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**Microtus longicaudus.** By Michael J. Smolen and Barry L. Keller

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*Microtus longicaudus* (Merriam, 1888)

Long-tailed Vole


**CONTENT AND CONTEXT.** Order Rodentia, Family Muridae, Subfamily Arvicolinae (Carlton and Musser, 1984), Genus *Microtus*, Subgenus *Microtus*. The subgenus contains 12 extant species in the Nearctic (Hall and Cockrum, 1953). The species *Microtus longicaudus* contains 14 subspecies (Hall, 1981) as follows:

M. l. abditus Howell, 1923:36. Type locality Walker's Ranch, Pleasant Valley, 8 mi S Tillamook, Tillamook Co., Oregon.

M. l. alticola (Merriam), 1890:67, see above.

M. l. alticola Bailey, 1898:86, see above.

M. l. baileyi Goldman, 1938:492. Type locality Greenland Spring, head of Bright Angel Creek, 8,000 ft., Grand Canyon National Park, Coconino Co., Arizona.

M. l. bernardus Merriam, 1908:145. Type locality Dry Lake, 9,000 ft., at base of San Gorgonio Peak, San Bernardino Mountains, San Bernardino Co., California.


M. l. latus Hall, 1931:12. Type locality Wisconsin Creek, 8,500 ft., Toyaba Mountains, Nye Co., Nevada.

M. l. leucophaeus (Allen), 1894:320, see above.

M. l. littoralis Swarth, 1933:209. Type locality Shaken, Prince of Wales Island, Alaska. Hall (1981) noted a discrepancy in this type locality, namely that Shaken is located on Kusilku Island, and proposed that the locality should be Prince of Wales Island, opposite Shaken.

M. l. longicaudus (Merriam), 1888:934, see above (*mordax* Merriam a synonym).

M. l. macrurus Merriam, 1898:353, see above.

M. l. sierrae Kellogg, 1922:288. Type locality Tushumne Meadows, Yosemite National Park, 8,600 ft., Tuolumne Co., California.

M. l. vellerosus Allen, 1899:7, see above (*caustus* Allen a synonym).

**DIAGNOSIS.** The subgenus *Microtus* differs from *Herpetomys* and *Orchiniomys* in that the m3 of *Microtus* has three transverse loops and no closed triangles instead of two transverse loops and two median triangles. The three closed triangles of the m3 and eight mammae of *Microtus* separate it from the subgenera *Pitymys* and *Pedomyx* that have m3 with two closed triangles and four or six mammae (Bailey, 1900; Hall and Cockrum, 1953).

The long tail, incisive foramina, and nasals of *M. longicaudus* are useful in distinguishing them from other species in the subgenus. The relatively long tail in relation to head and body length and hindfoot length separates *M. longicaudus* from most other species of *Microtus*. The head and body length of *M. longicaudus* is from 1.6 to 1.9 times as long as the tail, and the tail is from 2.8 to 3.5 times the length of the hindfoot. Only *M. californicus* (2.0–2.5 times tail length; 2.3–2.6 times length of hindfoot), *M. pensylvanicus* (2.0–3.1 × tail length; 1.9–2.7 × length of hindfoot), and *M. townsendii* (2.2–2.4 × tail length; 2.2–2.6 times length of hindfoot) have head and body to tail or tail to hindfoot proportions that approximate those of *M. longicaudus* (Hall and Cockrum, 1953). The four closed triangles in M2 of *M. longicaudus* distinguishes it from *M. pensylvanicus* that has an M2 with five closed triangles. Incisors are hidden by nasals when viewed from above in *M. longicaudus* rather than being visible as in *M. townsendii*. Furthermore, the incisive foramina are tapered gradually or at least as wide posteriorly as anteriorly in *M. longicaudus* whereas the foramina are long, narrow, and constricted posteriorly in *M. townsendii*. *Microtus californicus* is more difficult to separate if tail-length proportions are not definitive (Maser and Storm, 1970).

**GENERAL CHARACTERS.** *Microtus longicaudus* is a small, thick-bodied vole characterized by a long, bicolor tail that is greater than one-third the total length of the animal (Fig. 1). Pelage color ranges from dull grayish through brownish gray to dark sepia brown. Numerous black tipped hairs occur on the dorsal and lateral portions of the animal. The sides are more grayish and the ventral surface varies from grayish-white to a dull buff (Hall and Cockrum, 1953). Ears are large and haired, and eyes are large. There are four inguinal and four pectoral mammae. The skull is long and flattened (Fig. 2). The braincase is wide and buccal areas are large and round. The rostrum is long (Bailey, 1900; Hall and Cockrum, 1953; Maser and Storm, 1970).

The dental formula is 1/1, c/0/0, p/0/0, m 3/3, total 16 (Fig. 3). The m1 has a distinct anterior cusp with two shallow reentrant angles and one confluent pool of dentine, and is followed by five triangles each with their own isolated dentine pool (terminology that of van der Meulen, 1978). The posterior lobe is crescent-shaped and directly adjoins m2. The m2 consists of four separated

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**Fig. 1.** *Microtus longicaudus abditus* collected from Miami River, Tillamook Co., Oregon. Photograph provided by Murray L. Johnson.
triangles and a posterior lobe. The m3 consists of three crescent-shaped triangles. The M1 has an anterior spherical triangle, and is followed by four closed triangles. The M2 resembles M1 but lacks a triangle. The M3 has a spherical triangle that is followed by two closed triangles. The posterior portion of M3 is variable and consists of a triangle and a large posterior crescent that may have confluent pools of dentine.

Means and ranges (in parentheses) of external measurements (in mm), and sample sizes, are recorded for adults for the following subspecies: *M. l. alticola* (Utah; Durrant, 1952) males followed by females, total length, 175 (169 to 179) 4 and 172 (164 to 180) 6; length of hind foot, 20.5 (20 to 21) 4 and 20 (19 to 21) 6; length of ear, 14 (13 to 15) 4 and 14 (13 to 15) 6; *M. l. angusticeps* (California; Kellogg, 1922) males and females combined, total length, 174.3 (162 to 194) 10; length of ear, 61.2 (56 to 74) 10; length of hind foot, 22.0 (21 to 23) 10; *M. l. bernardina* (California; Kellogg, 1922) males and females combined, total length 183.8 (170 to 198) 10; length of tail, 62.6 (53 to 68) 10; length of hind foot, 22.4 (21 to 23) 10; *M. l. incanus* (Utah; Lee and Durrant, 1960) males followed by females, total length, 172.6 (162 to 182) 5 and 170.4 (155 to 186) 12; length of tail, 52.8 (49 to 59) 5 and 53.1 (49 to 58) 12; length of hind foot, 21.4 (21 to 22) 5 and 21.1 (19 to 24) 12; length of ear, 14.0 (13 to 15) 5 and 14.3 (13 to 15) 12; *M. l. latum* (Utah; Hall, 1931) males and females combined, total length, 187 (180 to 197) 10; length of hind foot, 22.4 (21 to 24) 10; *M. l. leucophaeus* (Arizona; Hoffmeister, 1956) males (n = 12) followed by females (n = 8), total length, 171.6, 184.9; length of tail, 52.8, 57.9; length of hind foot, 22.3, 21.9; length of ear, 15.8, 15.8; *M. l. longicaudus* (Nevada; Borelli and Ellis, 1934) males followed by females, total length, 187 (174 to 196) 10 and 185 (171 to 197) 10; length of tail, 64 (57 to 68) 10 and 63 (57 to 70) 10; length of hind foot, 21.2 (20 to 22) 10 and 20.9 (20 to 22) 10; *M. l. maccrurus* (British Columbia; Anderson and Rand, 1944) males only, total length 197.6 (191 to 202) 5; length of tail 77.0 (70 to 81) 5; length of hind foot 22.7 (21.5 to 23.5) 5; *M. l. sierae* (California; Kellogg, 1922) males and females combined, total length, 196.0 (190 to 221) 51; *M. l. sierae* (California; Kellogg, 1922) males and females combined, total length, 175.3 (158 to 190) 6 and 176 (160 to 195) 21; length of tail, 61.3 (52 to 70) 6 and 60.6 (50 to 70) 21; length of hind foot, 20.8 (19 to 21) 6 and 21 (19.5 to 21.5) 21; length of ear, 14 (13 to 15) 6 and 14 (13 to 15) 21.

Means and ranges (in parentheses) of body mass (in g) and sample sizes for *M. l. latum* are as follows: males followed by females, 47.3 (39.0 to 56.8) 10 and 49.4 (46.0 to 58.4) 6; and for *M. l. longicaudus*, 46.5 (36.9 to 56.9) 10 and 46.9 (42.0 to 51.2) 10 from Nevada (Hall, 1946).

Means and ranges of cranial measurements (in mm) for 10 male and 10 female (respectively) *M. l. longicaudus* from Nevada (Hall, 1946) are: condylobasal length, 26.8 (25.6 to 27.7), 26.8 (25.6 to 28.4); occipital-nasal length, 26.9 (26.3 to 27.7), 27.0 (26.2 to 28.6); nasal length, 7.8 (7.4 to 8.1), 7.8 (7.1 to 8.1); zygomatic breadth, 15.3 (14.5 to 16.0), 15.2 (14.0 to 16.0); interorbital breadth 3.7 (3.5 to 3.9), 3.6 (3.5 to 3.8); mastoid breadth, 12.3 (11.8 to 12.7), 12.2 (11.5 to 13.2); alveolar length, 6.5 (6.2 to 6.9), 6.6 (6.2 to 6.9); rostrum width, 5.3 (5.0 to 5.5), 5.1 (4.7 to
5.3); palatal length, 13.2 (12.0 to 13.8), 13.3 (12.5 to 13.9); width of auditory bullae, 6.0 (5.7 to 6.3), 6.2 (5.5 to 6.5). Cranial measurements for the other subspecies are contained in the following: M. longicaudus (Kellogg, 1922), M. l. angusticeps (Kellogg, 1922), M. l. leucophaeus (Hoffmeister, 1956), and M. l. sierrae (Kellogg, 1922). There is no significant size dimorphism between the sexes, although males average slightly larger than females in length of hind foot and eight cranial measurements (Hall, 1946; Turner, 1974).

**DISTRIBUTION.** Microtus longicaudus occurs throughout most of western United States and Canada to eastern Alaska (Fig. 4). The eastern and southern boundaries usually consist of populations in coniferous forests restricted to high elevations of isolated mountains. The eastward extension into the Great Plains occurred in the Pleistocene (Hoffmann and Jones, 1970; Turner, 1974), and subsequent warming and floral changes associated with increased aridity stranded populations in the Big Belt, Crazy, Little Belt, Big Snowy, Laramie, and Big Horn mountains (Hoffmann and Jones, 1970) and Black Hills (Hoffmann and Jones, 1970; Turner, 1974). Similar isolations are believed to account for M. l. incaus (Lee and Durrant, 1960) being restricted to the Henry Mountains in Utah, and are suspected to account for the mountain top populations occurring in the San Bernardino Mountains in California (Kellogg, 1922), and in the Sacramento, Mimbres, and Graham mountains in New Mexico and Arizona (Fendley and Jones, 1962).

**FOSSIL RECORD.** Fossil remains of M. longicaudus, M. montanus, and M. pensylvanicus are difficult to identify because of the similarity in their dental and cranial morphologies. Current records of long-tailed voles range from late Wisconsin to Recent, and their identifications usually are based on "geographic probability" and "faunal assemblages" (Gibb et al., 1977). These sites are: Idaho, Moonshiner Cave, Bingham Co. (White et al., 1984); Wyoming, Agate Basin Site, Niobrara Co. (Walker, 1982), Little Box Elder Cave, Converse Co. (Anderson, 1968); Colorado, Chimney Rock Animal Trap, Larimer Co. (Hager, 1972); New Mexico, Burnet Cave, Eddy Co. (Schultz and Howard, 1935), Dry Cave, Eddy Co. (Harris, 1970).

**FORM.** The structure of the baculum is similar to that of M. pensylvanicus (Burt, 1960; Hooper and Hart, 1962), but differs in shaft proportions (Anderson, 1960). The proximal bone of the baculum is broad and straight. The shaft is broad and angular, and, when viewed from the end, is dumbbell-shaped with the greater concavity on the dorsal portion. The shaft tapers to a blunt point and has a cartilaginous connection with the three lateral segments that curve lateral and dorsal from the junction. The dorsal lobe of the glans penis is elevated slightly above the ventral rim of the crat and is nonpapillate. The remaining portions of the rim bear between five and eight spine-tipped fingers per side. The urethral process consists of two unmistakable lobs that are curved laterally (Hooper and Hart, 1962). An os clitoridis, when present, is situated anterodorsal to the urethra and well within the connective tissue of the clitoris (Ziegler, 1961). The structure is rod-shaped with each end slightly expanded and with only the distal half ossified.

**Dental abnormalities are known. Jones (1978) reported distinct lateral grooves on the incisors of a female vole from the Yukon. Flattened incisors appeared in 10 voles, and various degrees of malocclusion of both incisors and molars were described in 11 other voles in Oregon (Maser and Hooven, 1970). Harris and Fisher (1962) found an extra tooth in the right lower tooth row of a vole from New Mexico.**

Although many mammalogists list the presence of hip glands as a characteristic of the subgenus Microtus (Bailey, 1900; Hall and Cockrum, 1953), M. longicaudus usually does not possess such glands (Quay, 1968). The development of hip glands can be induced with testosterone injections (Jannett, 1975).

Long-tailed voles have a mean of 4.5 and a mode of three melibonian glands in each eyeld (Quay, 1954).

**FUNCTION.** Mean diameter of erythrocytes is 6.3 μm (range = 5.1 to 7.0, n = 11). Hemoglobin concentration (g/100 ml), hematocrit ratio, and mean corpuscular hemoglobin concentration.

M. longicaudus from 2,895 m is as follows: adult males, (n = 7) 16.2, 49.4, 32.9; pregnant females, (n = 4) 15.8, 49.4, 32.0 (Sealander, 1964).**


With the animal in nesting material, the thermoneural zone was from 20° to 30°C, and the metabolic rate was 2.62 cc O₂ g⁻¹ h⁻¹. The thermoneural zone extended from 25° to 30°C in animals outside of their nest, and mean body temperatures were 37.1°C at 5°C ambient air temperature, 37.5°C at 15°C, and 37.7°C at 25°C. Ambient temperatures above 32°C were lethal (Beck and Anthony, 1971).

**ONTOGENY AND REPRODUCTION.** The breeding season extends from May through October for populations in Nevada with most reproductive activity observed in June and July (Hall, 1946). Populations in Alaska have a breeding season from mid-May to mid-September (Van Horne, 1982), similar to that reported for Idaho (Davis, 1939).

Information concerning gestation, development, growth, and age at sexual maturity is lacking for long-tailed voles. The largest crown-rump measurement of an embryo was 24 mm (Hog, 1940).

Mean litter sizes followed by the ranges (in parentheses) and sample sizes are: Arizona, 4.9 (4 to 6) 10 (Hoffmeister, 1956); Nevada, 5.6 (2 to 8) 39 (Hall, 1946); Wyoming, 6.0 (5 to 7) 3.
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(Clark, 1973); Black Hills, South Dakota and Wyoming, 4.7 (4 to 6) 15 (Turner, 1974); Alaska, 5.0 (no data) 26 (Van Horne, 1982); and a laboratory colony of Colorado stock, 5.3 (1 to 7) 6 (Colvin and Colvin, 1970).

Females produce a maximum of two litters in their life, and no voles were observed to survive to their second reproductive season in Alaska (Van Horne, 1982). Long-tailed voles seldom live longer than 1 year (Jenkins, 1948). Females lived longer than males; 13.5 months is the maximum observed age of two females (Van Horne, 1982).

ECOLOGY. Populations of *M. longicaudus* occur in a wide variety of habitats throughout their range, varying from spruce-fir (*Picea sp.*-Abies sp.) forests (Findley and Jones, 1962; Findley and Negus, 1953; Findley et al., 1975), thickets (Armstrong, 1977; Borell and Ellis, 1984; Findley and Negus, 1953; Randall, 1978; Rickard, 1960), forest-meadow ecotones (Findley and Jones, 1962; Findley et al., 1975), riparian zones (Armstrong, 1977; Borell and Ellis, 1984; Hoffmeister, 1956; Long, 1940; Turner, 1974) and grassy or sagebrush areas (Borell and Ellis, 1984; Brown, 1967; Hoffmeister, 1956; Lindsdale, 1938; Randall, 1978; Stinson, 1981). Long-tailed voles are not found in old-growth forests in Montana, but are common in areas that were recently cut or burned (Halvorson, 1982).


The shrubs snowberry (*Symphoricarpos albus*), pearleaf wood's rose (*Rosa woodsi var. ultramontana*), Spalding's rose (*R. nakanasii* and chokeberry (*Prunus virginiana*), the grasses Idaho fescue (*Festuca idahoensis*), and bluebunch wheat grass (*Agropyron spicatum*), and the forbs one-flowered little sunflower (*Helianthella douglasi*), arrow-leaved balsamroot (*Balsamorhiza sagittata*), western hawkweed (*Hieracium albertianum*), and silky lupine (*Lupinus sericatus*) occur in habitats occupied by *M. longicaudus* in Washington (Beck and Anthony, 1971; Randall, 1978; Randall and Johnson, 1979) and Idaho (Rickard, 1960). Populations on the Malheur National Wildlife Refuge in Oregon are confined to marshes containing hardstem bullrush (*Scirpus acutus*), cattail (*Typha latifolia*), Baltic rush (*Juncus balticus*), and sedges (*Carex sp.*; Feldhamer, 1979). In Wyoming, long-tailed voles are found in wetter and structurally more complex areas (Clark, 1973), and are common to willow-alder (*Salix sp.-Alnus tenuifolia*), aspen (*Populus tremuloides*, with *Pop* sp. and *Agropyron spicatum* understory); and sedges (*Carex sp.*, *Spartina sp.*, *Triphorum sp.*, *Phlox sp.* and *Aguelegia sp.*; Brown, 1967). Grassland slopes in the lower montane zone in Colorado with ground cover consisting of shrubby cinquefoil (*Pentaphylloides flavulaeforme*),.wax currant (*Ribes cereum*), prairie sage (*Artemisia ludoviciana*), cheat grass (*Bromus tectorum*), blue gramna (*Bouteloua gracilis*), and Kentucky bluegrass (*Poa pratensis*) support vole populations (Stinson, 1978). Armstrong (1977) described *M. longicaudus* habitats as containing 31% willows, 20% logs, 17% spruce, 17% aspen (*Populus sp.*), and an understory containing 77% forbs and 11% graminoids.

Habitats of long-tailed voles in New Mexico range from montane forests consisting of alders (*Alnus sp.*), cottonwoods (*Populus sp.*), willows from 2,468 m to 2,895 m (Hall, 1942) and spruce and fir forest (Findley and Jones, 1962). They also were found on grass and scrub hillsides (Findley and Jones, 1962), vegetated by Kentucky bluegrass, yarrow (*Achillea lusitanica*), vetch (*Vicia americana*), and bedstraw (*Galium aparine*; Conley, 1976). *M. longicaudus* usually is restricted to scrubbly and grassy meadows and flats above 2,438 m in Arizona (Hoffmeister, 1956). The relationship of long-tailed voles to water is not known precisely. The presence of standing water is not considered essential (Borell and Ellis, 1934) and individuals have been taken as far as 0.81 km from water in Nevada (Hall, 1946), whereas in New Mexico long-tailed voles required water for daily sustenance (Findley et al., 1975).

Diet of both sexes are nearly identical, and *M. longicaudus* consume a variety of seeds, berries, and other food sources. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Erechtites, Fallopia, Melanthera, Polygonum, and Stachys were identified. Gut contents of 50 voles (Van Horne, 1982) showed a wide variety of seeds, and includes Carya, Ilex, Picea, Populus, and Salix. In addition, Carpesium, Chaenactis, Ereh
species of Microtus (D. V. Colvin, 1973; Randall, 1978). When M. longicaudus is found with M. montanus, the more aggressive M. montanus (Randall, 1978) seems to displace long-tailed voles as their density increases (Randall and Johnson, 1979). Intraspecific aggression increases with the density of M. longicaudus (Cenley, 1976).

Neonates produce ultrasonic sounds when disturbed or subjected to stressful conditions, and these calls attract the attention of the parents (M. A. Colvin, 1973).

GENETICS. Karyotypic variation has been observed for M. longicaudus. Individuals from Washington (Matthey, 1955), northern Oregon (Hu and Benirschke, 1969), Arizona, Colorado, and New Mexico (Judd and Cross, 1980) have a diploid number of 56, of which 30 autosomes are metacentric or submetacentric and 24 are subtelocentric or acrocentric. The large number of chromosomes for the subspecies is believed to be the result of fusions and pericentric inversions (Matthey, 1957, 1973). The X chromosome is a large submetacentric and the Y chromosome is a small acrocentric. Six other cytotypes have been reported from southern Oregon and northern California (2n = 57, 58, 59, 62, 66, and 70), and involve additions of supernumerary X-chromosomes, and pericentric inversions (Judd and Cross, 1980).

An albino female was described from New Mexico (Fries et al., 1982).

REMARKS. The name Microtus is Greek mikros meaning small and otus meaning ear; longicaudus is from the Latin longus meaning long and cauda meaning tail. The authors wish to thank M. L. Johnson for supplying the photograph appearing in this account.

LITERATURE CITED


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