

Spermophilus washingtoni.

By Eric A. Rickart and Eric Yensen

Published 12 April 1991 by The American Society of Mammalogists

Spermophilus Cuvier, 1825

Citellus Oken, 1816:842. No type designated. Not available (Opinion 417, International Commission on Zoological Nomenclature, 1956).

Anisonyx Rafinesque, 1817:45. Type species *Anisonyx brachiura* Rafinesque (= *Arctomys columbianus* Ord). Preoccupied by *Anisonyx* Latreille, 1807, a coleopteran.

Spermophilus Cuvier, 1825:255. Type species *Mus citellus* Linnaeus by original designation.

Colobotis Brandt, 1844:366. Type species *Spermophilus fulvus* Lichtenstein by original designation. Proposed as a subgenus.

Otospermophilus Brandt, 1844:382. Type species *Sciurus grammurus* Say by original designation. Proposed as a subgenus.

Ictidomys Allen, 1877:821. Type species *Sciurus tridecemlineatus* Mitchell by subsequent designation (Merriam, 1895). Proposed as a subgenus.

Xerospermophilus Merriam, 1892:27. Type species *Spermophilus mohavensis* Merriam by original designation. Proposed as a subgenus.

Ammospermophilus Merriam, 1892:27. Type species *Tamias leucurus* Merriam by original designation. Proposed as a subgenus.

Callospermophilus Merriam, 1897:189. Type species *Sciurus lateralis* Say by original designation. Proposed as a subgenus.

Ictidomoides Mearns, 1907:328. Type species *Sciurus mexicanus* Erxleben by original designation. Proposed as a subgenus.

Urocitellus Obolenskij, 1927:188. Type species *Spermophilus evermanni* Lichtenstein by original designation. Proposed as a subgenus.

Poliocitellus A. H. Howell, 1938:42. Type species *Arctomys franklinii* Sabine by original designation. Proposed as a subgenus.

Notocitellus A. H. Howell, 1938:44. Type species *Spermophilus annulatus* Audubon and Bachman by original designation. Proposed as a subgenus.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Subfamily Sciurinae, Tribe Marmotini, Subtribe Spermophilina (Black, 1963; Hafner, 1984; Hall, 1981; Moore, 1959). Hall (1981) recognized the subgenera *Spermophilus*, *Callospermophilus*, *Ictidomys* (including *Ictidomoides*), *Otospermophilus*, *Poliocitellus*, and *Xerospermophilus*. Gromov et al. (1965) recognized the subgenera *Colobotis*, *Urocitellus* (included in the subgenus *Spermophilus* by Nadler et al., 1982), and considered *Otospermophilus* (including *Callospermophilus*), *Ictidomys* (including *Poliocitellus*), and *Xerospermophilus* distinct genera. *Ammospermophilus*, named as a subgenus of *Spermophilus*, was recognized as a distinct genus by Bryant (1945) and is now regarded as such by most workers (Hafner, 1984). The prairie dogs (*Cynomys* Rafinesque, 1817) may be a sister group to the subgenus *Spermophilus*, and the genus *Spermophilus* as defined here may be paraphyletic (Dobson, 1985; Hafner, 1984). Honacki et al. (1982) listed 36 species worldwide. The following key (based on Corbet, 1978; Gromov et al., 1965; Hall, 1981; Nadler et al., 1982, 1984; Ognev, 1947) will aid in distinguishing the species.

- 1 Molars brachydont; parastyle ridge on M1 and M2 joining protocone without an abrupt change of direction; confined to Nearctic region 2
- Molars hypsodont; parastyle ridge on M1 and M2 joining protocone with an abrupt change of direction; occurring in Nearctic or Palearctic regions 12
- 2 (1) P3 with two cusps and a functional cutting edge, crown area >25% that of P4 Subgenus *Poliocitellus*, *S. franklinii*
- P3 simple, crown area <25% that of P4 3
- 3 (2) Tail >128 mm; upper parts of variegated black, white and buff Subgenus *Otospermophilus* 4

- Tail <128 mm; upper parts plain or striped 8
- 4 (3) Supraorbital foramen closed; pelage with some rufous areas; confined to subtropics 5
- Supraorbital foramen open; pelage without distinct rufous areas; not occurring in subtropics 6
- 5 (4) Tail >175 mm and ringed *S. annulatus*
- Tail <175 mm and not ringed *S. adocetus*
- 6 (4) Nape and shoulders without a dark median area *S. variegatus*
- Nape and shoulders with a dark median area 7
- 7 (6) Median area equally dark on head and back; south of 28° in Baja California *S. atricapillus*
- Median area darker on back than on head; north of 28° in Baja California *S. beecheyi*
- 8 (3) Dorsum with white or gray stripe on each side; greatest width of nasals >20% of zygomatic width; greatest length of skull >39 mm Subgenus *Callospermophilus* 9
- Dorsum without stripes; greatest width of nasals <20% of zygomatic width; greatest length of skull <40 mm Subgenus *Xerospermophilus* 11
- 9 (8) Confined to northern Mexico *S. madrensis*
- Occurring north of Mexico 10
- 10 (9) Golden mantle on head and neck and median dark stripes well defined; hind foot ≤44 mm; not occurring in Cascade Range of Washington and British Columbia *S. lateralis*
- Dorsal mantle and median dark stripes poorly defined; hind foot ≥44 mm; confined to Cascade Range of Washington and British Columbia *S. saturatus*
- 11 (8) Underside of tail white *S. mohavensis*
- Underside of tail yellowish *S. tereticaudus*
- 12 (1) Metaloph on P4 not continuous; dorsal pelage with stripes, spots, or plain yellowish-brown; confined to Nearctic region Subgenus *Ictidomys* 13
- Metaloph on P4 continuous; dorsal pelage plain, or with white or buff spots; occurring in Nearctic or Palearctic regions Subgenus *Spermophilus* 16
- 13 (12) Dorsum striped and spotted *S. tridecemlineatus*
- Dorsum without stripes 14
- 14 (13) Dorsum with spots in linear series *S. mexicanus*
- Dorsum plain or with non-linear spots 15
- 15 (14) Venter buff, dorsum plain or with buff spots *S. perotensis*
- Venter and dorsal spots grayish-white *S. spilosoma*
- 16 (12) Tail length >33% length of head and body 17
- Tail length <33% length of head and body 18
- 17 (16) Dorsum with fine white spots; tail length >40% length of head and body; diploid number 32; occurring in central and northeastern Asia west of the Lena River *S. undulatus*
- Dorsum with bold white spots; tail length <40% length of head and body; diploid number 34; occurring in northwestern North America and northeastern Asia east of the Lena River *S. parryi*
- 18 (16) Confined to Palearctic region 19
- Confined to Nearctic region 29
- 19 (18) Sole of hind foot entirely hairy or nearly so 20
- Sole of hind foot naked, except on side and tip of heel 24
- 20 (19) Dorsum with conspicuous spots; confined to eastern Europe *S. suslicus*
- Dorsum plain, or with faint spots or speckles 21
- 21 (20) Tail length 20-25% length of head and body; tail with well developed black-and-white edging at its tip; occurring in eastern Asia 22



FIG. 1. *Spermophilus washingtoni* from near Snake River, Franklin Co., Washington. Photograph by B. J. Betts.

- Tail length 25–33% length of head and body; black-and-white edging at tail tip weakly developed; occurring in Europe or Asia Minor 23
- 22 (21) Interorbital distance >9 mm; dorsum brownish, unspotted; diploid number 38 *S. alashanicus*
Interorbital distance <9 mm; dorsum yellowish with dark speckling; diploid number 36 *S. dauricus*
- 23 (21) Tail length ca. 25% of length of head and body; dorsum yellowish-brown with faint, diffuse white spots; diploid number 40; occurring in eastern Europe *S. citellus*
Tail length <25% of length of head and body; dorsum yellowish-brown with dark speckling; narrow bare stripe in middle of hind foot; diploid number 42; occurring in Asia Minor *S. xanthopymnus*
- 24 (19) Dorsum yellowish with dark speckles, without light mottling; color of venter not markedly lighter than dorsum *S. fulvus*
Dorsal pelage various, often with light mottling; venter markedly lighter than dorsum 25
- 25 (24) Cheek with distinct ginger, chestnut, yellowish, or rusty patch below eye 26
Cheek patch indistinct or absent 27
- 26 (25) Larger; tail >65 mm; hind foot usually >42 mm; cheek yellowish with rusty patch; occurring in eastern Europe and western Asia *S. major*
Smaller; tail <65 mm; hind foot usually <42 mm; cheek white with rusty or chestnut-brown patch; occurring in central Asia *S. erythrogenys*
- 27 (25) Dorsum pinkish-gray; tail length 23–32% length of head and body; maxillary tooththrow longer than diastema *S. relictus*
Dorsum yellowish-gray or brownish-gray; tail length 16–20% length of head and body; maxillary tooththrow shorter than diastema 28
- 28 (27) Dorsum yellowish-gray; no dark subapical band on tail; occurring north of Caucasus Mountains *S. pygmaeus*
Dorsum dark brownish-gray; dark subapical band on tail; confined to Caucasus Mountains *S. musicus*
- 29 (18) Dorsum plain 30
Dorsum spotted 34
- 30 (29) Hind foot <39 mm; ear pinnae inconspicuous *S. townsendii*

- Hind foot >39 mm; ear pinnae conspicuous 31
- 31 (30) Underside of tail buffy 32
Underside of tail grayish or reddish 33
- 32 (31) Hind foot <43 mm; diploid number 34; occurring in extreme southwestern Montana and areas south *S. elegans*
Hind foot >43 mm; diploid number 36; occurring in areas north and east of extreme southwestern Montana *S. richardsonii*
- 33 (31) Underside of tail grayish *S. armatus*
Underside of tail reddish *S. beldingi*
- 34 (29) Hind foot >43 mm *S. columbianus*
Hind foot <43 mm 35
- 35 (34) Dorsum brownish; ear pinnae conspicuous *S. brunneus*
Dorsum grayish; ear pinnae inconspicuous *S. washingtoni*

Spermophilus washingtoni (A. H. Howell, 1938)

Washington Ground Squirrel

Citellus washingtoni Howell, 1938:69. Type locality "Touchet, Walla Walla County, Wash[ington]."

CONTEXT AND CONTENT. Context noted in generic summary. *S. washingtoni* is in the subgenus *Spermophilus*. Howell (1938:71) described the subspecies *S. w. loringi*, which was synonymized with the nominate form by Dalquest (1948). A phenetic and karyotypic study by Hill (1978) also indicated that the species is monotypic.

DIAGNOSIS. The Washington ground squirrel (Fig. 1) differs from members of the subgenera *Callospermophilus* and *Ictidomys* in the lack of stripes or linear arrangements of large spots on the dorsum. It is distinguishable from the subgenera *Poliocitellus* and *Otospermophilus* by its smaller size (<250 mm total length) and relatively shorter tail (<33% of the length of head and body). Members of the subgenus *Xerospermophilus* have relatively longer tails and molars that are more brachydont. No members of the subgenera *Ictidomys*, *Otospermophilus*, *Poliocitellus*, or *Xerospermophilus* are sympatric with *S. washingtoni* (Hall, 1981; Howell, 1938).

Among Nearctic species of the subgenus *Spermophilus*, *S. washingtoni* is distinguishable from *S. armatus*, *S. beldingi*, *S. columbianus*, *S. elegans*, *S. parryi*, and *S. richardsonii* by its smaller size (length of hind foot <39 mm). It differs from *S. brunneus* in having smaller pinnae, grayish dorsal pelage with more conspicuous spots, a more distinct lateral line, a tail that is pinkish-cinnamon beneath without black and white guard hairs, larger auditory bullae, and a longer rostrum. Its distinct dorsal spotting, more bushy tail, and larger, narrower skull distinguish it from *S. townsendii*. Within the subgenus *Spermophilus*, only *S. beldingi* and *S. columbianus* occur sympatrically with *S. washingtoni* (Hall, 1981; Howell, 1938; Scheffer, 1941).

GENERAL CHARACTERISTICS. *Spermophilus washingtoni* is one of the smallest members of the subgenus *Spermophilus*. Ranges for external measurements (in mm) are: total length, 185–245; length of tail, 32–65; length of hind foot, 30–38 (Howell, 1938).

Dorsal coloration of spring pelage is pale smoke-gray, faintly washed with pinkish-buff. Worn pelage is more brown. The dorsum is flecked with grayish-white spots that are roughly square and 3–4 mm in breadth. Underparts are grayish-white washed with pinkish-buff. The feet are white, tinged with pinkish-buff. The tail is gray mixed with fuscous above, pinkish-cinnamon beneath, and edged with buffy white (Howell, 1938).

The skull (Fig. 2) is similar to that of *S. townsendii*, but is narrower through the braincase and interorbital region. Ranges for cranial measurements (in mm) are: greatest length of skull, 35.0–41.8; palatal length, 17.0–20.0; zygomatic breadth, 6.4–8.2; post-orbital constriction, 8.0–11.0; length of nasals, 12.3–15.6; and length of maxillary tooththrow, 7.3–8.2 (Howell, 1938).

DISTRIBUTION. *Spermophilus washingtoni* is restricted to that portion of the Columbia Plateau lying south and east of the Columbia River in Washington, and between the John Day River

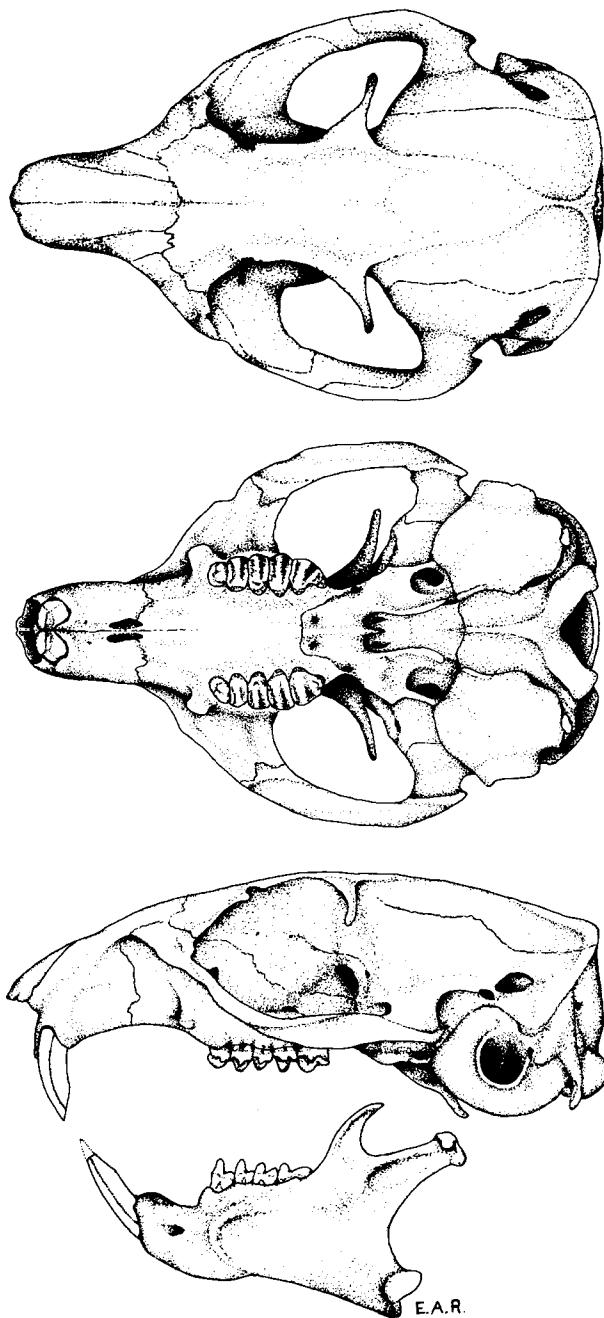


FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Spermophilus washingtoni* (United States National Museum 398334, male) from near Lind, Adams Co., Washington. Cranial length is 40 mm.

and the Blue Mountains in adjacent northeastern Oregon (Fig. 3). In southern Washington, *S. washingtoni* is separated from its ecological counterpart, *S. townsendii*, by the Columbia River (Howell, 1938; Scheffer, 1941). There is a possible historical restriction in range in eastern Washington due to competition with *S. columbianus* (Shaw, 1921). The range has been reduced in recent years through habitat loss to agriculture (Betts, 1990; Hill, 1978). Documented elevational range is from 90 to 450 m, within the upper Sonoran life zone (Bailey, 1936; Scheffer, 1941).

FOSSIL RECORD. Late Holocene specimens from eastern Washington identified as *S. townsendii* (Deavers and Greene, 1978), fall within the present range of *S. washingtoni* and probably represent the latter species (Rickart, 1987).

FORM AND FUNCTION. Washington ground squirrels have five pairs of mammae; one inguinal, two pectoral, and two

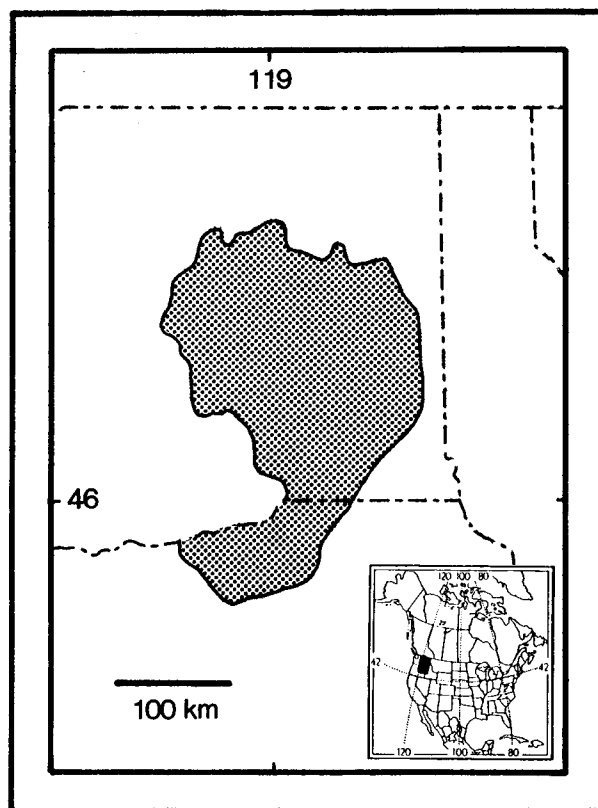


FIG. 3. Distribution of *Spermophilus washingtoni* in southeastern Washington and northeastern Oregon (after Hall, 1981).

abdominal (Bailey, 1936). Pelage is fresh in March, and worn in May and June (Howell, 1938). Timing of molt is unknown. As in other hibernating ground squirrels, weight fluctuates seasonally as a function of body fat content. Average body weights for adult males were 158 g in late February, and 257 g in late May (Scheffer, 1941). A hibernating captive male had a mean weight loss of 1.05 g/day, and rectal temperatures ranging from 3.3 to 9.4°C (Shaw, 1925).

ONTOGENY AND REPRODUCTION. *Spermophilus washingtoni* breed in late January or early February, soon after emergence from hibernation. A lengthy mating period of several weeks is indicated by the simultaneous presence in a local population of post-partum females and others in early pregnancy. One litter is produced each year, with births occurring in February and early March. At high elevations, emergence and breeding occur as much as a month later than at lower elevations (Bailey, 1936; Scheffer, 1941; Shaw, 1921). For 26 females, uterine litter size averaged 8, with a range from 5 to 11 (Scheffer, 1941). There is no information on age at first reproduction or age-specific fecundity.

By late March, young with body weights ranging from 22 to 44 g are weaned and appear above ground. By late April they are half-grown (89–139 g), and by late May they are nearly full-sized and are difficult to distinguish from adults (Scheffer, 1941).

ECOLOGY. Washington ground squirrels inhabit dry, open sagebrush (*Artemisia*) or grassland habitat. They occur in areas with sandy soils along hillsides, in ravines, and on river bottoms (Bailey, 1936; Howell, 1938). They are most numerous in areas of high grass cover, on deep, weaker soil with less clay (Betts, 1990). In favorable habitat, estimated total population densities range from 120 to 250 individuals/ha (Bailey, 1936; Dalquest, 1948).

The diet consists of succulent vegetation, flowers, roots, bulbs, seeds, seed pods, and insects. Documented food plants include a broad range of forbs and grasses; *Erodium* sp., *Sphaeralcea munroana*, *Plantago purshii*, *Bromus tectorum*, *Agropyron pauciflorum*, *Oryzopsis hymenoides*, and *Sisymbrium altissima*. Cultivated plants, including cabbage, green peas, corn, oats, wheat, rye, barley, and alfalfa also are eaten (Bailey, 1936; Howell, 1938). Badgers (*Taxidea taxus*) are considered to be the most important

predators of *S. washingtoni* (Bailey, 1936; Scheffer, 1941). A total of 150 badger-excavated burrows were reported in an area with a density of approximately 1,500 squirrel burrows/ha (Bailey, 1936). The ectoparasitic mites *Androlaelaps fahrenheitsi* and *Macrocheles* sp. have been reported from Washington ground squirrels (Whitaker and Maser, 1985).

Because of their diet and occurrence in an important grain-producing region, Washington ground squirrels have been considered agricultural pests and have been the subject of control programs (Bailey, 1936; Howell, 1938). They no longer occur at many localities where they were formerly abundant, primarily because of loss of habitat to agriculture. In 1988, squirrels were absent at 68 of 148 historically occupied sites in Oregon and Washington. Twenty-three vacated sites had lost squirrels during the previous decade, and 25 additional sites were considered vulnerable (Betts, 1990).

Washington ground squirrels have been trapped with live traps baited with apple, and with snap traps buried at burrow entrances (Hill, 1978; Scheffer, 1941). Captives have been maintained on diets of wheat, oats, sunflower seeds, carrots, and apples (Shaw, 1925).

BEHAVIOR. Washington ground squirrels have a protracted period of seasonal dormancy that encompasses the temperature extremes of both winter and summer. Adults emerge in late winter (late January to March) with males preceding females. Local timing of seasonal activity varies with elevation by as much as a month. Juvenile animals are born early in the active season and first emerge from natal burrows in late March. Squirrels enter dormancy in late spring and early summer. Adults emerge from late May to early June after an active season of 4–5 months duration, whereas juveniles remain active until late June or early July (Bailey, 1936; Scheffer, 1941; Shaw, 1921). A dormancy period of 244 days was recorded for a captive animal without access to food or water (Shaw, 1925).

Spermophilus washingtoni is strictly diurnal. During the late active season, animals avoid the heat of midday and are most active in the morning (Scheffer, 1941).

Burrows of *S. washingtoni* are simple and unbranched, reaching depths of up to 170 cm and lengths >7 m (Bailey, 1936; Howell, 1938). Fenced burrow systems and artificial nest boxes have been used to study hibernation in captivity (Shaw, 1925).

Captive squirrels have reduced appetites just before entering dormancy, and again immediately following emergence. During deep torpor, animals assume a rigid, curled posture (Shaw, 1925).

There are no studies dealing directly with social behavior of Washington ground squirrels. However, in favorable habitats they form colonies of up to 250 individuals/ha (Bailey, 1936). The alarm call is a soft, lisping whistle, similar to that of *S. townsendii mollis*. In responding to an alarm, animals generally assume an alert, upright posture ("picket pin") while calling, and quickly retreat to burrows if threatened (Bailey, 1936; Howell, 1938).

GENETICS. The diploid karyotype of *S. washingtoni* consists of 16 metacentric, 16 submetacentric, and 2 acrocentric autosomes, a submetacentric X chromosome, and a small acrocentric Y chromosome ($2n = 36$; $FN = 66$; Nadler, 1966). However, Hill (1978) described the 34 autosomes as biarmed. No significant karyotypic differences were found between populations separated by the Snake River in southeastern Washington (Hill, 1978). Both chromosomally and biochemically, *S. washingtoni* is similar to the Nearctic "big-eared" species, including *S. armatus*, *S. beldingi*, *S. elegans*, and *S. richardsonii* (Nadler, 1966; Nadler et al., 1982, 1984). This is in contrast to its apparent morphological similarities to Nearctic "small-eared" taxa that form the *S. townsendii* complex (Howell, 1938; Nadler et al., 1982).

REMARKS. Prior to the generic revision of Howell (1938), squirrels of this species were known under the name of *S. townsendii*. That was because the type locality originally associated with that name is imprecise (Howell, 1938; Rickart, 1987).

The generic name *Spermophilus* is derived from the Greek roots *sperma* (seed) and *philos* (loving). The specific epithet *washingtoni* refers to the state of Washington, where the species is primarily distributed. The vernacular name sage rat has also been applied to this species (Dalquest, 1948).

We thank B. J. Betts for providing a copy of his unpublished paper and the photograph for Fig. 1. R. S. Hoffmann, D. R. Johnson, and J. O. Murie reviewed the manuscript and provided many helpful

comments. This is contribution no. 89-5 of the Utah Museum of Natural History.

LITERATURE CITED

- ALLEN, J. A. 1877. Monographs of North American Rodentia. Reports of the United States Geological and Geographical Survey of the Territories, 11:631–939.
- BAILEY, V. 1936. The mammals and life zones of Oregon. North American Fauna, 55:1–416.
- BETTS, B. J. 1990. Geographic distribution and habitat preferences of Washington ground squirrels (*Spermophilus washingtoni*). Northwestern Naturalist, 71:27–37.
- BLACK, C. C. 1963. A revision of the North American Tertiary Sciuridae. Bulletin of the Museum of Comparative Zoology, 130:109–248.
- BRANDT, J. F. 1844. Observations sur les différentes espèces de sousliks de Russie. Bulletin de la Classe Physicomathématique de l'Académie des Sciences de St. Pétersbourg, 2:357–382 (not seen, cited in Howell, 1938).
- BRYANT, M. D. 1945. Phylogeny of Nearctic Sciuridae. The American Midland Naturalist, 33:257–390.
- CORBET, G. B. 1978. The mammals of the Palearctic region: a taxonomic review. British Museum (Natural History) and Cornell University Press, London and Ithaca, New York, 314 pp.
- CUVIER, F. 1825. Des dents des mammifères considérées comme caractères zoologiques. Paris, 255 pp. (not seen, cited in Howell, 1938).
- DALQUEST, W. W. 1948. Mammals of Washington. University of Kansas Publications, Museum of Natural History, 2:1–444.
- DEAVERS, K., AND G. S. GREENE. 1978. Faunal utilization at USAD2: a prehistoric archaeological site in the channeled scablands of eastern Washington. Tebiwa, 14:1–21.
- DOBSON, F. S. 1985. The use of phylogeny in behavior and ecology. Evolution, 39:1384–1388.
- GROMOV, I. M., D. I. BIBIKOV, N. I. KALABUKHOV, AND M. N. MEIER. 1965. Nazemnye belich'i [ground squirrels] (Marmotinae). Fauna SSSR, Mlekopitayushchie [Fauna of the USSR, mammals]. Nauka, Moscow-Leningrad, 3(2):1–466.
- HAFNER, D. J. 1984. Evolutionary relationships of the Nearctic Sciuridae. Pp. 3–23, in The biology of ground-dwelling squirrels (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.
- HALL, E. R. 1981. The mammals of North America. Second edition. John Wiley and Sons, New York, 1:1–600 + 90.
- HILL, T. G. 1978. A numerical taxonomic and karyotypic analysis of the Washington ground squirrel *Spermophilus washingtoni* (Rodentia: Sciuridae). Unpublished M.S. thesis, Walla Walla College, Walla Walla, Washington, 51 pp.
- HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPL (EDS.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.
- HOWELL, A. H. 1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. North American Fauna, 56:1–256.
- MEARNS, E. A. 1907. Mammals of the Mexican boundary of the United States. Part 1, families Didelphidae to Muridae. Bulletin of the United States National Museum, 56:1–530.
- MERRIAM, C. H. 1892. The geographic distribution of life in North America with special reference to the Mammalia. Proceedings of the Biological Society of Washington, 7:1–64.
- . 1895. (Review of) On a collection of mammals from Arizona and Mexico, made by W. W. Price, with field notes by the collector, by J. A. Allen. Science (new series) 2:417–418.
- . 1897. Notes on the chipmunks of the genus *Eutamias* occurring west of the east base of the Cascade-Sierra system, with a description of new forms. Proceedings of the Biological Society of Washington, 11:189–212.
- MOORE, J. C. 1959. Relationships among living squirrels of the Sciurinae. Bulletin of the American Museum of Natural History, 118:155–206.
- NADLER, C. F. 1966. Chromosomes and systematics of American ground squirrels of the subgenus *Spermophilus*. Journal of Mammalogy, 47:579–596.
- NADLER, C. F., R. S. HOFFMANN, N. N. VORONTSOV, J. W. KOEPL,

- L. DEUTSCH, AND R. I. SUKERNIK. 1982. Evolution in ground squirrels. II. Biochemical comparisons in Holarctic populations of *Spermophilus*. *Zeitschrift für Säugetierkunde*, 47:198-214.
- NADLER, C. F., R. S. HOFFMANN, N. N. VORONTOV, L. L. SHALTAROVA, AND Y. M. BORISOV. 1984. Chromosomal evolution in Holarctic ground squirrels (*Spermophilus*) II. Giemsa-band homologies of chromosomes and the tempo of evolution. *Zeitschrift für Säugetierkunde*, 49:78-90.
- OBOLENSKIY, S. 1927. A preliminary review of the Palaearctic sousliks (*Citellus* and *Spermophilopsis*). *Compte rendu de l'Academie des Sciences de l'URSS*, 12:188-193 (not seen, cited in Howell, 1938).
- OGNEV, S. I. 1947. *Zveri SSSR i prilozhashchikh stran* [Mammals of USSR and adjacent countries]. Vol. 5, Rodents. English translation, Israel Program for Scientific Translations, Jerusalem, 1963, 662 pp. Office of Technical Services, Washington, D.C.
- OKEN, L. 1816. *Lehrbuch der Zoologie—mit vierzig Kupfertafeln. Zweite Abtheilung, Fleischthiere*. (Preis: 2 Thaler.), August Schmid, Jena, 1,270 pp. (not seen, cited in Howell, 1938).
- RAFINESQUE, C. S. 1817. Descriptions of seven new genera of North American quadrupeds. *American Monthly Magazine*, 2: 44-46.
- RICKART, E. A. 1987. *Spermophilus townsendii*. *Mammalian Species*, 268:1-6.
- SCHEFFER, T. H. 1941. Ground squirrel studies in the Four-Rivers country, Washington. *Journal of Mammalogy*, 22:270-279.
- SHAW, W. T. 1921. Moisture and altitude as factors in determining the seasonal activities of the Townsend ground squirrel in Washington. *Ecology*, 2:189-192.
- . 1925. Observations on the hibernation of ground squirrels. *Journal of Agricultural Research*, 31:761-769.
- WHITAKER, J. O., JR., AND C. MASER. 1985. Mites (excluding chiggers) of mammals of Oregon. *Great Basin Naturalist*, 45: 67-76.
- Editors of this account were TROY L. BEST and KARL F. KOOPMAN. Managing editor was DON E. WILSON.
- E. A. RICKART, UTAH MUSEUM OF NATURAL HISTORY, UNIVERSITY OF UTAH, SALT LAKE CITY 84112, AND E. YENSEN, MUSEUM OF NATURAL HISTORY, THE COLLEGE OF IDAHO, CALDWELL 83605.