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Scapanus latimanus.

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Scapanus latimanus (Bachman, 1842)

Broad-footed Mole

Scalopus latimanus Bachman, 1842:34. Type locality "Santa Clara, [Santa Clara Co., California]" (vide Osgood 1907:52).
Scalops californicus Ayres, 1856:53. Type locality designated as "San Francisco, [San Francisco Co.,] California" by Jackson (1915:64).
Scapanus townsendii Peters, 1863:656. Misnaming of original type in Berlin Museum.
Scapanus dilatus True, 1894:242. Type locality "Fort Klamath, [Klamath Co.,] Oreg[on]."
Scapanus californicus True, 1896:52. Type locality "San Francisco, [San Francisco Co.,] California."
Scapanus latimanus Osgood, 1907:52. First use of name combination.

CONTEXT AND CONTENT. Order Insectivora, family Talpidae, subfamily Talpinae, tribe Scalopini, genus *Scapanus*, subgenus *Scapanus* (Hutchison 1987; Hutterer 1993; Yates 1984). Twelve subspecies are recognized currently (Hall 1981):

S. l. anthonyi Allen, 1893:200. Type locality "San Pedro Martir Mountains (alt. 7000 ft.), [Baja California, Mexico]." Ceballos and Navarro (1991) listed *anthonyi* as a distinct species but did not provide a published reference for the taxonomic change.
S. l. campi Grinnell and Storer, 1916:1. Type locality "Snelling, 250 feet altitude, Merced County, California."
S. l. caurinus Palmer, 1937:290. Type locality "Laytonville, Mendocino County, California."
S. l. dilatus True, 1894:242, see above (*truei* Merriam and *alpinus* Merriam are synonyms).
S. l. grinnelli Jackson, 1914:56. Type locality "Independence (altitude, 3,900 feet), Inyo County, California."
S. l. insularis Palmer, 1937:297. Type locality "Angel Island, San Francisco Bay, Marin County, California."
S. l. latimanus (Bachman, 1842:34), see above.
S. l. minusculus Bangs, 1899:70. Type locality "Fyffe, El Dorado Co., California."
S. l. monoensis Grinnell, 1918:423. Type locality "Taylor Ranch, two miles south of Benton Station, Mono County, California."
S. l. occultus Grinnell and Swarth, 1912:131. Type locality "Santa Ana Cañon at 400 feet altitude, Orange County, California."
S. l. parvus Palmer, 1937:300. Type locality "Alameda, Alameda County, California."
S. l. sericatus Jackson, 1914:55. Type locality "Yosemite, Mariposa County, California."

DIAGNOSIS. *Scapanus latimanus* (Fig. 1) can be distinguished from other members of the genus by its dark brown to silvery gray pelage (often with a coppery or brassy wash), unevenly spaced unicuspid teeth (especially the appression of U5 and U6), and relatively short and broad rostrum (Hall 1981; Ingles 1954; Jackson 1915; Verts and Carraway 1998). Winter pelage usually is darker (Jackson 1915) and individuals from semiarid areas are lighter in color than those from humid montane regions (Palmer 1937). Tail is nearly covered with silvery hair to tip and short hairs extend nearly to end of snout (Ingles 1965), distinguishing *S. latimanus* from other members of the genus. Aberrantly colored (e.g., light cinnamon yellow) individuals occur (Miller 1921).

GENERAL CHARACTERS. The broad-footed mole has a relatively short cylindrical body; conical, depressed head; long, pointed snout; crescentic, superior nostrils; minute eyes concealed by fur; small auricular orifices; keeled sternum (manubrium; Fig. 2a); short, stout legs; wide, scantily haired, and horny manus (Fig. 2b) permanently turned outward (Fig. 1) and widened by the os falciforme attached to the 1st digit; long, wide nails on the manus; relatively diminutive pes (Figs. 1 and 2c) with shorter, more pointed nails; and short, plush-like pelage (Ingles 1965; Jackson 1915; Sumner and Dixon 1953). Penis is directed posteriorly and scrotum is a slight bulge in the skin (Nowak 1991). Pinnae are absent (Hall 1946; Ingles 1965; Nowak 1991) and "auditory meatus [is] short (more developed than in *Scalopus*)" (Jackson 1915:56). The 8 mammae include 2 pairs pectoral and 1 pair each abdominal and inguinal (Jackson 1915).

Skull (Fig. 3) is conoidal with a broad braincase, moderately heavy mastoids, rectangular interparietal region about one-third as wide as long, flat frontal region, premaxillae extending beyond nasals, anteriorly opening nares, long and relatively heavy zygomata, oval foramen magnum, and elongate palate. Horizontal ramus of mandible is moderately heavy, curved upward posteriorly, and has an elongate coronoid process (Jackson 1915).

In general, broad-footed moles in more humid regions in northern and western portions of their range are larger than those in southern and more arid regions (Palmer 1937). In most populations, males are slightly larger than females. For California, averages and ranges of body dimensions (in mm—Palmer 1937) for 8 female and 10 male (in parentheses) *S. l. caurinus* from Mendocino Co. were: total length, 178.3, 154–192 (180.2, 164–190); length of tail vertebrae, 34.3, 23–39 (35.4, 32–38); and length of hind foot, 22, 20–24 (22, 21–23). Total length, length of tail vertebrae, and length of hind foot (in mm) for 1 female and 2 male (in parentheses) *S. l. insularis* from Marin Co. were: 182 (177, 183), 36 (36, 38), and 22.5 (23, 23.5). Averages and ranges of body dimensions (in mm) for 4 female and 4 male (in parentheses) *S. l. latimanus* from Santa Cruz Co. (Jackson 1915) were: total length, 171.5, 162–185 (175.8, 173–181); length of tail vertebrae, 32.5, 31–35 (33.3, 32–38); and length of hind foot, 20.8, 20–21 (20.8, 20–21); and for 2 females from San Mateo Co. and 3 males (in parentheses) from Santa Clara Co. of this subspecies (Palmer 1937) the same dimensions were: 170, 172 (171.7, 170–175); 32, 45 (34.7, 29–40); and 20, 20 (21.3, 20–22). Total length, length of tail vertebrae, and length of hind foot (in mm) for 1 female and 1 male (in parentheses) *S. l. parvus* from Alameda Co. were: 159 (160), 30 (33), and 20 (18). For *S. l. dilatus*, means and ranges for the same dimensions (in mm) for 5 females from Shasta Co. and 4 males (in parentheses) from Lassen Co. were: 167, 152–183 (173.2, 160–185); 34.6, 29–43 (36, 34–40); and 22, 21–23 (22, 21–25—Palmer 1937). The same dimensions for 2 male *S. l. minusculus* from El Dorado Co. were: 164, 175; 30, 30; and 20, 21. For 7 female and 11 male (in parentheses) *S. l. sericatus* from Mariposa Co., means and ranges for total length, length of tail vertebrae, and length of hind foot (in mm) were: 161.7, 152–171 (164.2, 150–174); 32.1,

FIG. 1. Ventral view of *Scapanus latimanus*. Photograph 1606, courtesy of the Archives, Museum of Vertebrate Zoology, University of California, Berkeley. Reprinted with permission.

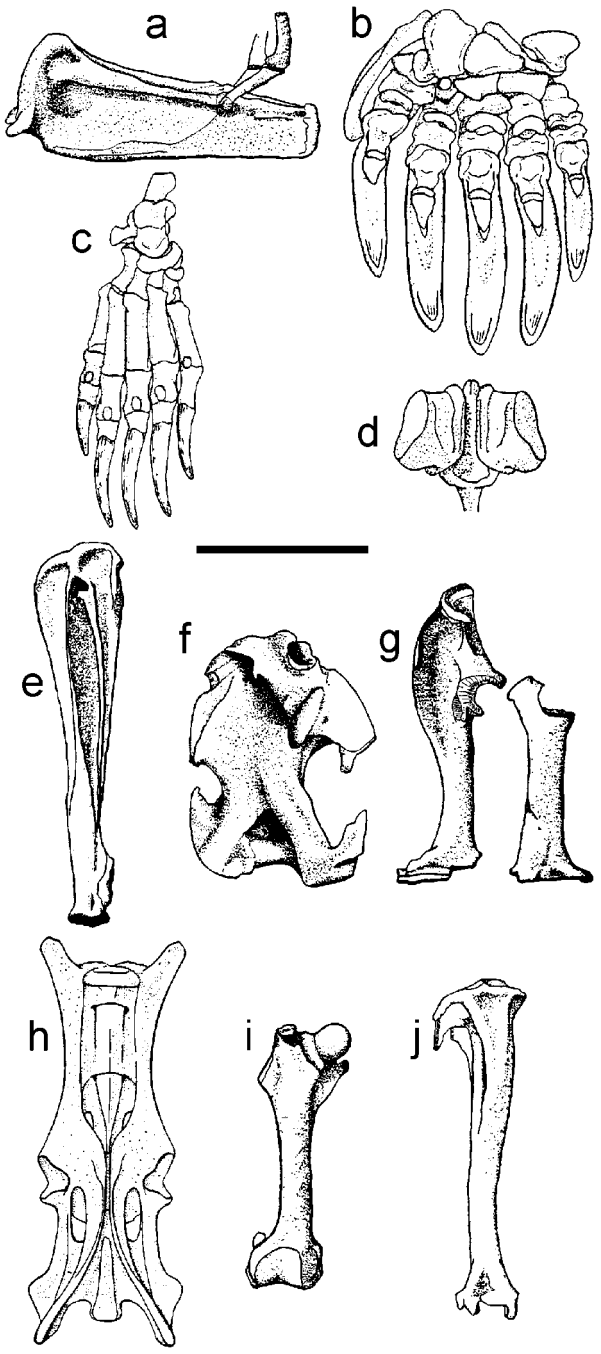

FIG. 2. Components of the right appendicular skeleton of *Scapanus latimanus*: a, manubrium, left lateral aspect; b, manus with os falciforme (leftmost), right palmar aspect; c, pes, right dorsal aspect; d, clavicle, anterior aspect; e, scapula, dorsal aspect; f, humerus, posterior aspect; g, radius and ulna, anconeal aspect; h, pelvis and sacrum, ventral aspect; i, femur, anterior aspect; and j, tibiofibula, anterior aspect (Reed 1951:figures 2a, 2e, 3a, 5b, 6a, 7a, 8b, 9a, 10a, and 12d). Scale bar is 10 mm. Used with permission of The American Midland Naturalist and C. A. Reed.

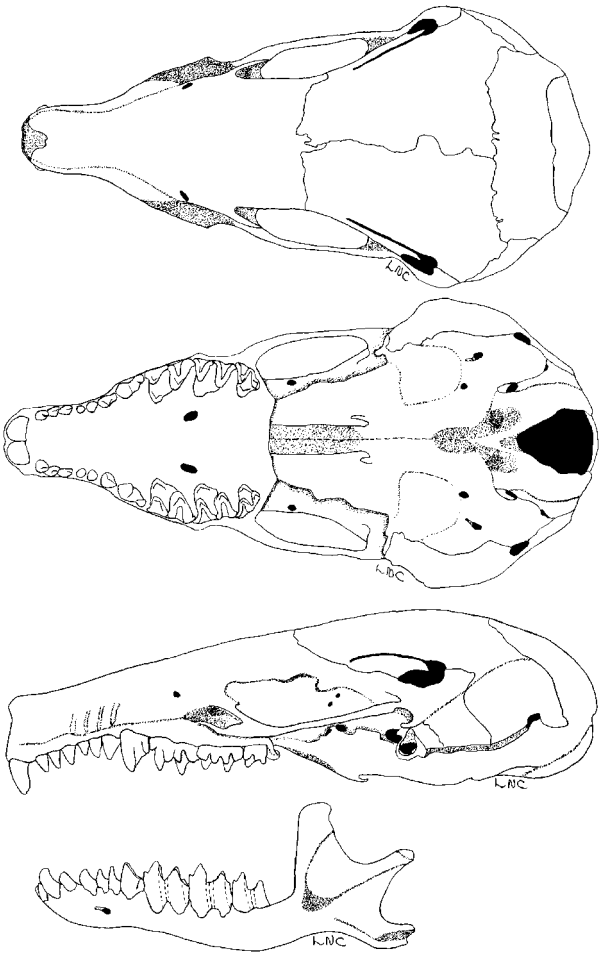

FIG. 3. Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Scapanus latimanus* (Oregon State University Fisheries and Wildlife [OSUFW] 3009) from 8 miles S Klamath Falls, Klamath Co., Oregon. Condylobasal length is 34.53 mm.

27–35 (32, 25–36); and 21.1, 19–22 (21.1, 20–24); whereas for 4 *S. l. campi* of each sex (male in parentheses) from Fresno Co. these measurements were: 151.3, 140–160 (161.5, 156–170); 28.8, 26–32 (34.2, 32–38); and 20, 19–21 (19.5, 19–20). For 6 *S. l. monoensis* of each sex (male in parentheses) from Mono Co., means and ranges for total length, length of tail vertebrae, and length of hind foot (in mm) were: 149.8, 136–161 (161.2, 150–170); 32.7, 29–36 (33.7, 31–36); and 20.3, 20–22 (21.7, 21–22); whereas for 5 female and 2 male (in parentheses) *S. l. grinnelli* from Inyo Co., the same dimensions were: 156.8, 147–168 (155, 156); 32.2, 26–36 (21, 35); and 20.3, 20–21 (20, 21—Palmer 1937). Means and ranges for total length, length of tail vertebrae, and length of hind foot (in mm) for 6 female and 7 male (in parentheses) *S. l. occultus* from Los Angeles Co. were: 152.2, 140–161 (149.4, 132–157); 29.3, 29–34 (31.2, 27–34); and 19.3, 18–20 (19, 18–21—Palmer 1937); and for 13 males from the same area they were: 151.9 (140–165), 25.3 (22–29), and 18.3 (17.5–19.5—Jackson 1915). From Baja California, Mexico, total length, length of tail vertebrae, and length of hind foot (in mm) for 1 female and 3 male *S. l. anthonyi* were: 143 (143, 141–146); 31 (32, 30–34); and 19 (18.2, 18.0–18.5).

Averages and ranges of external measurements (in mm) for 7 or 8 female and 11 or 12 male (in parentheses) *S. l. dilatus* from Oregon (Verts and Carraway 1998) were: total length, 173, 150–183 (170, 150–192); length of tail, 39, 30–55 (33, 25–41), and length of hind foot, 22, 21–23 (21, 16–25). In Nevada (Hall 1946), the same body dimensions for 5 male *S. l. dilatus* were: 168, 151–190; 35, 31–41; and 22, 21–22; and for 1 female and 3 male (combined) *S. l. monoensis* they were: 166, 162–169; 36, 34–38; and 21, 20–22.

Body mass (g) averaged 73.2 (66.7–73.9) for 3 female and 65.5 (55.6–73.9) for 5 male *S. l. dilatus* from Oregon (Verts and Carraway 1998) and 75.7 (65.5–85.0) for 3 males from Nevada (Hall 1946). Body mass for 4 *S. l. monoensis* from Nevada averaged 60.6 (52.2–69.5—Hall 1946). Six *S. l. occultus* from southern California weighed an average of 55.0 g (range, 50.2–59.5—Grim 1958).

Skull dimensions of the broad-footed mole, as for body dimensions, tend to decrease from north to south (Palmer 1937). Averages and ranges for skull dimensions (in mm) for 8 females and

12 males (in parentheses) of *S. l. dilatus* from Oregon (Verts and Carraway 1998) were: greatest length of skull, 35.36, 34.37–35.86 (35.41, 33.57–38.13); maxillary breadth, 10.45, 10.19–11.06 (10.31, 9.73–10.90); least interorbital breadth, 7.77, 7.49–8.14 (7.69, 7.36–8.16); cranial breadth, 17.24, 16.89–17.91 (17.02, 15.98–17.93); length of maxillary toothrow, 11.79, 11.46–12.02 (11.96, 11.50–13.09); length of mandible, 22.86, 22.09–23.47 (22.88, 21.19–24.63 [incorrectly reported as 22.00]); and length of mandibular toothrow, 11.67, 11.35–11.93 (11.77, 11.07–12.94).

In California (Palmer 1937), averages and ranges for skull dimensions (in mm) of 8 female and 10 male (in parentheses) *S. l. caurinus* from Mendocino Co. were: greatest length of skull, 36.5, 35.7–37.3 (36.4, 35.5–37.4); mastoid breadth, 17.3, 16.8–17.7 (17.2, 16.7–17.8); least interorbital breadth, 8.2, 7.7–8.4 (8.1, 7.9–8.6); length of maxillary toothrow, 11.4, 11.2–11.6 (11.4, 11.2–11.6); and length of mandibular molar–premolar row, 10.8, 10.6–11.2 (10.9, 10.6–11.3). The same dimensions (in mm) for 5 female and 7 male (in parentheses) *S. l. latimanus* from Marin Co. were: 36.0, 35.3–36.6 (37.1, 36.6–37.4); 16.9, 16.7–17.2 (17.3, 17.0–17.8); 7.7, 7.4–8.1 (7.8, 7.5–7.9); 11.1, 10.8–11.4 (11.3, 11.1–11.6); and 10.8, 10.3–11.1 (11.0, 10.7–11.4); measurements for 4 of each sex (males in parentheses) of the same subspecies from Santa Cruz Co. were: 34.7, 34.4–35.0 (36.1, 35.7–36.6); 13.8, 13.4–14.1 (14.2, 13.8–14.6); 7.8, 7.7–8.0 (7.8, 7.5–8.0); 10.7, 10.4–10.9 (11.0, 10.8–11.1); and 10.3, 10.1–10.5 (10.6, 10.5–10.8—Jackson 1915). For several dimensions, Palmer (1937) reported values ranging slightly smaller for this subspecies. The same dimensions (in mm) for 7 female and 11 male (in parentheses) *S. l. sericatus* from Maricopa Co. were: 33.7, 33.1–34.7 (34.1, 32.5–35.1); [no values] (16.5, 16.2–16.8); 7.5, 7.3–7.7 (7.5, 7.2–7.8); 10.7, 10.4–11.1 (10.8, 10.5–11.1); and 10.4, 10.0–10.6 (10.4, 10.2–10.8—Palmer 1937). For 6 female (Palmer 1937) and 13 male (in parentheses—Jackson 1915) *S. l. occultus* from Los Angeles Co. the dimensions (in mm) were: 31.7, 30.3–33.1 (31.6, 30.7–32.8); 15.9, 15.4–16.1 (12.3, 12.1–12.8); 7.3, 6.9–7.7 (7.1, 6.9–7.4); 9.9, 9.4–10.4 (10.0, 9.7–10.3); and 9.5, 9.0–9.9 (9.5, 9.3–9.9), and for 4 males from San Diego Co. (Jackson 1915) the measurements were: 32.9, 32.6–33.5; 12.9, 12.7–13.2; 7.3, 7.2–7.5; 10.3, 10.1–10.5; and 9.8, 9.6–10.0. *S. l. anthonyi* in Baja California, Mexico, is the smallest subspecies (Palmer 1937) with skull dimensions (in mm) for 1 female and 3 males (in parentheses) of: 29.7 (30.9, 30.3–31.9); 15.3 (15.7, 15.6–16.0); 6.9 (7.2, 7.0–7.4); 8.6 (9.5, 9.4–9.5); and 8.8 (9.1, 9.0–9.3).

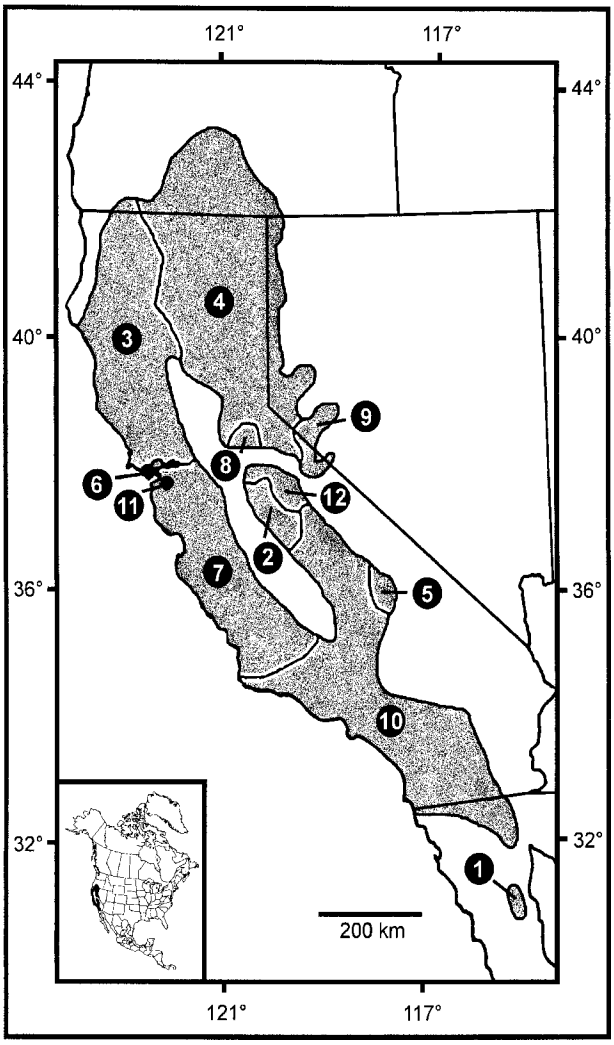

FIG. 4. Distribution of *Scapanus latimanus*. Subspecies are: 1, *S. l. anthonyi*; 2, *S. l. campi*; 3, *S. l. caurinus*; 4, *S. l. dilatus*; 5, *S. l. grinnelli*; 6, *S. l. insularis*; 7, *S. l. latimanus*; 8, *S. l. minusculus*; 9, *S. l. monoensis*; 10, *S. l. occultus*; 11, *S. l. parvus*; and 12, *S. l. sericatus*. Map redrawn from Hall (1981) with modifications from Ingles (1965) and Verts and Carraway (1998).

DISTRIBUTION. *Scapanus latimanus* occurs in southern Oregon (Jackson, Josephine, Klamath, and Lake counties), south through California, except for the northwestern corner (i.e., western parts of Del Norte and Humboldt counties), Central Valley region, and southeastern desert areas, into Baja California, Mexico, as far as La Grulla (Fig. 4; Hall 1981; Ingles 1965; Verts and Carraway 1998). The species also occurs in extreme western portions of Nevada (Douglas, Lyon, Ormsby, Story, and Washoe counties—Hall 1946). Altitudinally, the broad-footed mole ranges from sea level to ca. 3,000 m (Grinnell and Storer 1924; Palmer 1937).

FOSSIL RECORD. Fossils of members of the genus *Scapanus* date to the late Miocene (Clarendonian) of Oregon (Hutchison 1968) with records also from the Pliocene (Blancan) of Idaho, Oregon, and eastern Washington (Hutchison 1968; Kurtén and Anderson 1980). A probable ancestor of *Scapanus* likely was *Scapanoscapter simplicidens* from the Barstovian (Miocene?) of Oregon (Hutchison 1968). The closest morphological ancestor of *S. latimanus* is *S. malatinus* from Irvingtonian-age (ca. 1.8×10^6 years ago) deposits in San Diego Co., California (Hutchison 1987). Fossils referrable to *S. latimanus* were obtained from 21 sites (5 extralimital) in California; 1 site was middle Irvingtonian ($0.7–1.5 \times 10^6$ years ago) and the remainder were Rancholabrean (Hutchison 1987).

FORM AND FUNCTION. Individual hairs of broad-footed moles, as in other members of American Talpinae, consist of pigmented, cylindrical sections 1–2 mm long alternating with finer, flat, and usually unpigmented sections 0.2–0.5 mm long (Jackson 1915; Miller 1921). Flat sections function as hinges where hairs easily bend, producing the velvet-like texture of the pelage and permitting broad-footed moles to move forward or backward in their tunnels with little friction (Jackson 1915).

Dental formula usually is i 3/3, c 1/1, p 4/4, m 3/3, total 44; incisors, canines, and first 2 premolars commonly are referred to as "unicuspid teeth" and designated by "U." A tendency for reduction in antemolars occurs in southern populations, with *S. l. anthonyi* in Baja California, Mexico, uniformly lacking 1, and commonly 2, antemolars (probably premolars) in both upper and lower toothrows (Palmer 1937; Ziegler 1971). Appression of the unicuspid teeth is more pronounced in smaller races in which loss of teeth is more common (Palmer 1937); however, Huey (1936) considered the character sufficiently distinctive among specimens from Mexico to warrant elevating *anthonyi* to species level. In none of the Insectivora is dP4 and dp4 replaced (Kindahl 1967), and all milk teeth in *Scapanus* are small and virtually nonfunctional (Ziegler 1971). Absence of well-developed milk teeth in fossorial insectivores is considered an advanced character (Ziegler 1971).

In *S. latimanus* with 44 teeth, P3 has a posterobasal cusp and P4 is much larger and more cuspidate. Upper molars are W-shaped with an anterointernal V-shaped unlobed cusp-like shelf; M1 and M2 are nearly equal in size, but M3 is much smaller. First 7 lower teeth are small and conical, and, except for the smaller i1 and i3, nearly equal in size. The p4 is much larger and more cuspidate. Lower molars are M-shaped, with a bilobed anterointernal cusp; m1 has a posterointernal basal accessory cusp, m2 has both postero- and anterointernal basal accessory cusps, and m3 has an anterointernal basal accessory cusp. Like upper molars, m1 and m2 are subequal, and m3 is much smaller (Jackson 1915).

Vertebral formula was reported as 7 C, 14 T, 5 L, 6 S, 14 Ca, total 46 (Slonaker 1920). However, True (1896) reported 1 fewer caudal vertebrae in some individuals and Reed (1951) counted only 5 sacral vertebrae. Eight "antigenous hypophysial ossicles" (= hypapophyses) are interposed ventral to interspaces between lumbar vertebrae; the posteriormost is largest and is located between posterior lumbar and 1st sacral vertebrae (Slonaker 1920:356). Eight pairs of almond-shaped ossicles also occur ventral to interspaces of caudal vertebrae in young animals, but paired bones fuse in older individuals to form an H-shaped ossicle; the anteriormost is largest and is situated between 1st and 2nd caudal vertebrae. Lumbar ossicles may function as a fulcrum to increase lateral movement and caudal ossicles may function in movements of the tail (Slonaker 1920).

In contrast with some other fossorial mammals (e.g., Geomyidae—Hill 1937), the appendicular skeleton and accompanying musculature of *S. latimanus*, as in other talpid moles, is more highly modified for excavation of earth as required by the subterranean mode of life. The clavicle (Fig. 2d) of *S. latimanus* is extremely short and heavy, and articulates distally "with the greater tuberosity of the humerus instead of with the acromion of the scapula" (Reed 1951:533). With shortening of the clavicle, the M. atlantoscapularis anterior and M. trapezius anticus disappeared resulting in greater strength of the humeroclavicular joint and more solid anchoring of anterior end of scapula. Scapula (Fig. 2e) is markedly elongated, heavy, and rugged. Glenoid fossa is an ellipse; its long axis lies at an angle of 70° to plane of the subscapular surface. Tuberosity of the scapular spine is reduced in height because of the greater length of scapula; the spine is obliterated at both ends of the infraspinatus fossa and rises at the acromion as a bump. Supraspinatus fossa is small, but the M. supraspinatus originates on spine and fossa. "[T]eres fossa" serves as origin of the greatly enlarged M. teres major (Reed 1951). The broad-footed mole has 14 pairs of slender and pliable ribs (Slonaker 1920).

Humerus (Fig. 2f) is extremely broad; it is shifted laterodorsally until its distal end lies beside the skull. On the highly modified humerus, M. biceps brachii traverses the bicipital notch between the teres tubercle and the pectoral crest. Distal part of the much reduced pectoral ridge on the humerus serves for insertion of the enlarged M. pectoralis superficialis anticus. In *S. latimanus*, M. acromiodeltoideus inserts on "a slightly raised and roughened surface of the distal angle of the deltoid area" of humerus rather than on the pectoral ridge as it does in *Sorex* and *Neurotrichus* (Reed 1951:544). However, the M. spinodeltoideus inserts on the distal part of the deltoid process as in other insectivores. The long axis of the head of the humerus points mediodistally from the long axis of the humerus at ca. 20°. The joint is between the head of humerus and the glenoid fossa, thus motion of the humerus is limited to retraction, extension, and rotation. Raising and lowering the distal humerus can occur only by rotation of the scapula; therefore, the broad-footed mole cannot bring the manus beneath the body. The dramatically altered position of the talpid humerus has led to much confusion regarding naming its various parts (Reed 1951). The enlarged and elongated proximal processes of humerus are for attachment of powerful muscles associated with fossorial life. Distal humeral surfaces articulate with the ulna and radius (capitulum and trochlea) and do not allow lateral and medial shifts, thus the elbow joint is rigid (Reed 1951). Olecranon fossa is a deep pit near the distal end of the humerus and serves as origin of the great ligament of M. flexor digitorum profundus.

In *S. latimanus*, radius and ulna (Fig. 2g) are relatively short, but greatly thickened throughout their length; they lie parallel instead of the radius crossing the ulna. This torsion has been termed "pseudosupination," which in moles is such that "the long axes of the distal ends of the radius and ulna are at right angles to the transverse axis of the proximal crest of the olecranon" (Reed 1951: 549). The extremely high posterior crest of ulna serves as origin of many extensor muscles of the hand and for part of M. flexor digitorum profundus. The crest also serves to strengthen the ulna opposite the articular surface, a point of great stress. Distal end of the ulna forms a right-angle hinge with ulnare (= cuneiform—Carroll 1988) and pisiform bones. Capitular process of radius (a process found only in talpids) articulates with posterior surface of humeral capitulum and serves to strengthen the elbow (Reed 1951).

Manus (Fig. 2b) is pentadacylous and possesses a sickle-shaped bone (os falciforme) on the pollex side of carpus and metacarpus. Os falciforme is unique to talpines; it broadens the manus making it a more efficient earth mover. Proximally, it touches, but does not articulate with, the radiale (= scaphoid—Carroll 1988). Manus is webbed to end of 2nd phalanx and claws are exceptionally large (>50% of total length of hand). M. flexor digitorum profundus consists of a few small muscular heads and a wide ligamentous band that extends from the medial epicondyle of the humerus to the distal phalanges of the manus. The ligament is the primary flexor of the digits; it is involved when the humerus is rotated posteriorly by M. teres major, M. latissimus dorsi, M. subscapularis, and M. pecoralis superficialis posticus. Engaging these shoulder muscles to flex the digits increases speed of action while retaining great power (Reed 1951).

Sacrum (Fig. 2h) of *S. latimanus* consists of firmly ankylosed vertebrae with spinous processes united into a solid ridge that extends its entire length. Sacral spines serve as origins of M. gluteus maximus, M. femorococcygeus, M. tenuissimus, and parts of M. gluteus medius and M. semitendinosus. The exceptional strength of the sacrum is related to the great thrust provided by the hind legs, a possible adaptation for fossorial mode of life (Reed 1951). Ilium and ischium are ankylosed to all 5 vertebrae such that pelvis lies essentially parallel to the sacrum. These bones serve as origin for M. gemellus, M. quadratus femoris, M. biceps femoris, M. semimembranous, M. caudofemoralis, and part of M. semitendinosus. Acetabulum is displaced posteriorly and high on innominate bone; thus, the rear is depressed permitting free movement of hind legs in low-roofed tunnels. Before birth, posterior ends of pubes are connected by a symphysis pubis, but after birth, the cartilaginous symphysis is lost whereupon posterior ends of pubes diverge and anterior ends approach to form a pseudosymphysis. Thus, urogenital and digestive tracts pass ventral to pseudosymphysis. The narrow pelvis may aid the broad-footed mole in passing its massive foreparts over its rearparts when it changes direction within its burrow system; however, the relative width of the pelvis in some nonfossorial relatives is equal or less than that of *Scapanus*. Thus, the narrow pelvis may not be an adaptation to fossorial life (Reed 1951).

Proximal end of femur (Fig. 2i) is wide and trochanters are well developed to provide insertion of abductor and rotator muscles. These muscles produce great leverage on the femur that aids in use of the hind leg "in a lateral or twisted position . . . while bracing for burrowing and while pushing soil through the burrow" (Reed 1951:574). Also, when moving underground, *S. latimanus* straddles the burrow with both pedes and manus (Howell 1923). To compensate for the posterior and dorsal position of the acetabulum, the angle between the head and the shaft of the femur is greater in *S. latimanus* than in nonfossorial talpids. The shaft of femur is stout and rounded; the sesamoids on the lateral epicondylar ridge to which the tendons of the M. plantaris and M. gastrocnemius lateralis attach are massive. Femur also serves as origin of M. popliteus; this muscle strengthens the knee against a force that would rotate the shank (Reed 1951).

Tibia and fibula (Fig. 2j) of *S. latimanus* are fused for the distal two-thirds of their length to form a tibiofibula. These bones (crus) are relatively short, probably an adaptation for power at the expense of speed (Reed 1951). The short crura aids the broad-footed mole in bracing the pedes against the tunnel wall while digging or pushing excavated soil along the tunnel. Tibia has a large hook (falciform process) proximally that, in part, serves as origin of M. tibialis anticus; tibia also serves as origin of M. extensor hallucis longus, which extends and adducts the hallux, and M. flexor digitorum tibialis, which abducts the hallux and broadens the foot. The proximal head of the fibula is concave and supports the lateral condyle of the tibia. The fibula also has lateral and posterior processes that serve as the origin of M. peroneus longus, M. peroneus brevis, and M. peroneus digiti quinti; these muscles rotate the foot laterally. Seemingly, these processes of the fibula are unique to talpids (Reed 1951). Fibula also is origin of M. soleus that flexes the foot, M. tibialis posticus that pulls the foot medially, and part of M. flexor digitorum fibularis (remainder originates on tibia) that flexes the digits and foot. Shaft of crus is straighter, thicker, and more rugged than in near relatives. Distal end of crus is grooved both anteriorly and posteriorly for passage of muscles or tendons. Malleolus of crus extends over astragalus such that ankle is a hinge allowing movement of the foot in only 1 plane.

Pes (Fig. 2c) is pentadactylous and relatively short and broad. Nevertheless, the calcar is relatively long, permitting powerful extension of the foot by M. soleus and M. gastrocnemii through Achil-

les tendon. Claws, although somewhat shorter and more pointed than those of the forefoot, are relatively long (Reed 1951). Five tiny bundles of Mm. flexores breves originate, in part, on a broad tarsal ligament; 2 bundles each serve the 2nd and 3rd digits and 1 serves the 4th digit. The function of these degenerate muscles is uncertain (Reed 1951). The M. abductor hallucis originates on the tarsus; it serves to broaden the foot.

In a comparative study of 7 pectoral muscles (only 4 occur in *S. latimanus*) in 5 species of burrowing mammals, the muscles of *S. latimanus* had "a predominance of cells containing high, constant amounts of glycogen" (Goldstein 1971:523). Muscles in these moles also contained both white and red fibers (the latter synthesize glycogen more rapidly), but no fibers of intermediate type. Diameters of white fibers (28–48 μm) in all muscles and red fibers (22–29 μm) in 3 of 4 muscles examined were significantly smaller than those in California ground squirrels (*Spermophilus beecheyi*), against which the 4 other burrowers were compared (Goldstein 1971). Differences in strength of muscles of *S. latimanus* and sciurids were believed related to the proportion of fibers of the different types; broad-footed moles were considered to develop greater forces because of more muscle per unit of body mass and greater mechanical advantage rather than possessing more of a specific type of muscle fiber (Goldstein 1971).

Malleus in *Scapanus* differs from that of *Scalopus* by its small size and straight manubrium. Processus longus is thinner and shorter, and processus brevis is much longer than in *Scalopus*. Height of stapes is ca. equal in the 2 genera, but in *Scapanus* it is only one-half as wide as in *Scalopus* (Stroganov 1945).

Estimated metabolic rate (O_2 g^{-1} h^{-1}) for a 95-g adult *S. latimanus* based on calculations of Schmidt-Nielsen (1964) was 1,100 mm^3 (Goldstein 1971). Based on failure of the calcium precipitation method to reveal the presence of alkaline phosphatase in kidney tissue of *S. latimanus* in which the enzyme was detected by the azo-dye technique, Finegan (1963:194) concluded that this species possessed "two or more kinds of alkaline phosphatases with differing abilities to react with a wide range of substrates."

ONTOGENY AND REPRODUCTION. In California, an adult male broad-footed mole was captured in early January "in breeding condition" and "nearly grown young" were captured at the end of May (Grinnell and Storer 1924:46). Others collected in early June also were probably young-of-the-year. Probably, only 1 litter with an average of ca. 4 offspring is produced annually by *S. latimanus* (Sumner and Dixon 1953). At 10 days of age, young are 72–75 mm long, and by 30–35 days, they leave the nest (Ziegler 1972a).

Initially, primordia of deciduous teeth are connected to oral epithelium by dental lamina. As buds develop, they extend anteriorly beyond the lamina into an ingrown region of oral epithelium that diverges anterolaterally from the laminar neck (i.e., lateral string—Ziegler 1972b). Deciduous teeth obtain the 2nd connection to the oral epithelium from anterior to posterior along the toothrow. Developmental buds (i.e., primordia) of di1 appear by the time crown–rump length of the embryo is 12 mm; those of dI1–dI3, di2–di3, dP2–dP4, dp2–dp4, dM1–dM2, and dm1–dm2 by 17 mm; dm3 by 23 mm; dP1 by ca. 26 mm; and dM3 by ca. 30 mm. As deciduous teeth develop, the lateral string and attachment to the oral epithelium degenerate. Both are gone shortly after parturition. Material that forms di1–di3, dc1, dp1–dp4, dm1, and the anterior two-thirds of dm2 originates from the dental lamina. The posterior portion of dm2 and all of dm3 are formed from materials that originate from the lateral string as it extends posteriorally (Ziegler 1972b).

Except for dP1 and dp1, all milk dentition of *S. latimanus* erupts 10–35 days after birth. Eruption of dP1 coincides with eruption of replacement antemolars, but eruption of dp1 is slightly earlier, although somewhat later than other milk dentition. Neither dP1 nor dp1 is replaced, but function throughout life with the permanent dentition (Ziegler 1972a). Only extreme tips of anterior deciduous antemolars protrude through the gums, and probably are nonfunctional in independent feeding. However, dP3 and dP4 protrude somewhat more above the gum; combined with partially erupted molars, these teeth possibly are functional in mastication. Most deciduous dentition probably is lost within a few days of young leaving the nest (Ziegler 1972a).

ECOLOGY. Based largely on presence of raised-surface runways (commonly referred to as "mole-runs" or "surface galleries"—Hall 1946; McCully 1967) and mounds of excavated earth, the broad-footed mole occurs in moist, fairly rich soils with scant vegetation. In Oregon, a specimen was collected in shrub–steppe (with big sagebrush [*Artemisia tridentata*]—Whitaker et al. 1979). In Baja California, Mexico, *S. l. anthonyi* was considered a characteristic species of the California Biotic Province in which forests of yellow pine (*Pinus ponderosa*) and sugar pine (*P. lambertiana*) dominated higher elevations and lower slopes were vegetated by manzanita (*Arctostaphylos glauca*), chamiso (*Adenostoma fasciculatum*), palo amarillo (*A. sparsifolium*), and California holly (*Heteromeles arbutifolia*—Goldman and Moore 1946).

Broad-footed moles rarely occur in heavy clay, gravelly, or stony soils; 3 individuals from gravelly soils were young-of-the-year, suggesting they were dispersers (Palmer 1937). Rocky areas and bodies of water likely are barriers to distribution of the species, although 1 race (*insularis*) is endemic to Angel Island in San Francisco Bay and individuals swimming in rivers have been recorded (Palmer 1937). At Point Lobos, California, mole-runs made by *S. latimanus* were in roadways, pure sand, recently cultivated ground, and grasslands with little vegetation. Similar sign occurred in an area with hard soil devoid of vegetation, but sprinkled with castings of earthworms (Oligochaeta—Grinnell and Linsdale 1936). In California, surface galleries extended into the intertidal zone of a littoral environment where broad-footed moles probably fed on beach hoppers (*Orchestoidea californiana*—McCully 1967). Areas where soils become dry seasonally, such as margins of riparian zones, may be occupied only temporarily (Hall 1946; Palmer 1937). However, Hall (1946:111) claimed that an assistant was able to capture moles in "relatively dry areas by saturating with water the ground around a mole sign before setting a mole trap." Sandy and other loose soils usually are not occupied because they either lack sufficient food resources or are unsuitable for construction of tunnels. Sumner and Dixon (1953) suggested that broad-footed moles could not survive where the soil remains frozen for long periods. However, Grinnell and Storer (1924:46), although claiming that such "conditions would certainly seem unfavorable for active existence of moles," were less certain that the broad-footed moles could not survive in montane regions where soils are "frozen to a considerable depth." One individual was captured in a trap set in a tunnel from which "a pocket gopher had been caught the day before"; Bailey (1936: 353) suggested that both species apparently use the same tunnel systems.

Stomach contents of seemingly the only individual of *S. latimanus* analyzed (from Klamath Co., Oregon) consisted of 80% molluscs (Gastropoda) and 20% beetles (Coleoptera—Whitaker et al. 1979). In captivity, 4 individuals consumed a daily (for 15–20 days) average of 70.2% (range, 53.4–81.0%) of their body masses when fed dog food (95% horse meat) and 84.9% (range, 63.5–107.7%) of their body masses when fed earthworms for 3–4 days (Grim 1958). Body mass of 1 individual increased from ca. 55 g to ca. 68 g during the 20-day dog-food trial, but seemed to decline slightly when fed earthworms (Grim 1958). Four hours without food during the day left moles weaker than 11 h without food at night (Howell 1923). Also, captive individuals seem to require free water (Grim 1958).

Ectoparasites hosted by *S. latimanus* include fleas (Siphonaptera): *Corpsylla jordani* and *C. ornata*; a tick (Acarina): *Ixodes angustus*; and mites (Acarina): *Androlaelaps fahrenholzi, Haemogamasus keegani,* and *H. liponyssoides* (Yates et al. 1979). A single specimen of *S. latimanus* had no mites (Whitaker et al. 1979).

Broad-footed moles were eaten by pine martens (*Martes americana*) in eastern California except during winter; overall, moles contributed 3.5% of the volume and 3.6% of the mass, and were present in 2.6% of fecal samples (Zielinski et al. 1983). A few individuals were preyed upon by barn owls (*Tyto alba*), marsh hawks (*Circus cyaneus*), and red-tailed hawks (*Buteo jamaicensis*—Hafner 1974; Selleck and Glading 1943). Vulnerability to predation seems associated with reproduction and dispersal of young when "moles temporarily abandon their burrows" (Hafner 1974: 225).

BEHAVIOR. Broad-footed moles are fossorial; they rarely are active above ground although remains of these moles occasionally are found in regurgitated pellets of raptorial birds (Selleck and Glading 1943). Grinnell and Storer (1924) reported hearsay that

these moles were active above ground at time of mating, but admitted that they had no direct evidence for such.

When fed dog food, broad-footed moles scraped food into the mouth with "the almost prehensile nose"; those fed earthworms cleaned them with their front feet before consumption (Grim 1958: 268). Captive moles fed earthworms grasped and crushed them between their teeth "beginning at one end, progressing to the other, and back again" (Howell 1923:253). As the worm was consumed not only was dirt removed from the outside of the worm, but mud was forced from the worm's intestine (Howell 1923). When startled while feeding at a surface feeding station, broad-footed moles scurried back to their holes (Grim 1958).

When placed on a smooth concrete surface a broad-footed mole ran at 0.6 m/s and when placed in a 0.9-m-diameter tub of water, it swam for 6 min seemingly without tiring (Reed and Riney 1943). "The front feet were held semi-laterally and moved alternately, while the hind feet moved straight fore-and-aft in alternate strokes; the limbs of one side also moved alternately with reference to one another. The fore feet were depressed as much as possible, rather than being extended laterally as in burrowing. The fore foot was brought completely out of the water at the beginning of each stroke. The [broad-footed] mole changed direction at will by stopping the action of either fore foot" (Reed and Riney 1943:790). The body was held horizontally at the beginning of the session, but as the fur became wetted after 55 s, the rear of the body tilted downward at ca. 70°; when the broad-footed mole ceased to swim it became vertical in the water. It did not dive (Reed and Riney 1943).

Broad-footed moles construct subsurface runways ca. 2 cm underground using swimming strokes with the forefeet and upward pushing of soil with feet, head, and body. This action produces a ridge in the soil with many lengthwise cracks visible on the surface (Grinnell and Storer 1924). Ridges are produced as the broad-footed mole forages for insects and worms. Use of subsurface tunnels is irregular as indicated by great variation in the interval between setting traps along them and capture of a mole therein. Other tunnels are dug at much greater depth and earth excavated during the process is pushed upward through lateral and vertical shafts onto the surface to produce characteristically volcano-shaped mounds, considerably different from crescentic mounds produced by pocket gophers (Geomyidae). The core of a mound produced by a broad-footed mole is composed of the most recent earth used in its construction, but because the soil is pushed from beneath it is rarely visible on the surface of the mound (Grinnell and Storer 1924). During construction of mounds, the broad-footed mole is never exposed above ground. Each burrow system is occupied by only 1 individual, but reoccupation of a burrow upon removal of the occupant often occurs within 1 or 2 days (Grinnell and Storer 1924).

GENETICS. The diploid chromosome number in *S. latimanus* is 2n = 34 (Lynch 1971). The autosomal complement of a female from Marin Co. and a male from Contra Costa Co., California, consisted of 28 metacentric to submetacentric and 4 subacrocentric macrochromosomes (Lynch 1971).

An electrophoretic study of 18 loci in 7 species (including 5 genera) of talpids showed that populations of *S. latimanus* in Madera and Sonoma counties, California, have fixed alleles for Alb, Got-1, Ipo, LAP, Ldh-1, Ldh-2, Mdh-1, Mdh-2, Pgm, 6Pgd, and Sdh (Yates and Greenbaum 1982). Three of these, Ldh-1, Mdh-1, and Mdh-2, were fixed for all genera except *Condylura*. Populations of *S. latimanus* were polymorphic for the Got-2 locus, but for all other species the locus was fixed. Average heterozygosity was 0.007 for 7 specimens from Sonoma Co. and 0.014 for 4 specimens from Madera Co. Genetic similarity (S) between the 2 populations examined was 0.868 and genetic distance (D) was 0.128. Of other species examined, *S. latimanus* was most similar to *S. orarius* (S = 0.701 and 0.722, D = 0.325 and 0.341, respectively, for populations in Madera and Sonoma counties—Yates and Greenbaum 1982).

REMARKS. The generic name *Scapanus* was derived from the Greek prefix *skapanetes* meaning a digger (Jaeger 1978). The specific name *latimanus* is from the Latin *lat* meaning broad or wide and *manu* meaning a hand in reference to the broad hands of this mole (Borror 1960).

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