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Neurotrichus gibbsii. By L. N. Carraway and B. J. Verts

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Neurotrichus Günther, 1880

Neurotrichus Günther, 1880:441. Type species Urotrichus gibbsii
Raird

CONTEXT AND CONTENT. Order Insectivora, Superfamily Soricoidea, Family Talpidae, Subfamily Talpinae, Tribe Urotrichini, Genus *Neurotrichus*. Honacki et al. (1982) recognized one living species.

Neurotrichus gibbsii (Baird, 1858)

Shrew-mole

Urotrichus gibbsii Baird, 1858:76. Type locality "White River [Pass], Cascade Mountains, W. T." Type locality restricted to Naches Pass, 4,500 ft., Pierce Co., Washington, by Dalquest and Burgner (1941:12).

Neurotrichus gibbsii: Günther, 1880:pl. 42; first use of current name combination.

CONTEXT AND CONTENT. Context same as for genus. Three subspecies are currently recognized (Hall, 1981):

N. g. gibbsii (Baird, 1858:76), see above (major Merriam, 1899, a synonym in part).

N. g. hyacinthinus Bangs, 1897:240. Type locality "Nicasio, Marin Co., Cal." (major Merriam, 1899, a synonym in part).

N. g. minor Dalquest and Burgner, 1941:12. Type locality "University of Washington campus, Seattle, [King Co.], Washington"

DIAGNOSIS. Neurotrichus is the only known vertebrate to possess a pigmented layer (the external layer of the pars ciliaris retinae) covering the anterior surface of the lens of the eye (Lewis, 1983). Neurotrichus is the only talpid known to possess a pair of ampullary glands and have external lobulation of the two bodies of the prostate gland (Eadie, 1951).

Shrew-moles may be distinguished from Scapanus (the only other sympatric talpid) by their much smaller size, 36 instead of 44 teeth, and the interior basal projection of M1 and M2 bilobed rather than single-lobed (Hall, 1981). Compared with Scapanus, Neurotrichus has forefeet only moderately modified for digging (Reed, 1951).

In the shrew-mole, the serratus anterior cervicis is divided into four distinct slips; in all other talpids the slips are fused (Campbell, 1939; Reed, 1951). The origins of the gemellus and quadratus femoris muscles in the shrew-mole are not fused as in *Scapanus* (Reed, 1951). *Neurotrichus* has a small medial trapezius that originates from the extreme posterior end of the nuchal ligament and inserts "into the tuberosity of the scapular spine immediately anterior to the insertion of the [posterior trapezius]"; apparently this muscle is absent in *Scapanus* and *Sorex* (Reed, 1951:616).

Neurotrichus can be distinguished from its nearest relative, Urotrichus, by the presence of six upper and seven lower molariform teeth (Fig. 1), a less hairy tail, no pinnae (Fig. 2), and an autosomal diploid number of 38 (Brown and Waterbury, 1971; Tsuchiya, 1979). The dental characters that distinguish Neurotrichus from Urotrichus are (Storch and Qiu, 1983:102): P2 is double-rooted, encircled by a cingulum, and has a posteriorly centered paracone; P4 and M1 each have an ectocingulum; M2 has a metacingulum connected to the metastyle; p3 is double-rooted with "a longitudinal groove along the posterior wall of the protoconid"; and p4 has a high metaconid and a posteriorly centered protoconid.

GENERAL CHARACTERS. Neurotrichus gibbsii is small (total length usually <120 mm) and has inconspicuous rudimentary eyes 0.7-1.0 mm in diameter (Lewis, 1983). The ears are composed of an external auditory meatus in the form of a slit parallel with the

body; they are positioned far back on the side of the skull between the forelegs. The nose, elongate and flattened dorsoventrally, is 4 mm wide and 2 mm deep at the incisors and extends 8 mm anterior to the incisors (Dalquest and Orcutt, 1942). Eight pairs of vibrissae 6-12 mm long are located about 5 mm anterior to the eyes. A fringe of bristles about 0.5 mm long occurs on the sides of the terminal 5 mm of the nose (Dalquest and Orcutt, 1942).

The digitigrade, pentadactyle feet are scaly. Tubercles on the soles of the forefeet are well developed and those of the hind feet

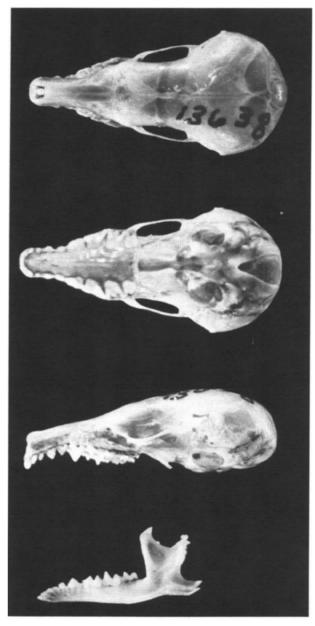


Fig. 1. Dorsal, ventral, and lateral views of the skull and lateral view of the mandible of an adult female *Neurotrichus gibbsii* (PSM 13638) from 2.88 km NNE Bandon, Coos Co., Oregon. Occipitonasal length of the skull is 20.77 mm.

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Fig. 2. Photograph of an adult *Neurotrichus gibbsii* from about 25 km E Eureka, Willow Creek, Humboldt Co., California.

poorly developed, opposite that of *Urotrichus* (Günther, 1880). The forefeet are equipped with long curved claws and have palms 4 mm wide, 5.4 mm long, and 2 mm deep (Dalquest and Orcutt, 1942). The forefeet are not webbed. The tail is about one-third of the total length, fat, sparsely haired, covered with transverse annular rows of scales (Jackson, 1915), and has a 4.4-mm-long tuft of hairs on its blunt end (Dalquest and Orcutt, 1942).

The pelage of *Neurotrichus* was described as nearly black (Cowan and Guiguet, 1975; van Zyll de Jong, 1983) to sooty blueblack (Banfield, 1974); it is not plush as in other moles (Banfield, 1974; Cowan and Guiguet, 1975). The hair of the tail is the same color as the body pelage.

Means and ranges (in parentheses) of external measurements (in mm), in order of total length, length of tail, and length of hind foot, for 85 specimens of N. g. minor from the type locality (Dalquest and Burgner, 1941) were: 107 (100-117); 35.3 (31-39); 15 (14-16). The same measurements for a sample of 48 from Bothell, King Co., Washington (Dalquest and Burgner, 1941) were: 104.4 (100-112); 34.7 (30-39); 14.3 (13-16). For two specimens of N. g. hyacinthinus from the type locality (Bangs, 1897) these measurements averaged: 123.8, 39.7, and 17. The same dimensions for a series of 33 N. g. gibbsii from Sumas, British Columbia (True, 1896) were: 113.6 (maximum 123); 37.1 (maximum 41.5); 16.6 (maximum 17.5); for two specimens from Tye, Stevens Pass, King Co., Washington (Dalquest and Burgner, 1941) the external measurements were: 121.5 (121-122), 45, 18. The external measurements for a N. g. gibbsii from Hope, British Columbia were 125, 42, 17.5 (Dalquest and Burgner, 1941) and ranges of measurements of shrew-moles from Oregon were 100-126, 32-50, 14-17 (Maser et al., 1981). Although Hall (1981), Nowak and Paradiso (1983), and Yates and Pedersen (1982) stated that pinnae are absent in all North American talpids, Maser et al. (1981) indicated that shrewmoles have pinnae 2-6 mm long obscured by dense fur. The external measurements for N. g. major from the type locality (Jackson, 1915) were: 119.7 (118-121), 40.3 (39-42), 17. There is no sexual dimorphism (Yates and Pedersen, 1982).

Means and ranges (in parentheses) of cranial measurements (in mm) for 25 topotypes of N. g. minor (Dalquest and Burgner, 1941) were: greatest length of skull, 21.7 (21.1-22.3); interorbital breadth, 5.1 (4.9-5.3); cranial breadth, 9.9 (9.7-10.0); length of maxillary toothrow, 9.7 (9.5-10.0); breadth of maxillary toothrow, 5.8 (5.4-6.0). The same dimensions for two N. g. gibbsii from Stevens Pass, King Co., Washington (Dalquest and Burgner, 1941) were: 23.5; 5.4 (5.3-5.5); 10.5; 10.5 (10.4-10.5); 6.0 and for the specimen from Hope, British Columbia, 23.7, 5.5, 10.5, 10.5, and 6.3. For N. g. hyacinthinus, only measurements for the type specimen have been published (Bangs, 1897): basilar length, 19.8 and mastoid breadth, 11.4. Means of these same dimensions for 18 N. g. gibbsii from Sumas, British Columbia (True, 1896) were: 18.4 and 10.2. Length and width (in mm) for some osteological elements were (Campbell, 1939): sternum, 6.5, 3.2; scapula, 12.2-12.6, 2.8-2.9; and humerus, 6.5-7.0, 1.5. Clavicle length was 3.5-3.6 mm (Campbell, 1939); however, Skoczeń (1980) reported a length of 4.08 mm. Length of the radius was 7.55-8.40 mm and its proximal width was 1.57-1.84 mm (Skoczeń, 1980).

The average body mass (Dalquest and Orcutt, 1942) of shrew-moles was 10 g (range, 9.5–10.5); however, Terry (1978) reported an average ($\pm SE$) of 7.8 \pm 0.5 g (n=4). The brain mass of shrew-moles calculated from cranial volume was 0.91 g (Mace et al., 1981).

DISTRIBUTION. Shrew-moles occur (Fig. 3) from the Fraser River region of British Columbia (van Zyll de Jong, 1983) south to Fremont Peak, Monterey Co., California, and from the Cascade and Sierra Nevada mountains of Washington, Oregon, and California (2,440 m elev.) west to the Pacific Ocean (Hall, 1981; Jackson, 1915). Williams (1975) provided extralimital records for Neurotrichus; however, these records are now within the recognized geographic distribution of Neurotrichus (Fig. 3). Shrew-moles also occur on Destruction Island, Washington (Aubry and West, 1984; Dalquest, 1948).

FOSSIL RECORD. Neurotrichus is Asiatic in origin. The oldest known ancestor for Neurotrichus is Quyania chowi from Ertemte 2, Huade Co., Inner Mongolia Region, China (Storch and Qiu, 1983) from the Upper Miocene or Lower Pliocene. Neurotrichus ?polonicus, found in Lower Pliocene to Middle Pleistocene deposits of Rebielice Królewskie I, Zamkowa Dolna Cave, and Kadzielnia, Poland, is thought to be an extinct phyletic lineage parallel to N. gibbsii (Skoczeń, 1980; Storch and Qiu, 1983). The Hemphillian form ?Neurotrichus columbianus from McKay Reservoir, Umatilla Co., Oregon (Hutchison, 1968), is considered to be closely related to Yanshuella primaeva (Tribe Scalopini) from Ertemte 1, Huade Co., Inner Mongolia Region, China. Storch and Qiu (1983) referred ?N. columbianus to Yanshuella columbiana and considered it a Hemphillian contemporary of N. gibbsii. No Pleistocene fossils of N. gibbsii are known (Kurtén and Anderson, 1980).

FORM AND FUNCTION. The rudimentary eyes of shrew-moles are characterized by "markedly proliferated tissue[s] of the central part of the iris, the loss of the vitreous body with collapse of the globe upon the lens and retina, the embryonal structure of the lens, the loss of rods and cones, the loss of any proximal bony attachment of the extraocular muscles, and the absence of a palpebral aperture" (Lewis, 1983:11). There is no Bowman's membrane, tenon's capsule is thin and occurs only posterior to the conjunctival angle, the conjunctival sac is broad and lined with epithelial cells, the sclera consists of 7-12 layers of fibroblasts, and the cornea is almost indistinguishable from the sclera (Lewis, 1983).

The shape of the stomach in Neurotrichus gibbsii is typical of that of soricids, but the relative percent area covered by particular glandular zones is fairly typical of other talpids (Myrcha, 1967). The pyloric region, unlike that of other talpids, is straight and elongated as in soricids. Shrew-moles have the smallest percent area of cardiac glands (1.1%) and of pyloric glands (4.0%), and the greatest percent area of fundic glands (89.2%) of 27 species of insectivores examined (Myrcha, 1967). A transition zone that contains parietal cells and no chief cells is located between each of the glandular areas; it comprises 5.7% of the stomach structure (Myrcha, 1967). The average area of the stomachs of five individuals was 3.52 cm² (Myrcha, 1967).

In Neurotrichus, the small size of the metacromion-acromion is related to the absence of the anterior atlanto-scapularis muscle and is associated with shortened clavicles and a stronger humeral-clavicular joint, thus allowing for a tighter anchoring of the anterior end of the scapula (Reed, 1951). Because the distal ends of the radius and ulna are twisted nearly 90°, the long axes of "the distal articular surfaces lie nearly at right angles to the proximal crest of the olecranon" (Reed, 1951:549), a condition intermediate between Sorex and Scapanus; however, the diaphysis of the radius and ulna remains long and slender. A sesamoid cap is located in the lateral tip of the venare "within the tendon of the [ulnar carpal muscle] where the tendon crosses the ulnare" (Reed, 1951:555). The manubrium is less than half as wide as long, and possesses a highkeeled ventral ridge, clavicular articulations on the anterior end of the dorsal surface, and a large anterior head. Shrew-moles also have exaggerated anterior expansions on the wings of the manubrium that serve as the origin for a portion of the subclavian muscle. The clavicles are compressed anteroposteriorly, the posterior half being elongated, and are 2.5 times as long as high (Reed, 1951). The ventral edge has two spines, the proximal for attachment of the sterno-clavicular ligaments and the distal serving as both the insertion for the ventral portion of the subclavius and origin of the proximal segment of the cleido-mastoid muscle. At the vertebral end of the scapula the suprascapular fossa is separated from the rhomboidal area; however, these surfaces are continuous in Scapanus (Reed,

The humerus has an indistinct pectoral crest and pectoral ridge, a poorly developed medial epicondyle, and a small brachialis fossa

(Campbell, 1939). From the shaft, the long axis of the head of the humerus points laterodistally at an angle of 25° in *Neurotrichus*, but points mediodistally at an angle of 20° in *Scapanus* (Reed, 1951). The sacrum is composed of five fused vertebrae; from the first to the third vertebrae is the ankylosed sacroiliac joint.

The head is turned and elevated by the splenius muscle which has one slip that originates on the nuchal ligment and inserts on the occipital bone, as in Scapanus, and a lateroposterior slip that originates on the anterior portion of the middorsal raphe of the posterior rhomboideus muscle and extends forward inserting into the first section of the splenius (Reed, 1951). The superior posterior-serratus muscle aids in elevating the ribs and bracing the posterior rhomboideus muscle in fossorial animals. In Neurotrichus, the superior posterior-serratus muscle originates from the third rib; in Sorex it originates from the muscle on both sides of the medial raphe of the thoracic vertebrae and, in Scapanus, on the third and fourth ribs. Neurotrichus and Scapanus do not have the anterior atlanto-scapularis muscle present in Sorex. The posterior rhomboideus muscle is not tendinous so it must contract with each digging stroke for the scapulae to be held together; in Scapanus, an interscapular ligament serves to hold the scapulae together (Reed, 1951).

Neurotrichus is able to elevate the humerus when burrowing or depress it during digitigrade locomotion because shrew-moles lack the pectoralis profundus muscle; Scapanus possesses this muscle, thus has less freedom of movement when burrowing (Reed, 1951). In the shrew-mole, the subscapularis muscle, which acts as a rotator of the humerus, is divided into a large head originating from an intermuscular septum beyond the coracoid border and a small head originating from the axillary border of the scapula. In Scapanus, this muscle has only one head originating in the intermuscular septum (Reed, 1951).

In Neurotrichus, the second through fourth digits and the hand at the wrist are flexed by the three heads of the flexor digitorum sublimus muscle as in Sorex; however, in Scapanus only one head, the flexor of the hand, is present (Reed, 1951). In the shrew-mole, the flexor digitorum profundus muscle is composed of five muscular heads, associated with a large ligament, with a common tendon that passes from the olecranon onto the palm; at the palm, the common tendon divides into five sections, each continuing into a digit to the distal phalanx (Reed, 1951). There is no transverse carpal ligament in the palm as in Sorex. In Scapanus, the muscle has only three heads, two of which are extremely small. The smaller size of the muscular heads is in response to the greater fossorial adaptation in Scapanus (Reed, 1951).

The falciform process of the tibia is thin and serves as the sole origin of the tibialis anticus muscle; the same muscle originates from both the process and the anterior surface of the tibia in Scapanus. This muscle elevates the skeleton at the shoulder joint in Neurotrichus; in Scapanus, the muscle has degenerated and is of limited use. The lateral process of the fibula is a delicate bar turned away from the tibia to such an extent "that its head fits into a groove on the lateral epicondyle of the femur" (Reed, 1951:577). In the knee joint of Neurotrichus, there is no ligamentous attachment between the lateral epicondyle of the femur and the proximal tip of the lateral process of the fibula; in Scapanus, there is a weak, and, in Sorex, a strong, ligamentous connection in the knee joint.

The origin of the intrinsic muscles of the foot is the proximal metatarsal sesamoid that lies on the proximal end of the plantar surface of the third through fifth metatarsals (Reed, 1951). The peroneus digiti quarti muscle acts as an extensor and abductor of the fourth digit in Neurotrichus; however, it acts only as an extensor in Sorex. Unlike Scapanus, the flexor digitorum fibularis muscle in the shrew-mole, which acts as a "flexor for the five digits and ventroflexor of the pes," has two separate bipinnate heads (Reed, 1951: 611). A single tendon from each head extends along the posterior surface of the shank of the fibula and the two tendons unite at the calcaneus. The width of the hind foot is 21.9% of its length in Neurotrichus (Reed, 1951).

The anterior trapezius is a well-developed, flat, triangular muscle that originates on the occiput and inserts on the acromion in shrew-moles. The latissimus dorsi muscle originates on the ribs, instead of the eighth or ninth thoracic spines as in most moles, and fuses with the teres major near the point of insertion. Unlike most moles, Neurotrichus has only a two-division rhomboideus thoracis muscle. The interscapularis muscle is fleshy instead of ligamentous. The panniculus carnosus muscle is one unit instead of dorsal and ventral segments, inserts entirely on the pectoral ridge, and is only

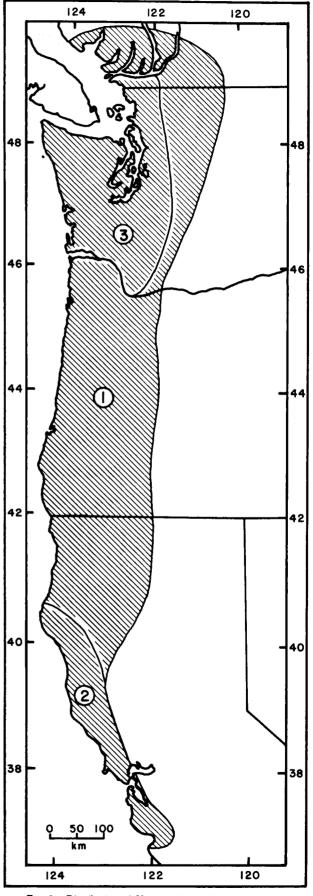


Fig. 3. Distribution of *Neurotrichus gibbsii*. Subspecies are: 1, *N. g. gibbsii*; 2, *N. g. hyacinthinus*; and 3, *N. g. minor*.

moderately developed. The strongly developed subclavian muscle originates on the second rib and on the side of the sternal keel and wing. The subscapularis is a simple one-unit muscle that originates on the subscapular fossa and inserts only on the lesser tuberosity. Origin of the teres major muscle is restricted to the vertebral end of the posterior margin of the scapula (Campbell, 1939).

Neurotrichus gibbsii has a typical mammalian ovary (Mossman and Duke, 1973); it is globose-shaped, located in the lumbar region, and has only a few lobes and a medium-sized rete. There is a complete bursa ovarica and a small epoophoron. The interstitial-gland tissue, composed of gonadal-adrenal type cells, of the ovarian medulla is a continuation of that associated with the epoophoron; it also "surrounds the rete at the hilus and extends to the cortex" (Mossman and Duke, 1973:199). In the ovarian medulla, the interstitial-gland tissue is intermingled with persistent medullary cords. Neurotrichus has a discoid placenta (Prasad et al., 1979). Mammae are arranged one pair pectoral, two pairs abdominal, and two pairs inguinal (Racey, 1929).

Accessory reproductive glands of male shrew-moles are composed of one large pair of ampullary glands, a bilobed prostate gland, a pair of Cowper's glands, and large perineal glands (Eadie, 1951). There are no seminal vesicles, preputial glands, or inguinal glands. When in breeding condition, the testes and epididymides may occupy cremaster sacs. The cauda epididymis is formed from the proximal end of the ductus deferens and contains a sperm reservoir. The posteriorly directed penis in 5 mm long (Günther, 1880) and terminates at a genital papilla "separated from a prominant anal papilla by a distinct perineal space" (Eadie, 1951:38). The penis is slightly enlarged on the end; it has longitudinal grooves, a surface covered with sharp, posteriorly directed, horny spines, and no baculum (Eadie, 1951). The spiny area ends at a truncated ridge that lies immediately posterior to the urethral opening. A narrow-pointed process projects terminally over the urethral opening. Located ventrolaterally to the bladder is the prostate gland that "consists chiefly of two lateral masses or lobes which are divided externally into finger-like lobules, giving the prostate a villous appearance reminiscent of the prostate in the shrew genus Sorex" (Eadie, 1951:38-39). The lobes of the prostate in shrew-moles are more coarse than in Sorex. Each lobe is drained by a pair of ducts into the urethra. The corpora amylacea are "involved in the formation of an unusual type of copulatory plug" in the female (Eadie, 1951:40); however, Eadie (1951) and subsequent authors did not describe the "unusual" nature of the plug. Cowper's glands of Neurotrichus are similar to those found in other moles and shrews in that they are located external to the body cavity with one on either side of the base of the tail, are shaped like a flattened ellipsoid, and have a layer of striated muscle that surrounds the compact, compound tubular-gland body. The large perineal scent glands are located dorsolaterally to the body of the penis and are composed of "an antero-ventral portion of probable sudoriparous origin and merocrine in type, and a posterio-dorsal portion of probable sebaceous origin and holocrine in type" (Eadie, 1951:40). The ducts of the glands end "on a small secondary papilla located on the anterior face of the large anal papilla" (Eadie, 1951:40).

Hairs of the shrew-mole are characterized by a poorly defined tumescent area, a gradually attenuated tip, a cortex with pigment adjacent to the medulla, a distinct cuticle, and a medulla thicker than the cortex and cuticle combined (Williams, 1938). Guard hairs are 10 mm long, ovoid, and about twice the diameter of the fur hairs (Williams, 1938).

The dental formula is i 3/3, c 1/1, p 2/2, m 3/3, total 36 (Ziegler, 1971). P1 and p1 have been lost, but it is uncertain if the remaining missing cheekteeth are P2 and p2 or P3 and p3 (Ziegler, 1971).

ONTOGENY AND REPRODUCTION. The breeding season for Neurotrichus is exceptionally long as a male in breeding condition was captured in February and two lactating females were captured in September (Dalquest and Orcutt, 1942). Most breeding occurs from early March to mid-May, but in this period almost 95% of the specimens taken were not in breeding condition. Litter size, based on counts of embryos of 1, 3, 3, 3, 4, and 4 (Dalquest and Orcutt, 1942; Racey, 1929) averaged 3.0. Length of gestation is unknown.

Neonates are pink, naked (lacking even vibrissae), and with no visible external opening to the ears. A 1-h-old neonate measured (in mm): total length, 26.0; length of tail, 5.0; and length of hind foot, 3.6; it weighed 0.67 g (Dalquest and Orcutt, 1942). There is no nail development on the digits at birth (Kritzman, 1972).

ECOLOGY. In Washington, Neurotrichus occurs in moist habitats with soft earth free of sod from sea level to 2,440 m (Dalquest, 1948). At lower elevations shrew-moles are most abundant in ravines characterized by black silt, usually >30.5 cm deep and with high content of humus (Dalquest, 1941, 1948; Dalquest and Orcutt, 1942; Terry, 1981). The dominant vegetation of these ravines (Dalquest and Orcutt, 1942; Terry, 1981) is big-leaf maple (Acer macrophyllum), vine maple (Acer circinatum), alder (Alnus oregona), flowering dogwood (Cornus nuttallii), red elderberry (Sambucus racemosa), salmonberry (Rubus spectabilis), thimbleberry (Rubus parviflorus), Devil's club (Oplopanax horrida), trailing blackberry (Rubus ursinus), Oregon grape (Berberis nervosa), sword fern (Polystichum munitum), mosses, and where standing water or mud occurs, skunk cabbage (Lysichiton americanum). Typically, ravine bottoms that support shrew-moles are covered with a layer of twigs and dead leaves interspersed with rotting logs and tree stumps.

Less commonly in Washington, shrew-moles occur in lake-shore swamp habitat that includes cat-tail (Typha) marshes, grassy meadows, and willow (Salix) thickets. Neurotrichus is found in the willow-thicket portions of these swamps (Dalquest and Orcutt, 1942). The soil of this habitat is soft with a duff of twigs and dead leaves. The water table is usually within 25-50 mm of the duff. On rare occasions, Neurotrichus is found in logged areas where the soil is dry, stony, and hard (Dalquest and Orcutt, 1942), in dry woods, or on burned-over land (Dalquest, 1941).

Following introduction of the European rabbit (Oryctolagus cuniculus) onto Destruction Island in about 1970, population levels of shrew-moles declined. This decline was attributed to habitat alteration and destruction of vegetation by the rabbits (Aubry and West, 1984).

In Oregon, Neurotrichus is most common in riparian alder and alder-salmonberry habitats (Maser et al., 1981). Less frequently shrew-moles occur in mature and immature conifer, riparian hard-wood, Sitka spruce (Picea sitchensis) with salal (Gaultheria sp.), skunkcabbage marsh, wet pastureland, headland prairie, and headland shrub habitats (Maser et al., 1981). Neurotrichus also occurs in montane areas with a low cover of lichen and few snags (Doyle, 1990). Shrew-moles were collected from July to September in coniferous forest composed primarily of Douglas fir (Pseudotsuga menziesii) on the Trojan Nuclear-Power Station near Prescott, Columbia Co., Oregon; however, none was collected in meadows composed of perennial grasses (Hedlund and Rickard, 1976).

In California, shrew-moles occur in habitats characterized by coast redwood (Sequoia sempervirens), near wet meadows, along streams, and at edges of forests within the narrow and humid coastal zone (Grinnell, 1933). Shrew-moles inhabit areas of virgin forest and occasionally occur in logged areas (Tevis, 1956).

Shrew-moles from forested areas in Washington treated with sewage sludge as fertilizer had liver and kidneys, respectively, with significantly higher levels (mg/kg) of cadmium ($\bar{X}=31$, range, 17-55; $\bar{X} = 65$, range, 33-128) and lead ($\bar{X} = 1.4$, range, 1.1-1.8; $\bar{X} = 8.6$, range, 7.2-10), but not of copper ($\bar{X} = 25$, range, 18-32; $\bar{X} = 30$, range, 26-34) or zinc ($\bar{X} = 93$, range, 77-113; $\bar{X} =$ 120, range, 96-150), than those from the five untreated areas combined (cadmium, $\bar{X}=5.5$, range, 0.1-30, $\bar{X}=15.3$, range, 0-110; lead, $\bar{X} = 0.38$, range, 0-1.0, $\bar{X} = 2.8$, range, 0.6-6.1; copper, $\bar{X}=22.2$, range, 15-39, $\bar{X}=25.9$, range, 14-73; and zinc, $\bar{X}=85.8$, range, 61-110, $\bar{X}=100.4$, range, 77-129— Hegstrom and West, 1989). However, no physiological damage caused by high levels of cadmium (Cd) and lead was detected. It is not known if the high levels of cadmium present in shrew-moles exposed to sludge are the result of "biomagnification along food chains or reflect high concentrations found in their invertebrate prey"; however, "the significance of the high levels of Cd found in . shrew-moles . . . may be in the transfer of Cd to their predators' (Hegstrom and West 1989:348).

In favorable habitats, the population size is about 12-15 animals/ha. However, densities as great as 247 Neurotrichus/ha were achieved after removal of all other small mammals (Dalquest and Orcutt, 1942).

The diet of N. gibbsii from western Oregon contained 11 items among which earthworms (Annelida) occurred most frequently (81.8%) and constituted the greatest volume (48.5%) of contents of 11 stomachs examined (Whitaker et al., 1979). The remainder of the foods eaten (percent frequency, percent volume) were centipedes (Chilopoda, 54.5%, 4.3%), snails and slugs (Mollusca, 9.1%, 4.1%), insects (Diptera, 45.5%, 9.9%, Coleoptera, 45.4%, 11.4%), un-

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identified insects (36.4%, 13.6%), and unidentified vegetation (18.2%, 0.6%). In September, the diet of Neurotrichus in the Cascade Mountains, Washington, was 75-88% invertebrates; by July, conifer seeds (36%) and lichens (32%) contributed the most to the diet (Gunther et al., 1983). Remnants of ingested food items occur in the feces within 35-40 min of ingestion (Banfield, 1974).

Mammalian associates of shrew-moles (Dalquest, 1941; Dalquest and Orcutt, 1942, Moore, 1940, 1942; Ostfeld and Klosterman, 1986; Terry, 1978, 1981; West, in press; S. D. West, in litt.) include Sorex bendirii, S. bairdii (Carraway, 1990), S. monticolus, S. pacificus, S. palustris, S. trowbridgii, S. vagrans, Scapanus orarius, S. townsendii, Aplodontia rufa, Tamias amoenus, T. townsendii, Tamiasciurus douglasii, Glaucomys sabrinus, Thomomys bottae, Reithrodontomys megalotis, Peromyscus maniculatus, P. oreas, Clethrionomys californicus, C. gapperi, Microtus californicus, M. longicaudus, M. oregoni, M. townsendii, Phenacomys longicaudus, Zapus trinotatus, Mustela erminea, and M. frenata.

Shrew-moles are preyed upon by Tyto alba, Bubo virginianus (Giger, 1965; Maser and Brodie, 1966), Aegolius acadicus (Forsman and Maser, 1970), and Canis latrans (Toweill and Anthony, 1988) in Oregon. Tyto alba also was reported to prey on shrewmoles in San Benito Co., California (von Bloeker, 1937) and at Crescent Beach, British Columbia (Cowan, 1942). In Washington (Dalquest and Orcutt, 1942), shrew-moles were found in stomach contents of Thamnophis o. ordinoides, Buteo borealis calurus, and Procyon lotor, and in pellets regurgitated by Otis asio. Shrew-moles are captured with equal frequency with old or new models of the museum special snap trap (West, 1985).

Capillaria maseri (Nematoda-Rausch and Rausch, 1973) and Eimeria heterocapita, E. neurotrichi, E. parastiedica, and Isopora neurotrichi (Coccidia: Eimeriidae-Duszynski, 1985) are the only endoparasites recorded from Neurotrichus. Recorded ectoparasites are Acarina: Hirstionyssus obsoletus (Jameson, 1950), H. utahensis (Jameson, 1950; Jameson and Brennan, 1957; Whitaker et al., 1979), Ixodes soricis (Easton and Goulding, 1974), I. angustus (Yates et al., 1979), Androlaelaps fahrenholzi (Yates et al., 1979), Haemogamasus liponyssoides hesperus (Radovsky, 1960), H. keegani (Jameson, 1952; Jameson and Brennan, 1957; Keegan, 1951; Whitaker et al., 1979), and H. occidentalis (Keegan, 1951; Whitaker et al., 1979), Bakerdania sp. (Whitaker et al., 1979), Eadiea neurotrichus (Jameson, 1949; Lukoschus et al., 1980; Whitaker et al., 1979), E. brevihamata (Jameson, 1949; Whitaker et al., 1979), Euryparasitus sp. (Whitaker et al., 1979), Eutalpacarus peltatus (Jameson, 1949; Whitaker and Maser, 1985; Whitaker et al., 1979), Laelaps kochi, Pseudoparasitus sp., and Pygmephorus johnstoni (Whitaker and Maser, 1985; Whitaker et al., 1979), P. forcipatus, P. horridus, P. plurispinosus, and P. whitakeri (Cudmore et al., 1987); Coleoptera: Leptinus occidentamericanus (Peck, 1982) and L. testaceus (Maser and Hooven, 1971); and Siphonaptera: Epitedia jordani (Hubbard, 1940b), E. scapani (Easton, 1983; Lewis and Maser, 1981; Yates et al., 1979), Catallagia sculleni chamberlini, Corypsylla jordani (Easton, 1983; Hubbard, 1940a, 1940c; Lewis and Maser, 1981; Yates et al., 1979), and C. ornata (Yates et al., 1979).

BEHAVIOR. Shrew-moles are active at all hours; they rest or sleep for 1-8 min at 2-18 min intervals (Dalquest, 1948; Dalquest and Orcutt, 1942). They are agile, but move about slowly and cautiously when not beneath cover. When startled, they rush to the nearest cover where they remain motionless for a minute or less (Dalquest and Orcutt, 1942). Neurotrichus is an active, agile, and deliberate climber. It descends from sticks or shrubs backwards. Shrew-moles are not known to jump. In captivity, a shrew-mole in climbing a twig examined bottoms of all leaves for insects (Dalquest and Orcutt, 1942).

Shrew-moles are powerful swimmers. The feet on each side of the body move alternately, thus creating an undulating motion of the body and tail (Dalquest and Orcutt, 1942).

Neurotrichus is completely blind and uses its long, prehensile nose to locate prey (Dalquest and Orcutt, 1942). When a prey item is located a shrew-mole taps its nose on the ground directly in line with the prey, then 40° to one side, then 40° to the other side; finally the shrew-mole moves one step forward (Dalquest and Orcutt, 1942). This process is repeated rapidly until the prey item is touched by the nose (Maser et al., 1981).

Captured earthworms were either bitten along their entire length and eaten, bitten over short sections and eaten (repeating the process section by section), or cut into small pieces and eaten. Shrew-moles used their nose to jerk insect pupae and isopods off balance after which the prey were "pounced upon and eaten completely" (Dalquest and Orcutt, 1942:394).

In captivity, shrew-moles emitted faint, high-pitched vocalizations audible only at short distances (Reed, 1944). Sounds from 8-30 kHz elicit a response from Neurotrichus (van Zyll de Jong, 1983). The role of sound in the behavior of shrew-moles is unknown.

A complex and interlocking network of runways are the primary avenues for hunting and movement of Neurotrichus. These runways are about 40 mm wide and 20 mm deep and appear as shallow troughs just beneath the duff (Dalquest, 1948; Dalquest and Orcutt, 1942). Less often, shrew-moles build narrow burrows ≤28 mm in diameter. Burrows usually are within 1.2-12.7 cm of the surface (Racey, 1929), but are never >30.5 cm from the surface (Dalquest and Orcutt, 1942). Small openings are made to the surface (ventilation ducts) at intervals along burrows; these occur above sleeping chambers (Dalquest and Orcutt, 1942). Burrows are dug by pushing dirt aside by lateral movements of the forefeet, a technique similar to that used by other talpids. Because the soil is soft, the dirt pushed aside is packed into the wall of the burrow instead of being pushed out of the burrow to form mounds as by Scapanus (Dalquest and Orcutt, 1942).

Neurotrichus is gregarious by nature (Dalquest and Orcutt, 1942; van Zyll de Jong, 1983); the former authors suggested that shrew-moles traveled in bands that may contain >11 animals. These bands appear to enter an area and remain for several hours to several days then move to another area. No information is available about size of home range or territory.

GENETICS. A female Neurotrichus gibbsii had an autosomal diploid number of 38 and a fundamental number of 72 (Brown and Waterbury, 1971). All of the chromosomes are biarmed. Yates and Greenbaum (1982) reported that shrew-moles had the highest average heterozygosity (0.05), based on examination of 18 loci of 10 specimens from two localities, of any North American talpid; three loci were polymorphic. However, after examination of = 21.9 loci of 28 specimens from several localities, Yates and Moore (1990) reported an average heterozygosity of 0.023. They determined that levels of average heterozygosity varied significantly from population to population (T. L. Yates, pers. comm.)

REMARKS. The generic name Neurotrichus is from the Greek prefix ne meaning not, oura meaning the tail, and thrix genitive trichos meaning hair (Jaeger, 1978); presumably this is in reference to its sparsely haired tail relative to that of Urotrichus Günther, 1880). The specific name gibbsii is a patronymic honoring George Gibbs who collected the type specimen.

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