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Arborimus longicaudus.

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Arborimus longicaudus True, 1890

Red Tree Vole

Phenacomys longicaudus True, 1890:303. Type locality "Marshfield, Coos Co., Oregon."

Phenacomys silvicolus A. B. Howell, 1921:98. Type locality "5 miles southeast of Tillamook, Tillamook Co., Oregon."

Phenacomys silvicola Miller, 1923:400. A renaming of *Phenacomys silvicolus* Howell.

Arborimus longicaudus Johnson, 1968:27. Elevation of the subgenus *Arborimus* to generic rank.

CONTEXT AND CONTENT. Order Rodentia, Suborder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Arvicolinae, (Musser and Carleton, 1993). Musser and Carleton (1993) recognized three extant species in the genus *Arborimus*, and Johnson and George (1991) recognized two subspecies of *A. longicaudus*.

A. l. longicaudus True, 1890:303, see above.

A. l. silvicola A. B. Howell, 1921:98, see above.

DIAGNOSIS. *Arborimus longicaudus* can be distinguished from all other sympatric arvicoline rodents by the combination of a reddish dorsum lacking a median stripe, a venter washed with reddish-orange hairs, and a well-haired tail that is not distinctly bicolored and is >50 mm long and >50% of length of head and body (Maser and Storm, 1970; Verts and Carraway, 1984). Skulls of the genus *Arborimus* can be separated from those of other arvicoline genera in the range of *A. longicaudus* by reentrant angles of the lower molars extending about two-thirds the way toward the labial side on the lingual side and about one-third the way toward the lingual side on the labial side. The skull of *A. longicaudus* can be distinguished from *A. albipes* by the combination of a pronounced longitudinal depression between the orbits that is bordered by a strong ridge, strongly recurved incisors, and wide incisive foramina (Maser and Storm, 1970). In contrast to *A. pomo*, *A. longicaudus* is generally larger overall, has nasals that extend further posteriorly relative to the maxillaries, lacks the abductor digiti secundi muscle and a full complement of lumbricales muscles, and differs in chromosome number and morphology (Johnson and George, 1991).

GENERAL CHARACTERS. *Arborimus longicaudus* is a small (mass 25 to 50 g) microtine rodent (Fig. 1.) The dorsal pelage is uniformly cinnamon (Hall, 1981) or bright rusty brown (True, 1890) with many hairs tipped in black in *A. l. longicaudus*, but a light (sayal) brown sparsely tipped with black in *A. l. silvicola* (Hall, 1981; Howell, 1921; True, 1890); the underparts are whitish in both subspecies (Hall, 1981). The tail is long and well-haired, varying from black to brown and not distinctly bicolored (Maser and Storm, 1970). Juveniles are duller, with less red and more brown in dorsal coloration and black tails (Maser and Storm, 1970). Melanistic forms of *A. l. silvicola* can occur.

There are six plantar tubercles on the hind foot and five on the forefoot (Hooper and Hart, 1962; Taylor, 1915). The claw on the first digit of the front foot is modified into a nail (Kesner, 1986). There are four inguinal mammary glands (Howell, 1926; Johnson, 1973; Taylor, 1915). The ears are 10–12 mm long in adults, with scant fine hair (Johnson, 1973).

The skull of *A. longicaudus* is heavy and moderately angular. The nasal bones extend beyond the incisors (Maser and Storm, 1970; Fig. 2.). The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16. The molariform teeth are rootless in juveniles and become rooted as the animal matures (Hooper and Hart, 1962; Howell, 1926). Rooted molars generally are considered to be an ancestral character for the subfamily (Carleton, 1985). Roots of the lower incisors extend slightly posterior and labial to M_3 (Hooper and Hart, 1962). The incisors are sharply recurved (Maser and Storm, 1970).

The cervical vertebrae are short and close together; the transverse processes of the lumbar vertebrae are large and flaring. The hyoid bone has short lateral processes and no spine or a reduced one. The acromion process of the scapula is narrow (Johnson, 1973).

On average, females are larger than males in most external and cranial measurements. Cranial or external measurements do not differ distinctly between subspecies (Johnson and George, 1991). Johnson (1973) gives ranges for diastema (6.1 to 7.5 mm; $n = 35$), minimum or maximum values for seven measurements, and qualitative descriptions of 22 morphological characteristics. Minimum and maximum mean values (mm) of 14 cranial measurements for 79 females grouped into seven geographic samples and 50 males grouped into four geographic samples (Johnson and George, 1991) are as follows (values for males listed first): greatest length of skull, 24.42 and 25.38, 24.81 and 26.08; zygomatic breadth, 13.80 and 14.50, 14.11 and 14.72; least interorbital width, 3.37 and 3.48, 3.22 and 3.59; mastoid breadth, 8.43 and 8.69, 8.47 and 8.86; length of nasals, 6.26 and 6.84, 6.50 and 6.85; length of maxillary toothrow, 5.56 and 5.86, 5.50 and 5.90; depth of braincase, 6.93 and 7.16, 7.02 and 7.23; nasal-maxillary distance, 0.44 and 0.56, 0.40 and 0.66; width of interparietal, 8.17 and 8.64, 7.83 and 9.02;

FIG. 1. An adult *Arborimus longicaudus* from Benton County, Oregon. Photograph by Stephen DeStefano.

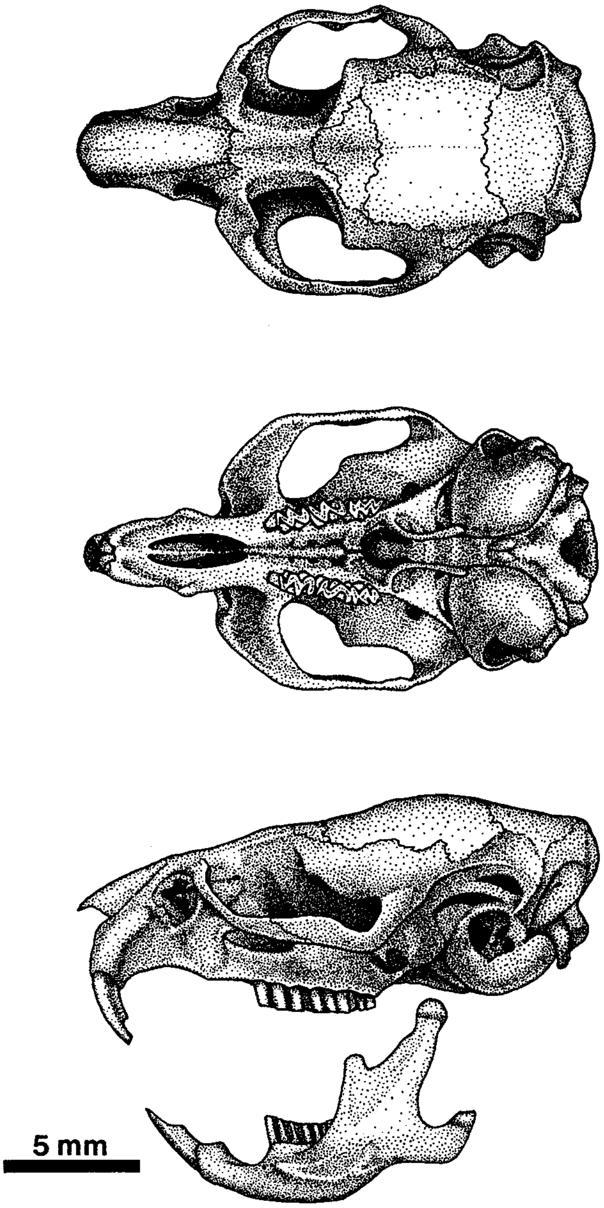

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Arborimus longicaudus* from 7 mi W Alpine, Alsea Falls Park, Benton Co., Oregon (female, Oregon State University, Department of Fisheries and Wildlife, mammal collection no. 3234). Drawing by G. Bracher.

length of interparietal, 3.16 and 3.40, 3.20 and 3.72; M2–M2 width, 5.49 and 5.78, 5.41 and 5.84; length of diastema, 6.84 and 7.14, 6.90 and 7.54; width of upper M2, 1.23 and 1.31, 1.21 and 1.35; and length of palatal foramen, 4.18 and 4.50, 4.24 and 4.69.

Mean external measurements (mm) and extremes (in parentheses) for six adult male and five adult female *A. l. longicaudus* (Hall, 1981) are as follows (values for males listed first): total length, 166 (158–176), 182 (170–187); length of tail, 67 (60–72), 73 (66–83); and length of hind foot, 20 (19–21), 21 (21–22). Measurements for one adult male and one adult female *A. l. silivicola* (Hall, 1981), respectively are total length, 193, 191; length of tail, 87, 81; and length of hind foot, 20, 22.

DISTRIBUTION. *Arborimus longicaudus* is restricted to coniferous forests west of the crest of the Cascade Mountains in Oregon and northern California (Johnson and George, 1991; Maser, 1965*a*; Murray, 1995; Fig. 3). Precise limits and extent of distribution in northern California, southern Oregon, extreme northwestern Oregon, and parts of the Oregon Cascades are uncertain. Johnson and George (1991) regard all California tree vole populations as *A. pomo*. Murray (1995) classifies red tree voles in northern California as *A. longicaudus* on the basis of genetic similarity. Johnson (1973) speculated that the genus *Arborimus* evolved in the Pacific Northwest during the Pliocene, but there are no known fossils of *A. longicaudus*.

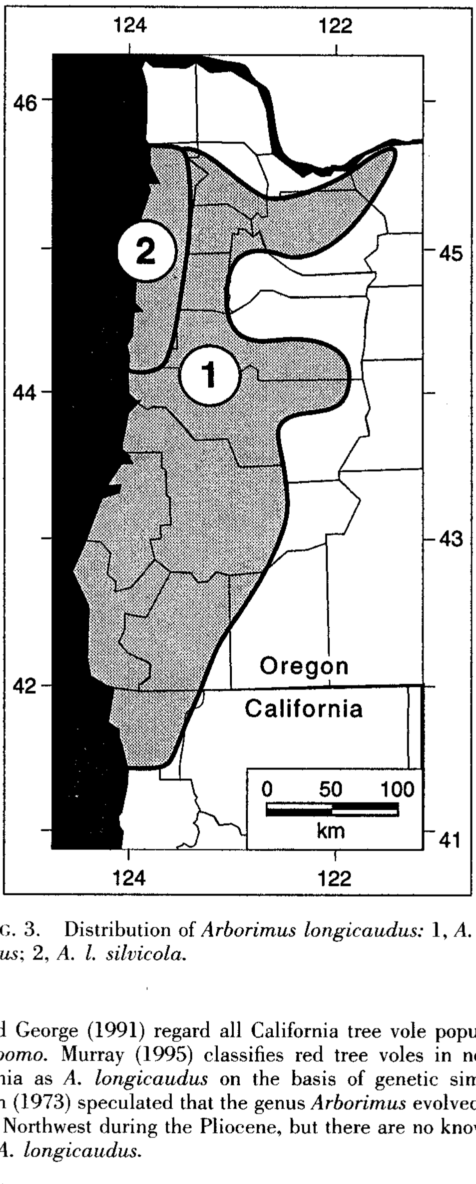

FIG. 3. Distribution of *Arborimus longicaudus:* 1, *A. l. longicaudus*; 2, *A. l. silvicola.*

FORM AND FUNCTION. In red tree voles, the palatal portion of the palatines is long; the basisphenoid is short, wide, and relatively shallow; and the auditory bullae are small and thin-walled (Hooper and Hart, 1962). The anterior longitudinal ridge of the diastemal palate is constricted and depressed in its middle area, with the medial area exposed and the incisive papilla not covered (Quay, 1954*b*).

The abductor pollicis brevis, abductor digiti quinti, and flexor digiti quinti brevis are present in the manus of *A. longicaudus* but absent from the manus of some other microtines. The adductor digiti secundi was absent from specimens referred to as *A. silvicola* (presumably *A. l. silvicola*) but present in specimens referred to as *A. longicaudus* (Kesner, 1986). According to Johnson and George (1991), specimens referred to as *A. longicaudus* by Kesner (1986) are actually *A. pomo,* but no locality information is provided by Kesner (1986). Specimens referred to as *A. longicaudus* were the only microtine specimens examined with a full complement of lumbricales muscles to digits II through V with a slip to II. In specimens referred to as *A. silvicola,* a complete complement of lubricales muscles was not present. Of the microtines examined, the palmaris transversus muscle was unique to the genus *Arborimus.* The palmaris transversus is a thin muscle originating from the radial aspect of the metacarpophalangeal joint of digit V and inserting into the ulnar aspect of the metacarpophalangeal joint capsule of digit II. Kesner (1986) concluded that modification of the palmaris transversus, presence of a nail on digit I, and retention of several muscles lost in other species are adaptations for food handling and for movement on terminal branches of trees; reasons for differences between specimens referred to as *A. longicaudus* and *A. silvicola* were not explained.

In general, the masticatory musculature of *A. longicaudus* is typical of most microtine rodents. The red tree vole differs from the typical microtine plan in having reduced posterodorsal insertion of the superficial masseter and a corresponding lateral process on the angular process of the mandible, and in lacking a distinct medial portion of the posterior belly of the diagastric muscle (Kesner, 1980).

The penis is heavily bowed in lateral view, corresponding to the shape of the baculum. The glans of *A. longicaudus* has extensive spines on the exterior surface. The dorsal lobe of the glans is relatively short with a single spine-tipped process on each side (Hooper and Hart, 1962).

The base of the baculum has a highly irregular proximal edge (Hooper and Hart, 1962) that is triangular (Hamilton, 1946) to semilunar (Dearden, 1958) or rounded (Hooper and Hart, 1962). The shaft is bow-shaped with a spatulate, almost trilobed head (Hooper and Hart, 1962). Three distal digital processes are cartilaginous (Dearden, 1958) or ossified (Hamilton, 1946). The distal digital processes are ankylosed in some individuals (Hamilton, 1946), but not in others (Dearden, 1958). More complete ossification and ankylosis may be more typical of older animals (Hooper and Hart, 1962). The baculum from a single specimen was 3.1 mm in length, with a shaft length of 2.75 mm and a median process 0.35 mm long (Hamilton, 1946).

Arborimus longicaudus possesses sebaceous, sudoriferous, and mucous glands of the oral lips and oral angle (Quay, 1965), but lacks posterolateral sebaceous glands (Quay, 1968). Number of tarsal glands in the eyelids from four individuals ranged from 15 to 19, with an average of 17 (Quay, 1954*a*).

ONTOGENY AND REPRODUCTION. Red tree voles exhibit postpartum estrus and effective postpartum mating in the wild (Brown, 1964). Reproductive biology of *A. longicaudus* is probably similar to that reported for *A. pomo* by Hamilton (1962), but no detailed studies of the species have been conducted.

ECOLOGY. Red tree voles occur in second-growth forests (Brown, 1964; Corn and Bury, 1986; Jewett, 1920; Maser, 1965*a*), but may be more numerous in mature or old-growth stands (Corn and Bury, 1986; Gilbert and Allwine, 1991). Some consider the species to be closely associated with the old-growth seral stage (Huff et al., 1992; Ruggiero et al., 1991).

Red tree voles most frequently are found in forests dominated by Douglas-fir (*Pseudotsuga menziesii*), but also occur in stands of grand fir (*Abies grandis*), Sitka spruce (*Picea sitchensis*), and western hemlock (*Tsuga heterophylla*; Jewett, 1920; Maser, 1965*a*; Walker, 1930). Red tree voles occur at elevations of sea level to 1300 m (Huff et al., 1992).

Nests typically are arboreal and are found in Douglas-fir trees, but they can occur in a variety of species of trees, including grand fir, Sitka spruce, or western hemlock (Gillesberg and Carey, 1991; Jewett, 1920; Maser, 1965*a*; Walker, 1930); one nest was located in a big-leaf maple (*Acer macrophyllum*; Maser, 1965*a*). Nests may be constructed by *A. longicaudus*, but in some areas the majority of nests used by red tree voles are built initially by other species (Maser, 1965*a*).

Red tree vole nests may be constructed on the base of a bird's nest or may have been abandoned by other mammals, including western grey squirrels (*Sciurus griseus*), Douglas squirrels (*Tamiasciurus douglasii*), woodrats (*Neotoma fuscipes*), and deer mice (*Peromyscus maniculatus*; Maser, 1965*a*). Nests built by *Arborimus longicaudus* have been simultaneously occupied by red tree voles and *Peromyscus maniculatus* (Brown, 1964) and by several species of invertebrates (Maser, 1965*a*). A nest built by *Sciurus griseus* was occupied simultaneously by *S. griseus* and *A. longicaudus* (Maser, 1965*a*).

Nests constructed by *A. longicaudus* often are in contact with the tree trunk, but also occur in branches away from the trunk, in cavities, or in dead tops of trees (Gillesberg and Carey, 1991; Maser, 1965*a*; Taylor, 1915; Wight, 1925). Nests are located at any height, are generally near a source of live needles, and are most abundant in the lower canopy. Nests are disproportionately common in large-diameter trees, but are found in trees as small as 10 cm in diameter at breast height. Often several nests are found in a single tree (Gillesberg and Carey, 1991; Maser, 1965*a*).

Nest construction begins with a platform of twigs with needles used for food. The platform is used as a latrine, and feces and urine accumulate on the nest. Over time, additional forage is brought to the nest, and the nest compacts with use. Red tree voles move discarded resin ducts to the sides of the platform, forming a cup-like depression. Additional resin ducts are positioned over the top of the depression, forming an enclosed nest chamber. Feeding takes place both inside and on top of the nest. The nest continues to grow as the inhabitant adds new twigs and deposits feces. Feces are found throughout the nest, except in the sleeping chambers and tunnels. The compacted feces anchor the nest to the tree (Maser, 1965*a*).

Of 117 red tree vole nests, 51% of the volume consisted of resin ducts, 19% of lichen, 13% of feces, and 9% each of needles and fine twigs (Gillesberg and Carey, 1991). Nests are sometimes tipped with freshly cut twigs with green needles (Jewett, 1930). Nests vary in size and may be up to 1 m in diameter (Taylor, 1915). Nest size, height, and form do not consistently differ between males and females. Mean height, width, and length (cm) of six nests occupied by males were 25, 28, and 32, respectively; those of 21 nests occupied by females were 28, 37, and 44. Nests vary in structure, but generally have a tunnel leading from the internal nest chamber to the bottom of the nest, one or two tunnels leading to the top of the nest, and a system of internal tunnels (Maser, 1965*a*).

Male and female *A. longicaudus* tend to occupy separate nests, although occasionally an adult pair will occupy a nest during breeding (Maser, 1965*a*; Walker, 1928). Nests may be used by multiple generations of red tree voles. There is no evidence of utilization of terrestrial nests by *A. longicaudus* (Maser, 1965*a*).

The northern spotted owl (*Strix occidentalis caurina*) is probably the principal predator of red tree voles (Forsman, 1976; Maser, 1965*b*), which comprise nearly 50% of the prey of spotted owls in some locations (Forsman et al., 1984). Other avian predators include great horned owls (*Bubo virginianus*; Maser, 1965*c*), long-eared owls (*Asio otus*; Reynolds, 1970), and northern saw-whet owls (*Aegolius acadicus*; Forsman and Maser, 1970). Raccoons (*Procyon lotor*), martens (*Martes americana*), and fishers (*M. pennanti*) are among the potential mammalian predators in some areas (Maser, 1965*a*; Maser et al., 1981).

Arborimus longicaudus and its sibling species, *A. pomo*, are unique among rodents in specializing on conifer needles for forage. The primary food of red tree voles is needles of Douglas-fir, but needles of other conifers and bark are sometimes consumed (Maser, 1965*a*; Walker, 1930; Wight, 1925). Captive individuals can be maintained exclusively on Douglas-fir needles and water (Brown, 1964). Hamilton (1962) has speculated that conditions in the Pacific Northwest (extensive coniferous forests with wet conditions and moderate temperatures) result in a unique environment that permits exploitation of this feeding niche.

Red tree voles probably obtain water from foliage or from fog or dew that collects on foliage (Maser, 1965*a*). Limited availability of water may restrict their eastern distribution (Hamilton, 1962; Maser, 1965*a*).

Ectoparasitic mites found on red tree voles included *Androlaelaps fahrenholzi*, *A. glasgowi*, *Glycyphagus hypudaei*, *Haemogamsus ambulans*, *H. pontiges*, *Hirstionyssus* sp., *Radfordia arborimus*, and a previously undescribed species of listrophorid mite (Maser, 1965*a*; Whitaker and Maser, 1979). The listrophorid was described as *Quasilistrophorus microticolus* by Fain et al. (1978). *Radfordia arborimus* was first described on the basis of a collection from *A. longicaudus* (Fain and Whitaker, 1975). Ticks found on red tree voles or in their nests include *Ixodes spinipalpis*, *I. angustus*, and larval *Haemaphysalis* sp. A flea (*Megabothris quirini*) was collected from a single individual, several unidentified fleas were collected from red tree vole nests, and an unidentified cestode was taken from an adult female (Maser, 1965*a*).

Logging activities are implicated in declines and extinctions of some red tree vole populations (Corn and Bury, 1986; Huff et al., 1992; Maser et al., 1981). Red tree voles may have limited dispersal capabilities and early seral stage forests may be a barrier to dispersal of *A. longicaudus* (Carey, 1989). *A. longicaudus* may be vulnerable to loss or fragmentation of old-growth Douglas-fir forests (Huff et al., 1992).

Arborimus longicaudus is difficult to capture. The only reliable method of capturing red tree voles is to disturb a nest and hand-capture the animal as it flees (Carey et al., 1991). There is one record of a red tree vole capture in a snap trap in a tree (Wight, 1925). Attempts to catch red tree voles in Sherman live traps or pitfall traps set in trees have been unsuccessful (Gillesberg and Carey, 1991). Pitfall traps in the ground catch red tree voles infrequently (Corn and Bury, 1986, 1988, 1991; Gilbert and Allwine, 1991).

BEHAVIOR. *Arborimus longicaudus* feeds on Douglas-fir needles in a stereotypical fashion. After biting a mature needle from a twig, they split off and discard the sides of the needle, including resin ducts, and eat the remainder, including the medullary portion (Benson and Borell, 1931; Hamilton, 1962; Taylor, 1915). Red tree voles sometimes consume young needles entirely, including the resin ducts (Benson and Borell, 1931; Maser, 1965*a*).

When disturbed, red tree voles run out on a limb, run down the tree head first, or jump to the ground (Jewett, 1920; Maser, 1965*a*). Red tree voles generally are arboreal, but occasionally exhibit terrestrial activity, evidenced by their capture in pitfall traps (Corn and Bury, 1986, 1988, 1991; Gilbert and Allwine, 1991). Much of their activity takes place close to source of live needles (Maser, 1965*a*). Red tree voles apparently are nocturnal (Maser et al., 1981), but no detailed studies of activity patterns, home range size, or home range utilization have been published.

GENETICS. *Arborimus longicaudus* typically exhibits a diploid number (2n) = 52, with 22 pairs of acrocentric or subtelocentric autosomes, three pairs of small submetacentric autosomes, a large submetacentric X, and a small metacentric Y chromosome (Hsu and Benirschke, 1974; Johnson and George, 1991). Of six specimens from Oregon, one from the southernmost locality had a 2n = 48, because of the substitution of two large metacentric pairs for four acrocentric pairs (Johnson and George, 1991).

Electrophoretic mobility of albumin in *A. longicaudus* was faster than that of *Phenacomys intermedius.* In addition, the globulin allele found in *A. longicaudus* had a faster electrophoretic mobility than that of *P. intermedius* (Johnson, 1968).

Murray (1995) analyzed restriction fragment length polymorphisms from amplified portions of mtDNA extracted from 12 *A. pomo*, 9 *A. longicaudus*, 3 *Microtus californicus*, *M. longicaudus*, and *Clethrionomys gapperi*, 2 *C. rutilus*, and 1 *A. albipes* and *Phenacomys intermedius.* Distinct northern and southern clades of tree voles were observed, consistent with the hypothesis that *A. longicaudus* and *A. pomo* are distinct species. Red tree vole specimens from Del Norte County, California clustered with specimens from Oregon, suggesting that the distribution of *A. longicaudus* extends into California. *A. albipes*, *A. longicaudus*, and *A. pomo* clustered together, but *Phenacomys intermedius* clustered with *Microtus*, forming a sister group to *Arborimus.* These data suggest that *Arborimus* is a distinct genus, and should not be considered to be a subgenus of *Phenacomys.*

REMARKS. The taxonomy of *A. longicaudus* remains controversial. At the generic level, some place *Arborimus* in the genus *Phenacomys* (Hall, 1981; Jones et al., 1992; McAllister and Hoffmann, 1988; Verts and Carraway, 1995). Hall (1981) provisionally accorded subgeneric rank to *Arborimus*, but Hooper and Hart (1962) argue that differences among species of *Phenacomys* do not even warrant subgeneric designation of *Arborimus.* Johnson (1968, 1973), Johnson and Maser (1982), and Murray (1995) argued that the subgenus should be elevated to genus. I recognize the generic rank of *Arborimus* primarily on the basis of genetic analyses (Murray, 1995) and supporting morphological data (Johnson, 1973; Johnson and Maser, 1982). Similarities between blood proteins suggest subspecific status of *A. silvicola* (Johnson, 1968), but no distinct morphometric or karyotypic differences between the subspecies have been detected in Oregon (Johnson and George, 1991).

Johnson and George (1991) and Murray (1995) provide compelling morphometric and genetic data indicating that southern tree vole populations constitute a sibling species, *Arborimus pomo.* Precise limits of the ranges of the two species are not known. In several works, the origin of specimens used is unknown; as a result, some cited references may refer to *A. pomo* rather than *A. longicaudus.* Differences in findings among studies, such as differences in baculum morphology reported by Hamilton (1946) and Dearden (1958), may be the result of differences between the species. The extent to which *A. longicaudus* and *A. pomo* differ for several behavioral, ecological, and morphological characteristics is not known. A historical account of early efforts to collect red tree voles is provided by Jobanek (1988).

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LITERATURE CITED

BENSON, S. B., AND A. E. BORELL. 1931. Notes on the life history of the red tree mouse, *Phenacomys longicaudus.* Journal of Mammalogy, 12:226–233.

BROWN, L. N. 1964. Breeding records and notes on *Phenacomys silvicola* in Oregon. Journal of Mammalogy, 45:647–648.

CAREY, A. B. 1989. Wildlife associated with old-growth forests in the Pacific Northwest. Natural Areas Journal, 9:151–162.

CAREY, A. B., B. L. BISWELL, AND J. W. WITT. 1991. Methods for measuring populations of arboreal rodents. United States Department of Agriculture, Forest Service, General Technical Report, PNW-GTR-273, 24 pp.

CARLETON, M. D. 1985. Macroanatomy. Pp. 176–253, *in* Biology of New World *Microtus* (R. H. Tamarin, ed.). Special Publication 8, The American Society of Mammalogists, 893 pp.

CORN, P. S., AND R. B. BURY. 1986. Habitat use and terrestrial activity by red tree voles (*Arborimus longicaudus*) in Oregon. Journal of Mammalogy, 67:404–406.

———. 1988. Distribution of the voles *Arborimus longicaudus* and *Phenacomys intermedius* in the central Oregon Cascades. Journal of Mammalogy, 69:427–429.

———. 1991. Small mammal communities in the Oregon Coast Range. Pp. 241–254, *in* Wildlife and vegetation of unmanaged Douglas-fir forests (L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords.). United States Department of Agriculture, Forest Service, General Technical Report, PNW-285, 523 pp.

DEARDEN, L. C. 1958. The baculum in *Lagurus* and related microtines. Journal of Mammalogy, 39:541–553.

FAIN, A., AND J. O. WHITAKER, JR. 1975. Two new species of Myobiidae from North American mammals (Acarina). Bulletin et Annales Societe Royale Belge d'Entomologie, 111:57–65.

FAIN, A., J. O. WHITAKER, JR., AND F. S. LUKOSCHUS. 1978. *Quasilistrophorus microticolus* gen. n. et sp. n. (Acari: Listrophoridae) from North American microtine rodents. Journal of Parasitology, 64:1097–1099.

FORSMAN, E. D. 1976. A preliminary investigation of the spotted owl in Oregon. M.S. thesis, Oregon State University, Corvallis, 127 pp.

FORSMAN, E., AND C. MASER. 1970. Saw-whet owl preys on red tree mice. Murrelet, 51:10.

FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs, 87:1–64.

GILBERT, F. F., AND R. ALLWINE. 1991. Small mammal communities in the Oregon Cascade Range. Pp. 257–267, *in* Wildlife and vegetation of unmanaged Douglas-fir forests (L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords.). United States Department of Agriculture, Forest Service, General Technical Report, PNW-285, 523 pp.

GILLESBERG, A., AND A. B. CAREY. 1991. Arboreal nests of *Phenacomys longicaudus* in Oregon. Journal of Mammalogy, 72: 784–787.

HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 2:601–1181 + *90.*

HAMILTON, W. J., JR. 1946. A study of the baculum in some North American Microtinae. Journal of Mammalogy, 27:378–387.

HAMILTON, W. J., III. 1962. Reproductive adaptations of the red tree mouse. Journal of Mammalogy, 43:486–504.

HOOPER, E. T., AND B. S. HART. 1962. A synopsis of recent North American microtine rodents. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 120:1–68.

HOWELL, A. B. 1921. Description of a new species of *Phenacomys* from Oregon. Journal of Mammalogy, 2:98–100.

———. 1926. Voles of the genus *Phenacomys.* North American Fauna, 48:1–64.

HSU, T. C., AND K. BENIRSCHKE. 1974. *Phenacomys longicaudus* (tree mouse). Atlas of Mammalian Chromosomes, 8(373):1–3.

HUFF, M. H., R. S. HOLTHAUSEN, AND K. B. AUBRY. 1992. Habitat management for red tree voles in Douglas-fir forests. United States Department of Agriculture, Forest Service, General Technical Report, PNW-GTR-302:1–16.

JEWETT, S. G. 1920. Notes on two species of *Phenacomys* in Oregon. Journal of Mammalogy, 1:165–168.

———. 1930. A nest of *Phenacomys silvicola* in Oregon. Journal of Mammalogy, 11:81–83.

JOBANEK, G. A. 1988. Searching for the tree vole: an episode of the biological survey of Oregon. Oregon Historical Quarterly, 89:369–400.

JOHNSON, M. L. 1968. Application of blood protein electrophoretic studies to problems in mammalian taxonomy. Systematic Zoology, 17:23–30.

———. 1973. Characters of the heather vole, *Phenacomys,* and the red tree vole, *Arborimus.* Journal of Mammalogy, 54:239–244.

JOHNSON, M. L., AND S. B. GEORGE. 1991. Species limits within the *Arborimus longicaudus* species-complex (Mammalia: Rodentia) with a description of a new species from California. Contributions in Science, Natural History Museum of Los Angeles County, 429:1–16.

JOHNSON, M. L., AND C. MASER. 1982. Generic relationships of *Phenacomys albipes.* Northwest Science, 56:17–19.

JONES, J. K., JR., R. S. HOFFMANN, D. W. RICE, C. JONES, R. J. BAKER, AND M. D. ENGSTROM. 1992. Revised checklist of North American mammals north of Mexico, 1991. Occasional Papers, The Museum, Texas Tech University, 146:1–23.

KESNER, M. H. 1980. Functional morphology of the masticatory musculature of the rodent subfamily Microtinae. Journal of Morphology, 165:205–222.

———. 1986. The myology of the manus of microtine rodents. Journal of Zoology, London (A), 210:1–22.

MASER, C. 1965*a*. Life histories and ecology of *Phenacomys albipes, Phenacomys longicaudus, Phenacomys silvicola.* M.S. thesis, Oregon State University, Corvallis, 221 pp.

———. 1965*b*. Spotted owl preys on dusky three (sic) mice. Murrelet, 46:46.

———. 1965*c*. Notes on the contents of owl pellets found in Oregon. Murrelet, 46:44.

MASER, C., AND R. M. STORM. 1970. A key to Microtinae of the Pacific Northwest (Oregon, Washington, Idaho). O.S.U. Book Stores, Inc., Corvallis, Oregon, 162 pp.

MASER, C., B. R. MATE, J. F. FRANKLIN, AND C. T. DYRNESS. 1981. Natural history of Oregon coast mammals. United States Department of Agriculture, Forest Service, General Technical Report, PNW-133, 496 pp.

MCALLISTER, J. A., AND R. S. HOFFMANN. 1988. Phenacomys intermedius. Mammalian Species, 305:1–8.

MILLER, G. S., JR. 1923. List of North American Recent mammals. U.S. National Museum Bulletin, 128:1–673.

MURRAY, M. A. 1995. Biochemical systematics of the genus *Arborimus.* M.A. thesis, Humboldt State University, Arcata, California, 46 pp.

MUSSER, G. G., AND M. D. CARLETON. 1993. Family Muridae. Pp. 501–756, *in* Mammal species of the world: a taxonomic and geographic reference. Second ed. (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C., 1,206 pp.

QUAY, W. B. 1954*a*. The meibomian glands of voles and lemmings (Microtinae). Miscellaneous Publications of the Museum of Zoology, University of Michigan, 82:1–17.

———. 1954*b*. The anatomy of the diastemal palate in microtine rodents. University of Michigan Museum of Zoology, Miscellaneous Publication, 86:1–41.

———. 1965. Comparative survey of the sebaceous and sudoriferous glands of the oral lips and angle in rodents. Journal of Mammalogy, 46:23–37.

———. 1968. The specialized posterolateral sebaceous glandular regions in microtine rodents. Journal of Mammalogy, 49: 427–445.

REYNOLDS, R. T. 1970. Nest observations of the long-eared owl (*Asio otus*) in Benton County, Oregon, with notes on their food habits. Murrelet, 51:8–9.

RUGGIERO, L. F., L. L. C. JONES, AND K. B. AUBRY. 1991. Plant and animal habitat associations in Douglas-fir forests of the Pacific Northwest: an overview. Pp. 447–462, *in* Wildlife and vegetation of unmanaged Douglas-fir forests (L. F. Ruggiero, K. B. Aubry, A. B. Carey, and M. H. Huff, tech. coords.). United States Department of Agriculture, Forest Service, General Technical Report, PNW-285, 523 pp.

TAYLOR, W. P. 1915. Description of a new subgenus (*Arborimus*) of *Phenacomys,* with a contribution to knowledge of the habits and distribution of *Phenacomys longicaudus* True. Proceedings of the California Academy of Science, Series 4, 5:111–161.

TRUE, F. W. 1890. Description of a new species of mouse, *Phenacomys longicaudus,* from Oregon. Proceedings of the United States National Museum, 13:303–304.

VERTS, B. J., AND L. N. CARRAWAY. 1984. Keys to the mammals of Oregon. Oregon State University Book Stores, Inc., Corvallis, Oregon, 178 pp.

———. 1995. Phenacomys albipes. Mammalian Species, 494:1–5.

WALKER, A. 1928. Some Oregon *Phenacomys.* Journal of Mammalogy, 9:254–255.

———. 1930. Notes on the forest *Phenacomys.* Journal of Mammalogy, 11:233–235.

WHITAKER, J. O., JR., AND C. MASER. 1979. Parasitic mites of voles of the genera *Arborimus* and *Lagurus* in Oregon. Northwest Science, 53:224–227.

WIGHT, H. M. 1925. Notes on the tree mouse, *Phenacomys silvicola.* Journal of Mammalogy, 6:282–283.

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