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Nectomys squamipes.

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Nectomys Peters, 1861

Nectomys Peters, 1861:151. Type species *M[us]. squamipes* Brants, 1827, by subsequent designation (Miller, 1912:180).

Potamys Liais, 1872:507. Type species *Potamys brasiliensis* Liais [=*Nectomys squamipes aquaticus* (Lund); *fide* Hershkovitz, 1944]. A homonym of *Potamys* Larranhaga, 1823.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Infraorder Myomorpha, Superfamily Muroidea, Family Muridae, Subfamily Sigmodontinae (Carleton, 1984; Carleton and Musser, 1984). Two species of *Nectomys* currently are recognized, although *N. squamipes* "may contain more than one species" (Honacki et al., 1982:429). *N. parvipes* is based on a single specimen of a female estimated to be 4.5 months old (Petter, 1979). A key to the species follows:

Length of hindfeet ≤ 37 mm, length of M3 ≤ 20% length of toothrow, frontal-parietal suture "V"-shaped with medial straight portion ..... *N. parvipes*

Length of hindfeet > 37 mm, length of M3 > 25% length of toothrow, frontal-parietal suture "V"-shaped without medial straight portion ..... *N. squamipes*

Nectomys squamipes (Brants, 1827)

Neotropical Water Rat

M[us]. squamipes Brants, 1827:138. Type locality Brazil, restricted by Hershkovitz (1944:32) "to the coastal town of São Sebastião," São Paulo state.

M[us] aquaticus Lund, 1841:240. Type locality Valle, do Rio das Velhas, near Lagôa Santa, Minas Gerais, Brazil (*fide* Hershkovitz, 1944).

Nectomys apicalis Peters, 1861:152. Type locality "Guayaquil," redetermined by Hershkovitz (1944:26) to be "Tena (altitude, 512 meters), at the base of the eastern Andes in Ecuador."

Potamys brasiliensis Liais, 1872:507. Type locality Minas Gerais, "possibly at or near Lagôa Santa" (*fide* Hershkovitz, 1944: 26). A renaming and redescription of *Mus aquaticus* Lund, 1841.

Nectomys palmipes Allen and Chapman, 1893:209. Type locality "south central part of the island, at a point twelve miles north of the southern coast and seven miles southeast of Princestown," Trinidad.

Nectomys grandis Thomas, 1897*b*:498. Type locality "valley of the Cauca . . . Concordia, Medellin, Colombia," restricted by Hershkovitz (1944:62) to the western slope of the valley, 1,790 m.

Nectomys magdalenae Thomas, 1897*b*:499. Type locality "W. Cundinamarca, in lowlands near Magdalena R.," Colombia.

Nectomys fulvinus Thomas, 1897*b*:499. Type locality "believed to be Quito." Redetermined by Hershkovitz (1944:27) as "somewhere east of the Andes" between Quito and the Río Napo.

Nectomys saturatus Thomas, 1897*a*:546. Type locality "Ibarra, [Imbabura Province,] N. Ecuador, alt. 2225 metres."

Nectomys Garleppii [sic] Thomas, 1899:41. Type locality "Ocobamba, district of Cuzco," Peru.

CONTEXT AND CONTENT. Context noted in the generic account. *Nectomys squamipes* contains 18 recognized subspecies (Hershkovitz, 1944, 1948) as follows:

N. s. amazonicus Hershkovitz, 1944:47. Type locality "Tauary, on the east bank of the lower Rio Tapajóz about fifteen kilometers below Aveiros, state of Pará, Brazil."

N. s. apicalis Peters, 1861:152, see above (*fulvinus* Thomas a synonym).

N. s. aquaticus Lund, 1841:240, see above.

N. s. garleppii Thomas, 1899:41, see above.

N. s. grandis Thomas, 1897*b*:498, see above.

N. s. magdalenae Thomas, 1897*b*:499, see above.

N. s. mattensis Thomas, 1903:238. Type locality "Santa Anna de Chapada, a village situated at an altitude of about 800 m., on the Serra do Chapada, some thirty miles N.E. of Cuyabá," Mato Grosso, Brazil.

N. s. melanius Thomas, 1910:185. Type locality "Lower Essequibo River, 12 miles from mouth. Alt. 40 feet," Demerara, British Guiana.

N. s. montanus Hershkovitz, 1944:57. Type locality "Hacienda Exito, on the Río Cayumbá, a small stream which enters the Huallaga next below the Río Chinchae, department of Huanuco, Peru; altitude, 3000 feet."

N. s. napensis Hershkovitz, 1944:56. Type locality "'San Francisco,' left bank of Río Napo above the mouth of the Río Challuacocha; latitude and longitude approximately 0°47′S., 76°25′W., Parish of La Coca, Napo-Pastaza Province, Ecuador; altitude, about 20 meters."

N. s. olivaceus Hershkovitz, 1944:41. Type locality "Five miles north of Therezopolis, Rio de Janeiro, Brazil."

N. s. palmipes Allen and Chapman, 1893:209, see above.

N. s. pollens Hollister, 1914:104. Type locality "Sapucay, Paraguay"; described by Hershkovitz (1944:42) as "a station on the railroad line about half way between Villa Rica and Asunción, in the region drained by the Tevicuarhy, a tributary of the lower Paraguay."

N. s. saturatus Thomas, 1897*a*:546, see above.

N. s. squamipes Brants, 1827:138, see above (*Hesperomys* [*Holochilus*] *robustus* Burmeister, 1854 a synonym).

N. s. tarrensis Hershkovitz, 1948:51. Type locality "Río Tarra, upper Río Catatumbo, department of Norte de Santander, Colombia; altitude, 250 meters."

N. s. tatei Hershkovitz, 1948:52. Type locality "San Antonio, about 15 km. east of Mount Turumiquire, Sucre, northern Venezuela; altitude 1,800 feet."

N. s. vallensis Hershkovitz, 1944:61. Type locality "Santa Ana, a semiarid, tropical pocket in the Río Urubamba Valley, department of Cuzco, Peru; altitude, 3480 feet."

DIAGNOSIS. *Nectomys* can be distinguished from most other Sigmodontinae by their relatively large body size and partially webbed hindfeet. *N. squamipes* is similar to species of *Holochilus* in external and cranial characters (Hershkovitz, 1962). *Nectomys* retains a more primitive cuspidate pattern on the cheekteeth, a pattern absent on the more specialized cheekteeth of *Holochilus* (Ellerman, 1941). Husson (1978) distinguished *Nectomys* from *Holochilus* in Suriname by the longer, less hairy ears and more glossy dorsal pelage of *Nectomys*. Pine (1973) noted the completely scaled heel of *Nectomys* as opposed to the partially scaleless heel of *Holochilus*. Compared to *Oryzomys*, the cheekteeth in *Nectomys* tend to become flat crowned earlier in life, the molars are more hypsodont, and the outer folds of the upper molars tend to be more isolated as enamel islands (Ellerman, 1941).

GENERAL CHARACTERS. *Nectomys squamipes* (Fig. 1) is the largest and most aquatic-adapted oryzomyine rodent (Hershkovitz, 1944). The pelage is long; wool hairs and guard hairs are well developed dorsally and ventrally. The glossy dorsal pelage is buffy to tawny, mixed with dark brown (Hershkovitz, 1944). The sides are paler, and the ventrum is gray-based, appearing whitish or grayish mixed with ochraceous. Ears have a thin coat of hair on both sides. The tail is sparsely haired, brown, and not bicolored; its length is at least 75% of the length of the head and body (Hershkovitz, 1944). Hairs are slightly shorter on the dorsal surface than on the ventral surface of the tail, and ventral hairs form a weakly

developed keel. The hindfeet are large, long, sparsely haired above, and naked and scutellated below (Hershkovitz, 1944). Hairs on the hindfeet form fringes. Webbing extends between all toes, but is reduced between the hallux and second toe and between the fourth and fifth toes. Hindfeet have five or six tubercles (Hershkovitz, 1944).

The skull (Fig. 2) is large and robust. Supraorbital ridges and lambdoidal crests are well developed. Temporal ridges also are present, but less distinctive. The zygomatic plate is broad; the zygomata are broadened posteriorly (Hershkovitz, 1944). The incisive foramina are wider posteriorly, and terminate anterior to M1. The posterior margin of the palate extends beyond the last molars. The auditory bullae are well developed and slightly inflated (Hershkovitz, 1944).

The incisors are strong and considerably decurved. Molars are hypsodont with low crests; mesostyle and mesoloph are well developed and fused. Anterior folds of the molars are isolated into two or more enamel islands or fused into a single island. Second and third upper molars are longer than wide. The dental formula is i 1/1, c 0/0, p 0/0, m 3/3, total 16 (Hershkovitz, 1944).

The ranges (compiled from Hershkovitz, 1944) of external and cranial measurements (in mm) are: combined length of head and body, 162 to 254; length of tail, 165 to 250; length of hindfoot, 43.5 to 54.9; condylobasal length, 36.2 to 47.8; zygomatic breadth, 20.2 to 26.7; breadth of braincase, 12.8 to 15.9; length of nasals, 15.0 to 21.5; length of alveolar row, 6.2 to 8.1; interparietal length, 2.0 to 5.6; interparietal width, 7.9 to 13.6. Body mass ranges from 160 to 420 g.

DISTRIBUTION. The geographic range of *Nectomys squamipes* (Fig. 3) extends from the northern coast of South America to southern Brazil and the vicinity of Misiones, Argentina, and from the eastern slope of the western cordillera of the Andes to the Atlantic coast of Brazil. The elevational distribution is from near sea level to approximately 2,200 m (Hershkovitz, 1944).

FOSSIL RECORD. Pleistocene fossils of *Nectomys* are known from a cave in Minas Gerais, Brazil (Paula Couto, 1952).

FORM. *Nectomys squamipes* has two pectoral and two inguinal pairs of mammae (Davis, 1947). The baculum has a slightly curved shaft with a broad, dumbbell-shaped base. Above the base, the shaft is compressed dorsoventrally; near the tip, it is flattened laterally. The distal tip has three narrow cartilaginous projections; the lateral ones are longer and more ventral than the medial one (Burt, 1960; Gardner and Patton, 1976). Dimensions from one specimen are length, 5.7 mm; width at base, 3.4 mm (Burt, 1960).

The stomach is primitive and sac-like (Hershkovitz, 1962), of the ancestral unilocular-hemiglandular type (Carleton, 1973). The glandular epithelium is more extensive than is common for this type, and extends past the opening of the esophagus and into the corpus (Carleton, 1973).

Measurements (in mm) of male genital structures, including accessory glands, are: urethra, 42.5; length of lateral preputial, 25.0; length and width of bulbo-urethral, 12.0 and 5.0; length and width of dorsal prostate, 12.0 and 12.5; length of medial ventral prostate, 20.0; length of lateral ventral prostate, 13.5; length and width of anterior prostate, 17.5 and 5.5; length and width of vesicular, 23.5 and 5.5; length and width of ampullary, 6.0 and 4.0 (Voss and Linzey, 1981).

ONTOGENY AND REPRODUCTION. Moojen (1952) reported that litter size is commonly five in *Nectomys s. squamipes*. Embryo counts of two trapped *N. squamipes* females were five and seven (Davis, 1947). One *N. s. palmipes* from Trinidad had three embryos (Vesey-Fitzgerald, 1936). Two captive females had litters of two (Mello, 1980) and three. Female *N. s. pollens* in Misiones, Argentina, are pregnant during October and November, and give birth to four to five young (Crespo, 1982).

ECOLOGY AND BEHAVIOR. *Nectomys squamipes* usually inhabits moist forested areas. Alho (1982) reported the occurrence of this species in the following vegetation complexes: seasonally flooded tropical evergreen rainforest (várzea), unflooded evergreen rainforest (terra firme), and cerrado (sensu lato). Captures (n = 94) in Venezuela reported by Handley (1976) included 18% in "tropical dry forest," 49% in "tropical moist forest," 21% in "tropical wet forest," 5% in "subtropical moist forest," and 1% in "subtropical wet forest." *N. squamipes* usually is found in or near

FIG. 1. Photograph of an adult *Nectomys squamipes*.

streams (Davis, 1947; Handley, 1976 [65%]; Hershkovitz, 1944; Mello, 1977), but also in other moist areas (19%; Handley, 1976) and in dry areas (16%; Handley, 1976). Most individuals reported by Handley (1976) were taken in areas with closed canopies (69%); some were caught in forest openings (13%), marsh edges (11%), and other open areas (7%). The most frequent capture site was in or near grass (Gramineae; 80%), but also near palms (Arecaceae), bananas (Musaceae), shrubs, and herbs (7%); among rocks and logs near streams (7%); and in or near human dwellings (6%). One individual was seen along a stream in a cave (Linares, 1969).

Paula (1983) considered *N. squamipes* to be a habitat specialist. He calculated a capture success (percent of trap-nights in which animals were caught) of 2.7% in flooded gallery forest without taboca de fogo (*Ichnanthus bambusiflorus*, Gramineae), and 0.5% for flooded gallery forest with taboca de fogo. No animals were captured in dry gallery forest, campo húmido, or campo cerrado.

Home-range size, determined by minimum area of monthly occupation calculated by the exclusive boundary strip method (Stickel, 1954), was 2,200 m² in central Brazil (Paula, 1983). Individuals were aggregated (Morisita's Index; Poole, 1974) in both the wet and dry seasons. Centers of activity (Hayne, 1949) occurred primarily along streams (Paula, 1983). In flooded gallery forest, *N. squamipes* was moderately exclusive in its use of area (index of relative exclusivity of use of space; Alho, 1979), but shared space primarily with *Philander opossum* (Paula, 1983).

Water rats of the genus *Nectomys* are nocturnal and semiaquatic (Moojen, 1952). They spend a considerable amount of time foraging in water (Alho, 1982). Their omnivorous diet includes fungi, plant matter, fruits, seeds, invertebrates (arthropods, snails), and vertebrates (Alho, 1981; Crespo, 1982).

Nectomys squamipes usually constructs nests in dense undergrowth or under logs and roots (Hershkovitz, 1944; Moojen, 1952). Miles et al. (1981) tracked one animal to its grass nest inside a rotten tree stump in a swampy area on the edge of a stream. The rat was able to enter the cavity through underwater openings.

The only reported instance of predation on *N. squamipes* was by a barn owl *Tyto alba* (Martins et al., 1981). Ectoparasites of *N. squamipes* include sucking lice (Anoplura): *Hoplopleura quadridentata* (Johnson, 1972); fleas (Siphonaptera): *Polygenis bohlsi, P. dunni, P. rimatus, P. roberti* (Johnson, 1957), *P. pradoi* (Botelho and Linardi, 1980), *P. tripus* (Guimarães, 1972), *Adoratopsylla intermedia* (Johnson, 1957), *Craneopsylla minerva* (Tipton and Machado-Allison, 1972); ticks and mites (Acarina): *Amblyomma* sp. (Jones et al., 1972), *Aitkenius ciscunctatus, Cotiscus desdendatus* (Brennan and Reed, 1975), *Parasecia aitkeni, Odontacarus tuberculatis* (Reed and Brennan, 1975), *Eubrachylaelaps rotundus, Gigantolaelaps goyanensis, Laelaps manguinhosi, L. mazzai* (Botelho et al., 1981), and *Ornithonyssus bacoti* (Saunders, 1975).

Endoparasites of *N. squamipes* include the fluke *Schistosoma mansoni* (Martins et al., 1955), and the nematodes *Litomosoides carinii* (Vaz, 1934), *Aspidodera raillieti*, and *Physaloptera getula* (Vicente et al., 1982). Caraparu-like virus, Venezuelan equine encephalitis (Jonkers et al., 1968), and Pacui virus (Aitken et al., 1975) also have been reported from *N. squamipes*. Skin lesions

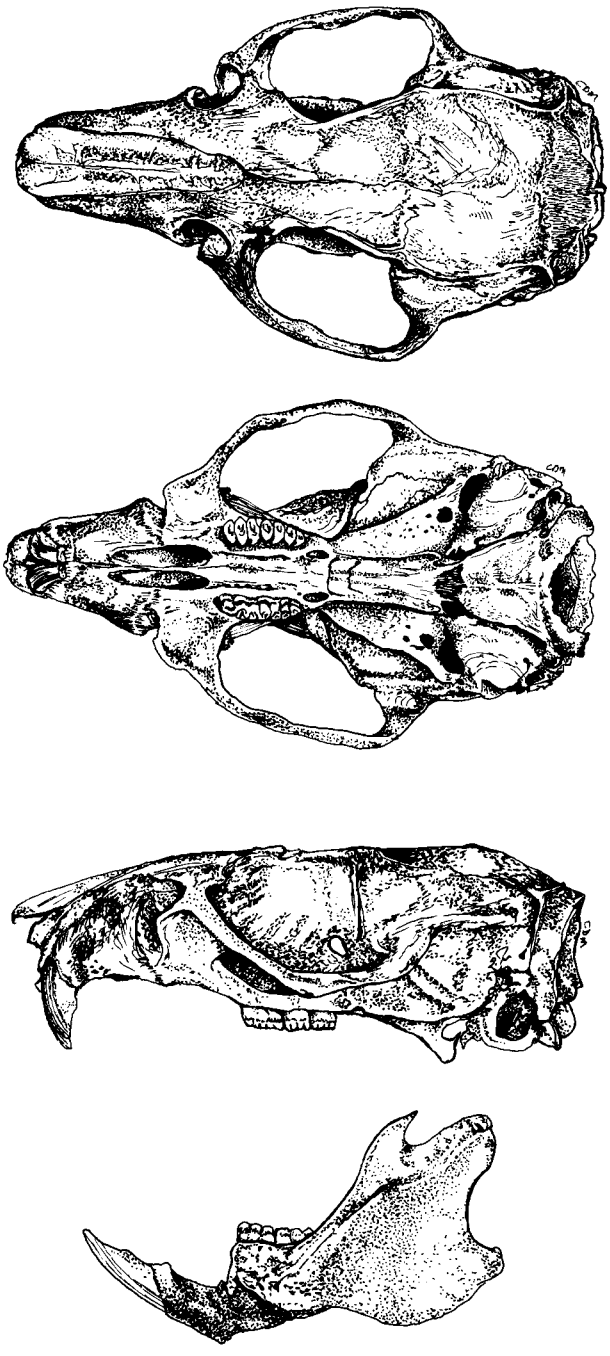

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *N. squamipes*. Specimen from Distrito Federal, Brazil; adult male, occipitonasal length 46.9 mm. Drawing by Coral McAllister.

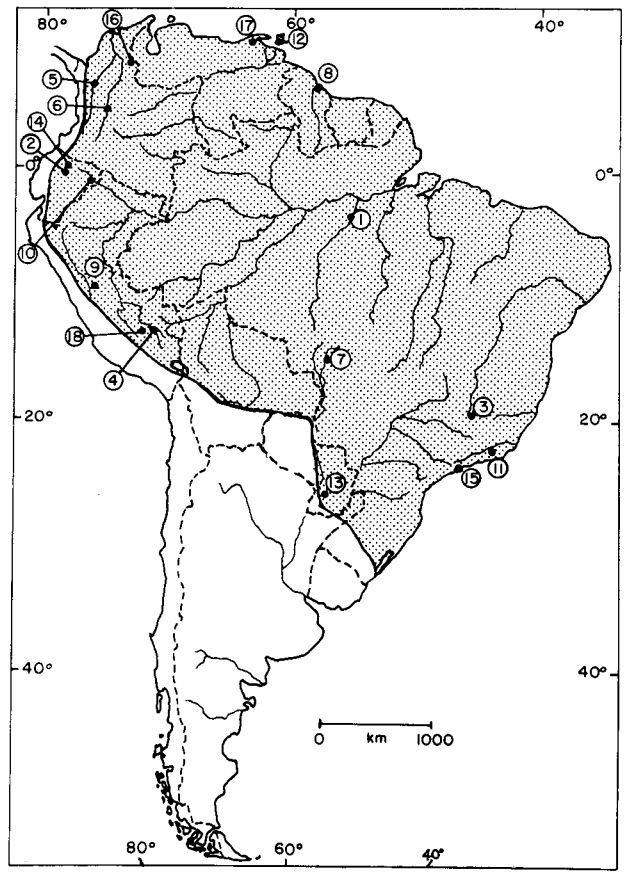

FIG. 3. Distribution of *Nectomys squamipes*. Dots represent type localities of the subspecies: 1, *N. s. amazonicus*; 2, *N. s. apicalis*; 3, *N. s. aquaticus*; 4, *N. s. garleppii*; 5, *N. s. grandis*; 6, *N. s. magdalenae*; 7, *N. s. mattensis*; 8, *N. s. melanius*; 9, *N. s. montanus*; 10, *N. s. napensis*; 11, *N. s. olivaceus*; 12, *N. s. palmipes*; 13, *N. s. pollens*; 14, *N. s. saturatus*; 15, *N. s. squamipes*; 16, *N. s. tarrensis*; 17, *N. s. tatei*; 18, *N. s. vallensis*.

caused by a species of the protozoan genus *Leishmania* were present in one of seven *N. squamipes* examined in Brazil (Lainson and Shaw, 1969). Pessôa (1974) found *Haemobartonella muris* and *Eperithrozoon* sp. in the blood of *N. squamipes*. None of 91 *N. squamipes* tested in Colombia carried the tapeworm genus *Echinococcus* (D'Alessandro et al., 1981).

Suitable baits for live-trapping include peanut butter (Paula, 1983), mixtures of peanut butter and fruit (Miles et al., 1981), and fruit and oat mixtures. Adults can be captured in Tomahawk live traps; juveniles and subadults (and rarely adults) will enter Sherman live traps. This species is maintained easily in captivity on a diet of rat chow, fresh fruit, and water.

GENETICS. Gardner and Patton (1976) found three karyotypically distinct groups of *N. squamipes* in Perú. Two males and two females had 2n = 52, FN = 52: one pair of small metacentric autosomes, 24 pairs of acrocentric autosomes, and subtelocentric sex chromosomes. One male had 2n = 42, FN = 40: 20 pairs of acrocentric autosomes, and acrocentric sex chromosomes. A third group (two males and two females) had 2n = 38, FN = 40: two large pairs of submetacentric autosomes, 16 pairs of acrocentric autosomes, and acrocentric sex chromosomes.

A study of 91 *N. squamipes* from three regions in Brazil revealed six karyotypic forms (Maia et al., 1984). Specimens from Pernambuco had complements of 2n = 52, FN = 52; 2n = 53, FN = 54; 2n = 54, FN = 56; 2n = 55, FN = 56; 2n = 56, FN = 56; and 2n = 57, FN = 57. Complements from São Paulo and Rio de Janeiro states were 2n = 55, FN = 56; 2n = 56, FN = 56; 2n = 57, FN = 58; 2n = 58, FN = 60; 2n = 59, FN = 62. Seventeen specimens from Rio Grande do Sul had complements of 2n = 56, FN = 56; 2n = 57, FN = 58; 2n = 58, FN = 60. X-chromosome types were acrocentric, subtelocentric, submetacentric, and submetacentric with a larger short arm. Y-chromosome types were subtelocentric, submetacentric, and metacentric.

Karyotypic variability in *N. squamipes* mainly is caused by supernumerary chromosomes (Maia et al., 1984). In 14 other rodent genera with supernumerary chromosomes, variability primarily is caused by Robertsonian rearrangements and pericentric inversions. Maia et al. (1984) concluded from its large cytogenetic variability that *N. squamipes* may include more than one species.

A color variant in *N. squamipes*, consisting of white patches of hair on the top of the head, was reported to occur in 6 of 56 specimens (Mello and Barbosa, 1974).

REMARKS. The skin of the type specimen of *Cercomys* Cuvier, 1829, and *C. cunicularis* is referable to *Nectomys squamipes* (*fide* Petter, 1973). The skull, however, is that of a *Proechi-*

mys, but the mandible is referable to *Echimys* (Petter, 1973). Petter (1973) suggested that the name *Cercomys cunicularis* was invalid, and the specific name *Trichomys apereoides* should be used for animals previously referred to *Cercomys*.

Vernacular names for *N. squamipes* include rata acuática, rata de agua, rato d'agua, rato lava-pés, quiara, Neotropical water rat, South American water rat, and Trinidadian water rat (for *N. s. palmipes*). The generic name *Nectomys* comes from the Greek νηκτός for swimming, and μῦς for mouse (Palmer, 1904). The specific name *squamipes* refers to the characteristic scales on the soles of the feet.

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