MAMMALIAN SPECIES No. 780, pp. 1–5, 3 figs.

Holochilus sciureus.

By Guillermo R. Barreto and Shaenandhoa García-Rangel

Published 20 December 2005 by the American Society of Mammalogists

Holochilus Brandt, 1835

Mus Desmarest, 1819:62. Type species *Mus brasiliensis*.
Holochilus Brandt, 1835:428. Type species *Mus* [*Holochilus*] *leucogaster*.
Hesperomys Waterhouse, 1839:75. Type species *Mus brasiliensis* by monotypy (Wagner 1842:288).
Holochilus Wagner, 1842:14. Type species *Holochilus sciureus* Wagner 1842:14. Elevation of name to genus rank.
Hesperomys Wagner 1845:147. Type species *Hesperomys leucogaster* Wagner 1845:147.
Holochilomys Peters, 1860:150. Type species *Holochilus* [*Holochilomys*] *brasiliensis* by monotypy.
Holocheilus Coues, 1874:176. Type species *Hesperomys leucopus* by monotypy.
Sigmodon Winge, 1887:21. Type species *Sigmodon vulpinus* (= *Holochilus brasiliensis*) considered by Hershkovitz (1955) as *Holochilus magnus*.

CONTEXT AND CONTENT. Order Rodentia, suborder Myomorpha, family Muridae, subfamily Sigmodontinae, genus *Holochilus*. *Holochilus* was considered a close relative of *Sigmodon* (Ellerman 1941), but penis morphology (Hooper and Musser 1964) and karyology (Baker et al. 1983) suggest a closer relationship to *Oryzomys* (Steppan 1995).

All of the named forms of *Holochilus* were referred to *H. brasiliensis* by Hershkovitz (1955), except *Holochilus magnus* (now *Lundomys molitor*). Massoia (1971) suggested *vulpinus* and *chacarius* (=*balnearum*) were valid species, but later Massoia (1981) considered *brasiliensis* (including *darwini* and *vulpinus*) included only populations of large rats with unexpanded paracones, vestigial mesolophs on M1 and M2, and distributed from northeastern Argentina throughout Uruguay to the southeastern states of Brazil. Reig (1986) listed *amazonicus*, *guianae*, and *venezuelae* as probable valid species. Karyotypic divergence among some geographic samples of *sciureus*-like rats suggest Venezuelan forms may be a distinct species (*H. venezuelae*—Aguilera and Perez-Zapata 1989). We keep the name *H. sciureus* for the Venezuelan form of *Holochilus* following Voss and Carleton (1993), Musser and Carleton (1993), and Soriano and Ochoa (1997).

At present, 3 extant species are recognized. The following key to species of *Holochilus* is based on Eisenberg (1989), Massoia (1981), Redford and Eisenberg (1992), and Voss and Carleton (1993):

1. Expanded paracones and no mesolophs on M1 and M2 ..... *H. sciureus*
   Unexpanded paracones and vestigial mesolophs on M1 and M2 2
2. Length of ear <20.5 mm; adult mass not >265 g; dorsum light orange chestnut, sometimes reddish with a few dark hairs ..... *H. chacarius*
   Length of ear >20.5 mm; adult mass >270 g; dorsum ochraceous tawny mixed with blackish ..... *H. brasiliensis*

Holochilus sciureus Wagner, 1842

Marsh Rat

Holochilus sciureus Wagner, 1842:17. Type locality "Río San Francisco, Minas Gerais, E. Brazil."
Holochilus nanus Thomas, 1897:495. Type locality "Source, Marajó Island, N.-E. Brazil."
Holochilus guianae Thomas, 1901:347. Type locality "Kanuku Mountains, [Guyana] British Guiana."
Holochilus venezuelae Allen, 1904:330. Type locality "El ll [Y] agual, [Edo. Apure] Central Venezuela."
Holochilus amazonicus Osgood, 1915:118. Type locality "Itacoara, Río Amazonas, Central Brazil."
Holochilus incarum Thomas, 1921:226. Type locality "Santa Ana, Cuzco district, Central Peru."

CONTEXT AND CONTENT. Context as above.

H. s. berbicensis Morrison-Scott, 1937:535. Type locality "Blairmont Plantation, Berbice, British Guiana," Guyana.
H. s. sciureus Wagner, 1842:17; see above.

DIAGNOSIS. *Holochilus sciureus* is distinguished from *H. brasiliensis* by its smaller size (lengths of head–body are 164 and 193 mm, respectively) and presence of expanded paracones but no mesolophs on M1 and M2. Tail is consistently shorter than head and body in *H. sciureus* but is about as long as head and body in *H. brasiliensis*. Tail of *H. sciureus* occasionally has a small hypothenar pad that does not occur in *H. brasiliensis*. *H. sciureus* has 8 or 10 mammae, whereas *H. brasiliensis* has only 8.

GENERAL CHARACTERS. Body form is ratlike. Dorsum is buffy or tawny, usually mixed with black. Sides are paler, and underparts vary from white to orange. Fur is short and close. Tail is thinly haired and is uniformly brown or somewhat paler beneath. Hindfeet noticeably larger than forefeet; 3 center digits considerably longer than outer 2. Hindclaws are prominent and toes are partially webbed. Webs are present between all adjacent digits but best developed between II and III and between III and IV. Natatory fringes are weakly developed along the plantar margins; these are longer hairs with a silvery cast.

Length of head and body of *H. sciureus* ranges from 130 to 220 mm and length of tail is 115–178 mm. Average body masses are 163.5 g (n = 7) in Surinam (Eisenberg 1989), 131.5 g (n = 351 females) and 198.5 g (n = 217 males) in Guyana (Twigg 1965), and 131.1 g (n = 314 females) and 130.2 g (n = 345 males) in Venezuela (Agüero 1979). Skull with very broad zygomatic plate and a blunt spinous process that extends its free dorsal edge, defining a deep zygomatic notch on each side of the rostrum (Fig. 2). Average ± *SD* cranial measures for females and males, respectively, in mm (sample sizes in parentheses) from Acarigua, Venezuela (Aguilera 1987), are greatest length of skull, 37.22 ± 1.83 (22), 39.50 ± 1.73 (25); condylobasal length, 34.85 ± 1.69 (21), 37.29 ± 1.71 (27); palatal length, 8.49 ± 0.6 (38), 8.69 ± 0.48 (39); basilar length, 30.69 ± 2.78 (21), 32.57 ± 1.63 (26); interorbital

FIG. 1. Female *Holochilus sciureus* from Calabozo, Venezuela. Photograph by G. R. Barreto.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Holochilus sciureus* from Calabozo, Venezuela (Museo de Ciencias Naturales Universidad Simón Bolívar MCNUSB 802, female). Maximum length of skull is 188 mm.

width, 4.82 ± 0.24 (38), 5.18 ± 0.31 (39); zygomatic width, 20.86 ± 1.19 (33), 21.67 ± 0.86 (37); length of mandible, 21.29 ± 1.43 (37), 22.13 ± 0.92 (39); depth of cranium, 10.96 ± 0.42 (21), 11.32 ± 0.48 (27). Both body-length data from Guyana and cranial measures from Venezuela suggest sexual dimorphism, males are larger than females when adults.

DISTRIBUTION. *Holochilus sciureus* occurs (Fig. 3) east of the Andes across northern South America in Venezuela, Guyana, and Suriname (Eisenberg 1989; Pons and Granjon 1998). It occurs in eastern Peru (Cocha Cashu), northern Bolivia, and in the State of Minas Gerais, Brazil (Emmons and Feer 1997; Honacki et al. 1982). *H. sciureus* is presumed to occur along the northern bank of the Amazon River, whereas *H. brasiliensis* occurs on the southern bank of the Amazon, mainly in the coastal states to the southeast of Brazil.

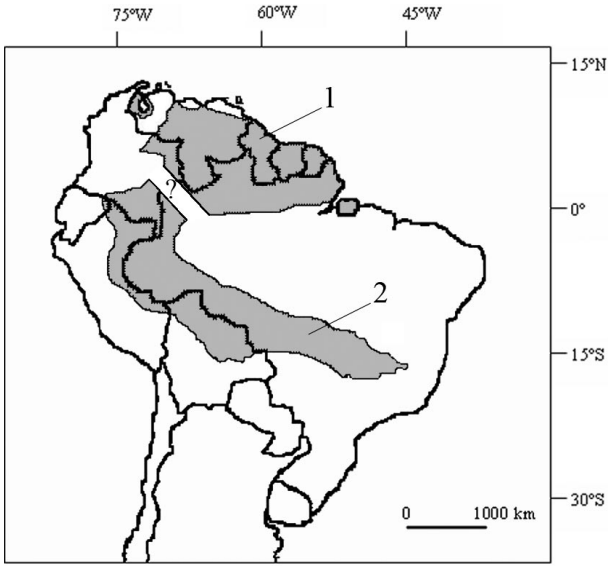

FIG. 3. Distribution of *Holochilus sciureus* in South America. Occurrence of the species along the southern bank of the Amazon River is doubtful. 1, *H. s. berbicensis*; 2, *H. s. sciureus*.

FOSSIL RECORD. Remains of 1 of the few extinct muroids known from South America are assigned to *Holochilus primigenius* (Steppan 1996). The fossils were recovered from the Ensenadan (middle Pleistocene) sediments of the Tarija Basin of Bolivia with a geologic age of 1.0–0.7 million years. *H. primigenius* may be the ancestor of its living congeners, including *H. sciureus* (Steppan 1996). Fossils of *H. sciureus* are not known.

FORM AND FUNCTION. Jugal is small and irregularly formed, and maxillary and squamosal are often in contact along the midportion of the zygomatic arch. In some samples of *Holochilus sciureus*, the mesopterygoid fossa often extends to or slightly between the M3. Subsquamosal fenestra is often occluded by an expanded hamular process or by an internal crest or septum of the periotic.

Dental formulae is i 1/1, c 0/0, p 0/0, m 3/3, total 16. Upper incisors are large, strong opisthodont teeth with yellow-orange enamel bands. Molars are flat-crowned with cusps and connecting lophs deployed in a single occlusal plane. Principal cusps are arranged in an alternating pattern and their labial and lingual margins are acutely angled (Voss and Carleton 1993).

Number of mammae varies from 8 to 10. In the latter case, individuals have a pair of thoracic teats in addition to the usual inguinal, abdominal, postaxial, and pectoral pairs.

ONTOGENY AND REPRODUCTION. Information on ontogeny and reproduction pertains to specimens from Venezuela and Guyana. Both sexes are fertile throughout the year. Fertility of males is 70–98% individuals with scrotal testes and fertility of females is >27% pregnancy along the year with some higher peaks (Twigg 1965). Rainfall increases fertility in both sexes (Twigg 1962, 1965). Testicular maturity is not correlated with mass or size of body but with testicular surface area according to an index that includes the number of spermatozoa and spermatids (Weir et al. 1996). The acceptance of the male by the female takes ca. 3.8 nights of courtship before mating. Probability of getting pregnant under laboratory conditions is ca. 66.7% (Aguilera 1987).

Gestation lasts ca. 29 days (Aguilera 1987). Mass of pregnant females increases ca. 48% (Aguilera 1987). Growth rates of fetal development is 0.12 g/day. *H. sciureus* tends to carry embryos in the right side of the uterus (Twigg 1965). Intrauterine mortality is 13–27%.

Parturition occurs at night or dawn, after which the female eats the placenta (Aguilera 1987). Litter size is affected by environmental conditions and increases with body mass and age (Agüero 1979; Twigg 1965). Mean number of embryos per litter is 5–6

in the Venezuelan Llanos (Agüero 1979), whereas mean litter size is 3.75 (range, 1–8) in the coastal region of Guyana (Twigg 1965). Large litters with a mean of 7.4 (*SD* = 0.3, *n* = 30 litters) embryos were reported for specimens from Acarigua, Venezuela (Cartaya 1983). Sex ratio at birth is 1:1 (Aguilera 1987).

Holochilus sciureus neonates are hairless except for mystacial vibrissae on top of the nose. Eyes and auditory meatus are closed, incisors have not emerged, and mass and body length at birth are ca. 7 g and 52 mm, respectively. Neonates exhibit no sexual dimorphism (Agüero 1979; Aguilera 1987). Within the 1st week, hairs start to appear, and by 15 days after birth, eyes and auditory meatus open. Incisor emergence occurs ca. 10 days after birth. Weaning occurs 10–15 days after birth, when infants weigh ca. 20–26 g (Agüero 1979; Aguilera 1987).

During the 1st month, growth rate is linear at 2.45 mm/day for length and 1.35 g/day for mass. During the 2nd month, growth rates become sex specific. Body mass of males increases at a rate of 10 g/week until the 5th month, after which growth declines to 4 g/week. Mass of females increases constantly through time at ca. 6 g/week. Increase in body length for each sex is also linear, but females grow faster (0.21 mm/week) than males (0.13 mm/week). This sexual difference enables females to reach their maximum head and body length (157 mm) before males (197 mm—Aguilera 1987).

Caloric content for adult males was 5.54 Kcal/g dry mass (*SD* = 0.59), and total lipids were 14.05% dry mass (*SD* = 5.22—Weir and Vivas 1988).

Body mass at which 50% of males have scrotal testes varies from 40 g (Twigg 1965) to 54 g (Agüero 1979). In a captive colony in which individuals were assigned to 3 age classes (juvenile, subadult, adults) based on body size and mass, males showed the transition from juvenile (body mass <90 g, M1 and M2 emerged) to subadult (body mass 90–150 g, M1 and M2 show differential wearing) at the end of the 2nd month, and the transition to adulthood (M1 and M2 show noticeable wearing) was at 3–4 months old, when individuals weighed 133 g and measured 160 mm total body length. For females, these stages show the same pattern of molar wear, although the subadult stage is attained earlier than in males, at ca. 1.5 months. Females reach adulthood later, at the end of the 4th month, when body mass is 100 g and body length is 140 mm (Aguilera 1987). Body mass at which 50% of females 1st become pregnant is 100 g (Aguero 1979; Twigg 1965). Percentage of pregnancy increases with body mass up to 93% for females >200 g (Agüero 1979).

ECOLOGY. Marsh rats frequent grasslands, savannas, marshes, and cultivated areas from sea level to 2,000 m. They live in open areas within rain forests (Emmons and Feer 1997). Diet of *H. sciureus* in rice fields in Venezuela (measured as percentage volume) was 84.3% grasses, 6% Cyperaceae, 5.8% invertebrates, 1.7% dicots, and 2.2 % unidentified material (Martino and Aguilera 1993). Rice (*Oryza sativa*) was the most commonly eaten grass, followed by *Leptochloa scabra* and *Chloris radiate*. Grass stems were the plant part most eaten. Rice seeds were also consumed. Despite abundant availability, Cyperaceae and dicots were eaten in low quantities (Martino and Aguilera 1993).

Mean home range size for marsh rats (*n* = 11) inhabiting a rice field in Venezuela based on mark–recapture data was 0.278 ha (*SD* = 0.403—Cartaya and Aguilera 1984).

Marsh rats account for 0.2–1.3% of total rodents captured in lowland and *Paspalum fasciculatum* savannas in the western Llanos of Venezuela (*n* = 34,455 trap nights—Utrera et al. 2000). Marsh rats occasionally become pests in cultivated crops, reaching densities of up to 713 rats/ha in rice fields of Venezuela. In a 1-year period, 180,606 marsh rats were caught by dogs and by hand in Blairmont, a 2,427-ha sugar state in Guyana; as many as 107 rats/ha were captured in some sugar fields (Twigg 1962). Such outbreaks, which are locally called "ratadas" (Cartaya and Aguilera 1985; Hershkovitz 1955; Twigg 1965), affect rice and sugar-cane production in Venezuela and Guyana (Agüero et al 1985; Aguilera 1985; Twigg 1965). Damage is caused to all developmental crop stages by gnawing and nest-building activities (Elías and Valencia 1984; Martino and Aguilera 1993; Twigg 1965). Crop losses are not accurately established, but may reach 50% of production in a harvest period. Anticoagulant baits are the principal control method.

Holochilus sciureus remains have been found in the stomachs of cayman (*Caiman crocodylus*) and rattlesnakes (*Crotalus*). Avian predators include barn owl (*Tyto alba*), savanna hawk (*Heterospizias meridionalis*), and white-tailed kite (*Elanus leucurus*). Crab-eating foxes (*Cerdocyon thous*) likely prey on marsh rats.

Thirteen parasites occur in *H. sciureus* (Guerrero 1985): Acarina (*Amblyomma ovale*, *Androlaelaps fahrenholzi*, *Eutrombicula alfreddugesi*, *E. batatas*, *Gigantolaelaps canestrini*, *G. mattogrossensis*, *Ornithonyssus bacoti*), Anoplura (*Hoplopleura contigua*, *H. quadridentata*), Nematoda (*Physaloptera*, *Stilestrongylus*, *Strongyloides*), and Siphonaptera (*Polygenis dunni*). Larvae of warble flies (*Cuterebra apicalis*), found mainly on the ventral surface and on heavier and older individuals, infect marsh rats in Guyana (Twigg 1965). No viruses linked with hemorrhagic fever have been reported in marsh rats. The Caño Delgadito virus (Fulhorst et al. 1997), Guanarito and Pirital viruses (Fulhorst et al. 1999), Machupo and Latino viruses (Webb 1975), and Sin Nombre virus (Calderón et al. 1999) have not been detected in laboratory or wild marsh rats.

BEHAVIOR. Marsh rats are mainly nocturnal. Females build spherical nests that are refuges for the female and her pups. Nests are usually found 0.5–1.5 m above the ground in sugarcane and rice fields and consist of an inner chamber made of shredded leaves and an outer layer of leaves by which the nest is attached to the crop stalk. Sometimes, nests consist only of a mass of fine leaves placed between soil cracks, under dense grass, tussocks, or on soil surface beneath remains of reaping (Twigg 1965, 1962).

GENETICS. Karyotypes reveal substantial divergence among geographic samples within the *Holochilus sciureus* complex (Voss and Carleton 1993). The karyotype of *H. sciureus* based on 28 individuals from Venezuela determined by Aguilera and Pérez-Zapata (1989) indicated the presence of 6 karyomorphs; the most frequent, and hence considered basic for the species, is 2n = 44 (FN = 56). This karyotype consisted of 7 pairs of metacentric chromosomes (5 large, 1 small, and 1 microchromosome) comprising 59.5% of the haploid set; 14 acrocentric pairs (9 small and 5 microchromosomes) representing 32% of the set; and the sexual pair, which is acrocentric and represents 6% (X) and 2.5% (Y) of the haploid set. Karyotypes from *sciureus*-like rats other than the Venezuelan form are 2n = 50, 2n = 56 (*n* = 1 male from Colombia and *n* = 1 male from Peru, respectively; Gardner and Patton 1976), and 2n = 55 (pair 1 is heteromorphic for a centric fusion, Brazil; Freitas et al. 1983). Chromosomal dimorphism in 44 specimens of *H. sciureus* was the result of 1 or 2 Robertsonian changes of the centric-fusion type, 1 pericentric inversion, and the presence of B chromosomes (Sangines and Aguilera 1991).

REMARKS. At present, the type species of *Holochilus* is *H.* (*Mus*) *leucogaster* Brandt 1835, a species known to be hystricomorphous and referable to the subgenus *Trinomys* of the genus *Proechimys*, thus rendering the names *Proechimys* and *Trinomys* junior synonyms of *Holochilus*. Voss and Abramson (1999) suggest conserving the name *Holochilus* Brandt 1835 for a genus of myomorphous neotropical marsh rats (family Muridae) and the names *Proechimys* J. A. Allen 1899 and *Trinomys* Thomas 1921 for hystricomorphous neotropical spiny rats (family Echyimidae). They propose *H. sciureus* Wagner 1842 be designated as the type of *Holochilus* (Voss and Abramson 1999).

We thank Dr. Marisol Aguilera for comments and literature. Comments by 2 anonymous referees are gratefullly acknowledged. We thank Decanato de Investigación y Desarrollo, Universidad Simón Bolívar (project CB 007 98) and FONACIT (S1 2001000690) for financial support.

LITERATURE CITED

AGÜERO, D. 1979. Análisis reproductivo de una población de *Holochilus brasiliensis* (Rodentia-Cricetidae) en cultivos de arroz en el Estado Portuguesa. Agronomía Tropical 28:101–16.

AGÜERO, D., J. QUEVEDO, I. TOVAR, A. FLORES, V. MARTÍNEZ, AND G. ESPINOZA. 1985. Estimación de daños y observaciones sobre la rata arrocera (*Holochilus venezuelae*) en caña de azúcar. Caña de Azúcar 3(2):63–70.

AGUILERA, M. 1985. Especies Plagas. Pp. 147–158 in El estudio de los mamíferos en Venezuela, evaluación y perspectivas (M. Aguilera, ed.). Fondo Editorial Acta Científica Venezolana, Caracas, Venezuela.

AGUILERA, M. 1987. Ciclo de vida, morfometría craneana y cariología de *Holochilus venezuelae* Allen 1904 (Rodentia, Cricetidae). Trabajo de Ascenso, Universidad Simón Bolívar, Sartenejas, Venezuela, 165 p.

AGUILERA, M., AND A. PÉREZ-ZAPATA. 1989. Cariología de *Holochilus venezuelae* (Rodentia, Cricetidae). Acta Científica Venezolana 40:198–207.

ALLEN, J. A. 1904. New mammals from Venezuela and Colombia. Bulletin of the American Museum of Natural History 20:327–335.

BAKER, R. J., B. F. KOOP, AND M. W. HAIDUK. 1983. Resolving systematic relationships with G-bands: a study of five genera of South American cricetine rodents. Systematic Zoology 32: 403–416.

BRANDT, J. F. 1835. Mammalium rodentium exoticum novorum vel minus rite cognitorum Musei Academici Zoologici descriptiones et icones. Mèmoires L'Acadèmie Impèriale des Sciences de Saint-Pètersbourg, series 6, 3(2):425–436.

CALDERÓN, G., et al. 1999. Hantavirus reservoir hosts associated with peridomestic habitats in Argentina. Emerging Infectious Diseases 5:792–797.

CAMERON, G. N., AND S. R. SPENCER. 1981. *Sigmodon hispidus*. Mammalian Species 158:1–9.

CARTAYA, E. 1983. Estudio de la comunidad de roedores plaga asociada a un cultivo de arroz (*Oryza sativa* L.) a lo largo de su ciclo de vida, en el Estado Portuguesa. Trabajo Especial de Grado, Universidad Simón Bolívar, Sartenejas, Venezuela, 89 p.

CARTAYA, E., AND M. AGUILERA. 1984. Area de acción de *Holochilus venezuelae* Allen, 1904 (Rodentia, Cricetidae) en un cultivo de arroz. Acta Científica Venezolana 35:162–163.

CARTAYA, E., AND M. AGUILERA. 1985. Estudio de la comunidad de roedores plaga en un cultivo de arroz. Acta Científica Venezolana 36:250–257.

COUES, E. 1874. Synopsis of the Muridae of North America. Proceedings of the Academy of Natural Sciences of Philadelphia 26:173–196.

DESMAREST, A. G. 1819. Noveau dictionnaire d'histoire naturelle, appliquèe aux art, principalement à l'agriculture et à l'economie rurale et domestique, par une societé de naturalistes. Nouvelle edition, Paris 29:40–71.

EISENBERG, J. F. 1989. Mammals of the Neotropics. Volume 1. University of Chicago Press, Illinois.

ELIAS, D., AND D. VALENCIA. 1984. La agricultura latinoamericana y los vertebrados plaga. Interciencia 9:223–229.

ELLERMAN, J. R. 1941. The families and genera of living rodents. Trustees of the British Museum, London, United Kingdom.

EMMONS, L. H., AND F. FEER. 1997. Neotropical rainforest mammals: a field guide. Second edition. University of Chicago Press, Illinois.

FREITAS, T. R. O., M. S. MATTEVI, AND L. F. B. OLIVEIRA. 1983. Chromosome relationships in three representatives of the genus *Holochilus* (Rodentia, Cricetidae) from Brazil. Genetica 61:13–20.

FULHORST, C. F., et al. 1997. Isolation, characterization and geographic distribution of Caño Delgadito virus, a newly discovered South American hantavirus (family Bunyaviridae). Virus Research 51:159–171.

FULHORST, C. F., et al. 1999. Natural rodent host associations of Guanarito and Pirital viruses (family Arenaviridae) in central Venezuela. American Journal of Tropical Medicine and Hygiene 61:325–330.

GARDNER, A. L., AND J. L. PATTON. 1976. Karyotypic variation in oryzomyni rodents (Cricetidae) with comments on chromosomal evolution in the neotropical cricetinae complex. Louisiana State University Publications of the Museum of Zoology 49:1–48.

GUERRERO, R. 1985. Parasitología. Pp. 35–91 in El estudio de los mamíferos en Venezuela, evaluación y perspectivas (M. Aguilera, ed.). Fondo Editorial Acta Científica Venezolana, Caracas, Venezuela.

HERSHKOVITZ, P. 1955. South American marsh rats, genus *Holochilus*, with a summary of sigmodont rodents. Fieldiana Zoology 37:639–673

HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL. 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Lawrence, Kansas.

HOOPER, E. J., AND G. G. MUSSER. 1964. The glans penis in neotropical cricetines (Muridae) with comments on classification of muroid rodents. Miscellaneous Publications, Museum Zoology, University of Michigan 123:1–57.

MARTINO, A. M., AND M. AGUILERA. 1993. Trophic relationships among four cricetid rodents in rice fields. Revista de Biología Tropical 41:131–141.

MASSOIA, E. 1971. Caracteres y rasgos bioecológicos de *Holochilus brasiliensis chacarius* ("rata nutria") de la Provincia de Formosa y comparaciones con *Holochilus brasiliensis vulpinus* (Brants) (Mammalia-Rodentia-Cricetidae). Revista de Investigaciones Agropecuarias Instituto de Investigaciones Agropecuarias 8:13–40.

MASSOIA, E. 1981. El estado sistemático y zoogeografía de *Mus brasiliensis* Desmarest y *Holochilus sciureus* Wagner (Mammalia, Rodentia, Cricetidae). Physis, Sección C 39:31–34.

MONES, A., AND L. R. CASTIGLIANI. 1979. Additions to the knowledge of fossil rodents of Uruguay Mammalia Rodentia. Palaeontologische Zeitschrift 53:77–87.

MORRISON-SCOTT, T. C. S. 1937. An apparently new form of Cricetinae from Bristish Guiana. Annals and Magazine of Natural History, Series 10, 20:535–538.

MUSSER, G. G., AND M. D. CARLETON. 1993. Family Muridae. Pp. 501–756 in Mammal species of the world: a taxonomic and geographic reference (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, Washington, D.C.

OSGOOD, W. H. 1915. New mammals from Brazil and Peru. Fieldiana Zoology 10:1–12.

PETERS, W. 1860. Derselbe über einige merkwürdige Nagethiere (*Spalacomys indicus*, *Mus tomentosus* und *Mus squamipes*) des Königl. Zoologischen Museums (mit 2 Tafeln). Abhandlungen der Königlichen Preussischen Akademie der Wissenschaften zu Berlin 139–156.

PONS, J. M., AND L. GRANJON. 1998. Liste des mammifères de Guyana française (Juillet 1997). Arvicola 10:12–15.

REDFORD, K. H., AND J. F. EISENBERG. 1992. Mammals of the Neotropics, the southern cone. Volume 2. University of Chicago Press, Illinois.

REIG, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404–440 in High altitude tropical biogeography (F. Vuilleumier and M. Monasterio, eds.). Oxford University Press, New York.

SANGINES, N., AND M. AGUILERA. 1991. Chromosome polymorphism in *Holochilus venezuelae* (Rodentia: Cricetidae): C- and G-bands. Genome 34:13–18.

SMITH, M. F., AND J. L. PATTON. 1999. Phylogenetic relationships and the radiation of sigmodontine rodents in South America: evidence from cytochrome b. Journal of Mammal Evolution 6: 89–128.

SORIANO, P., AND J. OCHOA. 1997. Lista actualizada de los mamíferos de Venezuela. Pp. 203–227 in Vertebrados actuales y fósiles de Venezuela (E. La Marca, ed.). Fundacite, Caracas, Venezuela.

STEPPAN, S. J. 1995. Revision of the tribe Phyllotini (Rodentia: Sigmodontinae) with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana Zoology 80:1–112.

STEPPAN, S. J. 1996. A new species of *Holochilus* (Rodentia: Sigmodontinae) from the middle Pleistocene of Bolivia and its phylogenetic significance. Journal of Vertebrate Paleontology 16:522–530.

THOMAS, O. 1897. Notes on some S. American Muridae. Annals and Magazine of Natural History, series 6, 19:494–501.

THOMAS, O. 1901. On a collection of mammals from the Kanuku Mountains, British Guiana. Annals and Magazine of Natural History, series 7, 8:346–366.

THOMAS, O. 1921. Report on the mammals collected by Mr. Edmund Heller during the Peruvian expedition of 1915 under the auspices of Yale University and the National Geographic Society. Proceedings of the U.S. National Museum 58(233): 217–249.

TWIGG, G. I. 1962. Notes on *Holochilus sciureus* in British Guiana. Journal of Mammalogy 43:369–374.

TWIGG, G. I. 1965. Studies on *Holochilus*, *sciureus berbicensis*, a cricetine rodent from the coastal region of British Guiana. Proceedings of the Zoological Society of London 245:263–283.

UTRERA, A., et al. 2000. Small mammals in agricultural areas of the western llanos of Venezuela: community structure, habitat

associations, and relative densities. Journal of Mammalogy 81: 536–548.

Voss, R. S., and N. I. Abramson. 1999. *Holochilus* Brandt 1835, *Proechimys* J. A. Allen 1899, and *Trinomys* Thomas 1921 (Mammalia, Rodentia) proposed conservation by the designation of *H. sciureus* Wagner 1842 as the type species of *Holochilus*. Bulletin of Zoological Nomenclature 56:1–7.

Voss, R. S., and M. D. Carleton. 1993. A new genus for *Hesperomys molitor* Winge and *Holochilus magnus* Hershkovitz (Mammalia, Muridae) with an analysis of its phylogenetic relationships. American Museum Novitates 3085:1–39.

Wagner, J. A. 1842. Beschreibung einiger oder minder bekannter Nager. Archives für Naturgeschichte 8:1–33.

Wagner, J. A. 1845. Diagnosen eineger neuen Arten von Nagen und Handfluglern. Archives für Naturgeschichte 1:145–149.

Waterhouse, G. R. 1839. The zoology of the voyage of H. M. S. Beagle, Part II. Mammalia. Edited and superintended by Charles Darwin. London, Smith, Elder & Co., London, England.

Webb, P. A. 1975. Infection of wild and laboratory animals with Machupo and Latino viruses. Bulletin of the World Health Organization 52:493–499.

Weir, E. H., and A. M. Vivas. 1988. Caloric and total lipid contents in adult male *Holochilus brasiliensis* (Rodentia: Cricetidae). Ecotropicos 1:41–43.

Weir, E. H., M. G. Muñoz, and A. M. Vivas. 1996. Madurez testicular en *Holochilus venezuelae* y *Sigmodon alstoni* (Rodentia: Cricetidae). Boletín del Centro de Investigaciones Biológicas 30:187–194.

Winge, H. 1887. Jordfundne og nulevende gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. E Museo Lundii 1(3): 1–200.

Associate editors of this account were Gail Michener and Pamela Owen. Editor was Virginia Hayssen.

Guillermo R. Barreto and Shaenandhoa García-Rangel, Laboratorio de Manejo y Conservación de Fauna, Departamento de Biología de Organismos, Universidad Simón Bolívar, Apartado 89000, Caracas 1080-A, Venezuela.