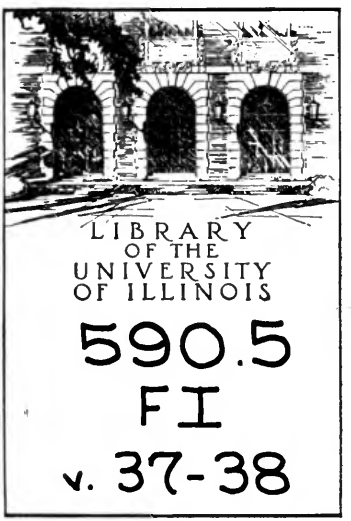

South American Marsh Rats, Genus *Holochilus*, With a Summary of Sigmodont Rodents

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Marsh rats, genus *Holochilus*, are large cricetines specialized for palustrine or semi-aquatic life. Their natural abode—in cane brakes, grass-lined stream banks and swamps—has predisposed the rats for successful occupation of sugar-cane plantations in the same regions. The vernacular name for the animal in Brazil is *rato de cana;* in Spanish-speaking countries it is *rata de agua*. The name used by the Guaraní Indians is *angudya pihta*. The generic name *Holochilus*, meaning "whole lip" in Greek, was proposed by Brandt in 1835 because the upper lip in two dried skins he described appeared to be entire. It has since been shown that the upper lip of marsh rats is normally cleft in the midline, as in all other rodents.

The marsh rats, *Holochilus*, the cotton rats, *Sigmodon*, the coney rat, *Reithrodon*, and the red-nosed vole, *Neotomys*, compose a natural, well-defined assemblage of cricetines to be known as the sigmodont group. Diagnostic characters of sigmodonts include reduced outer hind toes, webbed middle hind toes, spinous process of zygomatic plate, specialized posterior palatal region, simplified molars characterized by absence or obsolescence of a functional mesoloph (id) in, at least, $m\frac{1}{1}\text{–}\frac{2}{3}$, and the S-shaped enamel pattern of m_3.

Sigmodont rodents are inhabitants of open country, with a predilection for cultivated fields, where they usually become excessively abundant. They are abroad day and night and breed continuously throughout the year. Their young do not pass through a well-marked, protracted juvenal nestling stage. Instead, they acquire adult type pelage and, except for some delay in *Reithrodon*, fully erupted functional third molars very shortly after birth. They become active foragers while still occupying the maternal nest.

Sigmodont rodents are distributed from southern United States to Tierra del Fuego at the southern tip of South America (fig. 139).

Cotton rats occur throughout the North American portion of the range and the grass- and scrublands of the tropical zones of northern South America. The range of marsh rats is nearly as extensive. It overlaps that of *Sigmodon* in Venezuela, the Guianas, and the northeastern portion of the Amazonian basin. It continues southward along the eastern coast of Brazil and the swamps and grass-lined banks and tributaries of the Amazon and Paraná rivers, and terminates in the Argentine pampas. The red-nosed *Neotomys* has a limited distribution in the high Andean grasslands of Peru, Bolivia, and extreme northern Patagonia. The little coney rat, *Reithrodon*, of the treeless plains and pampas of Uruguay, Argentina and Chile, occupies the southern portion of the range of sigmodont rodents.

ABBREVIATIONS

The following abbreviations are used for designating the institutions that house the specimens examined: CNHM = Chicago Natural History Museum; MAHN = Museo Argentino de Historia Natural.

CHARACTERS OF SIGMODONT RODENTS

External characters.—Form variable, rat-like in *Holochilus*, cuniculoid in *Reithrodon*, vole-like in *Neotomys* and *Sigmodon* (= *Sigmomys*); size moderately large to among the largest of American cricetines; pelage soft or harsh; tail shorter than combined head and body length, except in *Holochilus magnus;* ear small; hind foot small to extremely large, claws well developed, about one-half of length of corresponding digits, except in *Reithrodon*, where they are somewhat shorter; outer digits of hind foot reduced, first and fifth toes, less claw, not extending distad of base of adjacent toes, except in *Holochilus*, where fifth toe, less claw, reaches middle of first phalanx of fourth; mammae 8 or 10.

Cranial characters (pls. 21–29).—Nasals truncate or rounded behind, and terminating on a line with, or slightly behind or in front of, fronto-maxillary suture, never with a long pointed process extending deeply between frontals; supraorbital edges square, ridged or beaded, never evenly rounded; zygomatic arches well expanded behind, convergent anteriorly; interparietal well developed, its width always greater than width across ridges at fronto-parietal sutures; infraorbital foramen, seen from dorsal surface of skull, deeply excised, with more than one-half to entire width of zygomatic plate exposed to view; zygomatic plate high and broad, its width more than one-half of least interorbital breadth, the anterior border convex, the upper

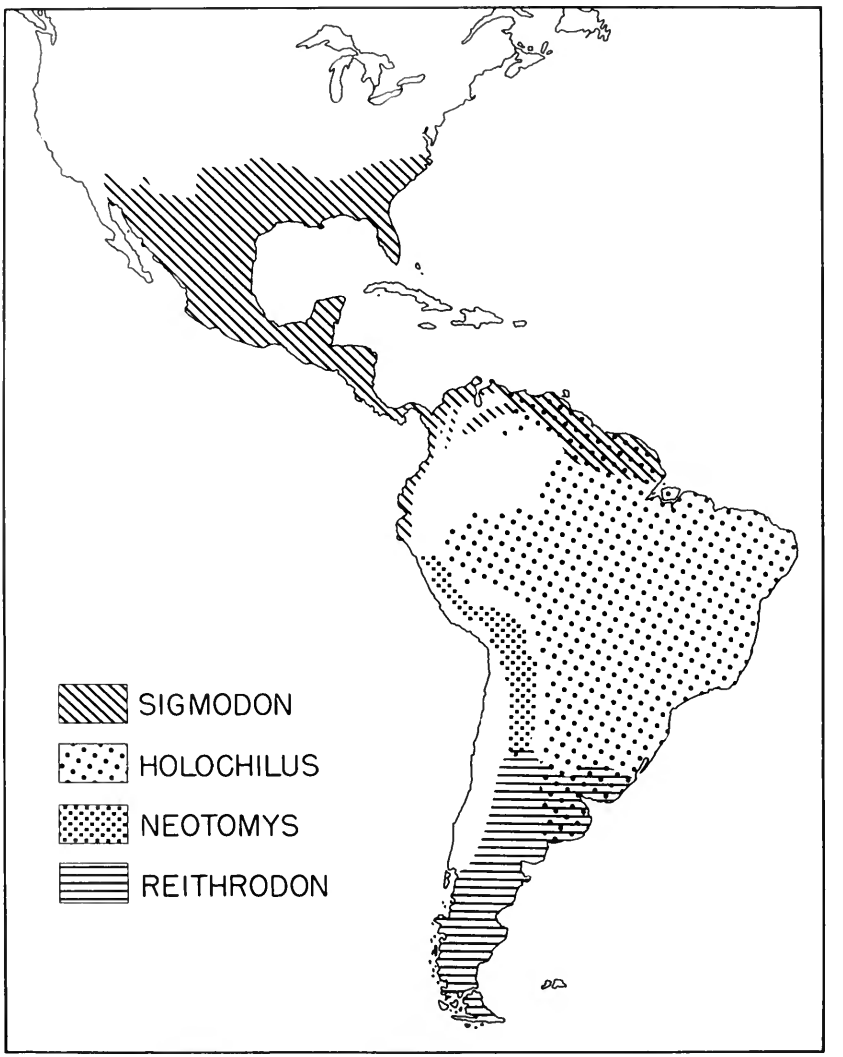


FIG. 139. Distribution of sigmodont rodents in North and South America.

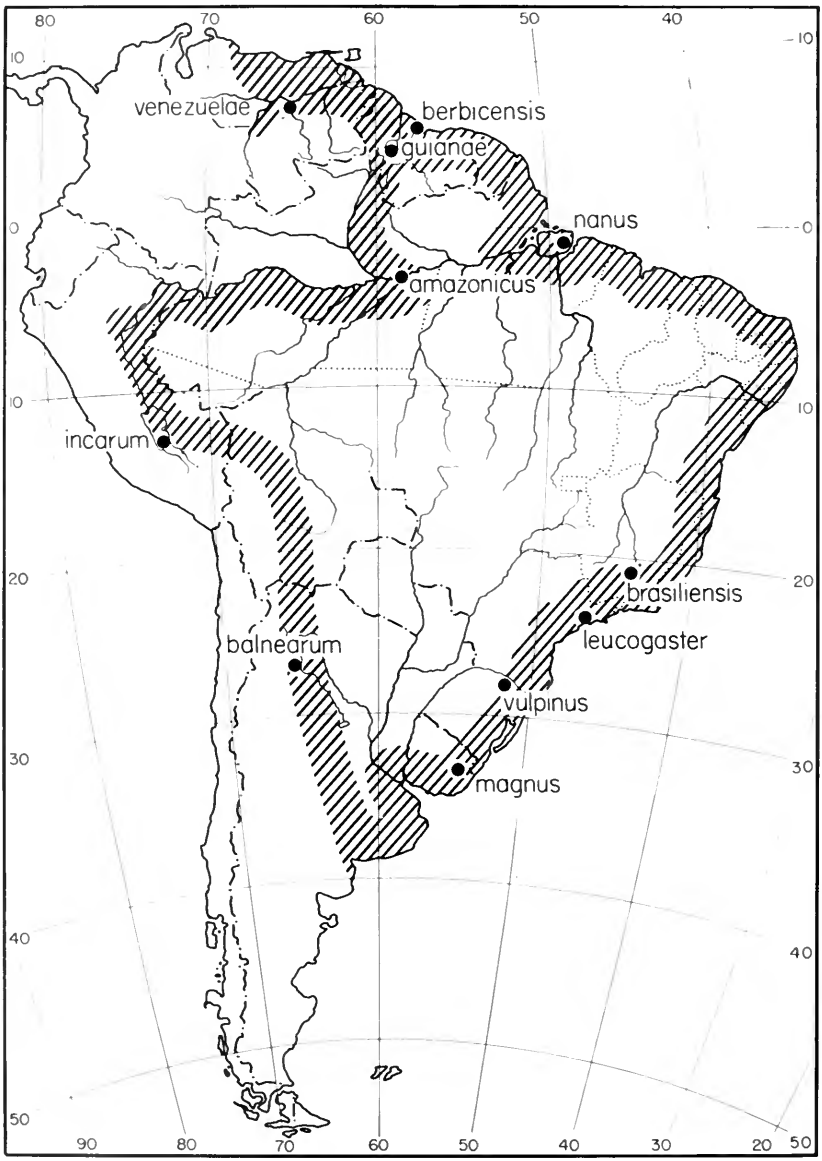


FIG. 140. Distribution of *Holochilus*. Diagonal lines = outer limits of range; dots = type localities of *H. magnus* and nominal subspecies of *H. brasiliensis*.

corner produced as a short, sharp spine; incisive foramina narrow, pointed behind; posterior border of palate situated slightly behind or in front of posterior plane of last molars; posterior portion of palate with two pitted fossae separated by a median ridge; parapterygoid fossa seen from ventral surface deep, the anterior corner usually undercut, the lateral walls well defined; sphenopalatine vacuities well opened or, sometimes, partially closed by a thin membranous bony tissue; bullae well inflated.

Dental characters (see fig. 144 and pp. 650–1 for explanation of terminology).—Upper incisors well developed, opisthodont or orthodont, their anterior face smooth or grooved; molar rows parallel-sided or slightly divergent posteriorly; molars large, crowns high, sometimes prismatic, with grinding surface flat or terraced; mesoloph rudimentary or absent in first two molars, present or absent in third upper molar; mesostyle absent or extremely small, never functional or associated with mesoloph, if present; occlusal surface of m_3 with S-shaped enamel pattern; major and primary folds deeply penetrating, the second primary of upper (first primary of lower) molars always extending medially beyond midline of tooth and apex of major fold; greatest length of first primary fold of upper molars one-half or more of length of second primary fold; major and first primary folds of m^3 often confluent and forming a lamina; second secondary fold (posterior cingulum) of m^{1-2} absent in adults, absent or extremely reduced in juvenals; internal folds absent; antero-internal fold sometimes present in first molar; first minor folds of m^{2-3} absent in adult, sometimes present in juvenal.

RELATIONSHIPS

Evolution of American cricetines has paralleled that of the New World Perissodactyla. The primitive brachyodont, buno-mesolophodont cricetines have survived, like the tapir, in forested parts of the range. Like the horse, the progressive branch of cricetines, with mesoloph absent or vestigial, has become increasingly specialized for life in open country and a diet of grasses. The young have lost, or are in process of losing, the distinctive juvenal phase of pelage comparable to the spotted coat of young tapirs and other woodland ungulates. The molars have become higher, their crown surfaces flatter and tending toward lamination. The third molar of grazing cricetines is nearly always precociously functional. This condition provides the needed maximum grinding surface which, in young ungulates, is supplied by deciduous premolars.

Sigmodont rodents are members of the relatively recently evolved, essentially grazing, New World mammalian fauna of open country. Morphologically, they merge into the phyllotine group (*Phyllotis, Hesperomys,* and others) by a recombination of characters. In both groups, the dentition is fundamentally similar. In sigmodonts, however, specialization of the posterior palatal region and the maxillary process of the zygoma is extreme. On the basis of dentition alone, the neotomyine rodents also appear to be nearly related. Cranially, however, wood rats conserve what may be regarded as the generalized cricetine posterior palatal region and zygomatic plate. A hypothetical common ancestor of sigmodont, phyllotine, and neotomyine rodents might have combined the cranial characters of a form like *Neotomodon,* and the bunodont but more brachyodont molars of a phyllotine like typical *Hesperomys.*

The two basic types of posterior palatal regions are repeated, with more or less modifications, throughout all myomorphs. Among mesolophodont cricetines, the short palate and undifferentiated pterygoids are found in true peromyscids, the long specialized palate in oryzomyines. Specialization of the posterior palatal region in the latter, however, has not affected the pterygoids at all, compared with the condition in sigmodonts.

THE MESOLOPH AND DEVELOPMENT OF M^3

In cricetines a well-developed, functional mesoloph (id) is always associated with brachyodont, bunodont molars of primarily forest-dwelling species. In living forms (e.g., *Oryzomys,* true *Peromyscus, Thomasomys, Aporodon*) the mesoloph (id) is locked with the mesostyle (id). A mesoloph (id) is vestigial or absent in specialized high flat-crowned molars of cricetines inhabiting open country, scrubland and, secondarily, forests (usually coniferous). Regressive loss of the mesoloph is associated with the evolution of grazers and grain-eaters from browsers and fruit-eaters (Hershkovitz, in preparation). In some cases it is lost in the bunodont stage of molar structure, in others its degeneration takes place in evolutionary stages of molar planation (figs. 141, 142) or of hypsodonty. In a given species ultimate disappearance of the element may have taken place during phylogeny, during ontogeny, or during both geneses. There is no vestige of a mesoloph (id) in even the newly erupted molars of *Sigmodon, Reithrodon,* and *Neotomys.* In *Holochilus magnus* a well-defined vestige is present in each upper juvenal molar (pl. 17); in newly erupted m_{1-2}, the vestige is smaller but still well marked

(pl. 18); in m_3 it is obsolete. In all cases the mesoloph (id) is nonfunctional and is completely lost in the young adult tooth. The molars of *H. brasiliensis* (pls. 17, 18) are more specialized, compressed anteroposteriorly, their crowns flat, the cusps triangulate, and the mesoloph (id) absent in all but m^3. Here the element is usually well developed and functional through juvenal and young adult stages (fig. 143). In some individuals, even juvenals, it may be obsolete or entirely lacking. Thus, in this species, the mesoloph may be lost either in phylogeny or during ontogeny.

Combined with the regressive, or palingenetic, nature of the mesoloph in m^3 is the caenogenetic character of lamination, a dental development for more efficient grinding of harsh grasses. In *Holochilus brasiliensis*, lamination of the anterior one-third of m^3 by confluence of major and first primary folds appears in the juvenal and advances into the subadult molar (fig. 143, C–E). Lamination of the postcingulum in the same tooth of this species is also incipient and marked by the emergence of a new element, the second minor fold. This enamel fold is confluent with both second primary and second secondary folds in the newly erupted molar, confluent only with the second primary in the worn juvenal and in the adult molar, or is an enamel island. In the dentally more primitive *Holochilus magnus*, lamination of the anterior one-third of m^3 appears only in the newly erupted tooth and there is no indication of a second minor fold or of lamination of the postcingulum (fig. 143, A, B). In *Sigmodon*, lamination of the anterior one-third of m^3 has progressed through ontogeny into a permanent adult character (fig. 143, F). Lamination of the postcingulum is a juvenal character in *Neotomys*, but here the second minor fold has become established as a trenchant adult character (fig. 143, G).

The extremely variable nature of the upper third molar stands in marked contrast with the comparatively stabilized lower third molar. The evolution of this tooth to the S-shaped pattern has been consistent in all sigmodont species (pl. 20).

Eruption of the third molar is advanced, often prenatal, in most cricetines with mesoloph vestigial or absent in adult dentition. The tooth becomes functional before it is structurally mature. Its development at this point may be at the same level as that of the uncut or newly erupted molar of the more primitive mesolophodont cricetines.

DIAGNOSTIC CHARACTERS AND KEY TO THE GENERA OF SIGMODONT RODENTS

1. Hamular processes of pterygoids converging anteriorly to form a Λ-shaped mesopterygoid fossa; incisive foramina extending posteriorly behind anterior plane of first molars; supraorbital region parallel-sided, the edges square, unridged; lateral outline of skull leporine, dorsal contour extremely arched; orbits large and high; interorbital vacuity extraordinarily large; condylar process of mandible deeply excavated internally; opisthodont upper incisors with a deep median groove; molars prismatic; second secondary fold of m^3 well developed but confluent with second primary in adult; procingulum of unworn m_1 trilobate; second primary fold of m_2 two-thirds or more of length of first primary fold; outer digits of hind foot extremely reduced, not reaching to base of adjoining digits; claws less than one-half of length of corresponding digits; sole hairy from back of heel to base of outer digits; ear comparatively large; mammae 2–2=8 ..... *Reithrodon* Waterhouse, 1837

   SYNONYMS: *Ptyssophorus* Ameghino, 1889; *Proreithrodon* Ameghino, 1908; *?Tretomys* Ameghino, 1889.

   SPECIES: *Reithrodon physodes* Olfers, 1818 (antedates *auritus* Desmarest, 1819).

   SYNONYMS: *Reithrodon typicus* Waterhouse, 1837; *R. cuniculoides* Waterhouse, 1837; *R. caurinus* Thomas, 1920; *R. olivensis* Rusconi, 1931 (Pleistocene); *Ptyssophorus elegans* Ameghino, 1889 (Pleistocene); *P. rotundatus* Rusconi, 1931 (Pleistocene); *?Tretomys atavus* Ameghino, 1889 (Pleistocene); *Proreithrodon chapalmalense* Ameghino, 1908 (Pleistocene); *P. incipiens* Ameghino, 1908 (Pleistocene). For discussion of the Recent subspecies see Osgood, 1943 (Field Mus. Nat. Hist., **30**: 220–224). (See pls. 19, 20, 25–29; text fig. 143.)

   Hamular processes of pterygoids parallel-sided or slightly divergent to form a Π- or M-shaped mesopterygoid fossa; incisive foramina extending posteriorly in front of or behind anterior plane of first molar; sides of supraorbital region parallel, convergent at midline, or divergent, with or without ridges; lateral outline of skull murine, dorsal contour of skull slightly or moderately convex; orbits not markedly enlarged; interorbital vacuity normal in size; condylar process of mandible not concave internally; upper incisors opisthodont or proodont, grooved or ungrooved; molars more or less hypsodont, never prismatic; second secondary fold of m^3 present or absent in adults; procingulum of m_1 semicircular, triangular, sometimes faintly trilobate; second primary fold of m_2 more or less than one-half of length of first primary; outer hind digits, less claw, reaching at least to base of adjoining digits; claw more than one-half of length of corresponding digits; sole bare or hairy on heel only; ears comparatively small; mammae 8 or 10 2

2. Anterior portion of nasals with a pronounced expansion; sides of supraorbital region parallel or convex midfrontally, the edges square and raised, but not beaded; temporal ridges obsolete or absent; width of mesopterygoid fossa at base of hamular processes less than width of parapterygoid fossa at same plane; diastema short, approximately equal to or less than alveolar length of molar row; posterior border of angle of mandible broadly rounded or truncate, not pointed, coronoid process weak; lower incisor short and broad, the cutting edge hardly extending above horizontal plane of molar crowns, tip of root not encased in projecting capsule; upper incisors opisthodont, the anterior surface flat with a pronounced inward slope when seen in cross section, lateral borders deeply grooved; postcingulum of m^3 well developed and always clearly defined in the adult by deeply penetrating second secondary and second minor folds; second primary fold of m_2 about one-half as long as first primary; minor folds of m_{2-3} absent, ear and hind foot extremely small, heel covered with hair; snout contrastingly colored reddish; mammae 2–2=8 ..... *Neotomys* Thomas, 1894

   SPECIES and SUBSPECIES: *N. ebriosus ebriosus* Thomas; *N. e. vulturnus* Thomas). (See pls. 19, 20, 25–29; text fig. 143.)

Anterior portion of nasals with normally tapered expansion; sides of supraorbital region parallel, convex midfrontally, or divergent, the edges square, ridged or beaded; temporal ridges well developed in adults; width of mesopterygoid fossa at base of hamular processes equal to or more than width of parapterygoid fossa at same plane; diastema always longer than alveolar length of molar row; posterior border of angle of mandible tapered to a blunt point, coronoid process well developed, as high as or higher than condylar process; lower incisor long and slender, cutting edge extending well above horizontal plane of molars, tip of root encased in projecting capsule; upper incisors opisthodont or orthodont, the anterior face normally convex, grooves, if present, near midline of tooth, never at lateral border; postcingulum of m^3 weakly developed or absent in juvenal, absent in adult; second primary fold of m_2 more or less than one-half of length of first primary; first minor fold of m_{2-3} present at least in juvenal; ear short or moderate in length; hind foot moderate to extremely large; heel bare, smooth; snout not contrastingly colored; mammae 3–2=10 3

3. Nasals truncate behind, not extending beyond fronto-maxillary suture; supraorbital region broadly divergent, edges beaded; frontal sinuses usually well inflated, midfrontal region convex in transverse outline; fronto-parietal sutures straight and forming an obtuse angle at midline; width across fronto-parietal sutures more than alveolar length of molar row and approximately equal to or more than length of diastema; incisive foramina extending posteriorly to or behind anterior plane of first molars; incisors opisthodont, grooved or ungrooved; molar crowns high, plane, principal cusps lozenge-shaped; vestige of mesoloph absent; apices of major and first primary folds opposed and touching in m^{1-2}, confluent in m^3; second secondary folds (posterior cingula) absent in upper molars; first secondary folds absent in lower second and third molars; anterior internal folds absent in first molars; second primary fold of m_2 short, less than one-half of length of first primary; external form vole-like; size moderately large; pelage coarse, often hispid, color pattern of upper parts and sides of body strongly agouti; tail shorter than combined head and body length; hind foot well developed, upper surface well haired, digital bristles usually as long as or longer than claws; first and fifth digits, less claw, not extending beyond base of corresponding adjacent toes ..... *Sigmodon* Say and Ord, 1825

SYNONYM: *Sigmomys* Thomas, 1901 (based on individuals of South American representatives of *S. hispidus* with grooved incisors).

SPECIES: Unrevised, but all named forms probably referable to *S. hispidus*. (See pls. 19, 20, 25–29; text fig. 143.)

Genus *Holochilus*, as described below.

Genus **Holochilus** Brandt

Holochilus Brandt, 1835, Mém. Soc. Imp. Sci., St. Petersb., (6), **1**: 428 (subgenus of *Mus;* included species: *leucogaster*, type; *anguya*); Wagner, 1842, Arch. Naturg., (8), **1**: 14 (generic rank, description, comparison with *Sigmodon;* species: *leucogaster, anguya, sciureus*); Wagner, 1843, Schreber's Säugth. Suppl., **3**: 548 (species: *brasiliensis, leucogaster, canellinus, sciureus, vulpinus*); Burmeister, 1854, Syst. Übers. Thiere Bras., **1**: 162 (part; subgenus of *Hesperomys;* description; species: *vulpinus, squamipes* [nec Brants], *physodes*); Ameghino, 1889, Act. Acad. Cienc., **6**: 116 (description; species: *vulpinus, multannus*); Trouessart, 1904, Cat. Mamm. Suppl., p. 411 (part; species: *multannus, brasiliensis, vulpinus, darwini, sciureus, guianae, canellinus, nanus, physodes, russatus*).

Holochyse (sic) Lesson, 1842, Nouv. Tabl. Reg. Anim., p. 137 (misspelling, name only listed).

Holochilomys (sic) Peters, 1861, Akad. Wiss. Berlin, **1860**: 150, 151; Hensel, 1873, Abh. Akad. Wiss. Berlin, Phys. Kl., **1872**: 32 (in synonymy of *Hesperomys vulpinus;* species: *brasiliensis*).

Holocheilus (sic) Coues, 1874, Proc. Acad. Nat. Sci. Philadelphia, **26**: 177, footnote (discussion).

Sigmodon Winge, 1888, E. Mus. Lundii, **1**, (3), pp. 12, 21 (comparisons; species: *vulpinus*); Merriam, 1895, Proc. Acad. Nat. Sci. Philadelphia, **1894**: 226 and footnote 6 (species: *vulpinus*).

Genotype.—*Mus* (*Holochilus*) *leucogaster* Brandt (=*Holochilus brasiliensis leucogaster* Brandt) and *Mus* (*Holochilus*) *anguya* Brandt (=*Holochilus brasiliensis leucogaster* Brandt); restricted to the first-named form by Miller and Rehn, 1901, Proc. Boston Soc. Nat. Hist., **30**: 89.

Included species.—*Holochilus brasiliensis* Desmarest; *H. magnus* sp. nov.

The following, listed in some current works as probable species of *Holochilus*, are referable to other genera, as shown.

Mus lutescens Gay, 1847=*Rattus norvegicus* Erxleben, 1771.

Mus Simpsoni Philippi, 1900=*Rattus norvegicus* Erxleben, 1771.

Mus agilis Philippi, 1900=*Oryzomys longicaudatus* Bennett, 1832.

DISTRIBUTION

Figure 140

Swamps, grasslands, and other moist, unforested situations from the coastal plains of Venezuela west into the Guianan lowlands, thence into suitable habitats in Brazil, Uruguay, Paraguay, the Amazonian basin in Peru and Bolivia, the Río Paraguay basin in Bolivia, and in Argentina the Paraná basin, the department of Buenos Aires, and possibly the department of Eva Perón; altitudinal range, sea level to approximately 2,000 meters above.

TAXONOMIC HISTORY

Holochilus was proposed by Brandt in 1835 as a subgenus of *Mus*. Improperly preserved dried skins gave Brandt the erroneous impression that the upper lip was not parted in the midline, as is normal in rodents. The mistake was corrected by later authors but the truly distinctive characters of marsh rats were regarded as of sufficient magnitude to validate *Holochilus* as a genus. Similarities in dental structure between *Holochilus* and *Sigmodon* came to the attention of Wagner (1842), and systematists have since regarded the two genera as very nearly related. Winge (1888) went farther and treated marsh rats as a species of *Sigmodon*. Merriam (1895) held conflicting views. In his haste to criticize the arrangement of Argentine cricetines pre-

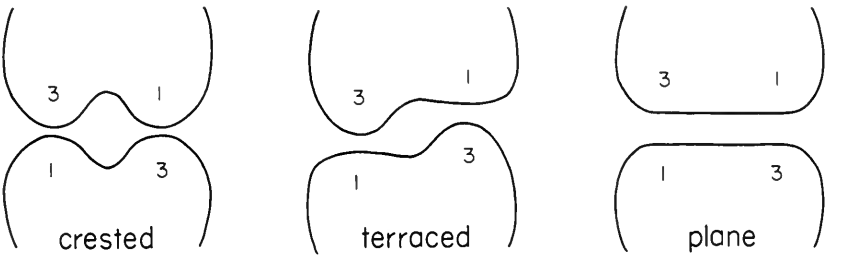


FIG. 141. Molar planation: three evolutionary stages, from primitive crested to specialized plane grazing type. 1 = protocone (id); 3 = paracone in upper, metaconid in lower teeth.

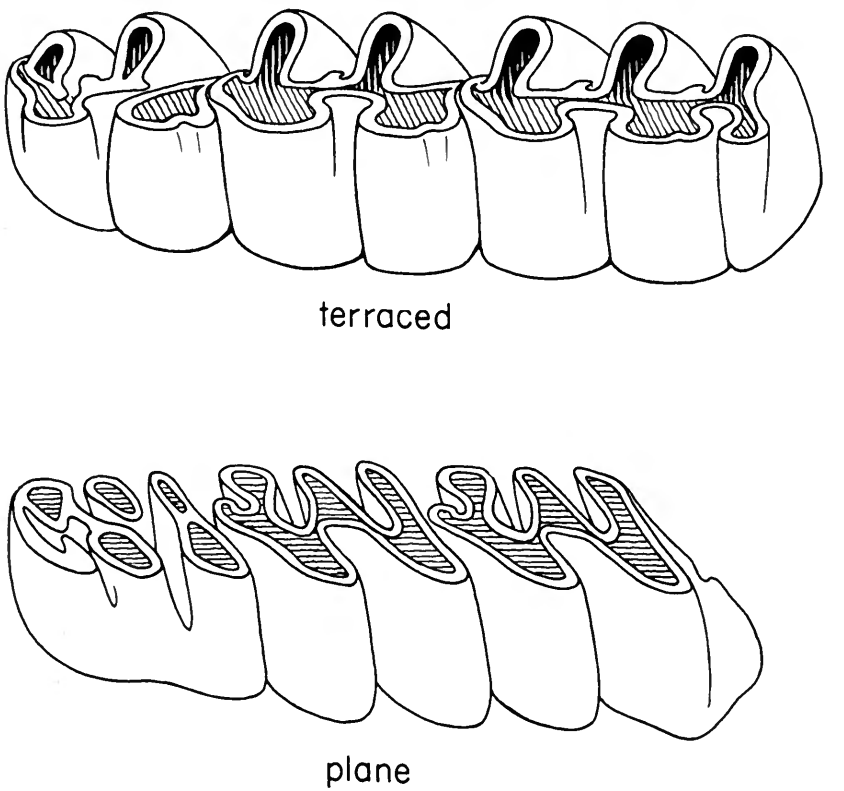


FIG. 142. Unworn terraced molars (right upper) of juvenal *Holochilus magnus* and unworn plane molars of juvenal *H. brasiliensis*.

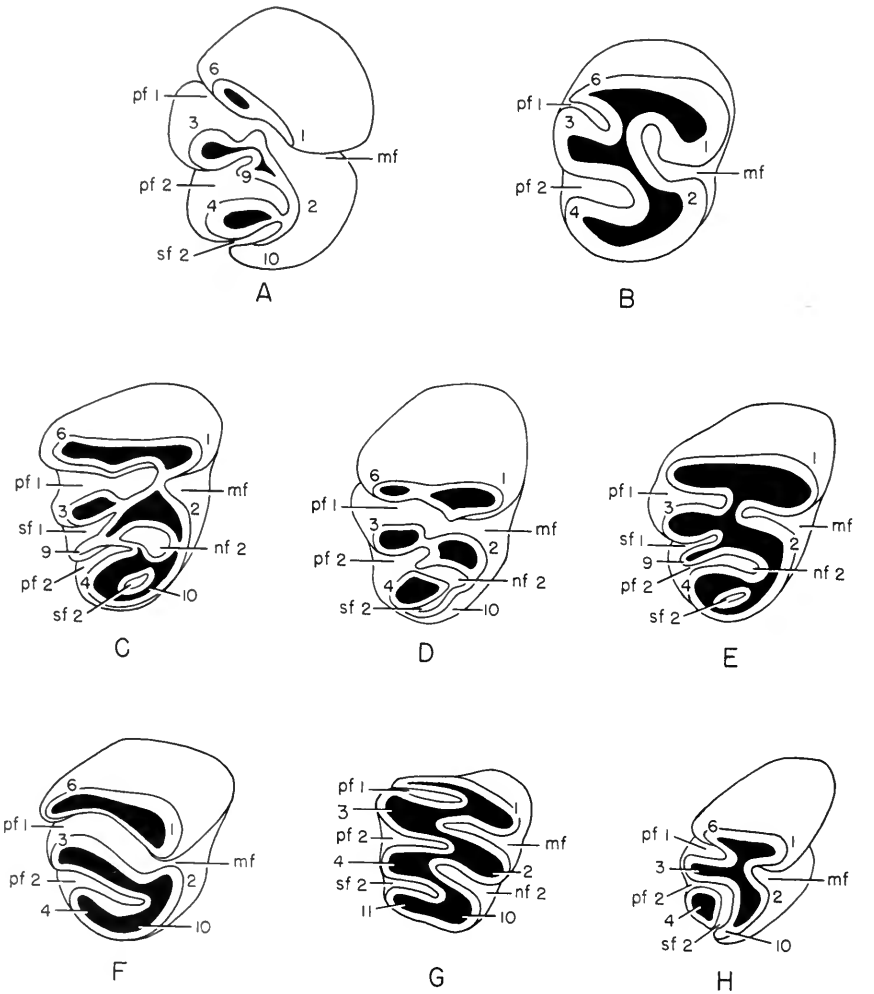


FIG. 143. Third right upper molar of A, *Holochilus magnus* (juvenal); B, *H. magnus* (adult); C, *H. brasiliensis* (juvenal with well-developed mesoloph); D, *H. brasiliensis* (juvenal with vestigial mesoloph); E, *H. brasiliensis* (adult with well-developed mesoloph); F, *Sigmodon hispidus* (adult); G, *Neotomys ebriosus* (adult); H, *Reithrodon physodes* (subadult). For explanation of symbols see below and page 651.

NAMES OF ENAMEL FOLDS (ALL MOLARS)

pf 1, first primary fold
pf 2, second primary fold
sf 1, first secondary fold
sf 2, second secondary fold
mf, major fold
nf, first minor fold
nf 2, second minor fold
amf, anterior median fold
aif, anterior internal fold
asf, anterior secondary fold
alf, anterior labial fold
alif, anterior lingual fold

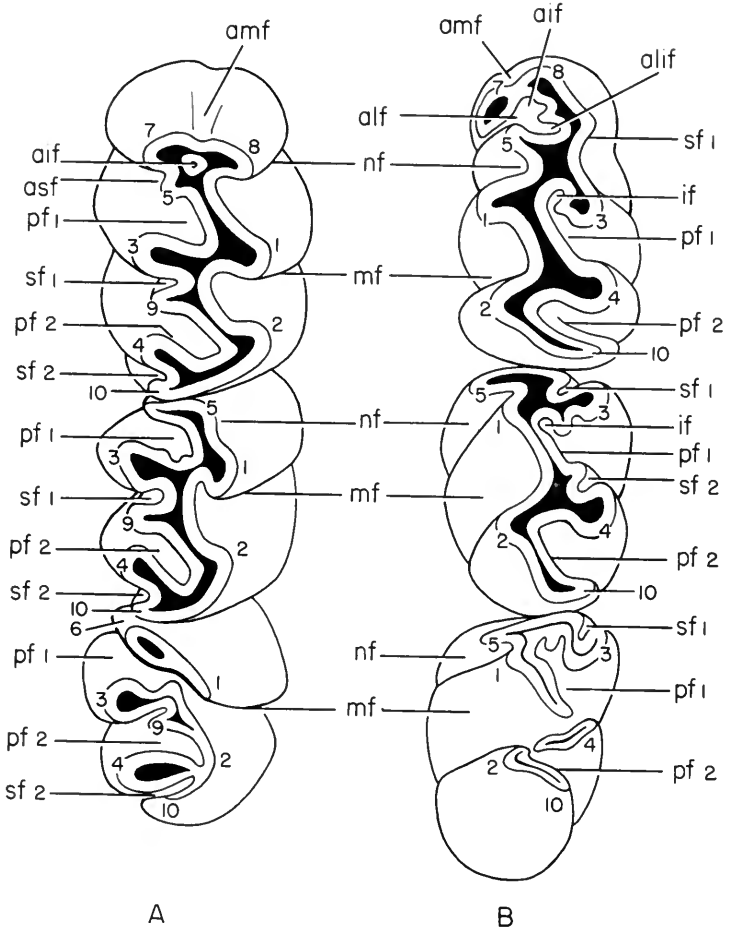


FIG. 144. Molars of *Holochilus magnus*. A, right upper molar row; B, left lower molar row. All dental elements present in sigmodont rodents are shown here. For explanation of symbols see below and page 650.

NAMES OF CUSPS, CINGULA AND LOPHS

Upper Molars		*Lower Molars*
1, protocone		1, protoconid
2, hypocone		2, hypoconid
3, paracone		3, metaconid
4, metacone		4, entoconid
5, anterolph	procingulum	5, anterolophid
6, anterior cingulum	procingulum	6, anterior cingulum
7, antero-labial conule	procingulum	7, antero-lingual conule
8, antero-lingual conule	procingulum	8, antero-labial conule
9, mesoloph		9, mesolophid
10, posterior cingulum	postcingulum	10, posterior cingulum
11, posteroloph	postcingulum	11, posterolophid

sented by Ameghino in 1889, Merriam pointed to the figures correctly determined as *Holochilus* by the former (Ameghino, 1889, atlas, figs. 11, 11, *a*, mandible and molars) and pronounced them *Sigmodon*. Paradoxically, he then decided that other specimens referred by Ameghino with equal justification to *Holochilus* were probably members of the over-inflated cricetine "subfamily" Neotominae Merriam!

CHARACTERS

External characters.—Form *Rattus*-like; size moderately large to among largest of cricetines; pelage soft, wool-hairs well developed; color of upper parts buffy, ochraceous or tawny, more or less mixed with blackish, especially mid-dorsally; sides distinctly paler, under parts varying from sharply defined white to uniformly ochraceous except for white or gray throat and, usually, inguinal region; basal portions of hairs of under parts white or gray; tail from more than three-fourths combined head and body length to nearly half again as long, coarsely scutulated, thinly haired, uniformly colored brown or slightly paler beneath than above; hind foot moderate to extremely large, thinly haired on upper surface, powerfully built and specialized for aquatic life; fifth toe, less claw, reaching to middle of first phalanx of fourth toe; first toe to base of second or slightly beyond; digital bristles sparse, shorter than claws; mammae (in *H. brasiliensis;* unknown for *H. magnus*), 2 pairs pectoral, 2 pairs abdominal, 1 pair inguinal.

Cranial characters (pls. 21–29).—Nasals truncate or rounded behind, terminating on a line with, or slightly behind or in front of, fronto-maxillary suture; sides of supraorbital region may be parallel, convex midfrontally, or slightly divergent, the edges square or ridged, not beaded; frontal sinuses hardly inflated, the midfrontal region concave in transverse outline; fronto-parietal sutures evenly curved or forming an angle at midline; width across fronto-parietal sutures more or less than alveolar length of molar row and less than length of diastema; incisive foramina not extending posteriorly behind anterior plane of first molars in adults; small jugal quite normal for cricetine rodents.

Dental characters (pls. 17–20, figs. 141–144; for explanation of terminology see pp. 650–1).—Incisors opisthodont, or nearly orthodont, without grooves; molar crowns moderately high, plane or terraced (figs. 141, 142); cusps ovate or sub-triangular; a more or less developed mesoloph often present in juvenal or subadult third upper molar; major and first primary folds of third upper molar opposed

and touching in adult, nearly or quite confluent in juvenal (fig. 143); second secondary folds (posterior cingula) present in juvenal, obsolete in adult upper molars; minor fold present in all lower molars; first secondary folds present at least in juvenal lower molars; anterior internal folds present at least in juvenal m_1; second primary fold of m_2 two-thirds or more of length of first primary fold.

COMPARISONS

Diagnostic and comparative characters of each genus of sigmodont rodent have been given above. The cotton rat *Sigmodon* is most nearly related to *Holochilus* and, in most respects, nearer *H. brasiliensis* than the latter is to its larger congener, *H. magnus*. *Sigmodon* averages smaller but the proportions of its limbs and ears are about the same as in *H. brasiliensis;* the pelage, which is generally harsh, often hispid, in *Sigmodon,* is usually soft, rarely harsh, in *Holochilus.* Tawny individuals of *Sigmodon* may resemble *Holochilus* spp., but the agouti pattern of the former is approached in the latter only by a fine ticking on the dorsum. Hind toes of *Sigmodon* are not conspicuously webbed like those of *Holochilus.* Cranial differences between *Sigmodon* and *Holochilus brasiliensis* are slight and chiefly concerned with the broader, more inflated frontals and shorter rostrum of the former. Young individuals of *H. brasiliensis,* however, hardly differ in these respects. In *H. magnus,* the frontals are narrower and more depressed than in the smaller member of the genus. Mandibles of *Sigmodon* and *Holochilus brasiliensis* are similar and readily distinguished from the elongated mandible of *H. magnus.* Incisors of *Sigmodon* are more recurved and the molar rows less parallel-sided, more divergent posteriorly. In its flat molar crowns and lack of mesolophs (ids), *Sigmodon* is more nearly like *H. brasiliensis.* On the other hand, the enamel folds of the molars of *Sigmodon* and *H. magnus* are oblique and the cusps are laminate or ovate, whereas in *H. brasiliensis* the folds are more nearly transverse and the upper cusps triangular in shape. Of the three named forms, the molars of *H. magnus* are more primitive in the following respects: retention of a rudimentary mesoloph in each juvenal molar, ovate cusps, crested paracone, metacone, metaconid and entoconid, less simplified procingulum of upper and lower first molars, and, in the juvenal molars, the presence of a vestige of the primitive enamel ridge originally separating primary and internal folds.

The oryzomyine water rat, *Nectomys squamipes,* is superficially similar to *Holochilus* in size, proportions, and swimming modifica-

tions. It differs, however, by well-marked juvenal pelage, more glossy, adpressed adult pelage, more gray under parts, less hairy ears, longer vibrissae, scaly heel, claws of hind feet a third shorter and more recurved, mammae with the oryzomyine formula, 2–2=8. Cranially, *Nectomys* differs in most of the more important diagnostic characters enumerated for the sigmodont group in general and *Holochilus* in particular; in addition, braincase more inflated, frontal sinuses comparatively well developed, posterior portion of frontals not depressed, palate always produced posteriorly beyond third molars, bullae from one-third to one-half size of those of comparably aged individuals of *Holochilus*. Dentally, *Nectomys* belongs to the primitive branch of cricetines characterized by bunodonty, presence of a functional mesolophostyle (id) complex in all molars, absence of lamination, and delayed eruption of the third molar. Its dentition has been described elsewhere (Hershkovitz, 1944, Misc. Publ. Univ. Michigan Mus. Zool. no. 58, pp. 14–17, 19, 23; figs. 4, 5). Resemblances between *Nectomys* and *Holochilus* are of the same order as those that occur in many small mammals with special adaptations for swimming. Actual relationship between the two genera is, of course, on the same level as relationships between the oryzomyine and sigmodont groups of cricetines.

Another oryzomyine rodent with which *Holochilus* has been confused in bibliographic citations and synonymies is *Oryzomys buccinatus* Olfers (antedates *Oryzomys angouya* Desmarest and authors). Resemblance between the two forms does not go beyond color, size, and characters common to cricetines in general. However, the first published descriptions gave no more information. This, plus the fact that the two species occur together in some regions, had created the illusion that anguyas and marsh rats were one and the same.

HABITS AND HABITAT

The larger species, *Holochilus magnus*, is more specialized for swimming than *H. brasiliensis*. Its molars, however, are transitional between the browsing-crushing and specialized grazing types. Both species are found together in some localities, but heretofore authors have not distinguished them. Possibly the mollusc-eating marsh rat mentioned below belongs to the new species, *H. magnus*.

In his notes on the nest and habits of marsh rats, Burmeister (1879, Descr. Phys. Rep. Argentine, **3**: 211–212) recorded: "The rat lives in swamps among tall reeds which grow to a height of 3 meters.

It builds its nest in September and attaches it to stems of the stoutest reeds. The abode is oval-shaped and may have a diameter as great as 40 centimeters. The nest is set at right angles to the reeds and about 30 or 40 centimeters above the surface of the water. Short pieces of reeds woven firmly together are used in the construction. The lower half of the living quarters is solid because of the large quantity of reeds pressed down on the bottom; the upper half is more lightly built and provided with a side entrance. The floor of the chamber is strewn with dry, gnawed reeds that make a soft litter for the occupant. Should the rat be disturbed by a strange sound, it leaps from its nest, plunges into the water, and swims swiftly amidst the thick vegetation until out of reach of possible danger. It remains at a safe distance for a long time before venturing back. My aide spent two hours to no avail watching from cover with the hope of seeing the animal swim back home. The rat rests quietly in its nest during the day. It feeds at night on swamp plants and molluscs." (Translation.) Burmeister does not mention the locality where observations were made. Presumably it is somewhere between the Paraná and Paraguay rivers, in extreme northern Argentina.

T. Ingalls, collector of the type specimen of *Holochilus chacarius* of the Paraguayan Chaco, reports (*in* Thomas, 1906, Ann. Mag. Nat. Hist., (7), **18:** 447) that the rat "raises a nest on weeds [reeds?] about a foot above water." Nests of marsh rats found in northern Argentina by Llanos (1944, Rev. Argent. Zoogeogr., **4:** 51–52) were built on the ground in sugar-cane fields. The living quarters are described as round and constructed of interlaced strips and scraps of cane. Means and extremes of weights and diameters of the nine nests measured are, respectively, 50 gms. (25–95 gms.) and 17.5 cm. (12–27 cm.).

According to Moojen (1943, Bol. Mus. Nac. Zool., **5:** 11), who observed and collected marsh rats in Ceará, Brazil, from four to six young are produced in a litter.

"RATADAS"

Under certain conditions and at certain times, marsh rats multiply rapidly and become plagues. Such plagues are known as *ratadas* in Latin America. Devincenzi (1935, Ann. Mus. Hist. Nat., Montevideo, (2), **4:** 71) reports *Holochilus* as the most abundant rat in Uruguay. Morrison-Scott (1937, Ann. Mag. Nat. Hist., (10), **20:** 535) quotes Dr. L. D. Cleare, collector of the type series of *Holochilus brasiliensis berbicensis*, as follows: "This rat is, I believe, fairly common on the coastland here [British Guiana] and is probably the more

usual form attacking sugar cane. They have caused considerable damage to cane on one sugar plantation where, during the past four months, over 100,000 have been destroyed—the outbreak appears to be confined to the county of Berbice."

A *ratada* of several species of cricetines, including *Holochilus*, was observed in southeastern Brazil by Giovannoni, Velloza, and Kubiak (1946, Arq. Biol. Tec. Inst. Biol. e Pesq., Curitiba, **1**: 185–195, pls. 52–60). They correlated the phenomenon with the fruiting season of the *taquara lisa* (smooth bamboo; *Merostichis* sp.). The *ratada* was the second recorded for the State of Paraná. The first occurred six or seven years before and coincided with the fruiting of the *taquara lixa* (rough bamboo; *Merostichis fistulosa* Doell). According to the investigators, the *taquara lisa* bore fruit in March and April, 1946. The seeds sufficed to nourish the rodents for two or three months. With depletion of this food supply, hordes of hungry mice turned to wheat, millet, potatoes, and other cultivated plants in fields and storehouses. Loss to farmers caused by the devastations of the rodents was considerable. During September a high mortality rate among the rats led to a rapid ebb of the *ratada*. A cause for the sudden decrease in population was not determined by the investigators. They suggested that the change in diet from *taquara* seeds to cultivated plants, or disease, might have contributed to the high death rate. Local destruction of the blossoming *taquara* was offered as the best remedy for prevention of *ratadas*.

An eruption of marsh rats in sugar-cane plantations in the Río San Francisco Valley, northern Argentina, was reported by Llanos (1944, Rev. Argent. Zoogeogr., **4**: 51–57). Inordinate increase in the marsh rat population began in February, 1944, and reached a peak in April. This was fo'lowed by a sharp decline in the number of individuals. Part of the drop was attributed to systematic destruction of rats by man. In July, when the *ratada* had run nearly its full course, Llanos set 367 traps in an area of 1,019.36 square meters and captured 96 rats. Of the catch, males outnumbered females nearly two to one. None of the captured females was gravid. This and other trapping statistics provided by Llanos are based on gross catch per gross number of traps set, rather than on the standard "trap-night" basis. After the period of maximum population, Llanos found many abandoned nests of marsh rats in the sugar-cane plantations. The rats were identified as *Holochilus balnearum*, said to be the resident species, and *H. chacarius*, an invader. No criteria were given for distinguishing one named form from the other, or for regarding

one rat as native and the other foreign to the area. Whatever the number of species involved, data supplied by Llanos indicate only a natural cyclic increase of native populations. *Oryzomys flavicans*, the only other cricetine trapped in the region, also figured in the *ratada*.

KEY TO THE SPECIES

Tail of adult more than 210 mm., always longer than combined head and body length; hind foot, with claw, more than 48 mm.; incisive foramina extending posteriorly to, sometimes behind, anterior plane of first molars; m^3 as long as wide, shorter than m^2; m^1 with three roots..... *Holochilus magnus* sp. nov.

Tail of adult less than 210 mm., and, normally, approximately equal to or shorter than combined head and body length; hind foot, with claw, less than 48 mm.; incisive foramina not extending posteriorly to anterior plane of first molars; m^3 longer than wide, longer than m^2; m^1 with four roots.
Holochilus brasiliensis Desmarest

Holochilus magnus sp. nov. Plates 17–21, 23, 25–29; text figs. 142–144.

Holochilus vulpinus Sanborn (nec Brants) 1929, Field Mus. Nat. Hist., Zool. Ser., **17**: 158—part, Uruguay (Treinta y Tres; Río Cebollati).

(?)*Holochilus vulpinus* Devincenzi, 1935, An. Mus. Hist. Nat., Montevideo, (2), **4**, no. 10, p. 71—Uruguay.

(?)*Hesperomys vulpinus* Hensel, 1873, Abh. Akad. Wiss. Berlin, **1872**: 34—part, Brazil (Porto Alegre, Rio Grande do Sul; one specimen in alcohol).

(?)*Sigmodon vulpinus* Winge, 1888, E. Mus. Lundii, **1**, (3), p. 23—part, Brazil (Lagôa Santa, Minas Geraes; one specimen in alcohol).

Type.—Adult male, skin and skull, Chicago Natural History Museum no. 29258; collected November 23, 1926, by Colin C. Sanborn.

Type locality.—Paso de Averías, Río Cebollati, about 40 kilometers south of Treinta y Tres, eastern Uruguay.

Distribution (fig. 140).—Known only from eastern Uruguay, but may range north as far as Minas Geraes in Brazil, and west into the Río Paraná basin of northern Argentina.

Characters.—Largest sigmodont rodent; hairs of under parts gray or ochraceous terminally, plumbeous basally; tail longer than combined head and body length; hind foot, with claw, from 28 to 35 per cent of combined head and body length in adults and subadults (longer in juvenals); sides of supraorbital region of skull narrower than in *brasiliensis* and evenly convergent midfrontally; frontoparietal sutures angular, not crescentic as in *brasiliensis;* incisive foramina extending posteriorly to, in juvenals behind, anterior plane of molars; ramus of mandible elongated, angle between base of body and ramus nearly straight, masseteric ridge not extending to anterior plane of first molar, coronoid process oblique, capsule of lower incisor

not projecting posteriorly beyond vertical plane of coronoid process; crowns of molars terraced (fig. 142), cusps and cingula ovate in outline and separated by comparatively broad folds; m^3 shorter than m^2 and approximately as long as wide; m^1 with outer middle root absent or extremely rudimentary; rudimentary mesoloph present in all juvenal molars, obsolete or absent in adult molars; anterior median fold present in all but extremely worn m^1, absent in m_1; anterior internal fold present in juvenal m^1 and in juvenal and adult m_1; long axes of major and primary folds oblique; apices of first primary and major folds opposed and touching in upper adult molars, confluent in juvenal m^3; second minor fold never present in m^3.

Measurements.—See Table 1.

Remarks.—Direct comparisons of *H. magnus* with *H. brasiliensis* and other sigmodont rodents have been made under the generic heading. The long tail and proportionately larger hind feet indicate that *magnus* is more highly specialized than *brasiliensis* for swimming. In molar structure *magnus* is least specialized. The first upper molar in this species, however, is three-rooted; in all other sigmodonts it is four-rooted.

Two specimens preserved in spirits and recorded as *vulpinus*, one by Winge (1888, supra cit.), the other by Hensel (1873, supra cit.), are, judged by published measurements (Table 1), referable to *H. magnus*. Neither authority suspected that two species of *Holochilus* live side by side. They described external characters of the genus from specimens of both *magnus* and *brasiliensis* preserved in spirits, and cranial and dental characters from skulls and skeletons of *brasiliensis* only.

It is surprising that of 18 names previously proposed for marsh rats, none applies to the present species. In view of the facility with which Thomas described a half dozen "species" of *Holochilus*, it is unlikely that he ever examined a specimen of *magnus*.

Specimens examined.—6. URUGUAY: Paso de Averías, Río Ceballati, Minas, 3 (CNHM); Treinta y Tres, Treinta y Tres, 3 (CNHM).

Holochilus brasiliensis Desmarest. Plates 17–20, 22, 24–29; text figs. 142, 143.

Distribution (fig. 140).—Same as for the genus. The species has been recorded also from Pleistocene cave deposits in Minas Geraes, Brazil, and from the Pleistocene pampean formations of Buenos Aires, Argentina.

Characters.—Larger than any sigmodont rodent except *Holochilus magnus;* hairs of throat and inguinal region usually white or buffy terminally, white or gray basally; tail normally less than combined head and body length (may measure longer in dry, contracted skin); hind foot, with claw, from 20 to 25 per cent of combined head and body length in adults and subadults (longer in juvenals); sides of supraorbital region of skull divergent; fronto-parietal sutures evenly curved, not forming an angle at midline; incisive foramina not extending posteriorly behind anterior plane of first molars; ramus of mandible subquadrate, angle between base of body and ramus pronounced, masseteric ridge extending anteriorly beyond first molar to border of mental foramen, coronoid process nearly vertical, capsule of lower incisor extending behind to emargination between coronoid and condylar processes; crowns of molars plane (fig. 142), cusps and cingula compressed antero-posteriorly, subtriangular in unworn tooth; m^3 longer than m^2 and longer than wide; m^1 with outer middle root normally present; mesoloph often present, and usually well developed in m^3, absent in remaining molars; anterior median fold not present in upper and lower first molars; anterior internal fold present in m_1, absent in m^1; long axes of major and first primary folds of upper molars transverse; major fold penetrating between first and second primary folds in m^{1-2}; major and first primary opposed in adult m^3, confluent in juvenal; second minor fold present, open to the margin in juvenals, an enamel island in adults.

Taxonomic history.—After recording and describing marsh rats under various names for more than three decades, Thomas (1928, Ann. Mag. Nat. Hist., (10), **2**: 260) concluded that he was "more and more convinced of the essential identity of all the *Holochilus* water-rats of the whole of the Amazonian drainage area, from Pernambuco to Peru, Guiana to Bolivia, and equally that of the Rio San Francisco." Accordingly, Thomas assigned all eastern Peruvian specimens to *Holochilus sciureus* Wagner, of the Rio São Francisco, Minas Geraes, eastern Brazil. Concerning *incarum,* from Cuzco, Peru, Thomas (op. cit.) thought it might "survive as a local highland subspecies [of *H. sciureus*]." As for *amazonicus* and *guianae,* Thomas had already (1920, Proc. U. S. Nat. Mus., **58**: 227) confessed to "considerable doubt as to whether [they] ought to have been separated from *H. sciureus.*" Another named form not specifically mentioned by Thomas but included, by his sweeping statement, in the synonymy of *sciureus,* is *Holochilus nanus.* This animal from the island of Marajó in the mouth of the Amazon was described as "scarcely half

the bulk" of *sciureus*. It proves to be nothing more than a juvenal of the common Brazilian marsh rat.

If there is but one species of *Holochilus* within the geographic limits fixed by Thomas, the earliest valid name that applies is not *H. sciureus* Wagner, 1842, but *Mus brasiliensis* Desmarest, 1819. The name was based on a specimen collected in Minas Geraes by Auguste St.-Hilaire. Its tail is said to be a little longer than the body, the under parts gray. Included with the description of the type is a reference to another specimen in the Paris Museum labeled "Rat du Brésil." In 1820, Desmarest decided that his *brasiliensis* was the same as the white-bellied, long-tailed species he had described as *Mus angouya* (=*Oryzomys buccinatus* Olfers, 1818). This was a mistake. Waterhouse examined the type and identified it as a *Holochilus*. The description of the dentition given by Gervais in 1849, though general, can apply only to *Holochilus* when external characters are taken into account. Subsequent authorities have sustained these opinions.

Mus vulpinus A. Brants, 1827, is the next available name for marsh rats. According to Lichtenstein (1830, Darstellung. . . . Heft 15, pl. 33, fig. 2 and text) the type is from Rio Uruguay, southeastern Brazil. This authority gives body length as 9″6‴ (=248 mm.), tail 6″6‴ (=170 mm.), hind foot with claw 2″3‴ (=59 mm.). The measurements exceed those of any type or other recorded or available specimen of the common Brazilian marsh rat. Nevertheless, the color, comparatively short tail and short hind foot (23.8 per cent of head and body), combined with the characters of the molars as described by Burmeister (1854, Syst. Übers. Thiere Bras., **1**: 163), leave no doubt of the identity of *vulpinus* as a large representative of *H. brasiliensis*.

Mus physodes A. Brants, 1827, appears to be another short-tailed member of the common species. Its type locality is given by Lichtenstein as São Paulo, Brazil. The name might be retained as a subspecies of *brasiliensis*, were it not preoccupied by *M. physodes* Olfers, 1818, a *Reithrodon*.

Mus (*Holochilus*) *leucogaster* and *Mus* (*Holochilus*) *anguya* were described in 1835 by J. F. Brandt. The original data (including color plates) and present knowledge of variation in Brazilian marsh rats, indicate that the two named forms represent the same species. The types of both were secured by Baron von Langsdorff, then Russian consul general in Brazil. No definite locality was given for either, but authors have identified marsh rats of the State of São Paulo, where

Langsdorff explored extensively, with *H. leucogaster*. Accordingly, the name *leucogaster* Brandt may replace the preoccupied *physodes* Brants. The name *anguya* Brandt is discarded not only as a synonym of *leucogaster*, but also as a homonym of *Mus angouya* Desmarest, an *Oryzomys*. The substitute name *canellinus* proposed by Wagner in 1843, together with his *russatus*, also from São Paulo are, therefore, synonyms of *leucogaster*.

Thomas (1897, Ann. Mag. Nat. Hist., (6), **19:** 496) suspected that *leucogaster* and *sciureus* might prove to be the same as *H. brasiliensis* Desmarest. Nevertheless, he was averse to conserving the name and proposed that the large marsh rat in the British Museum identified by Waterhouse in 1840 as *Mus braziliensis* (sic) be called *H. darwini* instead. The renaming cannot be justified. Waterhouse had compared his specimen with the type of *brasiliensis* in the Paris Museum and found the two identical. In addition, the description, color plate, and figure of skull and dentition, prove that his specimen is the same as the *sciureus* of Thomas, or *H. brasiliensis* of this paper.

The remaining named Recent forms are *Holochilus berbicensis* Morrison-Scott, *Holochilus venezuelae* J. A. Allen, *H. balnearum* Thomas, and *H. chacarius* Thomas. All show the diagnostic characters of *H. brasiliensis*. The first three are given here provisional subspecific rank. The last is indistinguishable from *vulpinus* of the same general region.

"*H*[*olochilus*] *chrysogaster* Waterhouse" is a misnomer published by Cabrera in his catalogue of specimens in the Natural History Museum of Madrid. No description or locality data accompanied the name and the specimen it designated. Possibly *chrysogaster* is a *lapsus* for *leucogaster*.

Holochilus multannus Ameghino, 1889, from Pleistocene formations of Buenos Aires appears to be a member of the common species and identical with *H. brasiliensis vulpinus*.

The subspecies.—Material at hand is insufficient for a comprehensive study of subspeciation in *Holochilus brasiliensis*. Present recognition of subspecies is based entirely on the availability of technical names for marsh rats in geographic areas where subspeciation *might* occur. There is absolutely nothing in the original descriptions to support the named forms as subspecific categories. The type specimens themselves are so imperfect as to be useless for comparative purposes. The distribution given here for each subspecies is for the convenience of systematists who may wish to identify marsh rats by trinomials.

Holochilus brasiliensis brasiliensis Desmarest

Mus brasiliensis Desmarest, 1819, Nouv. Dict. Hist. Nat., **29:** 62; 1826, Dict. Sci. Nat., **44:** 483 (redescription of type); Lesson, 1823, Manual Mammal., p. 270; P. Gervais, 1849, Dict. Univ. Hist. Nat., **10:** 731 (description of dentition); Osgood, 1943, Field Mus. Nat. Hist., Zool. Ser., **30:** 235 (*Mus brasiliensis* a *Holochilus*).

H[olochilus] brasiliensis Thomas, 1897, Ann. Mag. Nat. Hist., (6), **19:** 496 (possibly applies to "form I have provisionally called *H. sciureus*").

Hol[ochilus] sciureus Wagner, 1842, Arch. Naturg., (8), **1:** 16, 17—type locality, Rio São Francisco, Minas Geraes, Brazil (Spix, collector); 1843, Schreber's Säugth., Suppl., **3:** 553 (known from type only).

H[olochilus] sciureus Thomas, 1897, Ann. Mag. Nat. Hist., (6), **19:** 495 (compared with *nanus* Thomas).

Holochilus sciureus Thomas, 1901, Ann. Mag. Nat. Hist., (7), **8:** 149 (Bahia); 1920, op. cit., (9), **6:** 276—Pará; Moojen, 1943, Bol. Mus. Nac. Rio de Janeiro, Zool., **5:** 11—Crato, Ceará.

Sigmodon vulpinus Winge (nec Brants) 1888, E. Mus. Lundii, **1,** (3), p. 21, pl. 1, fig. 3 (head), fig. 4 (hind foot), pl. 2, fig. 5 (skull), fig. 5, *a* (molar)—part, Lagôa Santa, Minas Geraes (Pleistocene and Recent).

"*H[olochilus] chrysogaster* Waterhouse," Cabrera, 1912, Trab. Mus. Cienc. Nat., Madrid, no. 11, p. 102—"un ejemplar [cat. no.] 170, sin localidad comprado a la casa Verreaux de Paris" (a *nomen vanum,* probably a *lapsus* for *H. leucogaster*).

Mus angouya Desmarest (nec Desmarest), 1820, Mammalogie, **1:** 305—part (*Mus brasiliensis* in synonymy only).

Holochilomy (sic) *brasiliensis* Hensel, 1873, Abh. Akad. Wiss. Berlin, Math.-Phys. Kl., **1872:** 32—part (in synonymy of *Hesperomys vulpinus*).

Type.—Adult, sex unknown, Museum National d'Histoire Naturelle, Paris; collected by Auguste St.-Hilaire between December, 1816, and March, 1818.

Type locality.—"Brésil"; according to collector's itinerary, Minas Geraes, Brazil. Here restricted to Lagôa Santa, Minas Geraes.

Distribution.—Coast of Brazil, from the State of Minas Geraes northward to the mouth of the Amazon.

Measurements.—Those of the type and its synonyms are given in Table 2.

Remarks.—Under parts of the original *H. brasiliensis* are described as gray, those of the type of *sciureus,* white.

Holochilus brasiliensis vulpinus Brants

M[us] vulpinus Brants, 1827, Het Geslacht der Muizen, Berlin, p. 137—"Brazil."

Mus vulpinus Lichtenstein, 1830, Darstellung neuer oder wenig bekannter Säugeth., Heft 15, tab. 33, fig. 2 (col.) and text—type locality, Rio Uruguay.

H[olochilus] vulpinus Wagner, 1843, Schreber's Säugth. Suppl., **3**: 554; Thomas, 1897, Ann. Mag. Nat. Hist., (6), **19**: 496—Paraná and Uruguay river systems to La Plata; Goya, Corrientes.

Holochilus vulpinus Ameghino, 1889, Act. Acad. Nac. Cienc. Rep. Argent., **6**: 116, pl. 4, figs. 10, 11 (skull, molars)—Argentina (Recent and Pleistocene); Thomas, 1917, Ann. Mag. Nat. Hist., (8), **20**: 96—Argentina (Isla Ella, Delta del Paraná); Allen, 1916, Bull. Amer. Mus. Nat. Hist., **35**: 571—Brazil (Urucum, Mato Grosso); Marelli, 1924, Elenco Sistemático Fauna Buenos Aires, Min. Obras Publ., Buenos Aires, p. 670—Argentina (Corrientes; Entre Rios; Buenos Aires); Yepes, 1935, Rev. Inst. Bacteriol. Buenos Aires, **7**: 234, pl. 7 (animal); Gyldenstolpe, 1932, K. Sv. Vet. Akad. Handl., **2**: 63, pl. 6, fig. 2 (skull)—Argentina (Goya, Corrientes); Sanborn, 1929, Field Mus. Nat. Hist., Zool. Ser., **17**: 158—part, Uruguay (Trienta y Tres, one specimen only); Yepes, 1938, Rev. Centro Estud. Doc. Cienc. Nat., **2**: 15—Buenos Aires; 1938, An. Soc. Arg. Estud. Geogr., **6**: 52—Brazil and Argentina; Dennler, 1939, Physis, **16**: 231 (Guaraní name=*Angudya pihta*).

Hesperomys (*Holochilus*) *vulpinus* Burmeister, 1854, Syst. Übers. Thiere Bras., **1**: 163 (redescription of type; *Mus braziliensis* Waterhouse in synonymy); Burmeister, 1879, Descr. Phys. Rep. Argentine, **3**: 210 (description).

Hesperomys vulpinus Hensel, 1873, Abh. Akad. Wiss. Berlin, Math.-Phys. Kl., **1872**: 32, figs. 13, 23 (dentition)—Brazil (Porto Alegre, Rio Grande do Sul).

Holochilus multannus Ameghino, Act. Acad. Nac. Cienc. Rep. Argent., **6**: 117, pl. 4, fig. 12 (mandible and lower molars)—type locality, "Piso lujanense (pampeano lacustre) de la formación pampeana," Buenos Aires, Argentina.

Mus braziliensis (sic) Waterhouse, 1839 (nec Desmarest), Zool., Voy. "Beagle," Mamm., p. 58, pl. 19 (animal), pl. 33, fig. 3 (skull and dentition)—Argentina (Bahía Blanca, Buenos Aires).

H[olochilus] brasiliensis Wagner (nec Desmarest), 1843, Schreber's Säugth. Suppl., **3**: 551 (redescription of *Mus braziliensis* Waterhouse).

Holochilus brasiliensis Gray (nec Desmarest), 1843, List Mamm. Brit. Mus., p. 114—Argentina (Bahía [Blanca]).

H[olochilus] darwini Thomas, 1897, Ann. Mag. Nat. Hist., (6), **19**: 496 (new name for *Mus braziliensis* Waterhouse).

Holochilus darwini Thomas, 1910, Ann. Mag. Nat. Hist., (8), **5**: 242—Argentina (Los Ynglesas, Buenos Aires; type of *darwini* a female).

Holochilus chacarius Thomas, 1906, Ann. Mag. Nat. Hist., (7), **18**: 446—type locality, one league northwest of Concepción, Chaco, Paraguay; Yepes, 1938, Rev. Centro Estud. Doc. Cienc. Nat., **2**: 15—Paraguay (Concepción; Puerto Guaraní), Argentina (Tabacal, Salta; Chaco?; Formosa?).

Type.—Presumably in Zoologisches Museum, Berlin; collected by Herr Sello.

Type locality.—Rio Uruguay, southeastern Brazil. Brants states, "het vaterland van deze soort ist Brasilien." Lichtenstein specifies, "diese Art is von Herr Sello am Uruguay zuerst gefunden." This has

been transformed by some authors into Darwin's collecting locality, Maldonado, Uruguay!

Distribution.—Southeastern Brazil, in Mato Grosso and Paraná, southward into Uruguay, Paraguay, and northeastern Argentina, in the states of Misiones, Corrientes, Entre Rios, Buenos Aires, and possibly adjoining parts of Eva Perón.

Measurements.—See Tables 2 and 3.

Remarks.—Brants' and Lichtenstein's descriptions of *vulpinus* are of a large, short-tailed, white-bellied marsh rat. No cranial and dental characters are mentioned. However, Burmeister (1854, supra cit.) supplied a detailed description of the size, shape, and enamel pattern of the molars of the type. This removes any reasonable doubt regarding the identity of *vulpinus* with *brasiliensis*. Hensel (1873, supra cit.) also described and figured the molars of marsh rats from the type region under the name *Hesperomys vulpinus*. It is almost certain that his specimens were compared with the type of *vulpinus* in the Berlin Museum. In any case, authors (Winge, Thomas) have accepted the identity of Hensel's rats from Porto Alegre, Rio Grande do Sul, as representative. The "*Mus braziliensis*" of Waterhouse, from Bahía Blanca, is certainly the Brazilian species, but if it is subspecifically separable the name *vulpinus* applies. *Holochilus darwini*, proposed by Thomas for the Waterhouse specimen, is superfluous. A skull in the British Museum from Goya, Corrientes, Argentina, figured by Gyldenstolpe (1932, supra cit.) under the name *Holochilus vulpinus* shows clearly the diagnostic cranial and dental characters of *H. brasiliensis*. *Holochilus chacarius* Thomas from Paraguay is another form of *brasiliensis* and is quite like *vulpinus* on a subspecific level. Ameghino (1889, supra cit.) recorded an individual of *Holochilus vulpinus* from the Pleistocene of Buenos Aires. In the same formation he discovered the mandible of a smaller specimen and described it as *Holochilus multannus*. The published figure of the molars of the latter is poor. Whether the faulty representation is owing to the artist's liberties or to the imperfect condition of the fossil, it remains that *multannus* cannot be identified with any sigmodont rodent other than *H. brasiliensis*. The textual characterization of *multannus*, based on comparisons with fossil and living *vulpinus*, exposes only the variable dental characters of the species *H. brasiliensis*.

A very old individual at hand from Uruguay agrees almost exactly with Burmeister's description of the type; it is nearly as large, with upper parts ochraceous-tawny mixed with dark brown, the darker color disappearing on the sides; under parts white with ochraceous

wash on chest and belly, hairs slaty at the roots except on throat. Five specimens from the Paraguayan Chaco are younger, consequently smaller, their under parts more clearly defined, with less ochraceous, the hairs pale gray basally; in one specimen under parts nearly wholly white. Two juvenals from Mato Grosso are similar to the Paraguayan marsh rats.

Specimens examined.—8. BRAZIL: Urucum de Corumbá, 2 (CNHM). PARAGUAY: Río Pilcomayo, 15 miles above mouth, Chaco, 3 (CNHM); 30 km. northeast of Villa Militar, Chaco, 2 (CNHM). URUGUAY: Treinta y Tres, 1 (CNHM).

Holochilus brasiliensis balnearum Thomas

Holochilus balnearum Thomas, 1906, Ann. Mag. Nat. Hist., (7), **18:** 447; 1920, op. cit., (9), **5:** 190—Villa Carolina, Jujuy (specific distinction [from *brasiliensis*] doubtful); Yepes, 1938, Rev. Centro Estud. Doc. Cienc. Nat., **2:** 15—Jujuy and Tucumán; Llanos, 1944, Rev. Argent. Zoogeogr., **4:** 53—Río San Francisco Valley, Jujuy; Gyldenstolpe, 1932, K. Sv. Vet. Akad. Handl., **2:** 64, pl. 17, fig. 16 (upper molars of type).

Holochilus chacarius Llanos (nec Thomas), 1944, Rev. Argent. Zoogeogr., **4:** 53—Río San Francisco Valley, Jujuy.

Type.—Female, British Museum (Natural History) no. 4.10.2.5; collected June 18, 1904, by L. Dinelli.

Type locality.—Bañado de San Felipe, Tucumán, northwestern Argentina; altitude, 435 meters above sea level.

Distribution.—Northern Argentina, in departments of Tucumán, Jujuy, and Salta, to altitudes not exceeding 1,000 meters above sea level.

Measurements.—See Tables 2 and 4.

Remarks.—The original description is based on one specimen, a juvenal, hence the characterization of *balnearum* as "small." The oblique angle formed by the long axes of the molar rows, as described for the type, is not reproduced in any other known specimen. Molars of the type figured by Gyldenstolpe (1932, supra cit.) are those of the common species. In 1920, Thomas (supra cit.) recorded a large series of marsh rats from Villa Carolina, Jujuy, under what he now regarded as the doubtfully valid name *balnearum*. He also expressed remorse for the naming of this and other "species" of *Holochilus*.

Holochilus brasiliensis leucogaster Brandt

M[us] physodes Brants, 1827, Het Geslacht der Muizen, p. 139—type locality, Brazil (name preoccupied by *M. physodes* Olfers, 1818, in Eschwege, Neue Bibliothek Reisenbreschr., Weimar, **15:** 209, a *Reithrodon*).

Mus physodes Lichtenstein, 1830, Darstellung neuer oder wenig bekannter Säugeth., Heft 15, tab. 34, fig. 1 and text—type locality restricted to São Paulo, Brazil.

Hesperomys [*Holochilus*] *physodes* Burmeister, 1854, Syst. Übers. Thiere Bras., **1**: 167—São Paulo (*russatus* Wagner, a synonym).

Hesperomys physodes Pelzeln, 1883, K. K. Zool.-bot. Gesellsch., Wien, **33**, Beiheft, p. 71—Ypanema, São Paulo.

Holochilus physodes Leuderwaldt, 1929, Rev. Mus. Paulista, **16**: 27—São Paulo.

Mus (*Holochilus*) *leucogaster* Brandt, 1835, Mém. Soc. Imp. Sci., St. Petersb., (6), **1**: 92 (author's separate), pl. 12—type locality, "Brazil."

Holochilus leucogaster Giovannoni, Vellozo, Kubiak, 1946, Arq. Biol. Tec., Curitiba, **1**: 188, pl. 58, figs. 10, 11—Piraquara, Paraná.

Mus (*Holochilus*) *anguya* Brandt, 1835, Mém. Soc. Imp. Sci., St. Petersb., (6), **1**: 94 (author's separate), pl. 13—type locality, "Brazil."

Hesperomys russatus Wagner, 1848, Abh. Akad. Wiss., München, Math.-Phys. Kl., 1850, **5**: 312—type locality, Ypanema, São Paulo; Pelzeln, 1883, K. K. Zool.-bot. Gesellsch., Wien, **33**, Beiheft, p. 71—Ypanema, São Paulo.

H[*olochilus*] *canellinus* Wagner, 1843, Schreber's Säugth. Suppl., **3**: 552 (new name for *Mus anguya* Brandt, preoccupied by *Mus angouya* Desmarest, an *Oryzomys*).

Hesperomys (*Holochilus*) *brasiliensis* von Ihering, 1894, Os mammíferos de São Paulo, Catalogo, São Paulo, p. 19—São Paulo (also listed, *H. physodes, leucogaster, sciureus*).

Holochilus brasiliensis Pelzeln (nec Desmarest), 1883, K. K. Zool.-bot. Gesellsch., Wien, **33**, Beiheft, p. 73 (part, excl. syn.)—Ypanema, São Paulo.

Holochilus sciureus Thomas (nec Wagner), 1910, Ann. Mag. Nat. Hist., (8), **6**: 500—Serra de Ibiapaba, São Paulo.

Hesperomys squamipes Burmeister (nec Brants), 1854, Syst. Übers. Thiere Bras., **1**: 165—São Paulo (synonyms: *H. sciureus* Wagner, *anguya* Brants, *canellinus* Wagner).

Type.—Adult, sex unknown, presumably in Leningrad Zoological Museum; collected by Baron von Langsdorff.

Type locality.—Brazil, here restricted to State of São Paulo.

Distribution.—Known only from the coast and coastal mountain range of the states of Rio de Janeiro, São Paulo, and Paraná.

Measurements.—See Table 2.

Remarks.—The under parts of all described forms referred to *leucogaster* are white, some with an ochraceous wash. Subspecific status of *leucogaster* is maintained pending comparisons with typical *brasiliensis* and *vulpinus*.

Holochilus brasiliensis nanus Thomas

Holochilus nanus Thomas, 1897, Ann. Mag. Nat. Hist., (6), **19**: 495; Goeldi and Hagmann, 1904, Bol. Mus. Goeldi, Mus. Paraense, **4**, 1, pp. 76, 83 (Portuguese translation of original description).

Type.—Juvenal female, skin and skull from specimen originally preserved in spirits, British Museum (Natural History) no. 97.4.1.2; presented by E. A. Goeldi.

Type locality.—Soure (misspelled "Source" in original description), Ilha de Marajó, mouth of Amazonas, Pará, Brazil.

Distribution.—Known from type locality only.

Measurements.—See Table 2.

Remarks.—Characterized as a small species, the type proves to be a juvenal of the common Brazilian marsh rat. Presence of adult type of pelage and functional third molars in all but suckling young of most sigmodont rodents, misled a number of systematists into describing juvenals as distinct from adults of the same species. Pending comparisons with true *brasiliensis*, the name *nanus* must be retained as the oldest available for marsh rats of the Amazonian and Guianan regions.

Holochilus brasiliensis amazonicus Osgood

Mus (*Holochilus*) *brasiliensis* Gervais, 1855, in Castelnau, Expéd. Amér. du Sud, 7, Zool., pt. 1, p. 111—Bolivia (Santa Ana, Santa Cruz).

Holochilus sp. Osgood, 1914, Field Mus. Nat. Hist., Zool. Ser., **10:** 167—Peru (Tambo Yacu, San Martín).

Holochilus amazonicus Osgood, 1915, Field Mus. Nat. Hist., Zool. Ser., **10:** 188; Allen, 1916, Bull. Amer. Mus. Nat. Hist., **35:** 571—Brazil (lower Rio Solimões).

H[*olochilus*] *sciureus* Thomas, 1920, Proc. U. S. Nat. Mus., **58:** 227—Peru (Río Pachitea; *guianae* and *amazonicus* doubtfully distinct).

Holochilus sciureus Thomas, 1927, Ann. Mag. Nat. Hist., (9), **19:** 369 (Peruvian and lower Amazonian forms conspecific); op. cit., 1928, (10), **2:** 260—Peru (Cumeria; San Jerónimo); Tate, 1939, Bull. Amer. Mus. Nat. Hist., **76:** 192—Venezuela or Brazil (Rio Negro); Sanborn, 1949, Journ. Mamm., **30:** 285—Peru (Yarinacocha).

Type.—Adult male, Chicago Natural History Museum no. 20136; collected May 11, 1913, by Robert H. Becker.

Type locality.—Itacoatiara, north bank of Rio Amazonas, below mouth of Rio Madeira, Amazonas, central Brazil.

Distribution.—Amazonian basin of Brazil, Bolivia, Peru. The species is unknown from eastern Ecuador and Colombia.

Measurements.—See Tables 2 and 5.

Remarks.—The type series is represented by skins and skulls of four adults. In these, chest and belly are gray overlaid with ochraceous; throat, inguinal region and inner sides of limbs dirty white

faintly washed with buff. Osgood believed his *amazonicus* was larger than *nanus* and true *brasiliensis* as represented by Winge's *Sigmodon vulpinus* from Minas Geraes. It appears, however, that the type of *nanus* is a half-grown juvenal and the skull figured by Winge, basis for Osgood's comparison, is that of a subadult. Winge described other specimens with dimensions that exceed those of *amazonicus*.

Valid characters for distinguishing *amazonicus* may exist, but they cannot be determined with certainty in present material. Whatever the eventual disposition of the name, Amazonian marsh rats from Peru and Bolivia agree completely with the type series of *amazonicus*.

Specimens examined.—21. BRAZIL: Itacoatiara, Amazonas, 9, including type and 5 newborn young in alcohol (CNHM). PERU: Moyobamba, San Martín, 1 (CNHM); Yarinacocha, Río Ucayali, 8 (CNHM). BOLIVIA: Buenavista, Santa Cruz, 1 (CNHM); Marbán Province, Río Mamoré, Beni, 2 (MAHN).

Holochilus brasiliensis incarum Thomas

Holochilus incarum Thomas, 1920, Proc. U. S. Nat. Mus., **58**: 226, pl. 14, fig. 1 (skull of type).

Type.—Immature female, United States National Museum no. 194195; collected December 22, 1914, by E. C. Erdis.

Type locality.—Santa Ana, upper Río Urubamba Valley, Cuzco, Peru; altitude, 1,061 meters above sea level.

Distribution.—Known only from type locality.

Measurements.—See Table 2.

Remarks.—Of three specimens in the type series, the holotype is a juvenal, the others represented by skins only. Thomas (supra cit.) summed up the remarkably distinctive specific characters of *incarum* as "less buffy on flanks" than *sciureus* (=*brasiliensis*). He also observed that "it is not improbable that from Peru, at a comparatively low altitude, right down the Amazon to Pará and Pernambuco, only one species of the genus is found." Provisional subspecific status for *incarum* rests on nothing more than present indecision regarding the systematic position of *amazonicus*.

Holochilus brasiliensis guianae Thomas

Holochilus guianae Thomas, 1901, Ann. Mag. Nat. Hist., (7), **8**: 149.

H[olochilus] guianae Thomas, 1920, Proc. U. S. Nat. Mus., **58**: 227 (doubtfully distinct from *sciureus* [=*brasiliensis*]); Morrison-Scott, 1937, Ann. Mag. Nat. Hist., (10), **20**: 536 (comparison; discussion).

Holochilus sciureus Thomas, 1928, Ann. Mag. Nat. Hist., (10), **2**: 260 (*Holochilus* monotypic).

Type.—Adult male, British Museum (Natural History) no. 1.6.4.87; collected November 28, 1900, by J. J. Quelch.

Type locality.—Kanuko Mountains, southern British Guiana; altitude, 152 meters above sea level.

Distribution.—Known from type locality only.

Measurements.—See Table 2.

Remarks.—Morrison-Scott (supra cit., p. 537) states that Thomas wrote on the label of the type of *guianae* "=*sciureus*." It remains to be decided whether or not *guianae* is as much as subspecifically distinct from either typical *brasiliensis* or *nanus*. The status of *amazonicus* Osgood also depends on this decision.

Holochilus brasiliensis berbicensis Morrison-Scott

Holochilus sciureus berbicensis Morrison-Scott, 1937, Ann. Mag. Nat. Hist., (10), **20**: 535.

Type.—Adult male, British Museum (Natural History) no. 1937.6.24.2; collected April 10, 1937, by Dr. L. D. Cleare.

Type locality.—Blairmont Plantation, Berbice, coastal British Guiana.

Measurements.—See Table 6.

Remarks.—Two specimens from Nonpareil Plantation on the Demerara coast, just west of the type locality of *berbicensis*, are slightly darker throughout than the type series of *amazonicus* Osgood from the middle Rio Amazonas. On this basis, the difference between *berbicensis* and the geographically adjacent *guianae* must be insignificant, if at all real. In fact, Morrison-Scott refers a specimen from the Demerara River to *sciureus* (=*brasiliensis*). If *berbicensis* is at all valid, its range should include all the Demerara coast. Morrison-Scott did note that *berbicensis* was matched in color by a specimen of *venezuelae* J. A. Allen, from Carabobo, on the Venezuelan coast. However, the probability that *venezuelae* and *berbicensis* might be the same was discounted because of the larger feet and longer tail of the single Venezuelan specimen. Our near topotypes of *berbicensis*, however, have even larger feet and longer tails than Morrison-Scott's specimen from Carabobo.

The oldest available name for marsh rats of the Guianan region is *Holochilus brasiliensis nanus* Thomas, from the island of Marajó, Pará, Brazil. The fact that the type and only specimen of *nanus* is

represented by a skin and skull removed from a juvenal originally preserved in spirits seems to have encouraged authors to describe better-prepared specimens as new species.

Specimens examined.—2. BRITISH GUIANA: Nonpareil Plantation, Demerara, 2 (CNHM).

Holochilus brasiliensis venezuelae J. A. Allen

Holochilus venezuelae J. A. Allen, 1904, Bull. Amer. Mus. Nat. Hist., **20**: 330, 341—part (type only); Goodwin, 1953, Bull. Amer. Mus. Nat. Hist., **102**: 324 (type data; measurements).

H[olochilus] venezuelae Morrison-Scott, 1937, Ann. Mag. Nat. Hist., (10), **20**: 537—Carabobo, Venezuela.

Type.—Immature female, American Museum of Natural History no. 16973; collected March 20, 1901, by S. M. Klages.

Type locality.—El Llagual (Yagual), lower Río Caura, Bolívar, Venezuela.

Measurements.—See Table 2.

Remarks.—The original description of *venezuelae* is based partly on a "half grown female" and, chiefly, on a "very old male." The younger specimen, however, was designated as type because the unworn teeth "showed it to be a *Holochilus* and not a *Nectomys*." Allen's misgivings regarding the true identity of the adult prove to have been well founded. The designated cotype is shown by Goodwin to be a *Nectomys*. The description of *venezuelae*, like that of *nanus* Thomas, is, therefore, zoologically worthless. The relationship of the Venezuelan marsh rat to other described forms of northern South America remains to be determined.

TABLE 1.—Measurements of *Holochilus magnus* sp. nov.

Locality	Head and body	Tail	Hind foot	Greatest length of skull	Zygomatic breadth	Molar row Alveolar length
Río Cebollati[1]	210	230	62	44.9	25.6	8.5
Río Cebollati	230	280	66	48.3	27.0	9.0
Treinta y Tres[2]	160	230	61	40.3	....	8.5
Porto Alegre[3]	175	210	47[4]	....	....	...
Lagôa Santa[5]	185	208	50.5[4]	....	....	...

[1] Of type.

[2] Juvenal.

[3] Of juvenal in spirits, from Hensel (1873, Abh. Akad. Wiss. Berlin, **1872**: 34).

[4] Without claw; add 5 mm. for shrinkage and claw.

[5] Of juvenal in spirits, from Winge (1888, E. Mus. Lundii, **1**, (3), p. 23).

TABLE 2.—Measurements of *Holochilus brasiliensis* Desmarest and Synonyms

Unless otherwise indicated all measurements are of types from original descriptions

Name	Sex	Age	Head and body	Tail	Hind foot	Ear	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Molar row
brasiliensis[1]	..	Ad.	186	195	49	....	....	..	....	....
sciureus[2]	..	Ad.	196	161	39	....	....	..	....	....
vulpinus	..	Ad.	246	167	59	....	....	..	....	....
vulpinus[3]	..	.....	248	170	58.7	....	....	..	....	....
vulpinus[4]	..	.....	239	183	....	....	....	..	....	....
darwini[5]	♀	Ad.	215	196	51	15	....	..	....	9.0[5]
chacarius	♀	Subad.	175	164	38	17	36.7	..	19.5	6.9
balnearum	♀	Juv.	132[6]	133	35.5	18	35.0	..	20.0	7.5
leucogaster	..	.....	157	183	35	....	....	..	....	....
physodes	..	.....	174	150	37	....	....	..	....	....
physodes[7]	..	.....	183	157	37	....	....	..	....	....
physodes[8]	..	.....	174	165	....	....	....	..	....	....
anguya	..	.....	191	139	....	....	....	..	....	....
russatus	..	.....	165	150	37	....	....	..	....	....
nanus	♀	Juv.	122	112	32	14	....[9]	..	19	6.5
amazonicus	♂	Ad.	193	182	45[10]	41.2	38.2	..	....	7.4
incarum	♀	Juv.	128	132	34[11]	....	....	31	....	7.2
guianae	♂	Juv.	178	159	38.5[12]	15	37	..	20.6[13]	6.9[13]
venezuelae[14]	♀	Juv.	133	142	36.5	....	32.5	..	18.5	7.15

[1] From mounted skin of type, after Waterhouse (1839, Zool. Voy. "Beagle," p. 60).

[2] Converted from Old German inches to millimeters; 1 inch=26.1 mm.

[3] From Lichtenstein (1830, Darstellung . . . , Heft 15, tab. 33, text). [4] From Burmeister (1854, Syst. Übers. Thiere Bras., **1**: 163).

[5] Original measurements of type after Waterhouse (loc. cit.). The figures are not reliable. Cranial measurements taken by Waterhouse and Gyldenstolpe (1932, K. Sv. Akad. Handl., **2**: 142) are compared (in mm.) as follows (measurements of Waterhouse in parentheses): Nasals 12.0 ($7\frac{1}{4}$ lines = 15.4); least interorbital width 5.0 ($2\frac{1}{2}$ lines = 5.3); incisive foramina 8.0 ($4\frac{1}{4}$ lines = 9.0); molar row . . . ($4\frac{1}{4}$ lines = 9.0).

[6] Collector's measurements apparently "an undermeasurement; the skin looks contracted, but the head and body still measures over 140 mm." (Thomas, 1906, Ann. Mag. Nat. Hist., (7), **18**: 448, footnote.)

[7] From Lichtenstein (1830, Darstellung . . . , Heft 15, tab. 34, text).

[8] From Burmeister (1854, Syst. Übers. Thiere Bras., **1**: 167). [9] Skull perhaps is imperfect; basilar length given is 26.6.

[10] With claw. [11] With claw = 36 mm. [12] With claw = 42 mm.

[13] Zygomatic breadth 20.2, molar row 7.11, according to Morrison-Scott (1937, Ann. Mag. Nat. Hist., (10), **20**: 535).

[14] From Goodwin (in litt., Feb. 14, 1955); external measurements in original description are of the cotype, a *Nectomys*.

TABLE 3.—Measurements of *Holochilus brasiliensis vulpinus* Brants

Locality	Head and body	Tail	Hind foot	Greatest length of skull	Zygomatic breadth	Molar row Alveolar length
BRAZIL						
Rio Uruguay[1]	246	167	59	....	....	...
URUGUAY						
Treinta y Tres	...	...	55[2]	45.5	26.0	7.8
PARAGUAY						
Villa Militar	170	160	..	....	21.4	7.9
Río Pilcomayo	182	164	41	39.9	22.3	7.5
Río Pilcomayo	178	160	39	38.3	21.0	7.0
Concepción[3]	175	164	38	36.7	19.5	6.9
ARGENTINA						
Goya[4]	...	...	..	42.2	24.6	7.8

[1] Of type of *vulpinus* Brants, from original description.

[2] From dry skin.

[3] Of type of *chacarius* Thomas, "a young adult" (probably subadult), from original description.

[4] Of specimen in British Museum, from Gyldenstolpe (1932, K. Sv. Vet. Akad. Handl., **2**: 142).

TABLE 4.—Measurements of *Holochilus brasiliensis balnearum* Thomas

Locality	Head and body	Tail	Hind foot	Greatest length of skull	Zygomatic breadth	Molar row Alveolar length
San Felipe[1]	132	133[2]	35.5	35.0	20.0	7.5
Calilegua	187	153	42	39.3	21.3	7.6
	181	168	40	38.2	20.4	7.8
	168	160	43	37.9	20.5	8.0
	173	156	41	37.6	21.0	7.6
	168	158	41	37.5	20.5	7.7

[1] Of type, a juvenal, from original description.

[2] Skin "contracted."

TABLE 5.—Measurements of *Holochilus brasiliensis amazonicus* Osgood

Locality	Head and body	Tail	Hind foot	Greatest length of skull	Zygomatic breadth	Molar row Alveolar length
BRAZIL						
Itacoatiara[1]	193	182	45	41.2	....	7.6
	201	188	45	....	....	7.5
	194	180	42	40.2	22.0	7.6
	190	158	42	40.6	....	7.7
PERU						
Yarinacocha	185	143[+]	40	40.8	22.3	7.6
	170	165	36	39.8	21.0	7.7
	...	...	..	39.0	20.7	7.4
	162	140	..	37.7	19.6	7.4

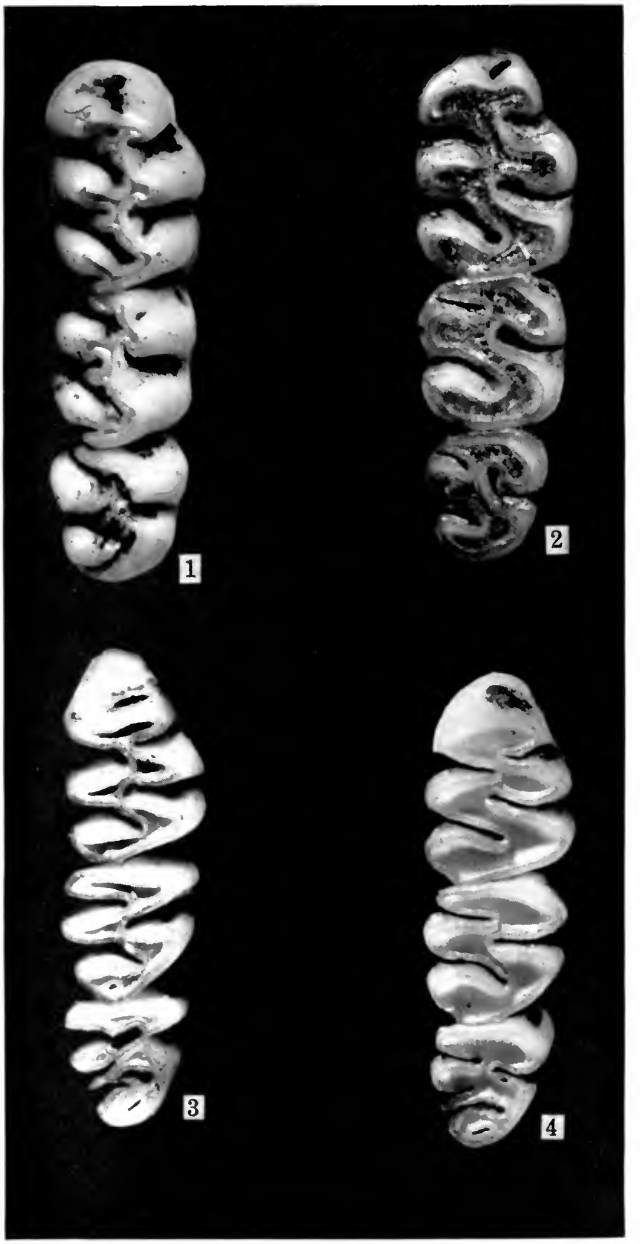
[1] First measurements are those of type.

TABLE 6.—Measurements of *Holochilus brasiliensis berbicensis* Morrison-Scott

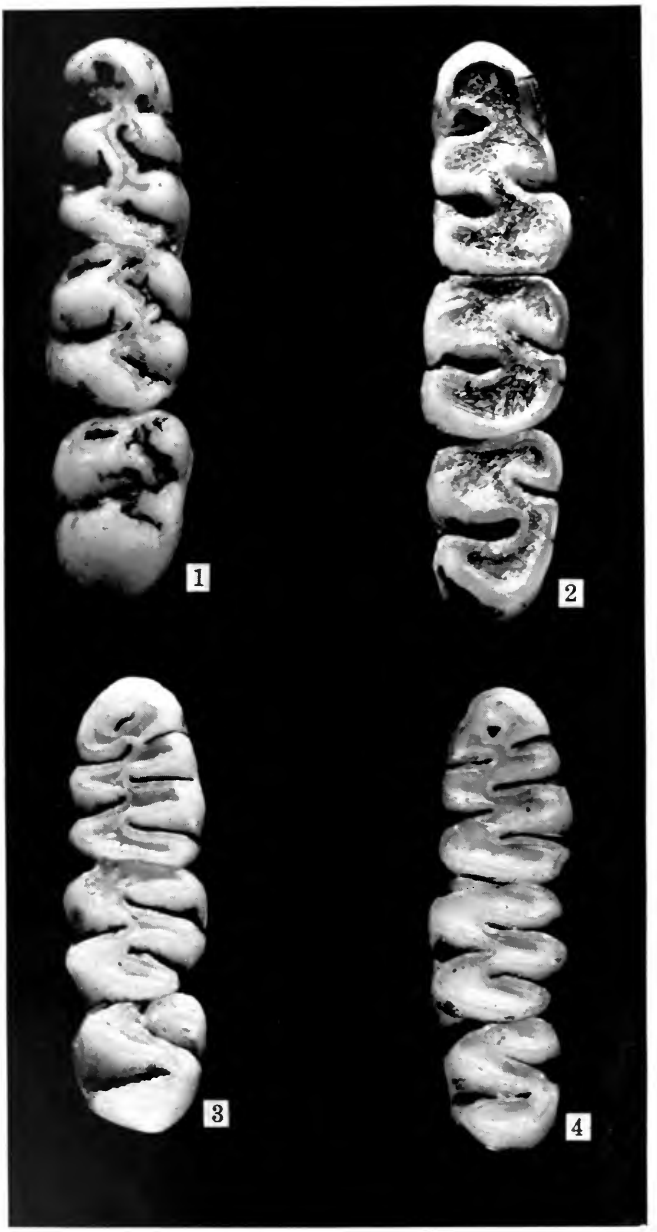
Locality	Head and body	Tail	Hind foot	Ear	Greatest length of skull	Condylo-basal length	Zygomatic breadth	Molar row
Berbice[1]	178	144	39	16	....	36.6	21.5	7.19
	190	145	35	17	....	36.3	21.3	7.29
	153	132	35	17	....	33.8	20.4	7.17
	140	117	35	16	....	31.9	19.2	7.22
	146	108	35	16	....	....	....	....
	142	139	35	16	....	....	....	....
	189	138	36	17	....	....	....	....
	170	150	37	15	....	....	....	....
Nonpareil	185	170	44[2]	..	40.1	37.9	22.2	7.5
	190	...	45[2]	..	....	....	....	7.2

[1] First measurements are those of type; the remainder, those of paratypes. All measurements from original descriptions.

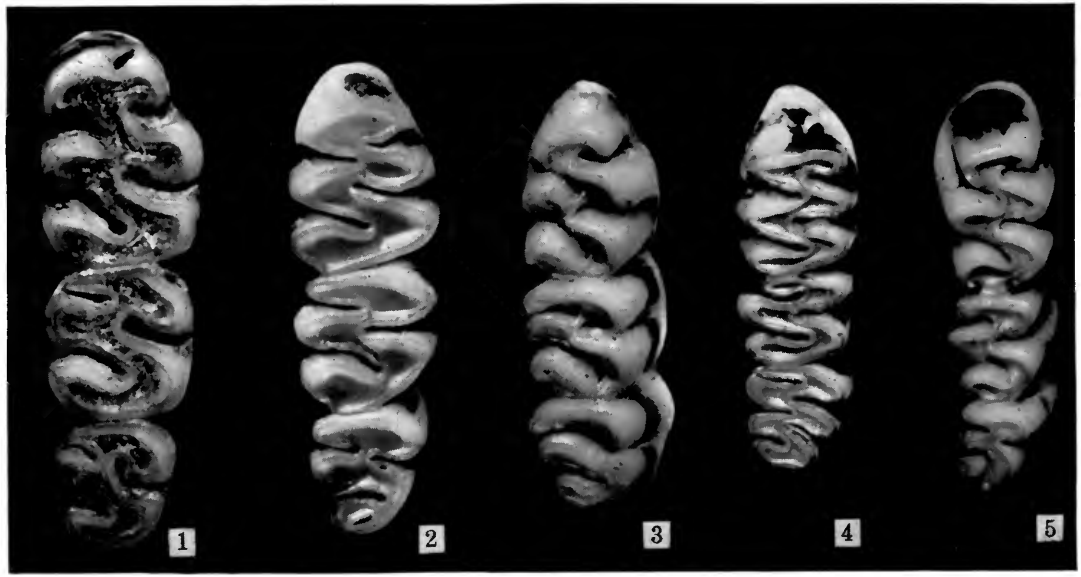
[2] Dry, with claw.



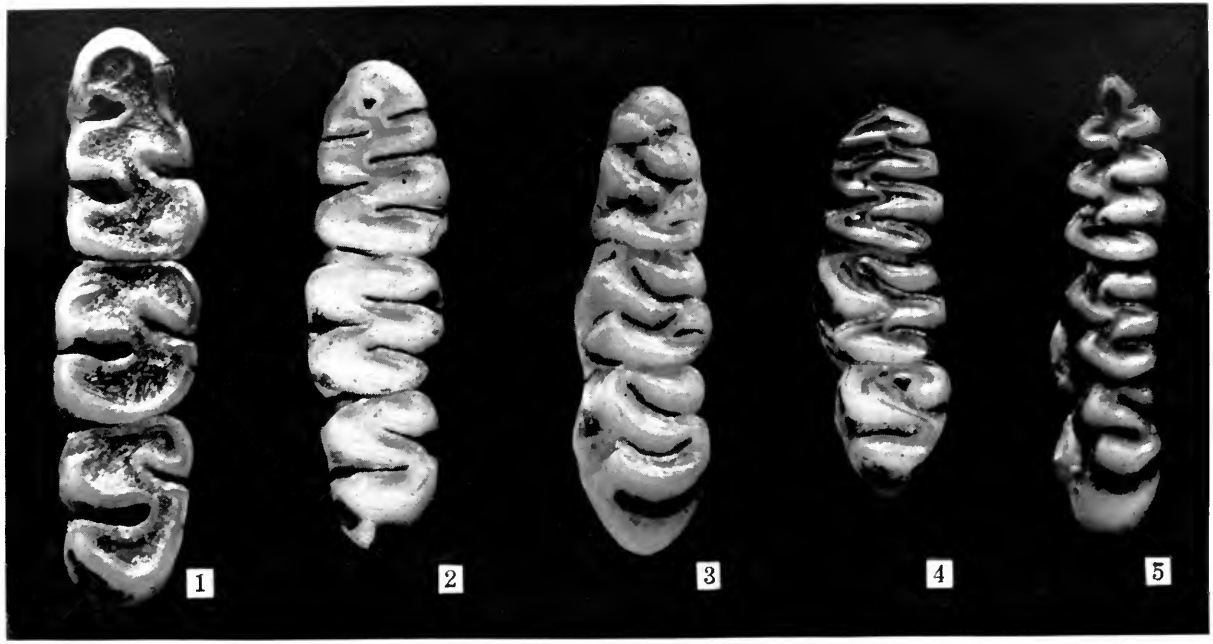
Upper molars: 1 and 2, juvenal and adult (type) of *Holochilus magnus;* 3 and 4, juvenal and adult of *H. brasiliensis.* Approximately × 8.



Lower molars: 1 and 2, juvenal and adult (type) of *Holochilus magnus;* 3 and 4, juvenal and adult of *H. brasiliensis.* Approximately × 8.

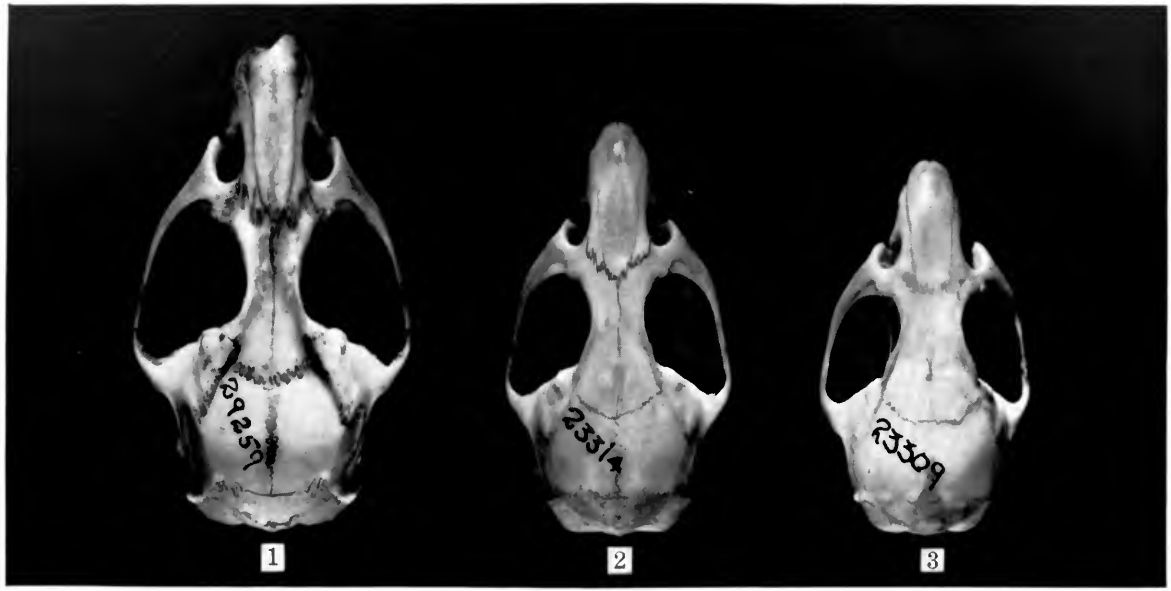


Upper molars: 1, *Holochilus magnus* (type); 2, *H. brasiliensis;* 3, *Sigmodon hispidus;* 4, *Neotomys ebriosus;* 5, *Reithrodon physodes.* Approximately × 8.



Lower molars: 1, *Holochilus magnus* (type); 2, *H. brasiliensis;* 3, *Sigmodon hispidus;* 4, *Neotomys ebriosus;* 5, *Reithrodon physodes.* Approximately × 8.

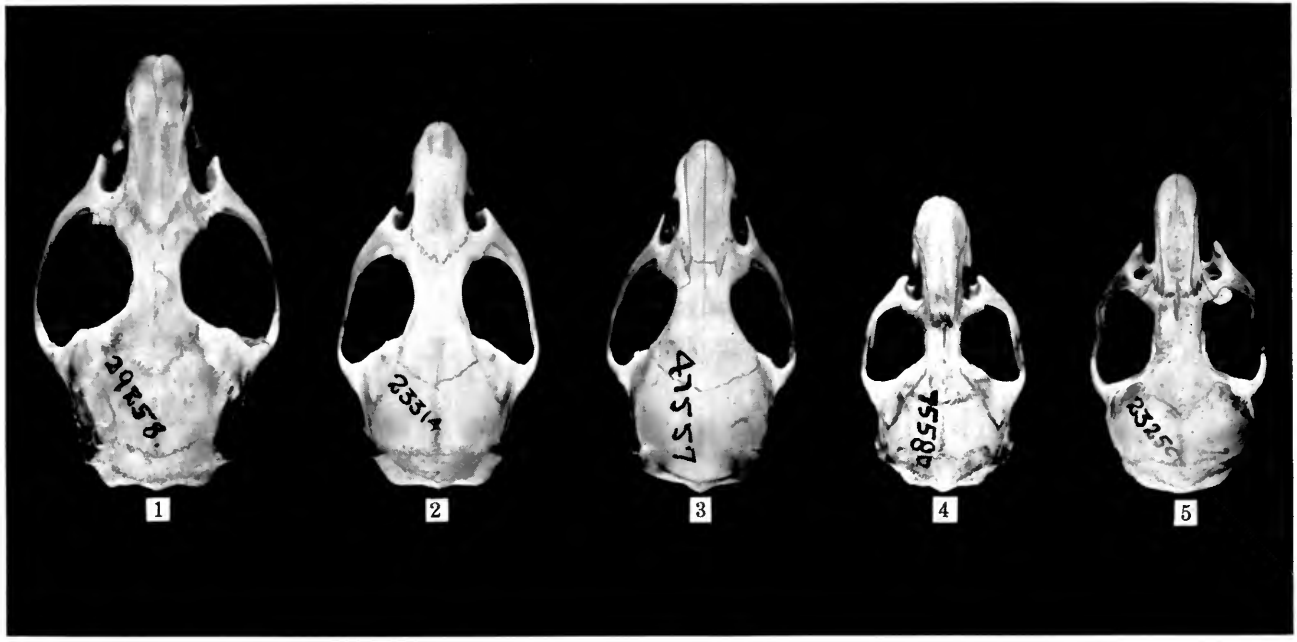
Dorsal surface of skulls of *Holochilus magnus:* 1, old male; 2, adult male (type); 3, juvenal female. Approximately × 3/2.



Dorsal surface of skulls: 1, *Holochilus brasiliensis vulpinus*, old adult; 2 and 3, *H. brasiliensis balnearum*, adult female and young male. Approximately $\times$ 3/2.

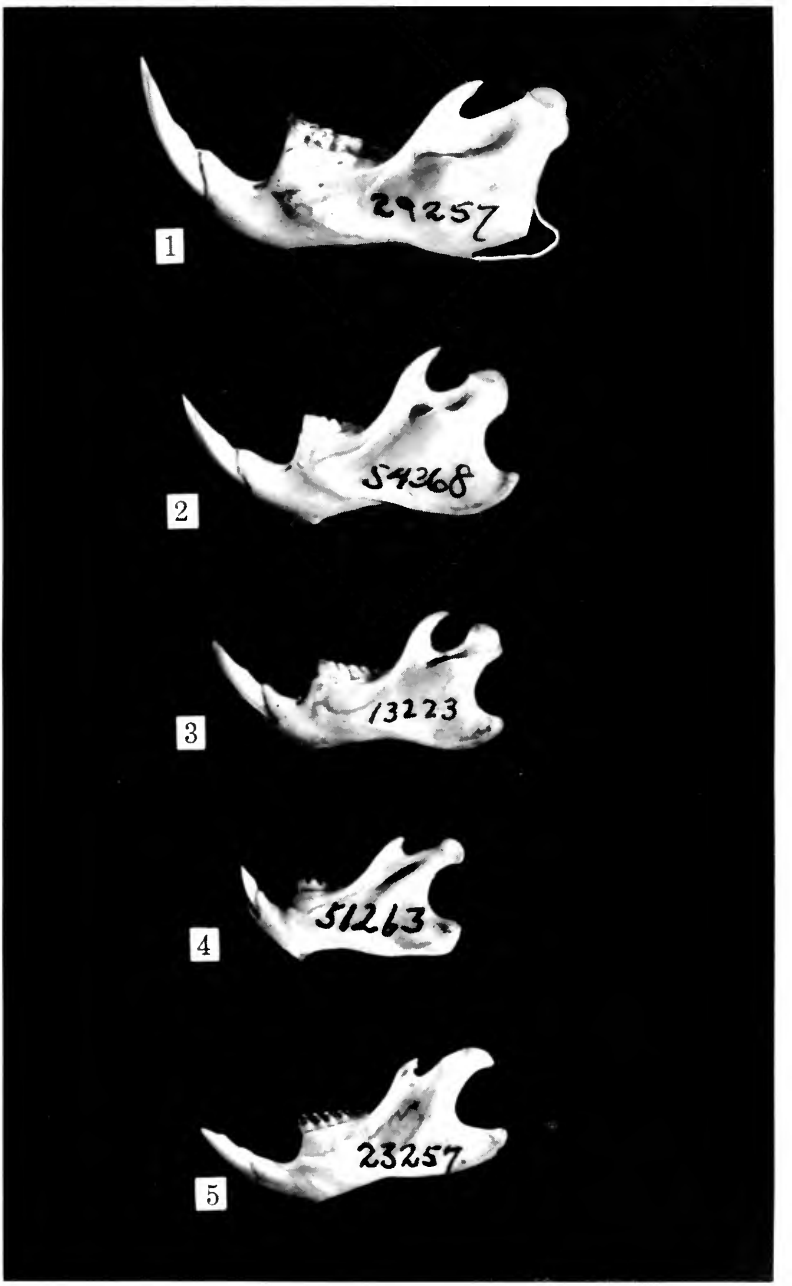
Ventral surface of skulls of *Holochilus magnus:* 1, old male; 2, adult male (type); 3, juvenal female. Approximately × 3/2.

Ventral surface of skulls: 1, *Holochilus brasiliensis vulpinus*, old adult; 2 and 3, *H. brasiliensis balnearum*, adult female and young male. Approximately $\times 3/2$.



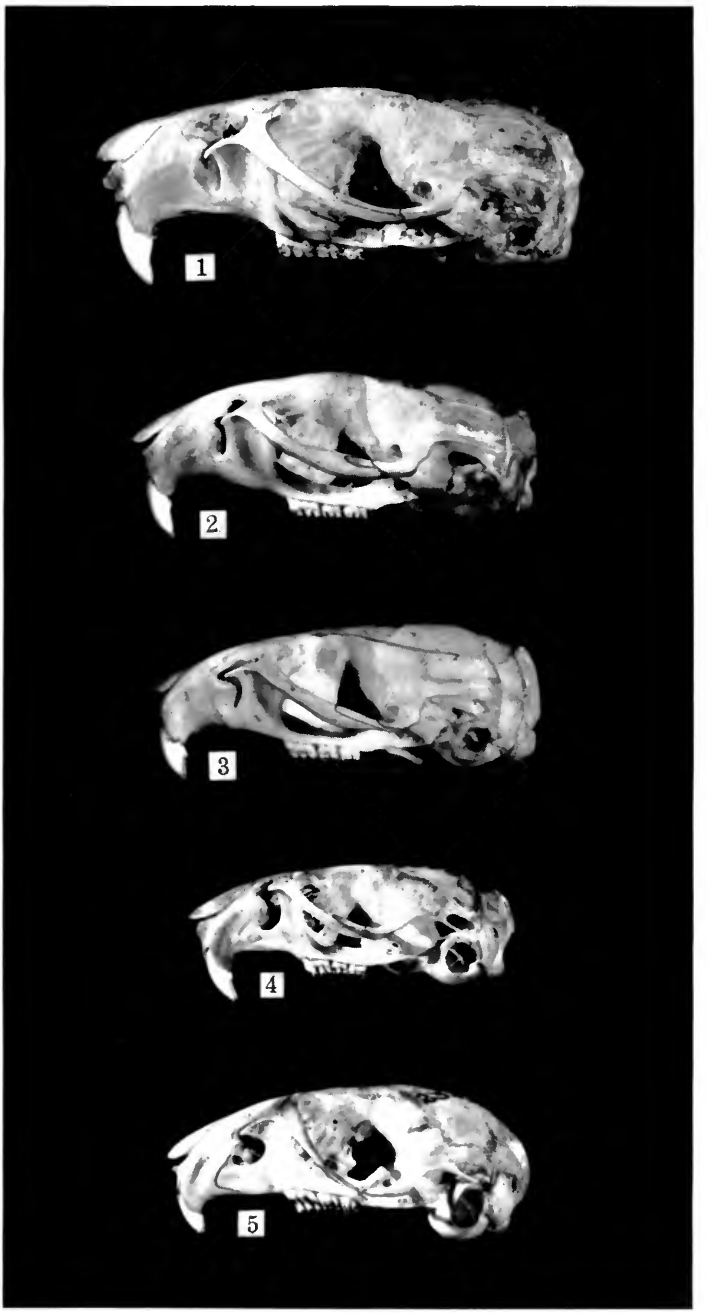
Dorsal surface of skulls: 1, *Holochilus magnus* (type); 2, *H. brasiliensis;* 3, *Sigmodon hispidus;* 4, *Neotomys ebriosus;* 5, *Reithrodon physodes.* Approximately × 4/3.

Ventral surface of skulls: 1, *Holochilus magnus* (type); 2, *H. brasiliensis;* 3, *Sigmodon hispidus;* 4, *Neotomys ebriosus;* 5, *Reithrodon physodes.* Approximately × 4/3.



Outer surface of mandibles: 1, *Holochilus magnus* (type); 2, *H. brasiliensis;* 3, *Sigmodon hispidus;* 4, *Neotomys ebriosus;* 5, *Reithrodon physodes.* Approximately $\times 9/5$.

Inner surface of mandibles: 1, *Holochilus magnus* (type); 2, *H. brasiliensis;* 3, *Sigmodon hispidus;* 4, *Neotomys ebriosus;* 5, *Reithrodon physodes.* Approximately $\times 9/5$.



Lateral surface of skulls: 1, *Holochilus magnus* (type); 2, *H. brasiliensis;* 3, *Sigmodon hispidus;* 4, *Neotomys ebriosus;* 5, *Reithrodon physodes.* Approximately $\times 4/3$.