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Sciurus alleni.

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Sciurus alleni Nelson, 1898

Allen's Squirrel

Sciurus alleni Nelson, 1898:147. Type locality "Monterey, Tamaulipas [=Nuevo Leon—Nelson, 1899:91], Mexico."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Family Sciuridae, Subfamily Sciurinae, Genus *Sciurus*, Subgenus *Sciurus* (Wilson and Reeder, 1993). Based upon structure of the hyoid bones, *S. alleni* also has been placed into the subgenus *Parasciurus* (Hoffmeister and Hoffmeister, 1991). The genus *Sciurus* contains 28 species (Wilson and Reeder, 1993). *S. alleni* is monotypic (Hall, 1981).

DIAGNOSIS. *Sciurus alleni* (Fig. 1) bears a close superficial resemblance to *S. carolinensis* of Texas (Nelson, 1899) and may be sympatric with *S. aureogaster* and *S. deppei*, but *S. alleni* differs from these species in having only one upper premolar instead of two (Fig. 2; Hall, 1981; Musser, 1968). The ranges of *S. oculatus* and *S. alleni* approach each other in San Luis Potosí, but these taxa are not sympatric (Hall, 1981). *S. alleni* and *S. oculatus* are similar (Baker, 1956; Dalquest, 1953), but *S. oculatus* has a smaller skull, smaller body, grayer feet, and whiter venter than *S. alleni* (Nelson, 1899). Compared with *S. alleni*, *S. oculatus shawi* in San Luis Potosí has: buff, rather than brownish or whitish feet; distinct, buffy postauricular patches; underparts that are deep-buffy rather than white. In *S. alleni*, postauricular patches usually are absent and, when present, usually consist of a tiny area where the pelage is slightly shorter and grayer than on the surrounding part of the head (Dalquest, 1950). In Coahuila, some *S. alleni* have conspicuous pale to dark buffy postauricular patches (Baker, 1956).

GENERAL CHARACTERS. In winter pelage, the back and sides of Allen's squirrel are yellowish brown, finely grizzled with gray and black, usually darker along the back, and grayer along the sides and flanks. The top of the head is similar to the back and sides, but usually a little darker. The eye has a distinct ring of dingy white, shaded with buff on the outer border. The sides of the head are grizzled dusky gray, often suffused with yellowish brown. The ears and basal patch are brownish gray. The forefeet and outside of the forelegs are whitish gray, frequently washed with buff. The hind feet are whitish gray, usually with a spot of dark buff on the middle of the upper surface. The outsides of the thighs are like the flanks, but often with a browner shade near the feet. The underparts are white. The colors of the upperparts and lowerparts usually are separated by a narrow line of pale grayish. The base of the tail is the same color as the back. Dorsally, the tail is black and heavily washed with white, with the yellowish-brown or yellowish-gray color often showing through. Ventrally, the tail has a broad median area of grizzled yellowish-brown or yellowish-gray, narrowly bordered with black and edged with white. The hairs of the back are black, with one or two rings of gray, buff, or buffy brown. In summer, the pelage is darker and more yellowish-brown than in winter due to the absence of most of the gray or white tips on the hairs (Nelson, 1899). In westcentral Nuevo León, no differences in color were found among seasons, populations, ages, or sexes (Morales, 1985).

The striking differences in anatomical proportions between *S. alleni* from the lowlands near Monterey, Nuevo León, and those from the mountains near Miquihuana, Tamaulipas (2,550 m elevation), are not accompanied by similar differences in color. In both locations, the upperparts vary from grizzled brown to nearly gray. One individual from San Pedro Mines, Nuevo León, had upperparts that were dark yellowish-brown, and was darkest (thinly washed with black) on the top of the head. The eye was surrounded by a ring of dark buff, the forefeet were washed with buff, and the hind feet with grayish white. Another Allen's squirrel in similar pelage occurred at Miquihuana in June (Nelson, 1899).

There is no sexual dimorphism, but females average larger in mass (Morales, 1985). Measurements (in mm) of three adult males from Sierra Guadalupe, Coahuila, and one adult female from Diamante Pass, Coahuila, respectively, are: total length, 433, 441, 440, 456; length of tail, 200, 219, 209, 216; length of hind foot, 55, 63, 61, 62; length of ear from notch, 30, 31, 31, 34; greatest length of skull, 59.0, 58.8, 58.7, 59.3; basilar length of cranium, 44.4, 45.1, 45.2; zygomatic breadth, 34.1, 32.2, 33.0, 33.5; length of nasals, 20.4, 19.8, 20.3, 20.2; width across posterior tongues of premaxillae, 16.4, 15.5, 14.8, 16.1; mastoidal breadth, 27.2, 25.9, 26.1, 26.5; postorbital constriction, 17.0, 18.3, 17.3, 18.5; alveolar length of maxillary toothrow, 10.4, 10.5, 9.5, 10.4 (Baker, 1956). Average external and cranial measurements (in mm) of specimens from near Monterey and from near Miquihuana, respectively, are: total length, 471, 465; length of tail, 217, 230; length of hind foot, 61, 66; basilar length of cranium, 50.4, 50.0; palatal length, 26.3, 25.6; interorbital breadth, 18.4, 18.1; zygomatic breadth, 33.7, 33.7; length of upper toothrow, 10.5, 10.3 (Nelson, 1899). In San Luis Potosí, averages of external and cranial measurements (in mm) are: total length, 481; length of tail, 230; length of hind foot, 61; greatest length of skull, 60.8; condylobasal length, 53.6; length of maxillary toothrow, 10.2; length of diastema, 15.0; postpalatal length, 20.4; zygomatic breadth, 33.8; interorbital breadth, 18.2; mastoid breadth, 24.7; breadth across upper second molars, 12.8 (Dalquest, 1953). In Coahuila, three non-pregnant females and three males weighed 452, 473, 507, 486, 490, and 491 g, respectively (Baker, 1956). In Nuevo León, mass of 14 adult males was 408 g (range, 290–485) and that of 11 adult females was 461 g (range, 345–510—Morales, 1985).

DISTRIBUTION. *Sciurus alleni* occurs in the Mexican states of Coahuila, Nuevo León, Tamaulipas, and San Luis Potosí

FIG. 1. *Sciurus alleni* in pine-oak forest at Iturbide, 1,500 m elevation, Nuevo León, Mexico. Photograph courtesy of J. A. Guevara G.

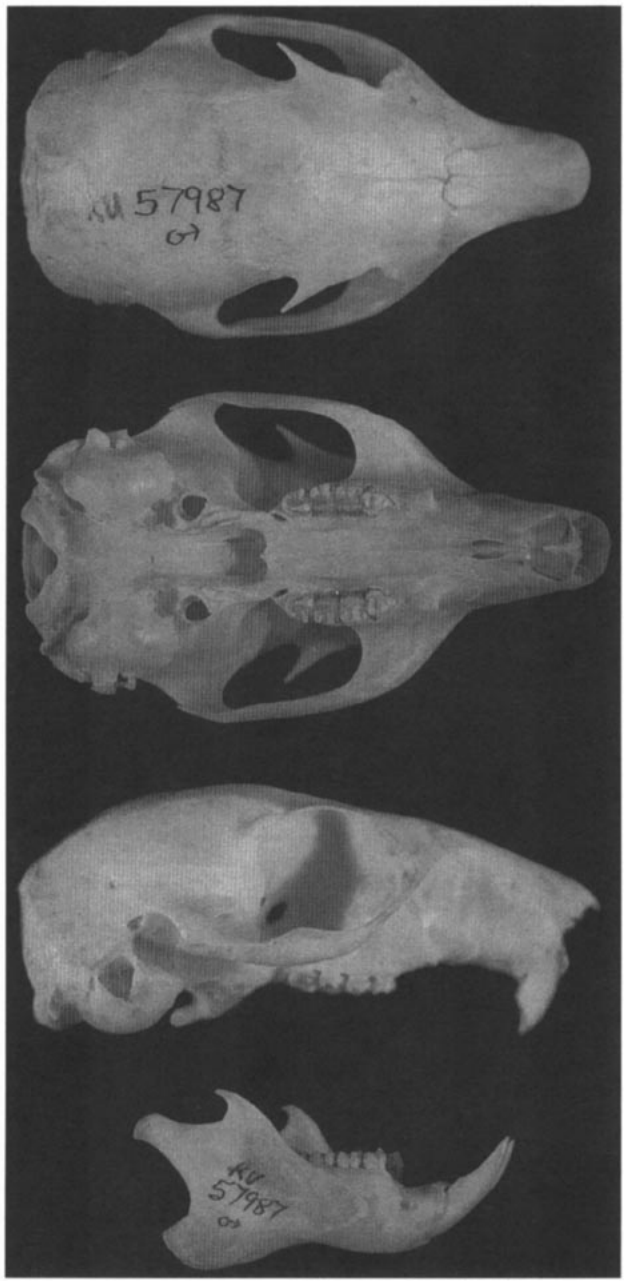

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Sciurus alleni* from 11.2 km S Aramberri, 1,140 m elevation, Nuevo León, Mexico (female, University of Kansas Museum of Natural History 57987). Greatest length of cranium is 55.7 mm.

(Fig. 3; Hall, 1981). It mainly occupies the lower Sonoran, upper Sonoran, and transition life zones at 900–1,500 m elevation, but Allen's squirrel has been reported at elevations of 600–2,550 m (Dalquest, 1953; Dice, 1937; Goodwin, 1954; J. A. Guevara G., pers. comm.; Hall, 1981; Kurtén and Anderson, 1980; Nelson, 1899).

FOSSIL RECORD. The genus *Sciurus* evolved by late Oligocene-early Miocene (Black, 1972; Hafner, 1984). *S. alleni* is known only from the Pleistocene (late Wisconsinan) fauna of San Josecito (Kurtén and Anderson, 1980).

FORM AND FUNCTION. The pelage on the back of Allen's squirrel is soft and dense, and the tail is full (Nelson, 1899). In Tamaulipas, *S. alleni* may be in fresh pelage or in old, faded, brown pelage in July (Goodwin, 1954). Near General Terán, Nuevo León, nearly one-half of *S. alleni* were black (Leopold, 1959), but no other melanistic individuals are known (Nelson, 1899).

The dental formula of Allen's squirrel is i 1/1, c 0/0, p 1/1, m 3/3, total 20 (Hall, 1981). The hyoid apparatus consists of a single basihyal and paired thyrohyals, ceratohyals, and stylohyals; the basihyal is thick, triangular in cross-section, long, and fuses with the short thyrohyals at an early age (Hoffmeister and Hoffmeister, 1991). The four pair of mammae are arranged as follows: one pectoral; two abdominal; one inguinal (Dice, 1937). Rectal temperature averages 39.9°C (range, 37.5–41.3—Morales, 1985).

The baculum of *S. alleni* (Fig. 4) is most like bacula of *S. deppei* and *S. granatensis*. The basal portion of the shaft is circular or nearly so in cross section. The shaft tapers distally, with an apparent twist, to its smallest diameter. At this point the shaft usually curves dorsally and expands into a broad circular disc that is concave on the right side and convex on the left. Ventral to this expanded disc is a spur. Compared to other *Sciurus*, the baculum of *S. alleni* is average in size and proportions, and lacks a supplementary spur. One specimen had a small tuberosity just posterior to the prominent spur. The posterodorsal edge of the expanded tip ends in a blunt point and an acute notch is formed with the shaft, which has a pronounced dorsal keel. Measurements (in mm) of two bacula from Nuevo León are: length, 11.0, 11.0; length of expanded tip, 3.1, 2.9; height of tip, 3.2, 3.0; height of base, 2.8, 2.9; width of base, 2.2, 2.3 (Burt, 1960).

ONTOGENY AND REPRODUCTION. In Coahuila, a female Allen's squirrel had two embryos averaging 25 mm in crown-rump length on 20 March, and two females were lactating on 23 April (Baker, 1956). In Nuevo León, adult males have scotal testes from January to August. Juveniles were present in January and April, and subadults were present from April to November. Some evidence of reproduction is present each month of the year, e.g., pregnancy and lactation (Morales, 1985). In Tamaulipas, a nest containing several small young was found 23 August in a hollow branch of a tree. On 21 July, a female had four embryos that were ca. 20 mm in length, and on 10 August, another female had four embryos ca. 37 mm in length (Dice, 1937).

ECOLOGY. *Sciurus alleni* occurs in the Tamaulipas biotic province (Goldman, 1951) in pecan (*Carya*), oak (*Quercus*), pine (*Pinus*), and other forests (Nelson, 1899). Allen's squirrel may be uncommon in some parts of its range (Davis, 1944), e.g., in Diamante Pass and east of San Antonio de las Alazanas, Coahuila, where coniferous timber predominates, and in other places it may be common, e.g., in oak groves in the Sierra de Guadalupe, Coahuila (Baker, 1956). In westcentral Nuevo León, relative abundance among localities had no relation to the type of vegetation, season of the year, presence of water, or proximity to areas disturbed by the activities of humans. At some localities >10 *S. alleni* were observed during the early morning hours, but at nearby, similar-appearing localities, it was uncommon (Morales, 1985).

In Nuevo León, Allen's squirrel occurs throughout deciduous and coniferous forests, from the lower elevations to the limit of trees on Cerro Potosí (Koestner, 1941). In Coahuila, *S. alleni* inhabits the mountains of the southeastern part of the state, and is known to occur in groves of pine and cedar (*Juniperus*) and in fir-pine-aspen (*Abies-Pinus-Populus*) associations. In Tamaulipas, Allen's squirrel is numerous in: oak woodlands and chaparral in the foothills of the Sierra Madre Oriental directly west of Ciudad Victoria (Baker, 1956); oak, pine, pecan, and madroña (*Arbutus*) forests (Dice, 1937); dry, open pine and oak woods (Goodwin, 1954; Hooper, 1953); stands of oak and hickory (*Carya*) trees that grow along streams and arroyos (Alvarez, 1963). In San Luis Potosí, Allen's squirrel lives in oak forests of the Sierra Madre Oriental and, where the lowlands to the east of the Sierra Madre are desert, *S. alleni* descends into the lowlands along streams and rivers. Where lowlands to the east of the Sierra Madre are tropical in San Luis Potosí, *S. alleni* is not present (Dalquest, 1953).

Along a river in Nuevo León, *S. alleni* frequented large cypress (*Taxodium*) trees, many of which had cavities (Davis, 1944). Nests may be inside natural cavities of trees or built of leaves and sticks placed on branches of trees. All nest cavities were observed in oaks at heights of 1.5–8 m; openings to nests were round and 5–8 cm in diameter. Nests placed on branches of trees were in pine and oak trees at heights of 7–13 m (Morales, 1985). In San Luis Potosí, nests are made of sticks and leaves, and one Allen's squirrel was living in a hollow tree (Dalquest, 1953).

In Coahuila, acorns seem to provide the basic food. *S. alleni*

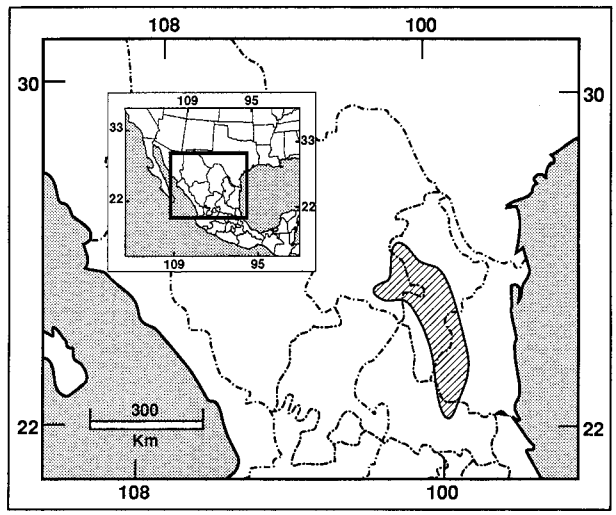

FIG. 3. Distribution of *Sciurus alleni* in Mexico (Hall, 1981).

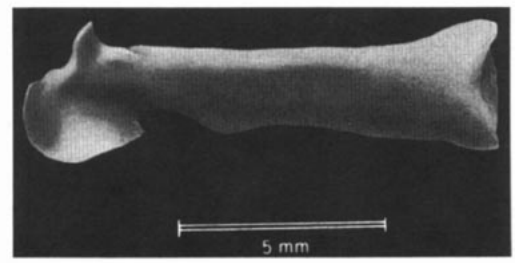

FIG. 4. Baculum of *Sciurus alleni* from Galeana, Nuevo León, Mexico (modified from Burt, 1960).

also may eat cones of *Pinus arizonica* (Baker, 1956). In Nuevo León, it consumes acorns, which are abundant from July to January, flowers and buds of oaks, and seeds of pines. Larvae and adult insects are common in the diet; peanuts, corn, oats, apples, peaches, mangos, plums, grapes, tomatoes, and anurans also are consumed (Morales, 1985). It occasionally enters cornfields and does considerable damage to the ripening corn (Davis, 1944). Allen's squirrel has suffered severe habitat loss through logging, burning, and the clearing of forests for agriculture (Leopold, 1959; Nowak, 1991).

Sciurus alleni may be sympatric with *S. aureogaster* (Musser, 1968). In Nuevo León, Allen's squirrel lives in forests of *Pinus montezumae* with *Microtus mexicanus, Peromyscus maniculatus, Thomomys, Sylvilagus floridanus* (Koestner, 1944), and *Spermophilis variegatus* (J. A. Guevara G., pers. comm.). Potential predators include rattlesnakes (*Crotalus*), hawks (*Accipiter striatus, Buteo jamaicensis*), golden eagles (*Aquila chrysaetus*), great-horned owls (*Bubo virginianus*), ringtails (*Bassariscus astutus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), and bobcats (*Lynx rufus*—Morales, 1985).

Ectoparasites include the lice *Neohaematopinus sciurinus, Enderleinellus longiceps* (Ferris, 1951), *E. arizonensis*, and *E. oculatus* (Kim, 1966), the ticks *Ixodes* and *Dermacentor*, and the fleas *Hoplopsyllus* (Morales, 1985), *Opisodasys robustus*, and *Orchopeas fulleri* (Traub et al., 1983). Endoparasites include the acanthocephalan *Moniliformis* (Moniliformidae) and nematodes of the families Physalopteridae (*Physaloptera*) and Trichostrongylidae (Morales, 1985).

BEHAVIOR. Allen's squirrel gives a soft "chirring" call. In Tamaulipas, it is active from sunrise to ca. 1000 h, and again late in the afternoon (Alvarez, 1963). In San Luis Potosí, *S. alleni* is active in summer, and often is seen on the ground and at the bases of trees. In winter, Allen's squirrel is extremely shy and retiring, and in November none was found in an area where it was common and prominent in summer (Dalquest, 1953). In Nuevo León, it is active from daylight to dark throughout the year at ambient temperatures of 2–30°C. Greatest activity occurs from sunrise to 1100 h and from 1700 h to dark (Morales, 1985). Nothing is known concerning the genetic characteristics of *S. alleni*.

REMARKS. *Sciurus alleni* is similar to *S. oculatus* (Nelson, 1899), and *S. alleni* has been considered to be a subspecies of *S. oculatus* (Moore, 1960). Squirrels ancestral to *S. nayaritensis, S. oculatus*, and *S. alleni* may have spread from western Mexico across the Mesa del Norte by way of mountains in western Coahuila, Durango, and Zacatecas (Baker, 1956).

Sciurus is from the Latin meaning squirrel (Jaeger, 1955). The specific epithet *alleni* is dedicated to J. A. Allen, former Curator of Mammals at the American Museum of Natural History (Nelson, 1898).

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LITERATURE CITED

ALVAREZ, T. 1963. The Recent mammals of Tamaulipas, México. University of Kansas Publications, Museum of Natural History, 14:363–473.

BAKER, R. H. 1956. Mammals of Coahuila, México. University of Kansas Publications, Museum of Natural History, 9:125–335.

BLACK, C. C. 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). Evolutionary Biology, 6:305–322.

BURT, W. H. 1960. Bacula of North American mammals. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 113:1–76.

DALQUEST, W. W. 1950. Records of mammals from the Mexican state of San Luis Potosi. Occasional Papers of the Museum of Zoology, Louisiana State University, 23:1–15.

———. 1953. Mammals of the Mexican state of San Luis Potosí. Louisiana State University Press, Baton Rouge, 229 pp.

DAVIS, W. B. 1944. Notes on Mexican mammals. Journal of Mammalogy, 25:370–403.

DICE, L. R. 1937. Mammals of the San Carlos Mountains and vicinity. University of Michigan Studies, Scientific Series, 12: 245–268.

FERRIS, G. F. 1951. The sucking lice. Memoirs of the Pacific Coast Entomological Society, 1:1–320.

GOLDMAN, E. A. 1951. Biological investigations in México. Smithsonian Miscellaneous Collections, 115:1–476.

GOODWIN, G. G. 1954. Mammals from Mexico collected by Marian Martin for the American Museum of Natural History. American Museum Novitates, 1689:1–16.

HAFNER, D. J. 1984. Evolutionary relationships of the Nearctic Sciuridae. Pp. 3–23, *in* The biology of ground-dwelling squirrels: annual cycles, behavioral ecology, and sociality (J. O. Murie and G. R. Michener, eds.). University of Nebraska Press, Lincoln, 459 pp.

HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1–600 + *90*.

HOFFMEISTER, R. G., AND D. F. HOFFMEISTER. 1991. The hyoid in North American squirrels, Sciuridae, with remarks on associated musculature. Anales del Instituto de Biologica, Universidad Nacional Autónoma de México, Serie Zoología, 62: 219–234.

HOOPER, E. T. 1953. Notes on mammals of Tamaulipas, México. Occasional Papers of the Museum of Zoology, University of Michigan, 544:1–12.

JAEGER, E. C. 1955. A source-book of biological names and terms. Third ed. Charles C Thomas Publisher, Springfield, Illinois, 323 pp.

KIM, K. C. 1966. The species of *Enderleinellus* (Anoplura, Hoplopleuridae) parasitic on the Sciurini and Tamiasciurini. The Journal of Parasitology, 52:988–1024.

KOESTNER, E. J. 1941. An annotated list of mammals collected

in Nuevo Leon, Mexico, in 1938. The Great Basin Naturalist, 2:9–15.

———. 1944. Populations of small mammals on Cerro Potosí, Nuevo Leon, Mexico. Journal of Mammalogy, 25:284–289.

KURTÉN, B., AND E. ANDERSON. 1980. Pleistocene mammals of North America. Columbia University Press, New York, 442 pp.

LEOPOLD, A. S. 1959. Wildlife of Mexico: the game birds and mammals. University of California Press, Berkeley, 568 pp.

MOORE, J. C. 1960. The relationships of the gray squirrel, Sciurus carolinensis, to its nearest relatives. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners, 13:356–363.

MORALES, D. M. 1985. Aspectos biologicos de la ardilla arborea *Sciurus alleni*, en el municipio de Santiago, Nuevo Leon, Mexico. Tesis Que Para Obtener el Titulo de Biologo, Universidad Autonoma de Nuevo Leon, Facultad de Ciencias Biologicas, Monterey, 47 pp.

MUSSER, G. G. 1968. A systematic study of the Mexican and Guatemalan gray squirrel, *Sciurus aureogaster* F. Cuvier (Rodentia: Sciuridae). Miscellaneous Publications of the Museum of Zoology, University of Michigan, 137:1–112.

NELSON, E. W. 1898. Descriptions of new squirrels from Mexico and Central America. Proceedings of the Biological Society of Washington, 12:145–156.

———. 1899. Revision of the squirrels of Mexico and Central America. Proceedings of the Washington Academy of Sciences, 1:15–110.

NOWAK, R. M. 1991. Walker's mammals of the world. Fifth ed. The Johns Hopkins University Press, Baltimore, Maryland, 1:1–642.

TRAUB, R., M. ROTHSCHILD, AND J. F. HADDOW. 1983. The Rothschild collection of fleas. The Ceratophyllidae: key to the genera and host relationships with notes on their evolution, zoogeography and medical importance. Academic Press, London, United Kingdom, 288 pp.

WILSON, D. E., AND D. M. REEDER (EDS.). 1993. Mammal species of the world: a taxonomic and geographic reference. Second ed. Smithsonian Institution Press, Washington, D.C., 1206 pp.

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