

*Microtus xanthognathus*. By Chris J. Conroy and Joseph A. Cook

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*Microtus xanthognathus* Leach, 1815

Taiga Vole

*Arvicola xanthognatha* Leach, 1815:60. Type locality "Hudson's Bay."

*Microtus xanthognathus* Miller, 1896:66. First use of current name combination.

**CONTENT AND CONTEXT.** Order Rodentia, Suborder Sciuromorphi, Family Muridae, Subfamily Arvicolinae, Genus *Microtus* (Musser and Carleton, 1993), Subgenus *Microtus* (Hall, 1981). The subgenus contains 12 extant species in the Nearctic (Hall and Cockrum, 1953). *Microtus xanthognathus* is monotypic (Hall, 1981).

**DIAGNOSIS.** Taiga voles are generally larger than other North American voles of the genus *Microtus*. *M. xanthognathus* and *M. chrotorrhinus* are similar in color but the former is much larger. Flank glands are present as with other species in North America (e.g., *M. richardsoni*, *M. miurus*, *M. abbreviatus*, and *M. chrotorrhinus*) but distinguish *M. xanthognathus* from species with hip glands (e.g., *M. pinetorum*, *M. californicus*, *M. montanus*, *M. oeconomus*, and *M. townsendii*) as well as from species that apparently lack sebaceous glands (e.g., *M. oregoni*, *M. umbrosus*, *M. longicaudus*, *M. mexicanus*, and *M. pennsylvanicus*—Quay, 1968). A lack of cementum from the posteriormost lateral reentrant angle of the M3 distinguishes *M. xanthognathus* from *M. richardsoni* and *M. pennsylvanicus* (Hallberg et al., 1974). *M. xanthognathus* has a shorter tail and larger ears than *M. richardsoni* (Bailey, 1900).

**GENERAL CHARACTERS.** *Microtus xanthognathus* is one of the largest species in the genus *Microtus*, and adults have a conspicuous rusty-yellowish color about the whisker area (Fig. 1). External measurements (in mm) are as follows: total length, 186–226; length of tail, 45–53; length of hind foot, 24–27 (sample size and sex not reported—Hall, 1981). No ear measurements have been published. Large adults often range from 140 to 160 g but have been reported up to 170 g (Hall and Cockrum, 1953; Lensink, 1954; Wolff and Lidicker, 1981). In color, upper parts are dark sepia to bistre and heavily lined with coarse black hairs on back. Sides of nose and ear patch are bright rusty yellowish. Venter is dusky gray. Tail is indistinctly bicolored: blackish above, dusky gray below. Body is 3.2–3.8 times as long as tail. Tail is 1.8–1.9 times as long as hind foot (Hall, 1981). Flank glands are elliptical and their size is a function of body mass (Wolff and Lidicker, 1980).

Skull is heavy, ridged, and angular (Fig. 2; Bailey, 1900). Nasals and incisive foramina are long and narrow, and bullae are large. The basal length of the skull of one adult specimen was ca. 34.5 mm (Bailey, 1900).

**DISTRIBUTION.** Taiga voles are known from scattered localities in the boreal taiga zone from the west coast of Hudson Bay northwestward to central Alaska, south to central Alberta, and north to the Arctic Coast (Musser and Carleton, 1993; Fig. 3). Records from Manitoba include Fort Churchill and Nelson River (Coues, 1877). Records from the Northwest Territories from east to west include Fort Smith, Fort Resolution, Great Slave Lake, Fort Rae, Fort Simpson, the Liard River, Fort Franklin, Fort Norman, Franklin Bay on the Arctic Coast, Fort Good Hope, and Fort McPherson (Bailey, 1900; MacFarlane, 1905; Preble, 1908). Records from Alberta include 30 miles above Pelican Portage on the Athabaska River as well as Cache Pecotte 40 miles east of Jasper House (Preble, 1908). Records from the Yukon Territory are from near Bern Creek (near Black River) and La Pierre House (Rand, 1945), Dominion Creek (head of the Indian River), and the Yukon-Alaska

boundary at 69°20'N latitude (Youngman, 1975). Alaskan records from east to west include the following: Eagle (Osgood, 1909), Charlie Village (Osgood, 1900), Fort Yukon (MacFarlane, 1905), the mouth of the Porcupine River (Bailey, 1900), south of Fairbanks (Dice, 1921), Toklat River in McKinley National Park (Dixon, 1938), the Hess Creek and Lake Minchumina area (Wolff and Lidicker, 1980), the Yukon River 200 miles southwest of the mouth of the Porcupine River (Bailey, 1900), the Hogatza River (University of Alaska Museum [UAM], unpublished), near the Kobuk and Reed River confluence (UAM), and near the mouth of the Takotna River (near the village of McGrath—Dice, 1921).

**FOSSIL RECORD.** Taiga voles lived south of the Laurentide ice sheet during the late Pleistocene (Guilday et al., 1977) and moved northwest following the Wisconsin glaciation. However, fossils from Alaska suggest they may also have been present in Beringia. Pleistocene *M. xanthognathus*, south of the Laurentide ice sheet, occurred in parkland habitat rather than taiga, which now characterizes most of its distribution (Hallberg et al., 1974). Fossils from late Illinoian to Holocene are known from Alaska, Arkansas, Illinois, Indiana, Iowa, Kentucky, Missouri, Nebraska, Pennsylvania, Quebec, Tennessee, Virginia, West Virginia, Wyoming, and Yukon Territory (Guilday et al., 1964; Richards, 1988, 1992; Voorhies, 1983; Zakrzewski, 1985). However, the fossil record for this species may not predate the Wisconsinan (Guilday et al., 1977; Richards, 1988). Holocene Alaskan fossils recorded by Repenning et al. (1964) and Guthrie (1968) were based on the size of a single M1 in each study. A mummified Pleistocene *M. xanthognathus* (AMNH 180252) was collected in Chicken, Alaska (Guilday and Bender, 1960; Youngman, 1975). The M3 of fossil *M. xanthognathus* cannot reliably be distinguished from that of extant and fossil *M. pennsylvanicus* and *M. chrotorrhinus* unless large sample sizes are used (Guilday, 1982). Late Pleistocene and modern specimens have few differences (Guilday and Bender, 1960).

**FORM AND FUNCTION.** *Microtus xanthognathus* has a basal metabolic rate, as measured by oxygen consumption (mean  $\pm$  SE) of  $1.44 \pm 0.089$  cm<sup>3</sup> g<sup>-1</sup> h<sup>-1</sup> ( $n = 5$ ), minimal thermal 'conductance' in terms of oxygen consumption of  $0.116 \pm 0.0057$  cm<sup>3</sup> g<sup>-1</sup> h<sup>-1</sup> °C<sup>-1</sup> ( $n = 22$ ), and a basal temperature of  $38.0 \pm 0.16$  °C ( $n = 21$ —McNab, 1992). Scent glands are present on flanks of both male and female taiga voles, and may be conspicuous in males. Two meibomian or tarsal glands (enlarged sebaceous-type glands) occur in the dorsal eyelid and one in the ventral eyelid ( $n$



FIG. 1. An adult *Microtus xanthognathus* from Hess Creek, 150 km NW of Fairbanks, Alaska. Photograph provided by J. O. Wolff.

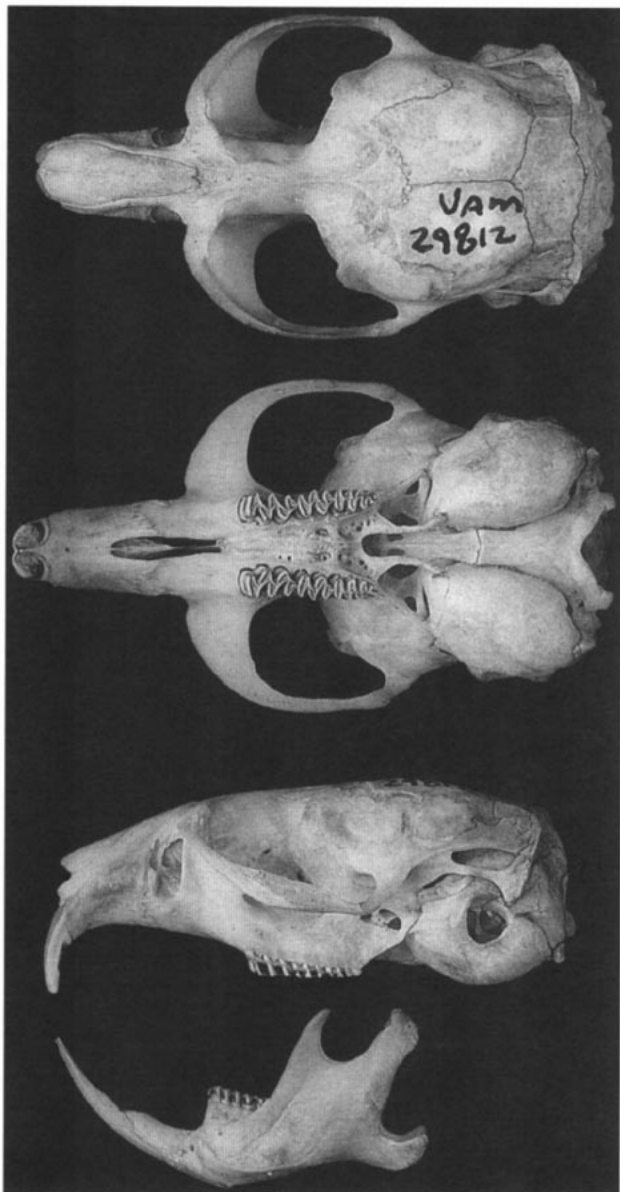


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of mandible of *Microtus xanthognathus* from 26 km north, 15 km east of the Nowitna and Little Mud Rivers, Nowitna National Wildlife Refuge, Alaska (adult female, University of Alaska Museum 29812). Greatest length of cranium is 32.8 mm.

= 1 individual—Quay, 1954). The penis is "ornate" (Lidicker and Yang, 1986:497) with dorsal papilla that have several secondary conules, urinary lappets that have two medial projections, and an entirely papillate outer crater rim. Baculum is robust and ossified (Martin, 1978).

Dental formula is  $i\ 1/1, c\ 0/0, p\ 0/0, m\ 3/3$ , total 16. The M3 has three closed triangles and the middle section of m3 is frequently divided into two nearly closed triangles (Hall and Cockrum, 1953). Upper molar row is up to 9.1 mm long and lower row is up to 8.4 mm long ( $n = 14$ —Guilday and Bender, 1960). The M3 has three lateral and four medial denticles, as well as divided rather than fused anterior pair of triangles. The m1 is asymmetrically trifoliate with a poorly developed anteromedial fold. Middle pair of lobes of m2 is divided but is fused on m3. Incisive foramina are long and narrow (Hall and Cockrum, 1953).

**ONTOGENY AND REPRODUCTION.** Taiga voles breed from early May to September and young do not breed during their first season (Douglass, 1977; Wolff and Lidicker, 1980; Youngman, 1975). Males reach reproductive competence two weeks prior to

first estrus in females (Wolff and Lidicker, 1980). Males achieve maximum length of seminal vesicles two weeks to one month after testis size declines (Wolff and Lidicker, 1980). Persistence of enlarged seminal vesicles, which may indicate sustained testosterone production, may be important to social integration of midden groups during winter (Wolff and Lidicker, 1980).

Males are territorial. The mating system is polygynous (Wolff, 1980, 1985) and, according to Wolff (1985), may qualify as resource-defense polygyny (Emlen and Oring, 1977). Litter size ranges from 6 to 13 ( $n = 85$  females—Lensink, 1954; Wolff and Lidicker, 1981; Youngman, 1975) and averages from 8 ( $n = 11$  females—Youngman, 1975) to 8.8 ( $n = 71$ —Wolff and Lidicker, 1981). Each year, the first litter is slightly smaller than the second litter (Wolff and Lidicker, 1980).

**ECOLOGY.** In general, taiga voles inhabit wet, highly productive, early successional stage forests (Swanson, 1996; Wolff, 1980). *M. xanthognathus* prefers recently burned, upland, black spruce (*Picea mariana*) forest in interior Alaska (West, 1979). Though they can occur in a wide variety of habitats, in the Northwest Territories they persisted over a 3-year period only in dense, black spruce forest (Douglass, 1977). Riparian forest edges and burned forest are ideal habitat in Alaska (Wolff and Lidicker, 1980). Availability of an abundant supply of rhizomes for winter food and good burrowing conditions, such as those found in heavy moss ground cover, are major requirements of taiga voles (Wolff and Lidicker, 1980).

In the Northwest Territories, Canada (65°54'N, 127°59'W), dried plant cuttings in runways included 89% *Carex*, 5% *Rumex arcticus*, 3% *Calamagrostis canadensis*, 2% *Vaccinium vitis-idaea*, and 1% *Equisetum* (Douglass and Douglass, 1977). Horsetail (*Equisetum*) and lichens have been found in stomachs of several taiga voles examined from central Alaska (Lensink, 1954). Cached rhizomes of *Equisetum* and *Epilobium* make up 90% of food during winter. The remainder of winter diet is from foraging below snow. Feeding trials and analysis of stomach contents (Wolff and Lidicker, 1980) suggested that grasses, horsetails, and berries are preferred summer foods.

Population dynamics of taiga voles have not been well studied. Irruptions may occur every 20 years (Youngman, 1975), and population size is highly variable (Rand, 1945, 1948). Annual fluctuations (100/ha maximum, 55/ha minimum, >2 years of data) may occur, but evidence is insufficient to support cyclic changes (Wolff and Lidicker, 1980). Both seasonal and multi-annual fluctuations suggest a "Chitty effect" (Chitty, 1952) when male voles >90 g are caught only at the highest population densities (Douglass, 1977). Taiga voles may maintain large populations (Lensink, 1954). This species is "very abundant most seasons in the far north, as well as along the arctic coast of Canada" (MacFarlane, 1905:735).

Dispersal is a conspicuous part of the life cycle (Lidicker and Patton, 1987). Maximum recorded dispersal distance is 800 m ( $n = 11$ —Wolff and Lidicker, 1980) and root-mean-square dispersal distance is 152 m (Lidicker and Patton, 1987).

*Microtus xanthognathus* is sympatric with masked shrews (*Sorex cinereus*), ermine (*Mustela erminea*), pine squirrels (*Tamiasciurus hudsonicus*), meadow jumping mice (*Zapus hudsonius*), red-backed voles (*Clethrionomys rutilus*), meadow voles (*Microtus pennsylvanicus*), heather voles (*Phenacomys intermedius*), and northern bog lemmings (*Synaptomys borealis*) in the Northwest Territories, Canada (Douglass, 1977). In the northwest corner of Denali National Park and Preserve in Alaska, *M. xanthognathus* coexists with red-backed voles (*Clethrionomys rutilus dawsoni*), brown lemmings (*Lemmus trimucronatus*), and "two species of *Microtus*" (Lensink, 1954:259)—probably *M. miurus*, *M. oeconomus*, and/or *M. pennsylvanicus*. *M. xanthognathus* was sympatric with *Sorex hoyi*, *Mustela erminea*, *T. hudsonicus*, *M. oeconomus*, *M. pennsylvanicus*, *C. rutilus*, and *Lepus americanus* in central Alaska (Wolff and Lidicker, 1980).

The only endoparasite reported for *M. xanthognathus* is the cestode *Taenia martis americana* (Rausch, 1977). Ectoparasites from taiga voles from Yukon Territory, include the botfly (*Cutebra cf. grisea*) and fleas *Amalaraeus dissimilis dissimilis* (as *Amalaraeus penicilliger cf. dissimilis*), *Amphipsylla sibirica pollionis*, *Megabothris calcarifer*, and *Megabothris groenlandicus* (Holland, 1985; Youngman, 1975). Ectoparasites from taiga voles from Alaska include the fleas *Ctenophthalmus pseudagyrtes* and *Megabothris groenlandicus* from 15 to 17 km west northwest of Galena; *Ama-*

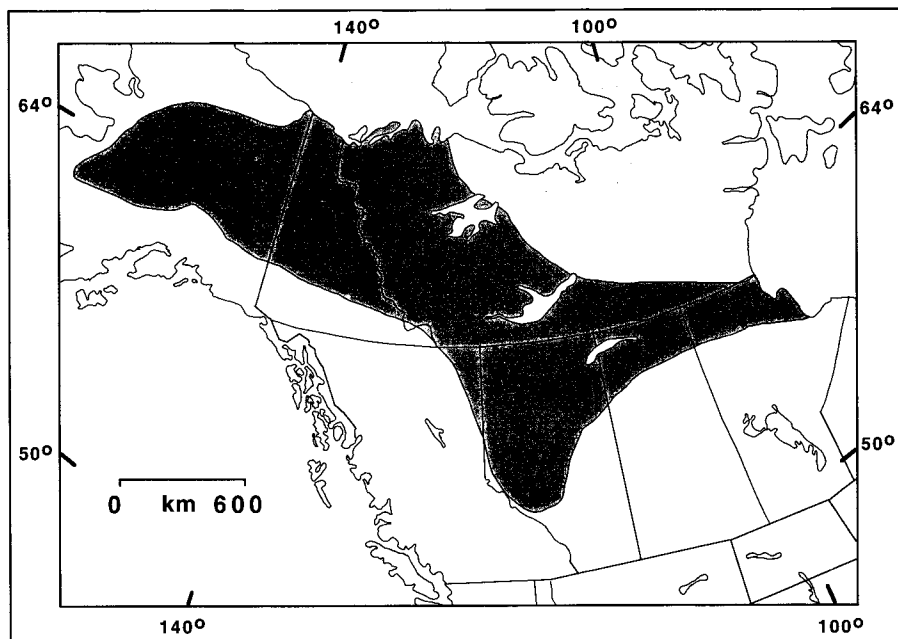


FIG. 3. Distribution of *Microtus xanthognathus* (modified from Hall, 1981).

*laraeus dissimilis* and *Catallagia dacenkoi* from 48 km north of Livengood, Alaska (Haas et al., 1989); and the louse *Hoplopleura acanthopus* from 150 km northwest of Fairbanks, Alaska (Wolff and Lidicker, 1980).

*Microtus xanthognathus* was found in the crop of a great gray owl (*Strix nebulosa*) and in the scat of marten (*Martes americana*)—Douglass et al., 1983; Lensink, 1954). Potential predators of taiga voles in Alaska include raptors—red-tailed hawk (*Buteo jamaicensis*), rough-legged hawk (*Buteo lagopus*), great gray owl (*Strix nebulosa*), northern hawk owl (*Surnia ulula*) and mammals—wolf (*Canis lupus*), red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), marten (*Martes americana*), ermine (*Mustela erminea*), least weasel (*Mustela rixosa*), and black bear (*Ursus americanus*)—Wolff and Lidicker, 1980).

**BEHAVIOR.** Communal winter nesting occurs in groups of five to ten individuals that are of mixed sex and age but that do not appear to be family groups (Wolff, 1980, 1984; Wolff and Lidicker, 1981). Nests have multiple entrances. Food caches have one entrance and are located near the nest. Food is gathered and stored from mid-August to mid-September. Both nests and caches are ca. 30 cm below ground, often under vegetative debris. Summer nests average 15 cm in diameter, are cup-shaped or round with an inner chamber, and are constructed of dried grass (*Calamagrostis*)—Wolff and Lidicker, 1980).

During the mating season, males are aggressive and territorial, and females are territorial around their nests (Wolff and Lidicker, 1980). Eleven aspects of copulatory behavior have been measured in *M. xanthognathus*: mount frequency, mount latency, intromission frequency, intromission latency, mean inter-intromission interval, thrust frequency, thrusts per intromission, ejaculatory thrusts, ejaculation frequency, ejaculation latency, and post ejaculatory interval (Dewsbury and Hartung, 1982). In *M. xanthognathus*, like *M. californicus*, *M. pennsylvanicus*, *M. pinetorum*, and *M. oeconomus*, multiple intromissions need not always precede ejaculation (Dewsbury and Hartung, 1982).

Taiga voles build and maintain extensive runways that are partially below ground and are located near water (Douglass and Douglass, 1977; Wolff, 1985; Wolff and Lidicker, 1980). Taiga voles will swim in lakes (Lensink, 1954; Youngman, 1975).

Taiga voles exhibit a diverse vocal repertoire (Wolff and Lidicker, 1980). Males and females of all age groups use a high pitched, possible alarm call (Wolff, 1980) during the mating season and in the autumn near nesting areas.

Scent marking may be important in recognizing individuals, indicating reproductive condition, or marking territorial boundaries (Wolff and Johnson, 1979). Scratching with hind feet stimulates flow

of sebum. Males perform scent marking more often than females and also scent-mark by dragging the anal gland.

**GENETICS.** The karyotype of *M. xanthognathus* has a diploid number of 54 and a fundamental number of 62 (Rausch and Rausch, 1974). The X chromosome is metacentric. The Y chromosome is near acrocentric. Most chromosomes have terminal to subterminal centromeres (pairs 2 through 24), and thus are subtelocentric or acrocentric. The primary structure of the hemoglobin  $\beta$ -chain of *M. xanthognathus* is known (Duffy and Genaux, 1977). Stratton et al. (1977) included *M. xanthognathus* in a comparative study of microtine hemoglobins. The mitochondrial cytochrome b gene for taiga voles (1,143 base pairs long—Conroy and Cook, in press) is slightly longer than that of most other mammals (Irwin et al., 1991), but base composition is similar and consists of 30.4% adenines, 29.7% cytosines, 13.7% guanines, and 26.3% thymines. Mean heterozygosity in *M. xanthognathus* is 0.06 ( $n = 20$ , 36 loci—Lidicker and Patton, 1987).

**REMARKS.** *Microtus xanthognathus* is named for its supposedly yellow cheek: *xantho-* (Greek for yellow) and *-gnathus* (Greek for jaw). This description is inaccurate because the conspicuous coloration is on the whisker area, not the jaw, and is not yellow. Vernacular names include yellow-cheeked vole, yellow-nosed vole, taiga vole, yellow-snouted vole, chestnut-cheeked vole, and fulvous-cheeked campagnol. Wolff and Lidicker (1980) suggested "taiga vole" was the most appropriate as it is a useful habitat indicator.

*M. xanthognathus* was placed in the subgenus *Microtus* by Miller (1896) and Bailey (1900), but Bailey noted that it showed "no close relationship to any other American species" (Bailey, 1900:57). *M. xanthognathus* may have affinities with the subgenus *Aulacomys*, which includes the *richardsoni* species group (Zagorodnyuk, 1990). Based on their shared taiga ecology, *M. chrotorhinus*, *M. richardsoni*, and *M. xanthognathus* may be part of a "lineage that has been evolving in North America since at least mid-Pleistocene, and perhaps earlier" (Hoffmann and Koepl, 1985:108). However, phallic morphology (Lidicker and Yang, 1986) and DNA sequences (Conroy and Cook, in press) suggest a sister relationship with *M. miurus*.

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