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Enlarging rodent diversity in west-central Argentina: a new species of the genus *Holochilus* (Cricetidae, Sigmodontinae)

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On the basis of an adult individual collected in 1955 plus 3 mandibles of latest Holocene age, we describe a new living species of the amphibious rat *Holochilus* (Sigmodontinae, Oryzomyini) from west-central Mendoza Province, Argentina. The new species is characterized by its short tail, broad zygomatic plate with rounded anterior–superior corner, bony palate without excrescences, large mesolophostyle in the upper first molars and complex upper third molar shorter than the second, and lacking the hypoflexus. The morphological traits displayed by this new *Holochilus* combine features observed in both the *H. brasiliensis* and *H. sciureus* groups with others unique among the genus (e.g., absence of hypoflexus). This new species is the southernmost expression of the genus along the western side of its current range, where it appears isolated in the middle part of the Río Atuel. The finding reported here uncovers and highlights unexpected diversity in southern South American arid lands.

Key words: *Holochilus brasiliensis*, *Holochilus chacarius*, *Holochilus sciureus*, Mendoza, Oryzomyini

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Within the extensive radiation of the sigmodontine rodents, few lineages developed full morphological adaptations to a semiaquatic way of life (e.g., Carleton and Olson 1999; Voss 1988). The genera *Amphinectomys*, *Holochilus*, *Lundomys*, and *Nectomys* are amphibious oryzomyines widespread along rivers and streams of tropical and subtropical South America (Musser and Carleton 2005; Weksler 2006). These rats are the largest living representatives within the tribe, but despite their abundance in the wild and in museum collections, particularly *Holochilus* and *Nectomys*, taxonomic diversity is poorly understood. Hershkovitz (1955) reviewed *Holochilus*, subsuming more than a dozen of nominal forms under *H. brasiliensis* and described 1 new species, *H. magnus* (now placed as a synonym of *Lundomys molitor*—Voss and Carleton 1993). Later, on the basis of external, cranial, and dental features, Massoia (1976, 1981) recognized 2 main groups within this genus, *brasiliensis* and *sciureus*. However, the contents of these groups and the validity of the several nominal forms proposed during the last 1.5 centuries (see Hershkovitz 1955) remains to be fully understood.

Holochilus reaches in its southernmost occurrence the northeastern limit of Patagonia, extending south of the Río Colorado in southern Buenos Aires Province by a few kilometers (Formoso et al. 2010). However, this rat had apparently continuous populations along that river and associated fluvial systems (such as Limay and Negro rivers) on the basis of abundant Holocene remains from several archaeological sites (Fernández et al. 2011; Pardiñas and Teta 2011). Apparently, these populations disappeared from northern Patagonia during the latest Holocene and there are no records of living marsh rats in Neuquén, Río Negro, or La Pampa provinces (Pardiñas et al. 2004).

In 1955 Humberto Lagiglia, formerly director of the Museo Municipal de Historia Natural de San Rafael (MHNSR, San Rafael, Mendoza, Argentina), obtained a marsh rat hand-trapped by a hunter near the margin of the lake known as Embalse Nihuil, about 60 km SW of San Rafael city. The specimen was prepared as skin, and the skull with the mandible (both poorly cleaned) were the only skeletal elements preserved. These

materials remained unstudied in the museum for decades, although Elio Massoia, at the end of the 1970s, took a quick look at the specimen (E. Massoia, pers. comm.). Very recently, after Lagiglia had died, one of the authors (FJF) encountered the specimen while recurating the zoology collection (MHNSR). In addition, 3 mandibles that also belong to this genus were retrieved from the faunal collection of Gruta del Indio, a famous archaeological site excavated by Lagiglia and collaborators (see Semper and Lagiglia 1962–1968). Both localities, Embalse Nihuil and Gruta del Indio, are in the middle of Río Atuel basin, within the Monte desert biome and the climatic region known as the South American Arid Diagonal (Abraham et al. 2009).

The study of all available specimens reveals a unique combination of morphological features, supporting that they collectively represent a new species of *Holochilus*. Here we describe and compare this new taxon with the *brasiliensis* and *sciureus* species groups (for brevity, hereafter referred to simply as *H. brasiliensis* and *H. sciureus*). We also briefly address the current records of *Holochilus* in southern South America, as well as the past distribution of the genus in this portion of the subcontinent.

Materials and Methods

We examined a total of 824 specimens of *Holochilus* from Argentina, Bolivia, and Brazil, including large series of craniodental remains derived from owl pellets (Appendix I). Those specimens referred to the new species ($n = 4$) described in this work belong to the collections of the MHNSR. We based morphological descriptions on the anatomical reviews of Carleton and Musser (1989), Voss (1988), and Weksler (2006); molar morphology nomenclature follows Reig (1977). We measured only specimens classified as adults according to the age criterion of Petter and Tostain (1981: figure 1). We took external measurements of the holotype from the dried skin, and recorded craniodental measurements with a digital caliper (nearest 0.1 mm) from those defined or listed by Hershkovitz (1962:109) and Carleton and Olson (1999). We performed a principal components analysis (PCA) of adult specimens without missing values (Table 1), using a reduced set of 15 craniodental and the STATISTICA software package (StatSoft 2001). Principal components were extracted from a variance–covariance matrix and computed from natural log transformations of the original measurements.

Results

Family Cricetidae Fischer, 1817
Subfamily Sigmodontinae Wagner, 1843
Tribe Oryzomyini Vorontsov, 1959
Genus *Holochilus* Brandt, 1835
Holochilus lagigliai, new species
Figs. 1 and 3

Holotype.—A skull with the right side partially damaged, pterygoid region crushed and both mandibles with the incisor tips and angular processes missing (MHNSR 564; Fig. 1), and a poorly prepared skin with the right hand missing and caudal skeleton preserved inside (MHNSR 558); both from a single adult individual, collected by Felipe Faliti on 15 January 1955. Sex and external measurements were not recorded on flesh.

Type locality.—The precise collecting locality of the holotype is unknown because the label indicates only "El Nihuil—San Rafael—Mendoza—Arg." El Nihuil is a dam constructed in 1947 on the middle course of the Río Atuel, with geographical coordinates 35°04′S, 68°43′W, 1,300 m above sea level (asl; Fig. 2).

Additional material.—Three right mandibles with broken incisors and m1–3 in place (MHNSR 231, 650, and 674), collected in the surface of Gruta del Indio by H. Lagiglia in January 1974. Gruta del Indio (34°45′S, 68°22′W, 660 m asl) is an archaeological and paleontological site located 28 km SE of San Rafael on the south side of the Río Atuel (Fig. 2).

Etymology.—This species is dedicated to Humberto A. Lagiglia, Argentinean archaeologist and naturalist (1938–2009) who founded and was the director of the MHNSR until his death. Professor Lagiglia promoted archaeological and biological research in Mendoza Province, Argentina over a remarkably prolonged, 5-decade period.

Measurements of the holotype (in mm).—Length of tail = 136.5; hind-foot length with and without claws, 41.7, 45.8; condylobasal length = 38.9; palatilar length = 20.5; length of incisive foramen = 7.8; width of incisive foramen = 2.3; breadth of zygomatic plate = 6.7; length of maxillary tooth row (alveolar) = 8.1; palatal breadth across M1s = 8.9; palatal bridge = 9.6; bullar width = 4.6; bullar length less tube = 6.1; interorbital breadth = 5.5; breadth of braincase = 16.2; breadth of rostrum = 7.9; length of diastema = 11.9; length of M1 = 3.1, width of M1 = 2.5; length of M2 = 2.3, width of M2 = 2.5; length of M3 = 2.0, width of M3 = 2.1; length of m1 = 3.5, width of m1 = 2.1; length of m2 = 2.3, width of m2 = 2.2; length of m3 = 2.8, width of m3 = 2.1; length of mandibular tooth row (alveolar) = 8.8. Measurements for additional material are (mean ± standard deviation; $n = 3$): length of m1 = 3.3 ± 0.04, width of m1 = 2.2 ± 0.06; length of m2 = 2.5 ± 0.00, width of m2 = 2.5 ± 0.06; length of m3 = 3.1 ± 0.08, width of m3 = 2.2 ± 0.03; length of mandibular tooth row (alveolar) = 9.1 ± 0.13.

Diagnosis.—A large species of *Holochilus* characterized by a unique combination of traits including a short tail, specially broad braincase, wide and anteriorly rounded zygomatic plate, bony palate without excrescences, M1 with subelliptical procingulum and persistent parastyle and protostyle, well-developed mesolophostyles on M1, M3 shorter than M2 and without hypoflexus and hypocone, m1 with anteromedian fossetid labially displaced and opened.

Description.—Dorsal coloration reddish brown, darker at the midline, and turning to buffy orangish on flanks; individual hairs have gray bases, with a broad yellowish median band and reddish to orangish tips; guard hairs are larger (~22 mm) and darker; venter covered by whitish hairs with gray bases; hairs on the chin, throat, and the inguinal area between the hind legs and tail base are completely white; an orangish, narrow, and

Table 1.—Descriptive statistics (in mm; mean ± standard deviation) for selected craniodental variables of adult specimens of *Holochilus*.

	H. lagigliai, sp. nov. ($n = 1$)	*H. brasiliensis* ($n = 27$)	*H. chacarius* ($n = 14$)
Length of incisive foramen	7.83	7.83 ± 0.54	7.81 ± 0.40
Breadth of incisive foramen	2.27	2.65 ± 0.23	2.55 ± 0.14
Palatilar length	20.5	19.71 ± 1.02	18.88 ± 0.48
Breadth of zygomatic plate	6.71	4.86 ± 0.39	4.75 ± 0.33
Length of maxillary tooth row	8.07	7.76 ± 0.22	7.23 ± 0.27
Palatal breadth across M1s	9.97	8.22 ± 0.33	7.09 ± 0.52
Palatal bridge length	9.58	9.12 ± 0.54	8.80 ± 0.35
Interorbital constriction	5.50	4.81 ± 0.19	4.79 ± 0.22
Length of diastema	11.86	11.57 ± 0.79	11.05 ± 0.53
Length of M1	3.10	3.15 ± 0.09	2.92 ± 0.09
Length of M2	2.30	1.99 ± 0.06	1.93 ± 0.06
Length of M3	2.05	2.21 ± 0.14	2.01 ± 0.14
Width of M1	2.55	2.37 ± 0.10	2.10 ± 0.09
Width of M2	2.50	2.31 ± 0.12	2.08 ± 0.07
Width of M3	2.10	1.93 ± 0.17	1.76 ± 0.08

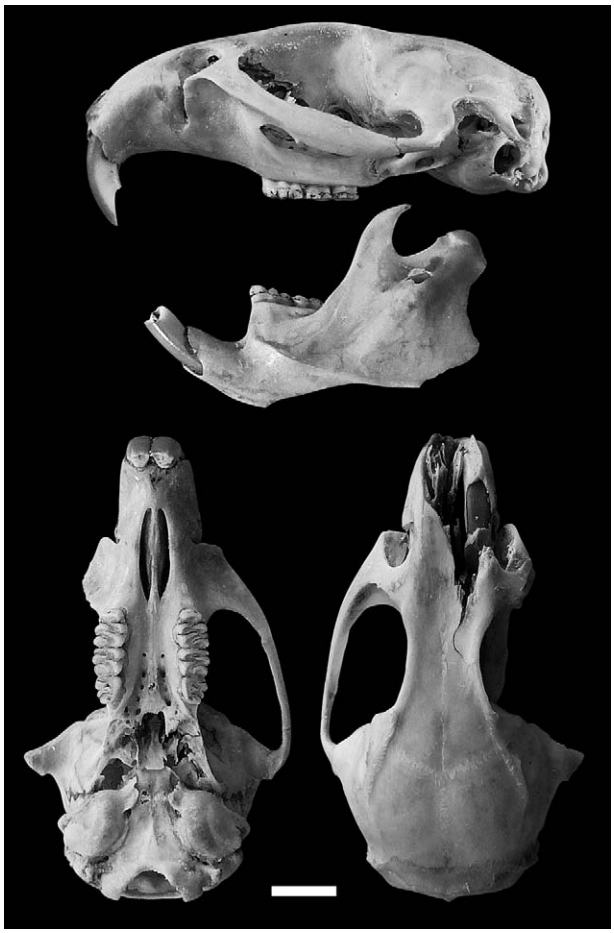

Fig. 1.—Holotype of *Holochilus lagigliai*, n. sp., from Nihuil, Mendoza, Argentina (MHNSR-564): skull in lateral (top), ventral (left), and dorsal (right) views, and left dentary in labial view. Scale = 5 mm.

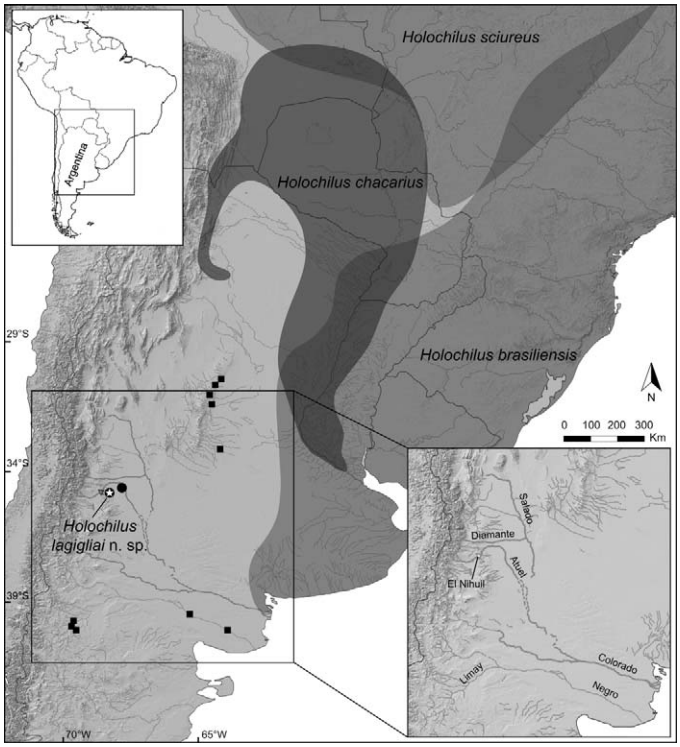

Fig. 2.—Geographic distribution of the genus *Holochilus* in southern South America (compiled from several sources). Star indicates the type locality of the new species described for Mendoza Province, Argentina. Squares are Late Holocene records for *H. brasiliensis* (after Pardiñas and Teta 2011). In the inset, main rivers dicussed in the text.

incomplete pectoral band is present between the forelegs; head reddish brown above and around the eyes and nose, checks buffy and slightly more yellowish than flanks; vibrissae short and brownish, not reaching the base of the ear; ears internally covered by short buffy hairs that slightly surpass the inner border of the pinna; tail bicolor and scarcely haired, reddish brown above and whitish below, with large, hexagonal epidermal scales visible to the naked eye; individual hairs on tail cover 2–2.5 scales; there are 3 hairs per scale; manus and pes are dorsally covered by whitish hairs; ungual tufts reach the mid-claw on manus, but are almost completely absent on pes; claws not keeled; manus with 5 palmar pads, 3 small interdigital and 2 large carpal; plantar surface hairless and densely squamated; interdigital pads on plantar surface large and oval; thenar pad is almost twice the size of the 2nd interdigital; there are no traces of a hypothenar pad; interdigital webbing present, extending beyond 1st interphalangeal joints of digits II, III, and IV.

Skull strongly built, with a short and broad rostrum, amphoral shaped and crested interorbital region and squared, broad, and especially short braincase (Fig. 1). Interorbital margins with moderately well-developed supraorbital crests that continue as distinct parietal ridges and end at the point where the lateral expansion of the parietal begins. Interparietal large. Zygomatic plate very broad and well excavated, with a

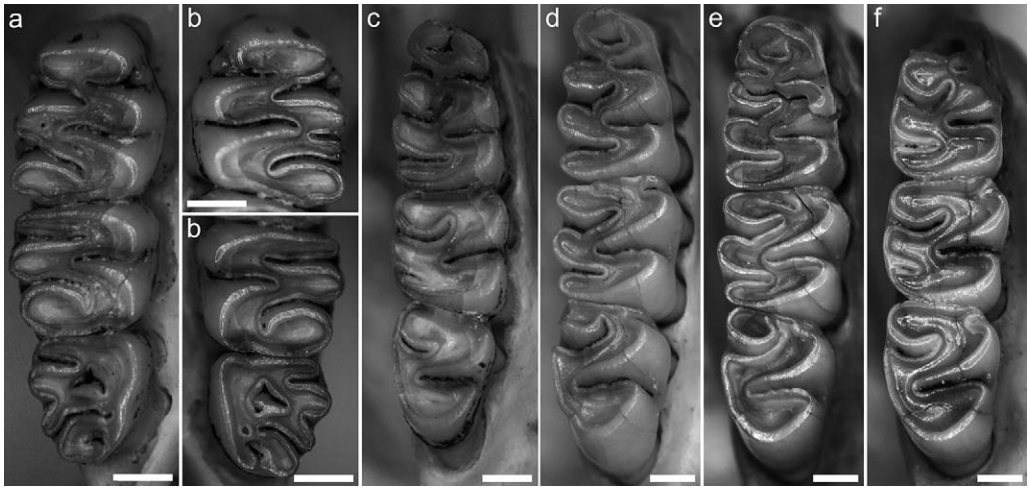

Fig. 3.—Occlusal view of upper and lower molars in *Holochilus lagigliai*, sp. nov., from Nihuil, Mendoza, Argentina; holotype (MHNSR-564), right (a) and left (b) upper and right lower (c) tooth rows; additional material, right lower tooth rows for MHNSR-231 (d), 650 (e), and 674 (f). Scale = 5 mm.

rounded upper corner and large free border that encloses a well-incised zygomatic notch; anterior border of the zygomatic plate very close to nasolachrymal capsule. Zygomatic arches robust and divergent posteriorly, dorsoventrally expanded in the middle portion and with a distinct spinous process on the inner margin. Jugal present but narrow. Postorbital ridge rounded. Postglenoid foramen large; subsquamosal fenestra partially occluded by a broad hamular process and an internal crest or septum of the periotic. Incisive foramina short, almost parallel side, ending well before the anterior face of M1; palatal process of premaxillary well developed, embracing posteriorly the median septum of the maxillary bone. Bony palate wide and long, with the anterior border of the mesopterygoid fossa slightly behind the plane defined by the 3rd molars; palatal bridge dissected by a median ridge and 2 deep lateral sulci; 4 to 5 small foramina are located in these grooves; anterior border of mesopterygoid fossa squared. Molar tooth rows slightly convergent forward. Alisphenoid strut broad; stapedial foramen absent, and the correlated absence of the sphenofrontal foramen and alisphenoid vascular groove provides evidence of a derived pattern of carotid circulation to the rostrum. Tympanic bullae globular with short and wide Eustachian tubes; periotic almost completely occluded in ventral view.

Dentary robust and high, with the coronoid nearly vertical and projected above the condyloid process; both the coronoid and the condyloid processes are broad and robust; sigmoid notch broad and nearly oval. Capsular projection well expressed and placed just below the sigmoid notch. Upper and lower masseteric ridges in the mandible typically fused at the level of the posterior root of m1 extending forward as a unique ridge to the level of the mental foramen (Fig. 1).

Upper incisors ungrooved, slightly opisthodont, with a curved dentine lake (sensu Steppan 1995: figure 10) and a well-defined lateral bevel (sensu Voss and Carleton 1993: figure 12). Molar crowns planate, with principal cusps arranged in opposite pairs and with lingual and labial margins rounded (Fig. 3). M1 subrectangular in outline; procingulum anterior–posteriorly compressed and subelliptical in outline; protostyle and parastyle present as small cusps that emerge from the base of the crown; anteromedian flexus absent; hypoflexus well expressed; posteroloph indicated by a smooth indentation on the anterior face of the tooth; mesoloph and mesostyle fused in left M1, mesostyle free in right M1; median mure wide and oblique in orientation; M2 squared in outline; hypoflexus transverse, reaching the midline of the tooth; labial lophs transverse in orientation, with the metacone bulbous and the hypocone larger than protocone; mesoloph indistinct; M3 subtriangular, with its posterior lobe reduced by the absence of hypocone; mesoloph well developed and obliquely directed backward; central fossette of uncertain homology present; m1 with main cusps slightly arranged in alternate pairs; procingulum circular with an internal fossettid open to the anterior-labial side of the tooth; mesostylid present in 1 specimen (MHNSR 650); mesolophid reduced to an inflexion of the median mure; lophids rounded; protostylid and metaflexid on m2 distinct, defining a well-expressed anterolophid; hypoflexid obliquely oriented, penetrating beyond the midline of the teeth; proto- and hypoconid faces oblique; m3 sigmoid shaped, with a persistent protostylid.

Compared with other species of *Holochilus*, *H. lagigliai* embraces a particular set of characters partially shared with the species in both the *brasiliensis* and *sciureus* groups.

The PCA analysis (Fig. 4) showed a clear separation of *H. lagigliai* from *H. brasiliensis* (including specimens of *darwini* [$n = 4$] and *vulpinus* [$n = 23$]) and *H. chacarius* (including *balnearum* [$n = 1$] and *chacarius* [$n = 13$]). The first 3 principal components summarized 71.35% of the total variation (Table 2). PC I is a general size axis, and heaviest loadings on each axis are defined by breadth measurements (e.g., palatal breadth across M1s, width of M1, width of M2, and width of M3 on PC I or breadth of zygomatic plate on PC II; Fig. 4, Table 2). Proportionally, *H. lagigliai* has broader teeth, palate, and

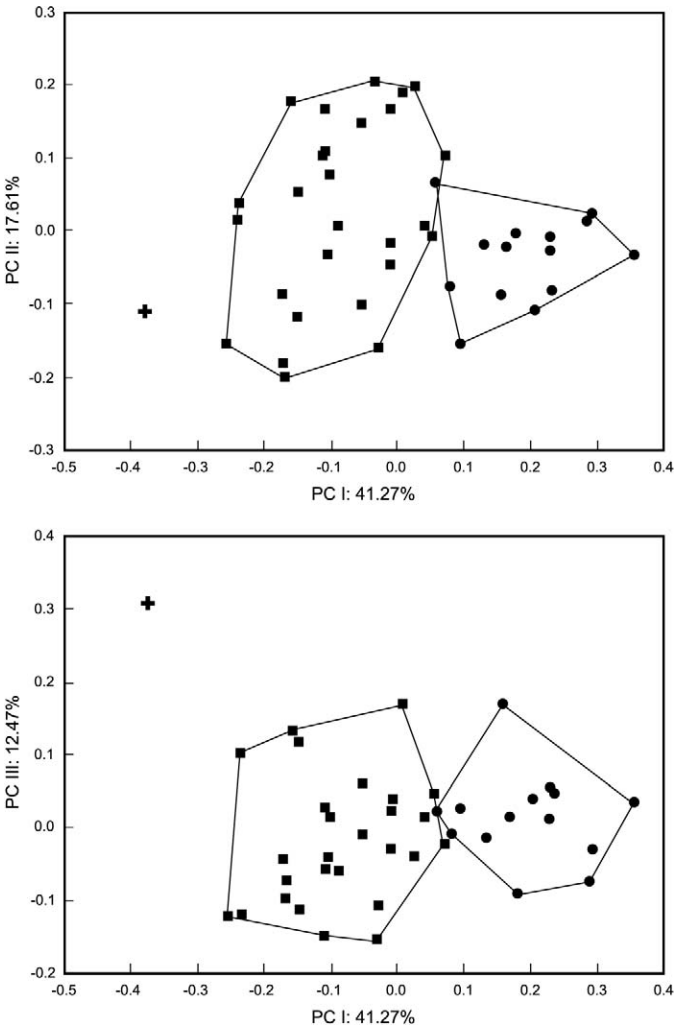

Fig. 4.—Specimen scores of adult individuals of *Holochilus* ($n = 42$) for principal components 1 and 2 (top) and 1 and 3 (bottom) extracted from the variance–covariance matrix of 15 craniodental distances (see text and Table 2). Symbols are: cross = *H. lagigliai*, sp. nov.; squares = *H. brasiliensis*; circles = *H. chacarius*.

Table 2.—Results of principal components analysis of 15 craniodental measurements of adult specimens of *Holochilus* ($n = 42$).

	PC I	PC II	PC III
Length of incisive foramen	−0.018725	−0.037220	−0.019491
Breadth of incisive foramen	−0.009789	−0.018957	−0.061244
Palatilar length	−0.032433	−0.027281	−0.005209
Breadth of zygomatic plate	−0.042915	−0.058351	0.035144
Length of maxillary toothrow	−0.035560	0.010535	−0.012651
Palatal breadth across M1s	−0.084137	0.001143	0.007094
Palatal bridge length	−0.026263	−0.021089	0.006256
Interorbital constriction	−0.005494	−0.004790	0.010813
Length of diastema	−0.039746	−0.039436	−0.003641
Length of M1	−0.025001	0.022847	0.002454
Length of M2	−0.026621	−0.000220	0.010589
Length of M3	−0.048841	0.014594	−0.046357
Width of M1	−0.060935	0.020459	0.006052
Width of M2	−0.056323	0.017267	0.004894
Width of M3	−0.052456	0.046724	0.012882
Eigenvalue	0.027340	0.011664	0.008266
% Variance	4.114.250	1.755.257	1.243.954

zygomatic plate. In addition, PCA also showed the morphometric distinction between the *sciureus* and *brasiliensis* groups, with no overlap between them.

The short tail of *H. lagigliai* is striking. Because it was measured in the dry specimen, we checked the length of tail of museum skins versus their original measurement taken when fresh for several specimens of *Holochilus*. In general terms we found the tail shortened by about 10% in dried versus fresh specimens. However, since museum skins had tails usually prepared in the standard way (i.e., filled by wire and cotton) and the tail of the holotype retained the vertebrae, we counted the number of caudal vertebrae present in the holotype and compared this number with vertebral counts for *Holochilus* spp. reported by Steppan (1995:43). The holotype of *H. lagigliai* had a count of 21 ± 1; those for *H. brasiliensis* varied between 25 and 35 and for *H. chacarius* ranged from 29 to 32. Although Steppan's (1995) "*brasiliensis*" is actually a mixture of *brasiliensis*, *chacarius*, and *sciureus*, *H. lagigliai* has a lower number of vertebrae in agreement with its shorter tail. According to Massoia (1976), adult *H. chacarius chacarius* has a tail length mean value of 167 mm, whereas *H. brasiliensis vulpinus* surpasses 224 mm. Tail is used in amphibious rats to change direction during swimming and as a point of rest against the bottom surface (Sierra de Soriano 1969). The length of the tail is probably correlated with general size and swimming capacities. Like the tail, the hind foot of *H. lagigliai*, from its dry skin, appears short, 41.7 mm in length without claws (45.8 mm with claws), a value that is intermediate between the average reported for *chacarius* (40 ± 2 mm, $n = 20$—Massoia 1976) and *brasiliensis* (51 ± 3 mm, $n = 20$—Massoia 1976). Clearly, these comparisons should be taken with caution due to the nature of the preserved evidence.

The posterior portion of the bony palate in *H. lagigliai* lacks osseous excrescences (sensu Musser et al. 1998:74), typically well developed in *H. brasiliensis*, being only a slightly bumpy close to the median suture. This condition is usually found in *H. sciureus*, although mature adult specimens of this species group display a medial bony mound, subtriangular in outline, which may also have lateral protuberances. The development and number of palatal pits in *H. lagigliai* are also more similar to the condition displayed by *H. sciureus* rather than that of *H. brasiliensis*. Particularly, the latter have large pits recessed into fossae located to the side of the anterior border of the mesopterygoid fossa, a trenchant difference with respect to the new species described here. In contrast, the posterior divergence of the zygomatic arch is more accentuated in *H. lagigliai* and *H. brasiliensis* than in *H. sciureus*; this condition modifies the geometry of the orbital space when viewed from above, with a subelliptical tendency in *H. sciureus* versus a compressed tear-drop morphology in *H. lagigliai* and *H. brasiliensis*.

The molar occlusal pattern in *H. lagigliai* is also striking among known members of the genus. Because of the variability displayed by large series of *Holochilus* (see Pardiñas and Galliari 1998; Petter and Tostain 1981) we suspected at first that the holotype of *H. lagigliai* was simply an abnormal individual. However, we discarded this hypothesis due to the concordance of lower dental morphology among the 4 available individuals (Fig. 3). Some dental traits of *H. lagigliai* resemble the pattern found in *H. sciureus*; for example the lingual emplacement of the anteromedian fossettid in the m1 versus its central location and larger size in *H. brasiliensis* (Pardiñas and Galliari 1998). Similarly, the persistence of a complex anterolophid in the m2 of *H. lagigliai* is more usually observed in *H. sciureus* than in *H. brasiliensis*. Furthermore, the more transverse disposition of the lophs and flexi, specially the hypoflexus of the M2, are also in line with the condition in *H. sciureus*. However, at least 2 molar features morphologically link *H. lagigliai* to *H. brasiliensis*. One of these is the presence of a mesolophostyle in the M1. This is a complex structure formed by the fusion of the anterior corner of the median mure, traditionally called "mesoloph" in *Holochilus* (Carleton and Olson 1999; Massoia 1971, 1976, 1981; Weksler 2006; but see the discussion in Pardiñas 2008) and the mesostyle. This condition is virtually absent in *H. sciureus* but widespread in *H. brasiliensis* (Massoia 1981). The 2nd feature is the rounded outer margins of the main molar cusps, versus the prismatic condition displayed by *H. sciureus* (Carleton and Olson 1999; Voss and Carleton 1993).

The discriminating value of other morphological features is difficult to evaluate, since some character states of *H. lagigliai* are typically found in *H. brasiliensis* (e.g., absence of hypothenar pad, degree of conjunction of the masseteric crests), although may also present in some populations of *H. chacarius* or *H. sciureus* (Voss and Carleton 1993).

Last, the fossil species "*Holochilus*" *primigenus* Steppan, 1996 can be easily separated from *H. lagigliai* by a list of anatomical features including more bunodont and less laminated teeth, reduced mesolophs in M1–M3, and oblique hypoflexus, among others. However, the M3 morphology in *H. primigenus* is partially convergent with those of *H. lagigliai* in the presence of an internal fossette and the hypoflexus reduction (Steppan 1996: figure 1G). The allocation of this fossil species from the Tarija basin, Bolivia, to *Holochilus* has been disputed by several authors (e.g., Carleton and Olson 1999; Pardiñas and Teta 2011).

In summary, *H. lagigliai* exhibits a mosaic of anatomical traits that correspond to the features seen in both *H. brasiliensis* and *H. sciureus* (Table 3). Available craniodental evidence is not sufficient to relate the new species to either of the groups of species of *Holochilus* with confidence.

Table 3.—Morphological comparisons using selected traits among species of *Holochilus*.

	H. lagigliai, sp. nov.	*H. brasiliensis* group	*H. sciureus* group
Number of caudal vertebrae	<23	>25	>25
Length of hind foot without claws (in mm)	<45	>47	<45
Palatal excrescences and posterolateral pits	Poorly developed	Well developed	Moderately developed
Mesolophs or mesolophostyles on M1–M2	Usually present	Usually present	Usually absent
Length of M3 to M2	M3 < M2	M3 > M2	M3 ≤ M2
Hypoflexus on M3	Absent	Present	Present
Molar design	Outer margins rounded	Outer margins rounded	Outer margins prismatic

Discussion

"As is true for so many South American mammals, the genus *Holochilus* requires critical revision" wrote Patton et al. (2000:93) after discussing the specific allocation of collected specimens in the western Amazon basin. This revision is still pending and despite minor contributions produced in the last 3 decades (e.g., Carleton and Olson 1999; Marques 1988; Voglino et al. 2004) the taxonomic scenario constructed by Massoia (1971, 1976, 1981) remains untouched. According to Massoia, 2 main morphological groups can be recognized in *Holochilus*: the *H. brasiliensis* species group, including the binomials *brasiliensis*, *leucogaster*, *vulpinus*, and *darwini*, all characterized by large general size, tail longer than combined head and body, length of hind foot without claws > 47 mm, absence of hypothenar pad, narrow interorbital constriction, well-developed palatal excrescences and posterolateral pits, rounded outer margins of lophs, mesolophs or mesolophostyles usually present on M1–M2, length of M3 clearly longer than M2, and postglenoid foramen not obliterated (Massoia 1976:62; see also Voss and Carleton 1993; Voglino et al. 2004); and the *H. sciureus* species group, including the binomials *sciureus*, *amazonicus*, *incarum*, *balnearum*, *nanus*, *guianae*, *berbicensis*, and *venezuelae*, and typified by small general size, tail equal to or shorter than combined head and body, length of hind foot without claws < 45 mm, minute hypothenar pad occasionally present, wide interorbital constriction, poorly developed palatal excrescences and inconspicuous posterolateral pits, outer margins of lophs with prismatic tendency, mesolophs or mesolophostyles absent on M1–M2, length of M3 equal to or smaller than M2, and postglenoid foramen usually obliterated (Massoia 1976:54; see also Voss and Carleton 1993; Voglino et al. 2004). As currently understood, the alpha taxonomy of *Holochilus* includes *H. brasiliensis*, *H. chacarius*, and *H. sciureus* as valid species, but which probably underestimates the real diversity in this widespread genus (Musser and Carleton 2005). Some authors recently ranked *H. vulpinus* as a full species (e.g., Bonvicino et al. 2008) without explanation.

Despite the poorly resolved systematics of *Holochilus*, neither the known morphological variation previously described for the genus nor the any of the available names apply

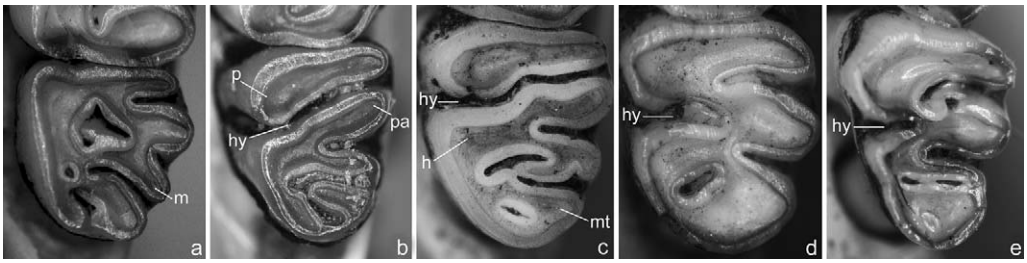

Fig. 5.—M3 occlusal morphology in several species of *Holochilus*. (a) *H. lagigliai*, sp. nov. (MHNSR 564, holotype); (b) *H. brasiliensis darwini* (CNP 1650); (c) *H. brasiliensis vulpinus* (CNP-E 68-1); (d) *H. chacarius balnearum* (CNP-E 657-1); (e) *H. chacarius chacarius* (CNP-E 656-1). Abbreviations are h, hypocone; hy, hypoflexus; m, mesoloph; mt, metacone; p, protocone; pa, paracone. No scale.

to the specimens now available from Mendoza Province. Indeed, it is difficult to allocate *H. lagigliai* to either of the 2 species groups of *Holochilus* currently recognized. As was discussed above, this new form combines a large craniodental size and mesolophostyle presence with a short tail and uncomplicated palate. And, in sharp contrast to the conservative morphology of the M3 among living, known *Holochilus*, *H. lagigliai* introduces a new pattern where both hypoflexus and hypocone are absent. Hershkovitz (1955:645) highlighted "the extremely variable nature of the upper third molar," a statement that was literally interpreted by Petter and Tostain (1981) and supported by at least 16 M3 occlusal figures in *H. sciureus* from Guiana. However, the assertion made by Hershkovitz (1955) must be interpreted in the context of his conception of the "Sigmodont rodents" (i.e., including *Sigmodon* and *Holochilus* plus *Lundomys*, *Reithrodon*, and *Neotomys*). These genera, now allocated to 4 separate tribes, display an important degree of M3 variation (Hershkovitz 1955: figure 143), although both hypoflexus and hypocone persist in each. In fact, hypoflexus loss is an unusual trait within the Oryzomyini (Weksler 2006) or even Sigmodontinae (Pacheco 2003). The remarkable morphology of the M3 in *H. lagigliai* is, in spite of everything, more congruent with that of the living *Holochilus* than the remaining oryzomyines (cf. Weksler 2006: figure 25). In fact, the tendency to lamination that characterizes the M3 of *Holochilus* is present, although masked by the loss of the hypoflexus and the hypocone, in the new form we describe herein from Mendoza (Fig. 5).

Holochilus lagigliai is biogeographically isolated in the northwestern corner of Patagonia, with nearest populations of living *Holochilus* located about 500 km to the east (*H. brasiliensis* in Buenos Aires Province) and 850 km to the north (*H. chacarius* in Tucumán province—Massoia 1976). During Late Holocene *H. brasiliensis* populations colonized important fluvial courses in northern Patagonia, including Colorado, Negro, and Limay rivers and reached the extreme southwest location at –40°S, –70°W (Fig. 2; Fernández et al. 2011; Pardiñas and Teta 2011). Importantly, at the same time period marsh rat populations were extensively recorded from the Pampa de Achala, a hilly plateau in western Córdoba Province (Teta et al. 2005). These *Holochilus* expansions were probably triggered by the warm and humid conditions of the Medieval Warm Period (Pardiñas and Teta 2011).

Marsh rats are closely associated with mesic microenvironments, such as grassy marshes, swampy savannas, and gallery forest along watercourses (Barlow 1969; Massoia 1976). In the context of episodes of expansion/contraction of *Holochilus* during the Holocene, a plausible hypothesis to explain its presence in Mendoza is the continuity of marsh rat populations along the Río Salado, a fluvial course that connects the Río Atuel with the Río Colorado (Fig. 2). The Salado dissects the arid lands in western La Pampa Province, where, until recently, dynamic flooding episodes generated extensive wetlands, the so-called "Bañados del Atuel." However, since the construction of dams (such as Nihuil) on major tributaries of the Desaguadero and Salado rivers, this fluvial basin has decreased its flow and is partially disconnected during most of the year (Spalletti and Isla 2003). An alternative route favoring the penetration of *Holochilus* into central Mendoza during glacial events might have been the saline chain present in the arid diagonal of Argentina from Santiago del Estero to Mendoza, including Ambargasta, Grandes, Pampa de las Salinas, Bebedero, and Telteca. An increase in the water surface of the salty lake Salinas del Bebedero and Río Desaguadero was recorded in association with the Last Glacial Maximum (about 24,000–18,000 years ago) and Little Ice Age (16th–19th centuries) events (González 1994; see also Cartwright et al. 2011). Additional amphibious mammals of subtropical affinities (such as the marsupial *Lutreolina crassicaudata*, and the caviomorph rodents *Hydrochoerus hydrochaeris* and *Myocastor coypus*) have patchy records in Mendoza Province (Roig 1991). Ecologically, it is interesting to note that *H. lagigliai* is a species of a genus found at least to elevations of 1,300 m asl. Neither *sciureus* nor *brasiliensis* surpass 1,100 m according to recent recorded localities. However, Late Holocene populations of *H. brasiliensis* in central Córdoba existed in an altitudinal gradient of about 1,000 to 1,800 m (Teta et al. 2005).

The new species of marsh rat reveals an unexpected diversity in west-central Argentina. In this region are currently recognized 36 rodent species including 5 major groups; 21 cricetid sigmodontines; 2 caviids; 3 ctenomyids; 7 octodontids; 1 myocastorid; and 2 chinchillids (Barquez et al. 2006, and references therein). During the last decades new rodents have

been described from this geographic area, such as the sigmodontines *Akodon oenos*, *Andalgalomys roigi*, *Salinomys delicatus* (Braun and Mares 1995; Braun et al. 2000; Mares and Braun 1996) and the octodontids *Pipanacoctomys aureus* and *Salinoctomys loschalchalerosorum* (Mares et al. 2000). Although some of these forms are now considered synonyms, all of these taxa represent mammals adapted to xeric environmental conditions. On the contrary, *H. lagigliai* is a novelty that enlarges the diversity of mammal fauna from the fluvial system normally characterized as poorly represented in southern South America.

Holochilus lagigliai was collected 57 years ago; the other 3 specimens referred to this form are from the Late Holocene. We do not know if this species still exists in the Atuel area although we have no evidence to believe that this is not true. The southern corner of Mendoza Province has been poorly prospected for mammals (Pardiñas et al. 2008), making any evaluation of the current status of this species difficult. It is clear that new collections are needed to obtain complementary evidences (e.g., karyotypes or DNA sequences), and also to evaluate adequately the conservation status of this apparently isolated, unique, and rare marsh rat.

Resumen

En base a un individuo adulto obtenido en 1955 y tres mandíbulas del Holoceno más tardúo se describe una nueva especie viviente de la rata anfibia Holochilus (Sigmodontinae, Oryzomyini) del centro-oeste de la provincia de Mendoza, Argentina. La nueva especie se caracteriza por su cola corta, placa zigomática ancha con el extremo anterodorsal redondeado, paladar œseo sin excrecencias, primeros molares superiores con mesolofostilos bien desarrollados y tercer molar superior complejo sin hipoflexo y más corto que el segundo molar superior. Los rasgos morfológicos que muestra esta nueva especie de Holochilus combinan características observadas en los grupos de especies de H. brasiliensis y H. sciureus como así también otras únicas en el contexto del género (e.g., ausencia de hipoflexo). Esta nueva especie es la expresión más austral del género en la porción occidental de su rango de distribución y parece estar aislada en el cauce medio del río Atuel. El hallazgo reportado aquí destaca una diversidad insospechada en las tierras áridas del sur de América del Sur.

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APPENDIX I

Specimens examined of *Holochilus* and *Lundomys* belonging to the following mammal collections: C, Colección Julio R. Contreras, Buenos Aires, Argentina; CEM, Colección Elio Massoia, Buenos Aires, Argentina; CNP, Colección de Mamíferos del Centro Nacional Patagónico, Chubut, Argentina; CNP-E, Colección de Material de Egagrópilas y Afines "Elio Massoia" del Centro Nacional Patagónico, Chubut, Argentina; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Buenos Aires, Argentina; MNRJ, Museu Nacional, Rio de Janeiro, Brazil. Sets of cranial remains recovered from owl pellets are indicated by a single collection number.

Holochilus brasiliensis vulpinus ($n = 626$): Argentina: Province of Buenos Aires, arroyo Méndez chico y Canal Arana (5 individuals,

CNP-E 7-4), Campana, Delta, Canal 6 (CEM 2572, CEM 3676, CEM 3684, CEM 3301, CEM 3306, CEM 2875, CEM 3298, CEM 3296, CEM 3305, CEM 3299, CEM 3683, CEM 3297, CEM 3685, CEM 1260, CEM 3307, CEM 1996, CEM 1220, MACN 18661, MACN 20334), Otamendi (MACN 19335, MACN 20388), Pilar, Zelaya (MACN 53–84, MACN 53–85, MACN 53–86), San Isidro (MACN 32-194). Province of Entre Ríos: Colonia Carmelo (21 individuals, CNP-E 6-4), Isla de las Lechiguanas (21 individuals, CNP-E 68-1), Parque Nacional El Palmar (MACN 18601), Villa Elisa (44 individuals, CNP-E 72-5). Province of Corrientes, Santo Tomé (509 individuals, CNP-E 650-3).

Holochilus brasiliensis darwini ($n = 35$): Argentina: Province of Buenos Aires, Arroyo El Pantanoso, Balcarce (CEM 3331, CEM 3332, CEM 3333), Arroyo Grande, Balcarce (CEM 3457, CEM 3458), Coronel Dorrego (CEM 3688, CEM 3687, CEM 3689, CEM 3690, CEM 3686, CEM 3691), General Lavalle (CEM 2705), González Catán (CEM 614, CEM 890, CEM 888, CEM 886, CEM 885, CEM 884, CEM 2732, CEM 3673, CEM 3672, CEM 3485, CEM 3484, CEM 3482), Luján (MACN 39–406), Mar del Tuyú (CEM 2714), Pergamino (MACN 18806), Reserva El Destino, Magdalena (5 individuals, CNP-E 1–5), río Quequén Salado (CNP 1650), Rojas (MACN 14405, MACN 16153).

Holochilus sciureus ($n = 8$): Brazil, State of Bahía (MNRJ 4205, MNRJ 4207, MNRJ 4208, MNRJ 4209, MNRJ 4166, MNRJ 4167). Bolivia, Department of Beni, río Mamoré (MACN 50.376, MACN 50.378).

Holochilus chacarius chacarius ($n = 140$): Argentina: Province of Chaco, Lote 16 (47 individuals, CNP-E 185-1); Province of Corrientes, El Sombrero (42 individuals, CNP-E 655-1); Province of Entre Ríos, Isla de las Lechiguanas (21 individuals, CNP-E 68-2), Paraná (8 individuals, CNP-E 69-2); Province of Formosa, Finca Yacaré (CEM 3398, CEM 3421, CEM 3422, CEM 3424, CEM 3425, CEM 3426, CEM 3559, CEM 3560, CEM 3564, CEM 3566, CEM 3567, CEM 3568). Paraguay: Department of Presidente Hayes, Asunción (10 individuals, CNP-E 656-1).

Holochilus chacarius balnearum ($n = 11$): Argentina: Province of Jujuy, San Salvador de Jujuy (MACN 33.24, MACN 33.169); Province of Salta, Escuela Agrotécnica Salta (6 individuals, CNP-E 657-1), Tabacal (MACN 33.24, MACN 17885). Bolivia: Santa Cruz, Uruma (MACN 13106).

Lundomys molitor ($n = 3$): Uruguay: Canelones, Tropa Vieja (C-2696, CEM 623, CEM 943).