about 3 August. From 4–18 August the home range became 32% larger than the smallest area, encompassing it and the second area as well as some surrounding land. From 18 August until 11 September she confined her movements to the woods near the nest site. Males and non-pregnant females are observed with greater frequency and have larger home ranges during the reproductive season than lactating females. After young emerge, lactating females increase their home range as much as 240%. Reproductive activity and availability of selected food plants appear to be most influential in altering the movement patterns (Martinsen, 1968).

Young are curious, bold, and fearless after emerging from the den. They are easy prey to the long-tailed weasel (*Mustela frenata*), goshawk (*Accipiter gentilis*), bobcat (*Lynx rufus*), coyote (*Canis latrans*), badger (*Taxidea taxus*), sparrow hawk (*Falco sparverius*), rattlesnake (*Crotalus viridis*), and *Buteo* sp. (Broadbooks, 1970*a*).

In a study of Colorado tick fever and Rocky Mountain spotted fever richettsia, the least important host animals were *T. amoenus* and *T. ruficaudus*, with about 37% infected with larvae, 41% infected with nymphs, and an average of 7.3 ticks/host. Larval activity was restricted to a 9–11 week period between mid-June and early September, peaking in late July and early August. Activity of nymphs remained constant until it declined after mid-August. Utilization of hosts largely depended upon availability, with *Neotoma cinerea*, *Spermophilus lateralis*, and *Peromyscus maniculatus* more abundant and having more ticks than yellow-pine chipmunks (Sonnenshine et al., 1976).

Yellow-pine chipmunks given innoculations of the virulent spotted fever agent, *Rickettsia rickettsii*, responded with rickettsemias detectable as early as 3 days and as late as 18 days after intraperitoneal inoculation. Antibody titers ranged from 1:16 to 1:64 after 23 days, with infection rates up to 11% noted in nymphal ticks that had fed as larvae on *T. amoenus*. Thus, *T. amoenus* is a significant source of the virulent *R. rickettsii* to ticks and, subsequently, of spotted fever to humans. Yellow-pine chipmunks were immune to non-virulent *R. montana* and *R. rhipicephali* following intraperitoneal inoculation and examination as nymphs (Norment and Burgdorfer, 1985).

In late summer, *T. amoenus* is heavily infested with bot fly warbles. In Craters of the Moon National Monument, Idaho, 6 of 8 *T. amoenus* had 13 unidentified warbles (probably *Cuterebra emasculator*) in August; three were under the skin in the neck area, four on the thorax, and one was scrotal. *C. approximata*, common on *Peromyscus*, was introduced as larvae into *T. amoenus*; over 14% became established and the host died 13 days later (Smith, 1977).

At Crater Lake National Park, Oregon, 51 of 110 *T. amoenus* were infested with fleas, 73 fleas were *Monopsyllus eumolpi*, 32 were *M. ciliatus*, 4 each were *Oropsylla idahoensis* and *Catallagia sculleni*, and 1 each were *Thrassis* sp. and *M. wagneri*. The significance is unknown, but about 67% of male *T. amoenus* were infested, compared to 27% of the females (Gresbrink and Hopkins, 1982). In central Oregon, *M. eumolpi* makes up about 85% of the total fleas collected from *T. amoenus* (Hopkins, 1985). Small numbers of *Oropsylla idahoensis*, *M. ciliatus*, and *Malaraeus euphorbi* were also found. Thirty-six female *T. amoenus* were collected, with 64% infested as compared to 71% of 35 males. Males had an average of 2.7 fleas/infested host, whereas females had 2.3. Nineteen males with descended testes had higher infestation rates (79%) and mean numbers of fleas (3/animal). Seventeen males with abdominal testes had only 65% infestation and an average of 2 fleas/animal. Among reproductively inactive females, 61% were infested with a mean of three fleas each, compared to 65% and two fleas per animal in breeding condition (Gresbrink and Hopkins, 1982). The mite, *Acarus monopsyllus*, was discovered in phoretic association as a parasite on the flea, *Monopsyllus eumolpi*, on *T. amoenus* in California (Fain and Schwan, 1954).

BEHAVIOR. Access to food and space is controlled in *T. amoenus* and *T. townsendii* by aggressive interactions, with *T. townsendii* dominant (Trombulak, 1985). Removal of *T. townsendii* led to an increase in the home range size of *T. amoenus* and also led to an increase in survival during winter, suggesting an advantage for increased size of home range. In western Alberta *T. amoenus* occupied forested valleys and lower slopes while *T. minimus* was on the higher ridges above tree line. This distribution appears to be at least partly because of interspecies competition, with *T. amoenus* dominant. *T. amoenus* was clearly dominant in 33 of 68 matches in laboratory experiments and *T. minimus* was dominant in only one. Variability in aggressiveness was shown by *T. amoenus*. One female never attacked a *T. minimus* yet lost in only three encounters and, even against a submissive *T. amoenus*, *T. minimus* did not display much aggressiveness. *T. amoenus* was more active than *T. minimus* in the experimental conditions, first to emerge from the next box in 60 contests compared with 11 for *T. minimus*. Also, *T. amoenus* was active >2,000 of the 3,000 min of observation, compared to only about 1,000 min for *T. minimus* (Sheppard, 1971).

T. amoenus was dominant to *T. minimus* when the two were simultaneously introduced into a large, structurally complex arena in the mountains of southern Alberta; however, if *T. minimus* was introduced one day before *T. amoenus*, the dominance was balanced, with each winning the same number of agonistic matches. Observation continued for three seasons in areas where the ranges of *T. amoenus* and *T. minimus* overlapped, and only four events of interaction between the two species were noted. No aggression was observed and the animals tended to avoid each other, possibly an indication of a previous aggressive experience, or an indication that, once dominance has been established, individuals may avoid their opponents in areas where aggression would not be beneficial. Structure of the habitat may affect the outcome of interactions as well as prior residence (Meredith, 1975, 1977). Interspecific aggression and possibly habitat selection are of far more importance than physiological adaptations in determining the lines of contact between altitudinally zoned, contiguously allopatric populations of *T. amoenus*, *T. alpinus*, *T. speciosus* and *T. minimus*. Interspecific aggression is an extension of intraspecific territoriality, selected for because of properties of the cover in their habitats and the seasonality and defendability of a limited food supply (Heller, 1971).

In central Oregon, activities of *T. amoenus* are placed in five behavior categories as follows: foraging, in which the animal engages in jerky, hesitant rushes, random searching, casual movement, digging without depositing anything or covering the hole; food gathering, handling, storing, or caching; protection, in which flight, conflict, alertness, retreat and alarm vocalizations are involved; positive social interaction such as chasing another animal, fighting, sexual behavior, tail twirling, nosing another animal, and threat posturing; and maintenance, in which grooming, dust bathing, gathering nest materials, and resting were involved. With high population density intraspecific competition increases for both *T. amoenus* and *T. townsendii*, although there was no observable change in the home ranges. Distributional zonation may result more from differences in habitat selection than from aggressive interactions. Most active foraging by *T. amoenus* did not occur until sunrise or until higher temperatures were reached on cloudy days. In areas of high daily temperatures, foraging was mostly in early morning and late afternoon in areas of shrub cover and shade. In cooler areas, the major foraging activity was during warmer parts of the day, especially where shade was available. There appeared to be a tendency to confine activity to dense cover in high wind. A high, positive orientation to trees occurred when ponderosa pine (*Pinus ponderosa*) cones opened to release their seeds, providing an abundance of food for winter storage. Alarm vocalizations had the effect of having each chipmunk serve, to some extent, as a lookout for others, especially noticeable in open sites. There was greater exposure to predators in open areas as was evident from more vocalizations and higher levels of watchfulness (States, 1976). Foraging away from cover was possible when the animals were more watchful (Broadbooks, 1970*b*). Territoriality suggested by Broadbooks appears to have resulted from observing females chasing other chipmunks away from their den sites (States, 1976).

In the Cascade Mountains of central Washington, Broadbooks (1970*a*) found *T. amoenus* active above ground about 7 months of the year. Winter dormancy, interrupted by brief activity and feeding about every 2 weeks, lasts about 5 months, from November through March.

Seasonal adjustment in *T. amoenus* involves changes in food consumption, fat storage, food storage, metabolism, growth, and activity. In general, hibernators store energy as fat, but chipmunks hoard food and build up little body fat, so have short periods of hibernation. *T. amoenus* is an intermittent or, in some areas, even a non-hibernator. It may even lose weight before entering the winter den so it survives mostly on stored food. Energy is conserved by entering various depths of torpor and decreased activity (Stebbins and Orich, 1977).

Dietary adjustments influence the control of body temperature by the central nervous system, and thus influence hibernation. Animals fed a diet rich in polyunsaturated fatty acids showed shorter periods of torpor, higher minimum body temperature, and higher metabolic rates. Males tended to emerge from hibernation 1–2 weeks ahead of females (Geiser and Kenagy, 1987).

When exposed to constant photoperiod and temperature for as long as 20 months, yellow-pine chipmunks showed both reproductive and hibernatory cycles that resembled the natural rhythms that were endogenously circannual and spontaneously repeated in a period of <1 year. Torpor was not required for the progression of the seasonal reproductive rhythm. Cycles of approximately annual periodicity are exhibited even when animals are isolated from environmental clues. Chipmunks live in strongly seasonal environments that demand a precise annual schedule, but during hibernation, exposure to environmental cues and also the sensitivity of the animals to cues is reduced. An endogenous annual temporal program should prepare them to meet their tight schedule that allows only one, 2–3 week breeding period directly following hibernation. Young born in early June coincide with strong summer productivity that follows the spring snow melt. Food supply and weather are natural conditions that influence the rather flexible onset of hibernation in chipmunks. Both reproduction and hibernation are influenced by exposure to different photoperiods. Eight of 12 h of light per day permit normal seasonal cycles, but 16 h of light per day block both gonadal cycle and hibernation. A variety of factors, including temperature, seasonal biotic productivity, social interactions, and length of day, synchronize the internal program with the external environment (Kenagy, 1981).

GENETICS. Characteristics of chromosomes of the subspecies of *T. amoenus*, except for *T. a. septentrionalis*, were determined through examination of karyotypes. The modal diploid number was 38, with five pairs of metacentric, six pairs of sub-metacentric, four pairs of acrocentric, and three pairs of small metacentric or acrocentric chromosomes. The sex chromosomes in the female consist of a pair of sub-metacentric X and, in the male, of a sub-metacentric X and a small acrocentric Y. Chromosomes of subspecies of *T. amoenus* were typical of karyotype B, a characteristic of all western *Tamias* species, except *T. cinereicollis* and seven of the subspecies of *T. minimus* that were karyotype A (Sutton and Nadler, 1969). The suggestion of two groups of species among the western chipmunks based on karyotypes disagrees with the existence of five groups based on morphology and pelage characters (Howell, 1929; Johnson, 1943), and three groups based on characteristics of the baculum (White, 1953*b*). There is no satisfactory explanation for the existence of the two karyotypes. A mechanism like stasipatric speciation is unlikely since chromosome rearrangement probably would not have occurred in widely scattered localities. Karyotype patterns are uniform among the *T. amoenus* subspecies, but chromosome characters have been of little value in determining taxonomic relationships among western chipmunks (Nadler, 1964; Sutton and Nadler, 1969).

Electrophoretic data for 20 proteins has been used to suggest that there are five subgroups within the Subgenus *Neotamias*, with *T. amoenus* along with *T. umbrinus* making up one of these subgroups. This *T. amoenus*-*T. umbrinus* species group is geographically cohesive, all taxa being in the Sierra Nevada, Pacific Northwest, and Rocky Mountains, so peripheral isolation or major allopatric speciation could have resulted (Levenson et al., 1985).

REMARKS. Two accounts in the literature call attention to taxonomic and/or distribution problems with *T. a. cratericus*. First, bacula from skins labeled as *T. amoenus* from Lardo Valley Co., Butte Co., and Boise National Forest, Idaho, are similar to those of *T. umbrinus* (White, 1953*b*). Second, the baubella of the five subspecies of *T. amoenus* that were examined are similar in form and size, but that of *T. a. cratericus*, like the male counterpart, is much larger in all characters and is similar to specimens of *T. ruficaudus* (Sutton, 1982). Since the *T. minimus* genital bones, as well as most morphological characters are similar to those of *T. amoenus*, it appears possible that diversity in the *T. minimus* chromosomal makeup may be the result of taxonomic confusion with *T. amoenus* (Sutton, 1982; Sutton and Nadler, 1969).

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