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Scapanus townsendii.

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Scapanus Pomel, 1848

Scapanus Pomel, 1848:247. Type species *Scalops townsendii* Bachman.

CONTEXT AND CONTENT. Order Insectivora, Family Talpidae, Subfamily Talpinae, Genus *Scapanus* (Yates, 1984). Honacki et al. (1982) recognized three living species. A key to the species adapted from Hall (1981) follows:

1 Pelage grayish with a coppery wash; fifth and sixth upper unicuspids appressed .... *S. latimanus*
Pelage blackish to purplish black; all upper unicuspids evenly spaced 2
2 (1) Total length >200 mm; hind foot >24 mm; total length of skull ≥40 mm; sublachrymal ridge prominent .... *S. townsendii*
Total length <200 mm; hind foot <24 mm; total length of skull <40 mm; sublachrymal ridge indistinct .... *S. orarius*

Scapanus townsendii (Bachman)

Townsend's Mole

Scalops Canadensis: Richardson, 1829:9. No type locality given. [Not of Desmarest or Harlan, which = *Scalopus aquaticus*]
Scalops Townsendii Bachman, 1839:58. Type locality "banks of the Columbia River." Type locality restricted to Vancouver, Clark Co., Washington, by True (1896:63).
Scapanus Tow[n]sendii, Pomel, 1848:247. First use of current name combination.
Scalops aeneus Cassin, 1853:299. Type locality "Oregon."
Talpa laeniata Le Conte, 1853:327. Type locality quoted from Bachman (1839) as "banks of the Columbia River." Specific name also spelled *taeniata*, apparently a lapsus.

CONTEXT AND CONTENT. Context same as for genus. Two subspecies are recognized currently (Johnson and Yates, 1980):

S. t. townsendii (Bachman, 1839:58), see above.
S. t. olympicus Johnson and Yates, 1980:1. Type locality "Hurricane Ridge, Olympic National Park, Clallam Co., Washington, elevation approximately 1615 meters."

DIAGNOSIS. *Scapanus townsendii* can be distinguished from *Sorex* (the only sympatric non-talpid insectivores) by presence of zygomatic arches, first upper incisor unicuspid, unpigmented teeth (Fig. 1), absence of pinnae, and body size. Of sympatric talpids, Townsend's mole can be distinguished from *Neurotrichus gibbsii* by possession of 44 teeth instead of 36, forefeet as wide as long, total length >130 mm, tail <25% of total length, and length of hind foot >18 mm; from *Scapanus orarius* by total length >200 mm, length of hind foot >24 mm, condylobasal length of skull usually ≥40 mm, and a prominent sublachrymal ridge; and from *Scapanus latimanus* by absence of a coppery wash on the pelage and fifth and sixth upper unicuspids evenly spaced. *Scapanus* may be distinguished from other North American talpid genera by the following characters (Hall, 1981; Ingles, 1965; Jackson, 1915; Silver, 1933; Yates and Pedersen, 1982): from *Scalopus* by presence of 44 teeth instead of 36 and the lack of webbed foretoes; from *Parascalops* by the lack of a densely haired tail, and presence of superior nostrils, complete auditory bullae, and simple lingual basal projections of upper molars instead of broad, lobed projections; and from *Condylura* by a tail <25% of total length, forefeet as wide as long, and absence of fleshy appendages around the nose.

GENERAL CHARACTERS. *Scapanus townsendii* (Fig. 2) is fossorial. The black velvet-like pelage is short and the body streamlined (True, 1896; Yates and Pedersen, 1982); the shoulders are heavy and the external appendages are muscular, short, and close to the body (Bailey, 1936; Cahalane, 1947; Silver, 1933). It has a long snout; a short neck; a short, essentially naked tail; small hind feet (Bailey, 1936; Elliot, 1901); and the front feet are shovel-like, as wide as they are long, and have large heavy claws (Cahalane, 1947). The ears have no pinnae and the eyes are minute (True,

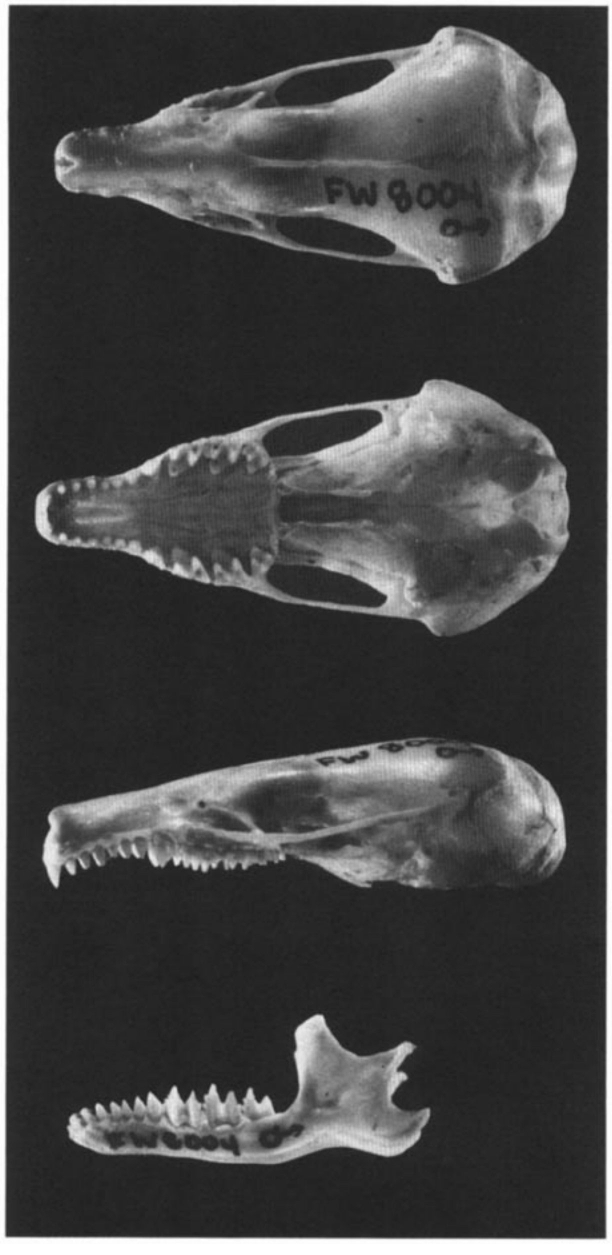

FIG. 1. Dorsal, ventral, and lateral views of cranium, and lateral view of the mandible of an adult male *Scapanus townsendii* (OSUFW [Oregon State University, Department of Fisheries and Wildlife mammal collection] 8004 from Corvallis, Benton Co., Oregon). Condylobasal length is 40.25 mm.

FIG. 2. Photograph of adult male *Scapanus townsendii* (OS-UFW 9271) from 1 mi. N, 1.5 mi. E Wilsonville, T3S, R1E, NW¼ Sec. 18, Clackamas Co., Oregon, collected on 7 August 1991.

1896). Females possess four pairs of mammae (Nowak and Paradiso, 1983).

Ranges of external measurements (in mm) of *S. townsendii* (Hall, 1981) are: total length, 195–237; tail length, 34–51; and length of hind foot, 24–28. These values were not exceeded by measurements provided by Bailey (1936), Ingles (1965), Jackson (1915), Johnson and Yates (1980), or by True (1896); however, Maser et al. (1981) reported tails of 61 mm and hind feet of 23–31 mm. Hall (1981), Nowak and Paradiso (1983), and Yates and Pedersen (1982) stated that pinnae are absent in all North American talpids; however, Maser et al. (1981) indicated that *S. townsendii* has ear pinnae 2–4 mm long. Body mass of adults average 141.7 g (range, 64–171 g—Dalquest, 1948; Maser et al., 1981; Pedersen, 1963); males average slightly larger than females (Yates and Pedersen, 1982). *Scapanus townsendii*, like all North American talpids, has a complete zygomatic arch but lacks jugal bones (Yates and Pedersen, 1982). The cranium is compressed dorsoventrally, the rostrum is long and narrow, and the interparietal is large and broad (True, 1896; Yates and Pedersen, 1982). Ranges of selected skull measurements (in mm) for 17 male and 17 female (in parentheses) *S. t. townsendii* from throughout the range (Jackson, 1915) are: greatest length of skull, 42.3–44.6 (41.2–44.1); mastoid breadth, 20.0–21.8 (19.3–20.4); interoribtal breadth, 8.7–9.5 (8.4–9.2); and length of maxillary toothrow, 13.5–14.4 (13.3–14.4). Means ($\pm SE$) for the same characters for eight male and nine female (in parentheses) *S. t. olympicus* are: 39.9 ± 0.32 (39.2 ± 0.13), 19.1 ± 0.11 (18.6 ± 0.11), 8.3 ± 0.06 (8.3 ± 0.09), and 12.9 ± 0.13 (12.8 ± 0.06—Johnson and Yates, 1980). The premolars are single rooted, upper molars are dilambdodont, and I1 is large, elongate, and flattened (Hutchison, 1968; True, 1896; Yates and Pedersen, 1982). The dental formula is i 3/3, c 1/1, p 4/4, m 3/3, total 44 (True, 1896). Brain mass of *S. townsendii* calculated from volume of the braincase averaged 2.02 g (Mace et al., 1981).

DISTRIBUTION. The geographic distribution of *S. townsendii* (Fig. 3) extends from Huntington, British Columbia, southward through the Olympic Mountains, Washington, Coast Range and interior valleys of Oregon to Ferndale, California, and eastward to the foothills of the Cascade Mountains, except in northern California where it is restricted to the coastal region. Altitudinally, Townsend's moles range from near sea level to at least 1,677 m in the Cascade Mountains (Taylor and Shaw, 1927) and 1,615 m in the Olympic Mountains (Johnson and Yates, 1980).

FOSSIL RECORD. Although fossil material of *Scapanus* dates to the Miocene (Clarendonian) and records of the genus from the Blancan are available for Idaho and eastern Washington (Kurtén and Anderson, 1980), no fossils of *S. townsendii* are known. The probable ancestor of *Scapanus* is *Scapanoscapter simplicidens* from the Barstovian (Miocene?) of Oregon (Hutchison, 1968).

FORM AND FUNCTION. The skin of Townsend's moles is characterized by a thin epidermis except on the palms, snout, and rostral areas. The surface of the palms is covered with short, rounded rete ridges with villi between them. Blunt papillae on the snout penetrate into the dermis and have individual organs of Eimer (Giacometti and Machida, 1965). The dermis has no papillary layer, a few horizontally distributed collagen fibers, and almost no elastic fibers. However, the eyelids have elastic fibers. Many blood vessels, but only a few superficial capillaries, serve the dermis (Giacometti and Machida, 1965). Nerve filaments, strongly reactive for alkaline phosphatase, surround the large arterioles of the deep dermis. Above the dermis of the palms is a simple network of nerves that serve the rete ridges. The palms do not contain Meissner-like corpuscles or encapsulated nerve terminations (Giacometti and Machida, 1965).

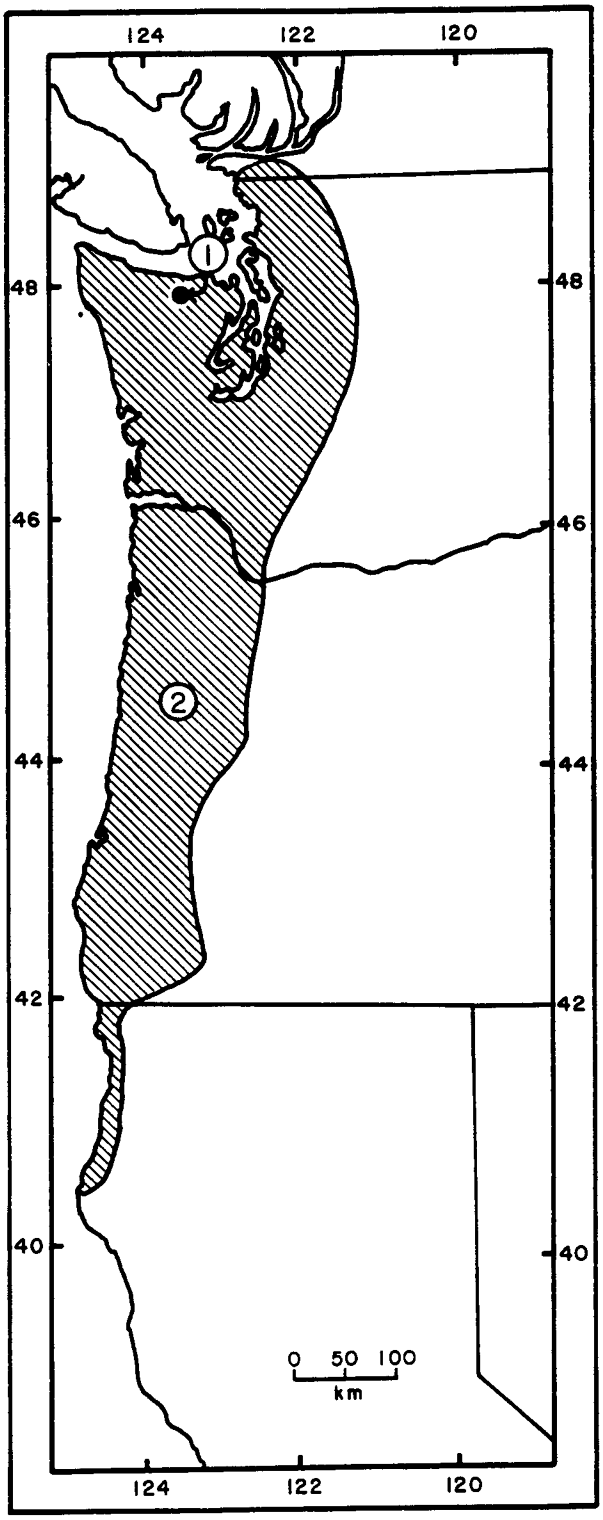

FIG. 3. Geographic distribution of *Scapanus townsendii* (redrawn after Hall [1981] and Johnson and Yates [1980]). Subspecies are: 1, *S. t. olympicus* (known only from type locality); 2, *S. t. townsendii.*

A cross section of the deep dermis of the torso shows "a polygonal rete of fine nerves which enclose islands of hair follicles" (Giacometti and Machida, 1965:32). The greatest level of specialization in the development of nerve endings is in the organs of Eimer in the papillae on the snout. These organs are composed of about 20 nerve fibers that penetrate each papilla; the nerve fibers form a helical structure that passes through the epidermis and terminates in the stratum corneum (Giacometti and Machida, 1965). At the most internal level of the dermis are nerve bundles that supply the organs of Eimer and end at the base of each papilla in the form of "an elongated, short, encapsulated end-organ" (Giacometti and Machida, 1965:32).

The hair follicles are long, slender, extend inward to the stratum adiposum, and are surrounded by a ring of fine nerve endings that test positive for alkaline phosphatase (Giacometti and Machida, 1965). In the dermis, the bulbs of the hairs are slanted; however, the slope is lost as the hairs emerge through the skin. This accounts for the ability of mole hairs to bend in any direction. The torso pelage is characterized by 3,000 hairs/cm^2, hair follicles in clusters of five or six, guard hairs in a growing phase, and quiescent underhairs (Giacometti and Michida, 1965). The number of guard hairs equals that of underhairs. "The guard hairs have a discontinuous, pigmented medulla, interrupted at regular intervals by air spaces; the fine [underhairs] have no medulla and often terminate in long whip-like tips" (Giacometti and Machida, 1965:32); the guard-hair follicles contain glycogen. Hair follicles grow singly on the rostrum and lips. The dorsum has slender arrectores pilorum muscles; these muscles are absent from the chest and venter.

Townsend's moles have sweat and sebaceous glands (Giacometti and Machida, 1965). Sweat glands occur in conjunction with the pelage, open direclty on the surface of the skin, are distributed 600/cm^2 on the dorsum and venter, and have nerves that test positive for alkaline phosphatase, not cholinesterases as in most mammals. The fundi of the sweat glands are in the deep dermis. The narrow and straight excretory ducts of the middermis enlarge before reaching the surface of the skin. The enlarged section of the sweat glands is lined with a layer of cuboidal epithelium. On the chest and venter, the sweat glands are small, partially coiled, and surrounded by myoepithelial cells that contain glycogen and dermal collagen. In the deep dermis, associated with each hair follicle, are one or two subaceous glands. The acini of the sebaceous glands are small, spherical, and have short, narrow ducts; none contains glycogen, is surrounded by phosphatase-reactive capillaries, or is supplied by cholinesterase-reactive nerves. On the rostrum and perianal areas, the sebaceous glands are large and lobulate. "The meibomian glands, situated deeply in the thick tarsal plate, are large and multiacinar" (Giacometti and Machida, 1965:33).

The humerus is slightly longer than wide. The tibia, slightly longer than the femur, is joined by a short fibula that only extends a little above the midpoint of the tibia (True, 1896). The scapula of *Scapanus* "has a prominent tubercle at the distal extremity of the inferior spine" (True, 1896:50). "The clavicles are about two-thirds as long as broad, deeply notched on the inferior border, and not pierced by a foramen" (True, 1896:50). The vertebral formula is 7C, 14T, 5L, 6S, and 13–14Ca, total 38–39 (True, 1896). Seven invertebral ossicles are located from the 14th thoracic vertebra to the 5th lumbar vertebra. The sternum has five small sections and a large manubrium equal in length to the remainder of the sternum (True, 1896). The manubrium is characterized by an expanded anterior end, grooved and slightly incurved borders, and a keel whose depth is less than one-third its length. The two sides of the narrow pelvis do not meet posterior to the acetabula. The dorsal surface of the junction of the sacral vertebrae and pelvis is covered by osseous bridges except for two pairs of moderate-sized foramina (True, 1896).

The baculum of Townsend's mole is situated in the extreme distal portion of the glans penis, is relatively transparent, and varies considerably in size and shape. It averages 0.42 mm long by 0.27 mm wide (range, 0.36–0.59 by 0.18–0.42, n = 6—Maser and Brown, 1972). The glans penis was depicted, but not described, by Maser and Brown (1972; Fig. 4).

The blood of Townsend's moles (n = 5–7) is characterized by (Yates and Pedersen, 1982) a hemoglobin of 16.92 g/100 cm^3 (range, 11.60–21.63), a hematocrit of 46% packed-cell volume (range, 35–60), 5,721 white blood cells/mm^3 (range, 2,750–8,150), 48 polymorphonuclear neutrophils/100 cells (range, 25–70), 50 small lymphocytes/100 cells (range, 30–74), 2.2 monocytes/100 cells (range, 0–7), and 6.12 million erythrocytes/mm^3 (range, 5.48–7.03). A urinalysis of Townsend's moles (n = 11) indicated the presence of some triple phosphate and uric acid crystals, an albumin level of 3–4, a reaction (presumably pH) of 6.5–8.0, and at least a trace of sugar present in five animals (Pedersen, 1963); it is unclear whether these were captive or freshly killed animals.

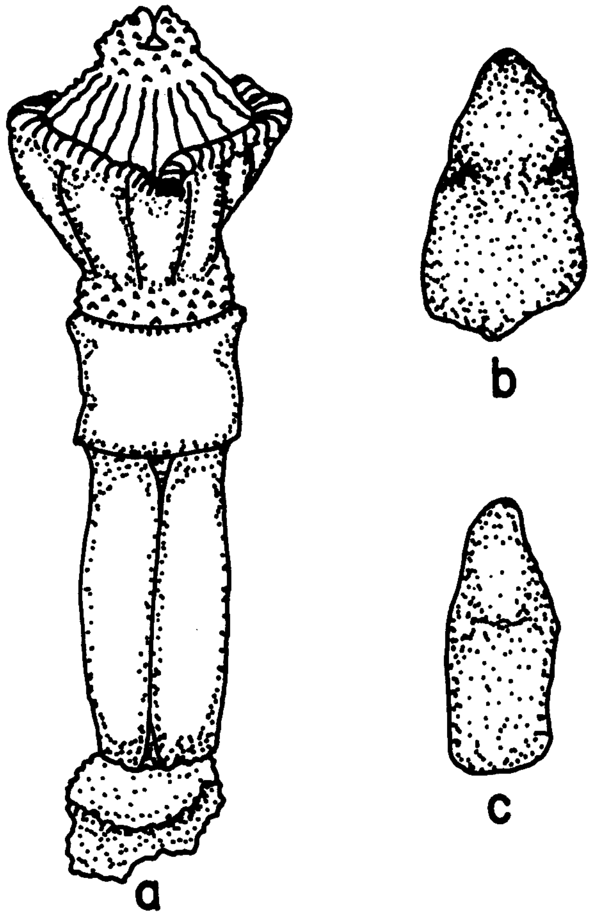

FIG. 4. Drawings of: a, glans penis; b, dorsal view of baculum; c, lateral view of baculum of *Scapanus townsendii*. Baculum is 0.36 by 0.19 mm in greatest dimension. Scale of penis is unknown; redrawn after Maser and Brown (1972).

ONTOGENY AND REPRODUCTION. Reproductive activity in *S. townsendii* near Tillamook, Oregon, was considered to commence in November with the first evidence of enlargment of the testes; testis size began to decrease by February (Pedersen, 1963). The breeding season of Townsend's moles had begun before collection of animals began on 7 February in western Oregon; this was based on males considered to have fully enlarged testes. All nine males examined before 14 March were so classified (Moore, 1939). However, none of 14 caught between 17 March and 20 April was considered in breeding condition. The first obviously pregnant female was taken on 13 March, although a female with a vaginal plug was taken on 22 February. In another study conducted nearby, the first evidence of pregnancy was detected in a specimen collected on 22 February, and well-developed embryos were found by 8 March (Pedersen, 1963). Two females caught on 3 and 4 April were considered to have given birth 3 days earlier and no pregnant females were captured after 12 April (Moore, 1939). In the same region, a female with embryos deemed too small to weigh (other embryos as small as 0.14 g were weighed) was captured on 4 April (Pedersen, 1963). Gestation is unknown but assumed to be 4–6 weeks (Yates and Pedersen, 1982). Thus, the breeding season in males seems too restricted for females to produce more than a one litter annually.

Of nine pregnant female *S. townsendii* from near Netarts, Oregon, three had two embryos, four had three, and one each had four and six ($\bar{X}$ = 3.1); six postpartum females had an average of 3.1 (range, 3–4) implantion sites (Moore, 1939). Of 18 females with visible embryos from Tillamook, Oregon, examined by Kuhn

FIG. 5. Photograph of four *Scapanus townsendii* mounds in field recently planted to grain with grain drill in Polk Co., Oregon.

et al. (1966), 1 had one embryo, 7 had two, and 10 had three ($\bar{X}$ = 2.5). Kuhn et al. (1966) examined 94 nests containing young; 1 contained one young, 23 contained two, 57 contained three, and 13 contained four ($\bar{X}$ = 2.87). Pedersen (1963) examined 43 nests with a total of 119 young ($\bar{X}$ = 2.76; range, 1-4); L. W. Kuhn (pers. comm.) indicated that this was a subsample of that reported on by Kuhn et al. (1966).

Neonates weigh about 5 g (Kuhn et al., 1966), are naked, pink, without teeth and distinguishable eyes, and the claws are soft (Pedersen, 1963). The size of the manus seems exaggerated. By 10 days of age, the color of the young has changed from pink to gray. At 15-20 days of age, young weighed about 35 g and their pelage had begun to develop (Pedersen, 1963). By 30 days of age, young were furred completely and weighed 60-80 g (Kuhn et al., 1966). Reproductive competence is attained at about 10 months of age.

Warm cow's milk fed to 70- and 76-g young at 4-h intervals sustained them although the former lost 4 g and the latter gained only 1 g in 3 days (Pedersen, 1963). After 10 days in captivity, the young refused milk, but ate earthworms (presumably *Lumbricus*) and lean ground beef; after attaining a mass of 88 g, the smaller of the two began to lose mass and died after 33 days in captivity, the heavier attained a mass of 142 g after 51 days in captivity. The latter mole died after 179 days in captivity on a diet of ground beef and water.

ECOLOGY. *Scapanus townsendii* occupies moist meadows, lowlands, and river flood plains (Dalquest, 1948; Johnson and Yates, 1980; Yates and Pedersen, 1982). *S. t. townsendii* in Oregon has been found in prairie and shrub habitats (Maser et al., 1981) and, in Washington, it frequently inhabits fir (*Abies*) forests (Dalquest, 1948). In contrast, the habitat of *S. townsendii olympicus* consists of heavy sods of grasses, a sedge (*Carex albonigra*), American bistort (*Polygonum bistortoides*), subalpine lupine (*Lupinus latifolius*), and subalpine fir (*Abies lasiocarpa*) that occur in clumps in deep, moist soils at edges of meadows, in cirques, and on ridge tops in a restricted area of the Olympic Mountains at 1,370-1,675 m (Johnson and Yates, 1980).

In Tillamook Co., Oregon, as many as 12.4 moles/ha were found in the most heavily populated areas (Kuhn et al., 1966). Densities as low as 0.42 moles/ha occur in areas with poor drainage and scarcity of earthworms (Giger, 1973). Eight nest mounds were located in a 6.1-ha field near Tillamook, Oregon (Kuhn et al., 1966). In the same region, 70 *S. townsendii* and 2 *S. orarius* were removed from a 37.1-ha field and 51 of the former species and 1 of the latter were removed from a 49.4-ha field; mole activity ceased in both fields (Giger, 1973).

Of 180 juveniles marked in April-May as ≤4-week-old nestlings in 62 nests on a 150-ha study area in Tillamook Co., Oregon, 58 (32.2%) were found dead in the nests in June (mostly from trampling by cattle), 44 (24.4%) were recaptured after mid-September, and the status was unknown for the remaining 78 (43.3%). Of the 44 recaptured after mid-September, 38 had dispersed <305 m from their natal dens and 27 had dispersed <152 m. Average dispersal movements were 181 m (range, 15-856 m) for juvenile females and 166 m (range, 15-722 m) for juvenile males (Giger, 1973). Three young crossed paved roadways during dispersal.

Scapanus townsendii primarily eats earthworms (Oligochaeta) and insects (Cahalane, 1947; Gabrielson, 1921; Kuhn, 1970; Silver, 1933; Wick and Landforce, 1962; Wight, 1928; Yates and Pedersen, 1982). The stomachs of 306 Townsend's moles from the Willamette Valley, Oregon, contained an average by volume of 72.5% earthworms (Wight, 1928). The percent frequency of occurrence for each food item in the 306 stomachs was 85.6% earthworms, 30.7% earthworm cocoons, 31.0% insect larvae and pupae, 13.0% centipedes (Chilopoda), 2.6% each for slugs (Pulmonata) and adult insects, and 2.6% was categorized as miscellaneous which included a wild bulb, grain, and unidentified starchy granules (Wight, 1928). Contents of stomachs of 106 male Townsend's moles collected from 1961 to 1963 in Tillamook Co., Oregon, averaged 63.7% earthworms and 36.3% grass roots by volume and that of 76 female moles averaged 65.8% earthworms and 39.2% grass roots by volume (Whitaker et al., 1979). Thirty-six stomachs (19.8%) contained cylindrical (10 by 5 mm), dark brown, compact "root balls" (Whitaker et al., 1979:271). Insect exoskeletons were found in six (3.3%) stomachs and one stomach contained 100% slugs (Whitaker et al., 1979). Stomachs of 28 Townsend's moles collected from 1970 to 1972 in Tillamook and Benton counties, Oregon, contained earthworms (54.9% by volume, 92.9% frequency of occurrence), centipedes (1.4%, 32.1%), snails and slugs (1.6%, 17.9%), spiders (Araneae; trace, 3.6%), insect larvae (10.7%, 85.7%), insect pupae (0.2%, 10.7%), adult insects (2.0%, 53.6%), insectivore or mouse remains (2.1%, 7.1%), seeds (6.8%, 10.7%), other vegetation (9.4%, 60.8%), and unidentified material (11.0%, 42.9%—Whitaker et al., 1979). Stomachs of 42 Townsend's moles from Tillamook and Hillsboro, Oregon, and near the coastal border of Oregon and California contained an average volume of 76.1% earthworms, 5.6% two-winged flies (Diptera), 0.93% butterflies and moths (Lepidoptera), 0.5% centipedes, 0.3% beetles (Coleoptera), 0.07% bees, wasps, and ants (Hymenoptera), 0.002% crickets and grasshoppers (Orthoptera), a trace of spiders, and 15.9% vegetable matter (Moore, 1933). Vegetable matter was found in 57.1% of the 42 stomachs; tulip bulbs, tigridia bulbs, iris bulbs, garden peas, soft white wheat, sweet corn, Irish potatoes, parsnips, and carrots in addition to earthworms and insects were considered to form a substantial portion of the diet of the species (Moore, 1933). However, another authority indicated that Townsend's moles may eat succulent vegetation only when deprived of the large amount of water needed for survival (Wight, 1928). These moles may need to eat one-third to two-thirds their own mass daily (Cahalane, 1947) and one mole may eat ca. 18 kg of food each year (Wick and Landforce, 1962).

Neurotrichus gibbsii, *S. orarius*, and *S. townsendii* have different burrow depths and "habitat orientation" (Whitaker et al., 1979:271). These three species seem to partition the available food resources, thereby decreasing interspecific competition for food (Whitaker et al., 1979).

Townsend's moles construct extensive permanent tunnel systems 15-20 cm deep and some 1-3-m-deep tunnels are formed under fencerows, building foundations, and roadbeds (Silver, 1933; Wick and Landforce, 1962; Yates and Pedersen, 1982). Deeper tunnels may be used by more than one individual and are used more frequently than surface tunnels (Kuhn, 1970; Wick and Landforce, 1962; Yates and Pedersen, 1982). Shallow surface tunnels are constructed during foraging and generally are used only once (Cahalane, 1947; Kuhn, 1970; Wick and Landforce, 1962). These shallow tunnels range from 5.1 to 15.2 cm below the surface (Wick and Landforce, 1962). *S. townsendii* produces mounds of dirt on the surface of the ground along runway systems (Fig. 5); one male produced 302 mounds in 77 days (Nowak and Paradiso, 1983) and as many as 805 mounds/ha were reported (Yates and Pedersen, 1982). The mole mound is conical and often relatively cloddy (Wick and Landforce, 1962).

During the breeding season, spherical nesting cavities about 1,639 cm^3, with three to 11 tunnel entrances, are dug in areas of little disturbance such as along well-established fence lines (Kuhn et al., 1966; Pedersen, 1966; Wick and Landforce, 1962). These nesting cavities may or may not be reused by the same female mole in following years. Nesting cavities range from 7.6 to 50.8 cm deep; however, usually they are from 15.2 to 20.3 cm deep (Kuhn et al., 1966; Pedersen, 1966). Nursery nests usually are close enough to the surface of the ground to be warmed by the sun (Scheffer, 1949). The nest is constructed of an inner core of fine, dry grass and an outer core of grass, moss, or leaves usually still green and damp (Kuhn et al., 1966; Pedersen, 1966; Silver, 1933; Wick and Landforce, 1962). The outer cover is ca. 5 cm thick and is compact; additional fresh grass occasionally is added to the outside of the nest during the month that young are in the nest (Kuhn et al., 1966; Pedersen, 1966). As green vegetation on the outside of the nest decays, warmth is provided for the young moles in the nest (Kuhn et al., 1966; Pedersen, 1966). Nest cavities contain a bolt hole for escape; this tunnel leads from the bottom of the nest downward for several centimeters then turns upward and enters another tunnel or burrow (Kuhn et al., 1966; Pedersen, 1966). Shelter nests and nurseries are connected by deep runways (Scheffer, 1949). Many nests built in pastures are destroyed by farm machinery and cattle (Kuhn et al., 1966).

Because *Scapanus townsendii* is largely subterranean, it avoids most predation other than that by humans (Yates and Pedersen, 1982). Other documented predators on the Townsend's mole include the red-tailed hawk (*Buteo jamaicensis*—Roest, 1952; Silver, 1933), barn owl (*Tyto alba*—Giger, 1965), coyote (*Canis latrans*—Toweill and Anthony, 1988), great horned owl (*Bubo virginianus*—Maser and Brodie, 1966), "small weasels" (*Mustela* sp.—Silver, 1933:9), rubber boa (*Charina bottae*—Maser et al., 1981) and domestic dogs and cats (Kuhn, 1970; Maser et al., 1981). Neither dogs nor cats have been observed to eat moles that they kill (Maser et al., 1981; Silver, 1933). Stomach contents of more than 2,000 hawks and owls contained only 13 moles (Silver, 1933). The frequency of occurrence of remains of Townsend's moles found in fresh barn owl pellets, known to have been deposited during the previous month (n = 724), was approximately 17.0% in May, 4.0% in June, and 2.0% in December (Giger, 1965). All skulls (for which age could be determined) in pellets collected during May and June were those of juveniles (Giger, 1965) and 13 of 14 Townsend's moles killed on highways in Tillamook Co., Oregon, in June were juveniles (Pedersen, 1963). From this information, Giger (1965:6) concluded that "a marked amount of juvenile dispersal must therefore take place on the surface of the ground at night."

Recorded mammalian associates of *S. townsendii* are *Sorex trowbridgii*, *S. vagrans*, *Thomomys bulbivorus*, *Microtus canicaudus*, *M. oregoni*, *M. townsendii*, *Mus musculus*, *Ondatra zibethicus*, *Neotoma fuscipes*, *Peromyscus maniculatus*, *Zapus trinotatus*, and *Marmota olympus* (Couch, 1924; English, 1923; Giger, 1973; Hooven et al., 1975; Johnson and Yates, 1980; Kuhn et al., 1966; Wight, 1928).

Ectoparasites reported to infest *S. townsendii* include Acarina: chiggers: *Neotrombicula brennani* (Yates and Pedersen, 1982; Yates et al., 1979), *N. cavicola*, *N. microti* (Brennan and Wharton, 1950); other mites: *Proctolaelaps* sp., *Scalopacarus scapanus* (Fain and Whitaker, 1981), *Androlaelaps fahrenholzi* (Strandtmann, 1949; Whitaker and Maser, 1985; Whitaker et al., 1979; Yates and Pedersen, 1982; Yates et al., 1979), *Glycyphagus hypudaei*, *Protomyobia brevisetosa*, *Eulaelaps stabularis*, *Haemogamasus occidentalis*, *H. reidi* (Whitaker and Maser, 1985; Whitaker et al., 1979; Yates and Pedersen, 1982), *H. ambulans* (Keegan, 1951; Whitaker et al., 1979; Yates and Pedersen, 1982), *H. keegani* (Jameson, 1952; Whitaker and Maser, 1985; Yates and Pedersen, 1982), *H. liponyssoides occidentalis* (Keegan, 1951; Yates and Pedersen, 1982; Yates et al., 1979), *Echinonyssus blarinae* (Yates and Pedersen, 1982; Yates et al., 1979), *E. obsoletus* (Herrin, 1970; Whitaker and Maser, 1985; Whitaker et al., 1979; Yates and Pedersen, 1982), *Listrophorus mexicanus* (Whitaker and Maser, 1985; Whitaker et al., 1979), *Macrocheles polypunctatus* (Krantz and Whitaker, 1988), *Eadiea scapanus* (Fain and Whitaker, 1975; Whitaker and Maser, 1985; Whitaker fain et al., 1979), *Radfordia arborimus*, *Pygmephorus lutterloughae*, *P. mahunkai* (Whitaker and Maser, 1985), *Pygmephorus* sp. (Whitaker et al., 1979; Yates and Pedersen, 1982), *Bakerdania* sp., *Euryparasitus* sp. (Whitaker et al., 1979); and a tick: *Ixodes angustus* (Easton and Goulding, 1974; Yates and Pedersen, 1982; Yates et al., 1979); and Siphonaptera: fleas: *Catallagia charlottensis*, *C. s. sculleni* (Lewis et al., 1988), *Corypsylla ornata* (Easton, 1983; Hubbard, 1940*a*; Lewis et al., 1988; Yates and Pedersen, 1982; Yates et al., 1979), *Epitedia scapani* (Hubbard, 1940*b*; Lewis et al., 1988), *Foxella ignota recula*, *Megabothris abantis*, *Nearctopsylla genalis hygini* (Lewis et al., 1988); *N. jordani* (Hubbard, 1940*a*, 1949; Lewis et al., 1988; Yates and Pedersen, 1982; Yates et al., 1979); and *N. martyoungi* (Lewis et al., 1988).

Moles damage some crops by eating or pushing up roots and by covering aboveground portions of plants with mounds of soil (Maser et al., 1981; Yates and Pedersen, 1982). In 1961, *Scapanus townsendii* caused an estimated annual loss of $100,000 to dairy farmers in Tillamook Co., Oregon, as a result of their burrowing activity (Wick, 1961); forage for cattle was reduced from 10–50% because of mole activity. Other effects of mole infestation and causes of reduction in quantities of cattle forage and monetary loss to farmers are: equipment stoppage and breakdown during harvest operations, soil from mounds mixed with crops resulting in poorer quality silage, seedbeds created for weeds in the mounds, and excessive drying of plant roots because of the tunnels (Wick and Landforce, 1962; Yates and Pedersen, 1982). *Sorex* sp., *Mus musculus*, *Microtus oregoni*, *M. townsendii* (and other *Microtus*) frequently inhabit mole runways (Couch, 1924; Silver, 1933; Wight, 1928) and are among the primary causes of garden damage for which moles frequently are accused (Couch, 1924). Upon examination of 71 mole systems, 30 were appropriated by *M. townsendii*, 1 by a "ground squirrel," 1 by a "gopher," and 1 by "rats" (Wight, 1928:30).

Trapping by use of scissor-jaw, Cinch, squeeze, diamond-jaw, or choker-loop traps is the most effective control method for Townsend's moles restricted to relatively small areas; trapping moles is inefficient and uneconomical for large commercial areas (Gabrielson, 1921; Silver, 1933; Wick and Landforce, 1962; Yates and Pedersen, 1982). In the past, chemical agents (thallium sulfate, strychnine, sodium monofluoroacetate [1080], and phosphorus compounds) were the most common control methods for moles, but most of these are now restricted by state and federal licensing regulations (Kuhn, 1970; Wick and Landforce, 1962; Yates and Pedersen, 1982). Commercial baits currently available include grain laced with strychnine and zinc phosphide (Kuhn and Edge, 1990), but these must be applied by a registered applicator. Also, baits containing an anticoagulant (chlorophacinone or diphacinone) that inhibits normal platelet function and results in internal hemorrhaging (Yates and Pedersen, 1982) are available for private use. Bait placement in the tunnels is critical in successful mole control. Because the diet of moles consists largely of invertebrates the effectiveness of baits is low (W. D. Edge, pers. comm.). Unfortunately, other small animals that occupy mole tunnels frequently are killed in greater numbers than moles (Yates and Pedersen, 1982). Dairy farmers in Tillamook Co., Oregon, destroy many young moles by excavating breeding nests (Kuhn et al., 1966).

Marking of individuals with size 6 (19 by 3.5 by 0.5 mm) monel butt-end bands placed on the hind leg was satisfactory. However, size 5 (16 by 3.5 by 0.5 mm) bands placed on the narrow base of the tail were not (Giger, 1973).

Moles are beneficial because they aerate and mix the soil layers and eat a substantial number of insects, insect larvae, and other invertebrate pests (Kuhn and Edge, 1990). Mole skins were used for clothing accessories such as caps, purses, tobacco pouches, and garment trimmings from the 17th through 19th centuries (Yates and Pedersen, 1982). Shortly after World War I, each *Scapanus townsendii* skin was worth $0.50–0.60 in the fur market (Scheffer, 1949). During the time that mole skins were used as fashionable clothing accessories, the mole-skin business was a $2–3 \times 10^6$ industry annually (Scheffer, 1922). Skins of *S. townsendii* no longer are marketed commercially.

BEHAVIOR. Juvenile *S. townsendii* appear to move about on the surface of the ground frequently from April through July; this was hypothesized to be related to dispersal of juveniles from natal nests (Giger, 1965). There is an inverse relationship between distances traveled by dispersing juveniles and suitability of habitat (Giger, 1973). Of 24 adults captured twice, the average ($\pm SD$) distance traveled between points of capture was 23 ± 15.5 m (range, 3–57.6 m); 14 adults captured three or more times averaged 40.5 ± 28 m (range, 15–116 m—Giger, 1973). Adult Townsend's moles in dry pastures with low fertility tended to travel farther than moles in highly fertile pastures (Giger, 1973). Apparently, a high degree of intolerance for conspecifics is the norm as indicated by strong agonistic behavior when individuals come in contact. For adults with established home ranges and interconnecting tunnel systems, there is no overlapping of movements (Giger, 1973). The concept of "community highways" used by many individuals (Pedersen, 1963: 24) apparently was rejected by Giger (1973). Interconnecting tunnel systems may be extensive (Scheffer, 1949), but seem to serve only as avenues of dispersal (Giger, 1973). During severe flooding large numbers of individuals may crowd onto islands or road banks (Giger, 1973).

Fourteen of 32 Townsend's moles artificially displaced 34–455 m (some across canals, roadways, or rivers) successfully returned to their former home ranges (Giger, 1973). Rising waters in winter caused four marked individuals to move 113–149 m; all returned to their home areas when the water receded. However, 62 dead *S. townsendii* were found on the 150-ha study area in Tillamook Co., Oregon, following flooding, indicating that many "were unable to orient in the direction of higher ground, possibly because of poor eyesight" (Giger, 1973:656). Familiarity with runway systems, scent, and chance exploration were cited as possible factors involved in successful homing by Townsend's moles (Giger, 1973).

Townsend's moles are excellent swimmers and sometimes pass through flooded tunnels (Giger, 1965; Moore, 1939). Occasionally, *S. townsendii* makes tunnel casts in the snow in the manner of pocket gophers (Geomyidae—Moore, 1939), but they are not as extensive (M. L. Johnson, pers. comm.).

During the breeding season Townsend's moles can dig nest cavities in 5 days. The amount of digging required produces a large quantity of soil that the female may push into either one large nest mound 75–125 cm in diameter, or a set of small mounds within a 1.83–3.1-m area (Kuhn et al., 1966; Pedersen, 1966). Females usually abandon disturbed nest mounds before parturition (Pedersen, 1966), but usually not after parturition (Kuhn et al., 1966).

GENETICS. In 12 *S. townsendii* from Oregon and Washington, Yates and Greenbaum (1982) found no polymorphisms at 18 loci examined.

Aberrantly colored pelages were reported in *S. townsendii* (Klein, 1944; Bachman, 1839; Merriam, 1885). Of 663 museum specimens of Townsend's moles examined for color aberrations (Carraway and Verts, 1991): 154 contained one to several white or pale brown spots <5 mm in diameter; 33 had one to three yellow, reddish yellow, or pale brown, irregularly shaped splotches occupying <1–100% of the pelage; 3 had similar yellowish splotches on gray or brown dorsal and gray or light gray ventral pelage; 5 had mottled pelages of gray, brown, grayish brown, and yellow on both dorsum and venter; 1 was white shading to yellow anteriorally on the dorsum and white shading to reddish yellow on the venter; and 1 was reddish yellow blending to pale brown and yellow on the head (except for a grayish brown sigma-shaped blaze), left shoulder, and venter; and posterior to a line from the right shoulder to the left lower thoracic region was grayish brown. Carraway and Verts (1991) inferred from the absence of seasonality in the occurrence of aberrancies, their failure to remove yellowish coloration with a solvent, and the homogeneous yellowish coloration of a splotch bisected by a molt line that the yellowish coloration was not derived from a waxy secretion from sudoriferous glands during the reproductive season as suggested by Eadie (1954). They further suggested that the high prevalence of aberrant pelages indicated that adverse pleiotrophic effects, if present, were minor. However, the high prevalence and inconspicuousness of the small white spots and low prevalence of individuals with large yellow splotches (especially on the dorsum) indicated that Townsend's moles with conspicuous markings probably were selected against.

REMARKS. The generic name *Scapanus* was derived from the Greek prefix *skapanetes* meaning a digger (Jaeger, 1978). The specific name *townsendii* is a patronymic honoring J. K. Townsend at the request of T. Nuttall (Bachman, 1839).

The specimen of *Scapanus townsendii* used in Fig. 2 was provided by C. Alexander. M. L. Johnson and R. G. Schwab commented on an earlier draft of this manuscript. This is Technical Paper No. 9549, Oregon Agricultural Experiment Station.

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