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Fossil history of the marsh rats of the genus *Holochilus* and *Lundomys* (Cricetidae, Sigmodontinae) in southern South America

Historia fósil de las ratas palustres de los géneros Holochilus *y* Lundomys *(Cricetidae,* Sigmodontinae*) en el Cono Sur de América del Sur*

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ABSTRACT

The sister genera *Holochilus* and *Lundomys*, plus the extinct forms *Carletonomys* and *Noronhomys* and the living *Pseudoryzomys*, constitute a small clade of amphibious sigmodontine rodents that inhabits in tropical and subtropical environments of the Neotropics. Based on almost all the available fossil evidence recovered in Argentina, Bolivia, southeastern Brazil, and Uruguay we revised the paleontological record of *Holochilus* and *Lundomys* in southern South America. Past distributions and chronologies indicate the following occurrences [biochrons] for the study area: *Holochilus brasiliensis* (Middle Pleistocene-Recent in Argentina, Late Pleistocene-Recent in Brazil), *H. chacarius* (Late Holocene-Recent in Argentina, Early Holocene-Recent in Bolivia), †*H. primigenius* (Middle Pleistocene in Bolivia), and *Lundomys molitor* (Middle Pleistocene-Late Pleistocene in Argentina, Late Pleistocene-Recent in Uruguay). Taking into account the present distributions and environmental requirements of these rodents we hypothesize several expansion/retraction episodes of their populations triggered by the occurrence of moist/dry climatic pulses during Pleistocene-Holocene times.

Keywords: Argentina, Bolivia, Brazil, *Holochilus*, *Lundomys*, Holocene, Pleistocene, Uruguay.

RESUMEN

Los géneros hermanos *Holochilus* y *Lundomys*, junto con las formas extintas *Carletonomys* y *Noronhomys* y la viviente *Pseudoryzomys*, constituyen un pequeño clado de sigmodontinos de hábitos anfibios, que habitan en ambientes tropicales y subtropicales del Neotrópico. Basándonos en la totalidad de la evidencia fósil disponible para Argentina, Bolivia, sudeste de Brasil y Uruguay se revisó el registro paleontológico de *Holochilus* y *Lundomys* de la porción austral de América del Sur. Las distribuciones en el pasado y sus cronologías indican las siguientes ocurrencias para el área de estudio: *Holochilus brasiliensis* (Pleistoceno Medio-Reciente en Argentina, Pleistoceno Tardío-Reciente en Brasil), *H. chacarius* (Holoceno Tardío-Reciente en Argentina, Holoceno Temprano-Reciente en Bolivia), †*H. primigenius* (Pleistoceno Medio en Bolivia) y *Lundomys molitor* (Pleistoceno Medio-Pleistoceno Tardío en Argentina, Pleistoceno Tardío-Reciente en Uruguay). Considerando en conjunto las distribuciones actuales, los requerimientos ambientales de estos taxones y los registros fósiles, se verifican varios episodios de expansión y retracción de sus poblaciones, posiblemente vinculados con pulsos climáticos húmedos y secos alternantes durante el Pleistoceno-Holoceno.

Palabras clave: Argentina, Bolivia, Brazil, *Holochilus*, *Lundomys*, Holoceno, Pleistoceno, Uruguay.

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Introduction

Marsh rats of the genus *Holochilus* Brandt, 1835 and *Lundomys* Voss & Carleton, 1993, are large oryzomyine rodents, semiaquatic in habit, and principally herbivorous in diet (Massoia, 1971, 1976). According to Carleton & Olson (1999), both genera, together with †*Noronhomys* and the extant *Pseudoryzomys* compose a small clade of tetralophodont sigmodontines that may have originated in riverine and palustrine habitats found within savanna enclaves of southern South America. Weksler (2006), based on morphological and molecular data, suggests that within the Oryzomyini radiation, *Holochilus* is the sister group of *Lundomys*, and that both genera are closely related to *Pseudoryzomys*. More recently, Pardiñas (2008) added to this group a new extinct large form from Argentinean Pleistocene, *Carletonomys*.

Both *Holochilus* and *Lundomys* have a rich fossil record in South America, especially in the Southern Cone, ranging from Middle Pleistocene to Recent (Pardiñas *et al*., 2002). Teeth, mandibles, and cranial remains of *Holochilus* and *Lundomys* are easily distinguishable from those of other sigmodontine genera. A proof of this is the almost complete absence of synonyms -at least at generic level- from the paleontological record, in clear contrast to many other large sigmodontines, such as *Reithrodon* or *Graomys* (Massoia & Pardiñas, 1993; Pardiñas, 1995, 2000). The oldest references of marsh rats in the paleontological literature (as *Holochius vulpinus*, *Sigmodon vulpinus*, *Holochilus multannus*, or *Hesperomys molitor*) were made by Herluf Winge (1887) and Florentino Ameghino (1889) in their classical works "Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Gerais, Brasilien" and "Contribución al Conocimiento de los Mamíferos Fósiles de la República Argentina," respectively. Since then, numerous fossil remains have been collected in Argentinean, Bolivian, Brazilian, Uruguayan, and Venezuelan deposits (e. g., Mones & Castiglioni, 1979; Oliveira, 1992; Steppan, 1996; Ubilla, 1996; Pardiñas, 1999a, 1999b; Pardiñas *et al*., 2002; Teta *et al*., 2004, 2005b; Rincón, 2005; Ubilla *et al*., 2004; Teta & Pardiñas, 2006). Steppan (1996) described the only known extinct species of the genus, †*H. primigenius*, from Tarija Basin, Bolivia, and discussed its generic affinities based on morphological evidences.

In this paper we review the fossil record of the living species of *Holochilus* and *Lundomys* in southern South America (Argentina, Bolivia, southern Brazil, and Uruguay). In addition, we offer an interpretation about the paleoenvironmental and paleoecological significance of these findings and their correlation with the major climatic events during Quaternary times. We put our emphasis in middle latitudes of Argentina and Uruguay because this area has a rich fossil record, represents the southern distributional limit of both genera, and its biota was largely affected by Pleistocene-Holocene climatic changes (Pardiñas, 1999).

Materials and Methods

We studied almost all fossil specimens of *Holochilus* and *Lundomys* housed in Argentinean and Uruguayan collections (Appendix 1). In addition, a complete search of the paleontological and archaeological literature was made and critically assessed through the direct examination of voucher materials when available. Regular series of recent *Holochilus brasiliensis* (Desmarest, 1819), *H. chacarius* Thomas, 1906, *H. sciureus* Wagner, 1842, and *Lundomys molitor* (Winge, 1887) individuals were used for comparative purposes (Appendix 2). Taxonomic criteria used in this paper follow Musser & Carleton (2005) and the synonym lists provided are those exclusively from paleontological literature. Tooth crown surface terminology follows Reig (1977). The chronostratigraphy follows Cione & Tonni (1999). The maximum length and width of molars were measured (in mm) using manual calipers and a micrometer eyepiece included in a binocular microscope. Abbreviations used in the text, tables, and figures are: † = extinct; AD = Anno Domini; kyr = kilo years ago (* 1,000 years ago); M1, M2, M3, m1, m2, m3 = first, second, and third upper and lower molars, respectively; myr = millions of years ago; ry BP = radiocarbon years before present. Geographic locations of collecting localities are presented in the Fig. 1 and Table 1.

Taxonomy and fossil record

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer, 1817
Subfamily Sigmodontinae Thomas, 1897
Tribe Oryzomyini Vorontsov, 1959
Genus *Holochilus* Brandt, 1835
Holochilus brasiliensis (Desmarest, 1819)
(Figs. 1a, 2, and 3, Tables 1, 2 and 3)

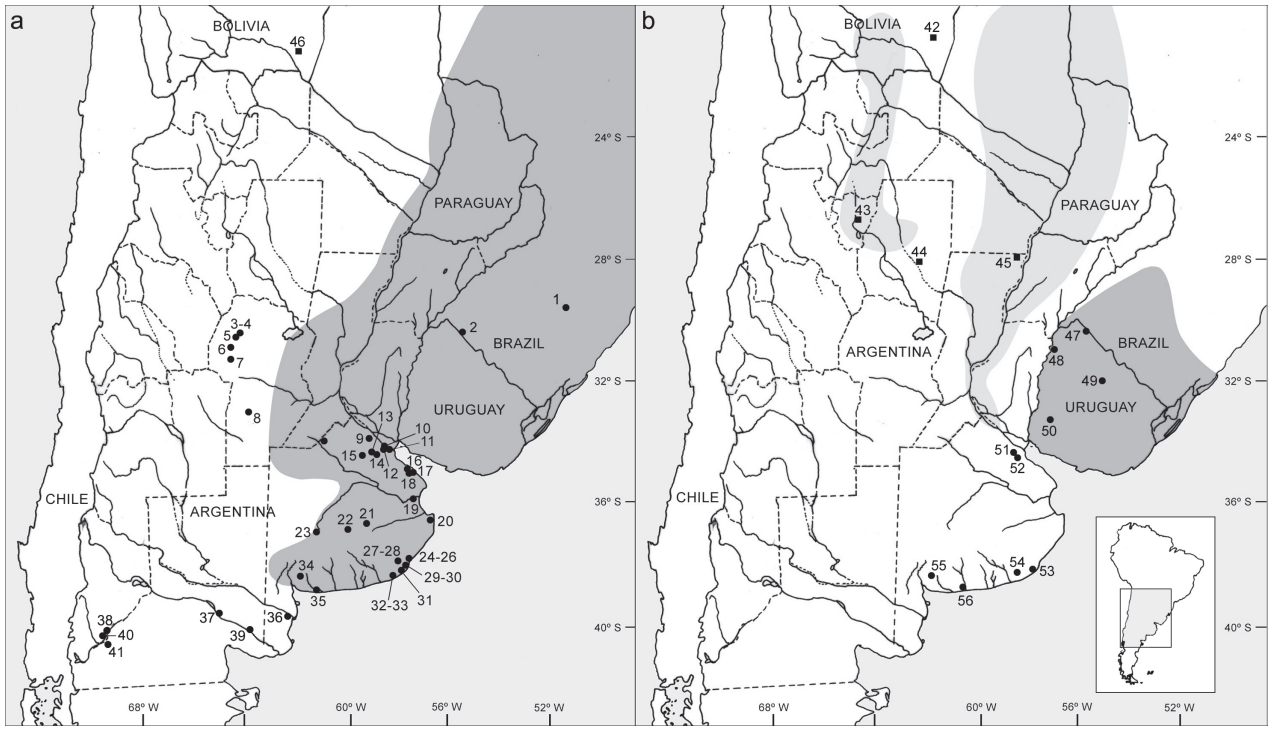

Fig. 1.—Recent distributional ranges (compiled from several sources; e.g., Massoia, 1971; Pardiñas, 1999; Teta *et al*., 2010) for *Holochilus brasiliensis* (dark gray; a), *H. chacarius* (light gray; b), and *Lundomys molitor* (dark gray; b), and fossil recording localities (in a, circles for *H. brasiliensis* and square for *H. primigenius*; in b, squares for *H. chacarius* and circles for *L. molitor*). For the reference numbers, see Table 1.

Holochilus vulpinus (sensu Ameghino, 1889:116)
Holochilus multannus Ameghino, 1889:117
Holochilus braziliensis (Ameghino, in schedis)
Sigmodon multannus (Ameghino, in schedis)

Recent distribution: From central-eastern Argentina throughout eastern Paraguay and Uruguay to the southeastern states of Brazil, including parts of the states of Minas Gerais and Bahia (Hershkovitz, 1955; Massoia, 1976, 1981; Marques, 1988; Fig. 1a).

Fossil record: Middle Pleistocene-Recent in central-eastern Argentina; Late Pleistocene-Recent in Brazil (Figs. 1a, and 3, Tables 1 and 2).

Taxonomy: We provisionally accept the arguments of Massoia (1976, 1981) and restrict the specific epithet *brasiliensis* [including *H. darwini* Thomas, 1897 and *H. vulpinus* (Brandt, 1827)] to the populations of large individuals (upper tooth molar-row length usually > 8 mm) with vestigial mesoloph-like structures on M1 and M2 (Fig. 2). Detailed descriptions are provided by Massoia (1976) and Pardiñas & Galliari (1998). Diagnostic characters for lower molars, the most common kind of remain in fossil assemblages, are summarized in Table 3.

Remarks: Although both *Holochilus* sp. and *H. brasiliensis* were mentioned for Uruguayan Late Pleistocene deposits (see Mones & Castiglioni, 1979; Ubilla, 1985), all the available materials is referred to *Lundomys* (see below). Passing mentions in archaeological Brazilian literature (e. g., Brentano *et al*., 2006; Rosa, 2006) indicate putative occurrences of *Holochilus* sp. in several Holocene sites of the State of Rio Grande do Sul; however, these records were not included in the present paper (Table 1) due to the impossibility to check voucher specimens. Musser & Carleton (2005:1120) incorrectly included *H. multannus* under the synonymy of *H. sciureus* (see Massoia & Pardiñas, 1993 for its attribution to *H. brasiliensis*).

Holochilus chacarius Thomas, 1906 (Figs. 1b, 2 and 3, Tables 1, 2 and 3)

Holochilus brasiliensis (sensu Hoffstetter, 1968:833; Marshall & Sempere, 1991:643)

Recent distribution: Northwestern and northeastern Argentina and central Paraguay (Massoia, 1976; Musser & Carleton, 2005; Fig. 1b). Populations from the lowlands of Bolivia were referred by Anderson (1997) to *H. sciureus* Wagner, 1842. However, two specimens from Santa Cruz Department found in the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" are undistinguishable of *H. chacarius* (see Appendix 2). Distributional limits between *H. chacarius* and *H. sciureus* are unclear and perhaps both species are sympatric in some areas of eastern Bolivia. Voglino *et al*. (2005) recently recorded *H. chacarius* in northeastern Buenos Aires province (Argentina), the southernmost point presently reached by the species.

Tabla 1.—Fossil collecting localities for *Holochilus* and *Lundomys* in southern South American (arranged by taxon and increasing latitude)

#	Taxon	Collecting locality	Age	Radiocarbon date (ry BP, except indication)	Main references
1	*H. brasiliensis*	Afonso Garivaldino Rodrigues (=RS-TQ-58) archaeological site (29º 34' N, 51º 38' W, Rio Grande do Sul, Brazil)	Early to Middle Holocene	9,439 ± 360 – 7,520 ± 350	de Queiroz (2004)
2	*H. brasiliensis*	Rio Quaraí (30º 06' S, 56º 48' W, Urugaiana, Rio Grande do Sul, Brazil)	Late Pleistocene	—	Oliveira (1992)
3	*H. brasiliensis*	C. Pun 39 archaeological site (31º 03' S, 64º 31' W, Córdoba, Argentina)	Late Holocene	716 ± 39 - 854 ± 39	Teta *et al*. (2005a)
4	*H. brasiliensis*	Las Chacras 2 archaeological site (31º 03' S, 64º 31' W, Córdoba, Argentina)	Late Holocene	—	Teta *et al*. (2005a)
5	*H. brasiliensis*	Puesto La Esquina 1 archaeological site (31º 09' S, 64º 37' W, Córdoba, Argentina)	Late Holocene	362 ± 43 - 365 ± 38	Teta *et al*. (2005a)
6	*H. brasiliensis*	Río Yuspe 1 archaeological site (31º 22' S, 64º 48' W, Córdoba, Argentina)	Late Holocene	1,170 ± 50	Teta *et al*. (2005a)
7	*H. brasiliensis*	Arroyo El Gaucho 1 archaeological site (31° 40' S, 64° 45' W, Córdoba, Argentina)	Late Holocene	3,595 ± 60	Teta *et al*. (2005a)
8	*H. brasiliensis*	Arroyo Santa Catalina, near San José (33º 06' S, 64º 28' W, Córdoba, Argentina)	Holocene lato sensu	—	Massoia *et al*. (1987)
9	*H. brasiliensis*	Río Areco near its mouth (33º 56' S, 59º 16' W, Buenos Aires, Argentina)	Late Holocene	—	López and Reboledo (1998)
10	*H. brasiliensis*	Las Vizcacheras archaeological site (34° 16' S, 58° 48' W, Buenos Aires, Argentina)	Late Holocene	1,090 ± 40 – 1,070 ± 60	Pardiñas (1999a), Teta *et al*. (2004)
11	*H. brasiliensis*	Laguna Grande archaeological site (34º 19' S, 58º 52' W, Buenos Aires, Argentina)	Late Holocene	—	Pardiñas (1999a), Teta *et al*. (2004)
12	*H. brasiliensis*	La Bellaca archaeological site 2 (34º 22' S, 58º 40' W, Buenos Aires, Argentina)	Late Holocene	680 ± 80	Pardiñas (1999a), Teta *et al*. (2004)
13	*H. brasiliensis*	Olivera (34º 37' S, 59º 15' W, Buenos Aires, Argentina)	Late Pleistocene	—	Ameghino (1889; holotype of *H. multannus*)
14	*H. brasiliensis*	Río de la Reconquista (34º 41' S, 58º 49' W, Buenos Aires, Argentina)	Early Holocene?	—	This paper
15	*H. brasiliensis*	Estación Manuel J. García (34º 42' S, 59º 32' W, Buenos Aires, Argentina)	Early Holocene	—	Pardiñas (1999a)
16	*H. brasiliensis*	La Higuera archaeological site (34º 53' S, 57º 48' W, Buenos Aires, Argentina)	Late Holocene	530 ± 50	Pardiñas (1999a)
17	*H. brasiliensis*	Streets 43 and 122, Ensenada (34º 54' S, 57º 55' W, Buenos Aires, Argentina)	Middle Holocene	4,730 ± 219	Tonni and Cione (1984), Pardiñas (1999a)
18	*H. brasiliensis*	La Norma archaeological site (34º 55' S, 57º 46' W, Buenos Aires, Argentina)	Late Holocene	—	Pardiñas (1999a)
19	*H. brasiliensis*	La Guillerma 5 archaeological site (35º 50' S, 57º 38' W, Buenos Aires, Argentina)	Late Holocene	—	This paper

Tabla 1 *(continuación)*.—Fossil collecting localities for *Holochilus* and *Lundomys* in southern South American (arranged by taxon and increasing latitude)

#	Taxon	Collecting locality	Age	Radiocarbon date (ry BP, except indication)	Main references
20	*H. brasiliensis*	Divisadero Monte 6 archaeological site (36º 23' S, 56º 56' W, Buenos Aires, Argentina)	Late Holocene	540 ± 60	Aldazabal *et al*. (2006)
21	*H. brasiliensis*	Azul (36º 46' S, 59º 41' W, Buenos Aires, Argentina)	Pleistocene lato sensu	—	This paper
22	*H. brasiliensis*	La Moderna archaeological site (37º 07' S, 60º 05' W, Buenos Aires, Argentina)	Early to Middle Holocene	Several from 7,510 ± 370 to 6,555 ± 160	Politis and Gutiérrez (1998), this paper
23	*H. brasiliensis*	Fortín Necochea archaeological site (37º 23' S, 61º 08' W, Buenos Aires, Argentina)	Middle to Late Holocene	6,010 ± 400 – 3,630 ± 60	Pardiñas (1991, 1999a)
24	*H. brasiliensis*	Camet Norte (37º 49' S, 57º 29' W, Buenos Aires, Argentina)	Late Pleistocene	24,550 ± 600	Pardiñas *et al*. (1998)
25	*H. brasiliensis*	Camet Norte (37º 49' S, 57º 29' W, Buenos Aires, Argentina)	Holocene lato sensu	—	This paper
26	*H. brasiliensis*	Complejo Ferroviario (37º 50' S, 57º 30' W, Buenos Aires, Argentina)	Middle Pleistocene	—	Pardiñas (2004)
27	*H. brasiliensis*	Cueva Tixi archaeological site (37° 57' S, 58° 02' W, Buenos Aires, Argentina)	Holocene	Several from 10,375 ± 90 to 170 ± 60	Pardiñas (1995, 1999a), Quintana (2001)
28	*H. brasiliensis*	Cueva El Abra archaeological site (37° 59' S, 58° 05' W, Buenos Aires, Argentina)	Late Holocene	958 ± 32	Quintana *et al*. (2002)
29	*H. brasiliensis*	Constitución (37º 59' S, 57º 33' W, Buenos Aires, Argentina)	Late Pleistocene	—	Pardiñas *et al* (2004b), this paper
30	*H. brasiliensis*	Playa La Serena (= Balneario Menta; 38° 06' S, 57° 34' W, Buenos Aires, Argentina)	Late Holocene	420 ± 90 – 1,125 ± 55	Pardiñas (1999a)
31	*H. brasiliensis*	Miramar (specific locality unknow, Buenos Aires, Argentina)	Late Holocene	1,870 ± 50	Tonni *et al*. (2002)
32	*H. brasiliensis*	Centinela del Mar (38° 21' S, 58° 00' W, Buenos Aires, Argentina)	Late Holocene	565 ± 50 - 250 ± 65	Pardiñas (1999a)
33	*H. brasiliensis*	Centinela del Mar (38° 21' S, 58° 00' W, Buenos Aires, Argentina)	Late Pleistocene	—	This paper
34	*H. brasiliensis*	Napostá Grande (38º 21' S, 62º 20' W, Buenos Aires, Argentina)	Late Holocene	1,960 ± 100 - 1,070 ± 60	Deschamps and Tonni (1992)
35	*H. brasiliensis*	Camping Americano (38º 59' S, 61º 21' W, Buenos Aires, Argentina)	Early Holocene	8,990 ± 55	Pardiñas (1999a, 2001)
36	*H. brasiliensis*	El Tigre archaeological site (39º 46' 49'' S, 62º 22' 32'' W, Buenos Aires, Argentina)	Late Holocene	ca. 500 – 1,000 AP	Stoessel *et al*. (2008)
37	*H. brasiliensis*	Negro Muerto archaeological site (39º 50' S, 65º 17' W, Río Negro, Argentina)	Late Holocene	483 ± 46 – 398 ± 43	Prates (2007)
38	*H. brasiliensis*	Alero Arias archaeological site (40º 02' S, 70º 00' W, Neuquén, Argentina)	Late Holocene	3,230 ± 60	Pardiñas (1999a), Teta *et al*. (2005b)

Tabla 1 *(continuación)*.—Fossil collecting localities for *Holochilus* and *Lundomys* in southern South American (arranged by taxon and increasing latitude)

#	Taxon	Collecting locality	Age	Radiocarbon date (ry BP, except indication)	Main references
39	*H. brasiliensis*	Angostura 1 archaeological site (40º 10' S, 64º 11' W, Río Negro, Argentina)	Late Holocene	938 ± 45	Prates (2007)
40	*H. brasiliensis*	Rincón Chico 2 archaeological site (40º 11' S, 70º 01' W, Neuquén, Argentina)	Late Holocene	710 ± 60 - 680 ± 65	Fernández and Crivelli Montero (2004), M. Silveira (pers. comm.)
41	*H. brasiliensis*	La Marcelina 1 archaeological site (40º 38' 24'' S, 70º 32' 53'' W, Río Negro, Argentina)	Late Holocene	<1,770	This work
42	*H. chacarius*	Quebrada de Ñuapua (20º 52' S, 63º 04' W, Tarija, Bolivia)	Early to Middle Holocene	7,200 ± 400 – 6,000 ± 370	Hoffstetter (1968), Pardiñas and Galliari (1998)
43	*H. chacarius*	Ruinas Jesuíticas de San José de Lules (Tucumán, Argentina)	Late Holocene	1650-1900 AD	Ortíz (2000)
44	*H. chacarius*	Lomas del Veinte archaeological site (ca. 28º 00' S, 63º 03' W, Santiago del Estero, Argentina)	Late Holocene	1000-1200 AD	Cione and Tonni (1981), this paper
45	*H. chacarius*	Cerro Aguará archaeological site (28º 00' S, 59º 05' W; Santa Fe, Argentina)	Late Holocene	—	Santiago (2004)
46	*H. primigenius*	Tarija and río Churumoya, Tarija Basin (Tarija, Bolivia)	Middle Pleistocene?	—	Steppan (1998)
47	*L. molitor*	Río Cuareim (30º 26' S, 56º 27' W, Artigas, Uruguay)	Late Pleistocene	—	Ubilla *et al*. (1994, 2004), this paper
48	*L. molitor*	Arroyo Sopas (31º 15' S, 57º 00' W, Salto, Uruguay)	Late Pleistocene	43,500 +/- 3,600 [TL/OSL age]	Ubilla *et al*. (1994, 2004)
49	*L. molitor*	Arroyo Malo (32º 03' S, 56º 07' W, Tacuarembó, Uruguay)	Late Pleistocene	58,300 +/- 7,400 [TL/OSL age]	Ubilla *et al*. (1994, 2004), this paper
50	*L. molitor*	Arroyo Perico Flaco near its mouth (ca. 33º 10' S, 57º 10' W, Soriano, Uruguay)	Late? Pleistocene	—	Mones and Castiglioni (1979), this paper
51	*L. molitor*	Pilar (34º 27' S, 58º 58' W, Buenos Aires, Argentina)	Middle Pleistocene	—	Teta and Pardiñas (2006)
52	*L. molitor*	Río de la Reconquista (34º 41' S, 58º 49' W, Buenos Aires, Argentina)	Middle Pleistocene	—	Pardiñas and Lezcano (1995)
53	*L. molitor*	Centinela del Mar (38º 26' S, 58º 13' W, Buenos Aires, Argentina)	Late Pleistocene	—	Bond and Massoia (1981)
54	*L. molitor*	Paso Otero (38º 34' S, 58º 42' W, Buenos Aires, Argentina)	Late Pleistocene	—	Pardiñas and Lezcano (1995)
55	*L. molitor*	Bajo San José (38º 34' S, 61º 41' W, Buenos Aires, Argentina)	Middle Pleistocene	—	Pardiñas and Deschamps (1996), Deschamps (2005)
56	*L. molitor*	Cueva del Tigre (38º 49' S, 60º 32' W, Buenos Aires, Argentina)	Late Pleistocene	—	Teta and Pardiñas (2006)

Fossil record: Late Holocene-Recent in northern Argentina, Early Holocene-Recent in southern Bolivia (Figs. 1b and 3, Tables 1 and 2).

Taxonomy: *H. chacarius* belongs to a morphologically cohesive assemblage of small forms of *Holochilus* (upper tooth molar-row length usually < 8 mm) without mesoloph-like structures on M1-M2 and with prismatic lophs/ids, usually included under the concept of *H. sciureus* (Massoia, 1976; Voss & Carleton, 1993; Carleton & Olson, 1999). Massoia (1976) reviewed the taxonomic status of the Argentinean population of *Holochilus* and considered *H. balnearum* Thomas, 1906 as subspecies of *H. chacarius* Thomas, 1906. Descriptions provided are by Massoia (1976) and Pardiñas & Galliari (1998). Diagnostic characters of lower molars are summarised in Table 3.

Remarks: Hoffstetter (1968) indicated that fossil remains of *H. chacarius* (cited as *H. brasiliensis*) characterized the Ñuapua 2 member in Quebrada de Ñuapua (Bolivia; see also Pardiñas & Galliari, 1998).

†*Holochilus primigenius* Steppan, 1996 (Figs. 1a, Table 1)

Holochilus primigenius Steppan, 1996: 524

Fossil record: Middle Pleistocene in Southern Bolivia (Steppan, 1996; Table 1).

Taxonomy: Steppan (1996) described *Holochilus primigenius* from the Middle Pleistocene of Bolivia. The molar morphology of this species is almost identical to those of *Lundomys molitor* except in size. However, Steppan (1996) provisionally included *primigenius* in the genus *Holochilus*, taken into account the following characters, which allowed him to distinguish it from *Lundomys*: mandible robust with steeply-angled coronoid process, incisive foramen not extending beyond the margin of the anterior alveolus of M1, and mesopterygoid fossa extending nearly to the posterior alveolus of M3. We partially disagree with this view, because some of these characters are not exclusive of *Holochilus*. First, the incisive foramina of *Lundomys* are extended posterior to or between the molar alveoli (in relation to the anterior surface of the molar alveoli) while in *Holochilus* are clearly shorter (Voss & Carleton, 1993). In *H. primigenius*, the incisive foramina "just reaching the anterior alveolus in the two specimens with intact anterior palates" (Steppan, 1996: 524), is not much different of the condition seen in *L. molitor*. Second, the position of the anterior border of the mesopterygoid fossa has some individual and age-related variation within populations of *Holochilus*, projecting conspicuously between M3s in some individuals, or extending even with or beyond the end of M3 in others (see Voss & Carleton, 1993). In fact, Steppan (1996) himself and Carleton & Olson (1999) recognized that the inclusion of the species *primigenus* within *Holochilus* is at least questionable. The remarkable similarity between the molars of *H. primigenus* and *L. molitor* gives support to the hypothesis that the former is an extinct species of *Lundomys* or, alternatively, a new extinct genus within this small clade of tetralophodont oryzomyines (Pardiñas, 2009).

Remarks: Hoffstetter (1963:197) earlier mentioned *Holochilus* (surely, *H. primigenus* Steppan, 1996) for the Tarija Basin fossil assemblage; however this taxon was omitted in subsequent contributions on this paleofauna (see Hoffstetter, 1986; Marshall & Sempere, 1991). Paleomagnetic analysis of

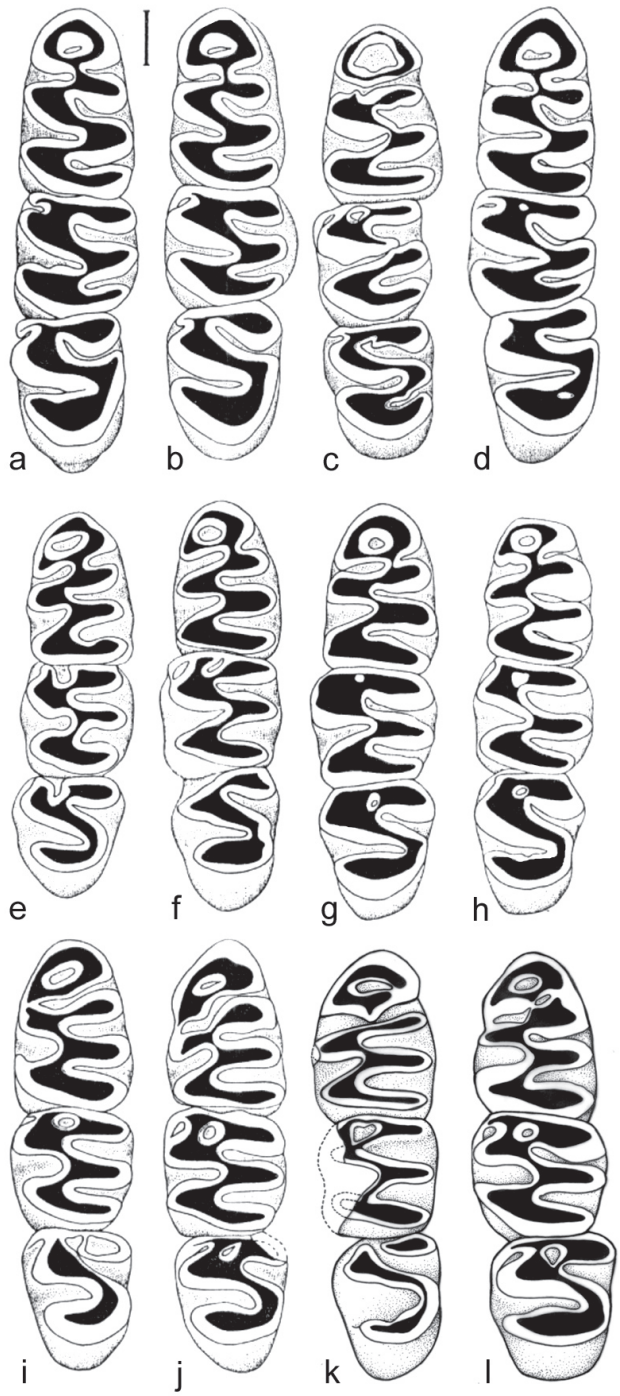

Fig. 2.—Left lower molars in occlusal view of: *Holochilus brasiliensis* (a, b, c, and d [CEM 3672, 888, 3683, and CAF 1042]), *H. chacarius* (e, f, g, and h [CEM s/n, s/n, 3424, and 3421]), and *H. sciureus* (i, j, k, and l [MNRJ 4209, 4207, 4167, and 4205]. Scale = 1 mm.

Tabla 2.—Lower and upper molar measurements of some *Holochilus* and *Lundomys* specimens from Quaternary deposits in Argentina and Uruguay

		m1		m2		m3		m1-m3
Specimen	Locality	length	width	length	width	length	width	length
H. brasiliensis								
AEG1 C2C10	Alero El Gaucho	3.30	2.30	2.50	2.50	—	—	—
AEG1 C2C6	Alero El Gaucho	3.80	2.40	2.50	2.60	2.90	2.30	8.90
C.Pun.39 C3C3	C.Pun.39	3.40	2.10	2.20	2.30	2.60	2.00	8.30
C.Pun.39 D1C1b	C.Pun.39	—	—	2.20	2.30	—	—	—
C.Pun.39 D1C1d	C.Pun.39	—	—	—	—	2.50	2.10	—
C.Pun.39 D3C2	C.Pun.39	3.50	2.20	2.30	2.30	2.50	2.00	8.50
C.Pun.39 D3C3a	C.Pun.39	3.50	2.10	2.50	2.30	—	—	—
MSC-C-13	Camet Norte	3.20	2.24	2.28	2.24	2.64	2.20	8.40
MLP 95-V-6-1	Camping Americano	3.40	2.16	—	—	—	—	—
MLP 84-X-20-40	Cueva Tixi	3.08	2.04	—	2.28	—	—	—
MLP 84-X-20-41	Cueva Tixi	3.04	2.08	2.40	2.20	—	—	—
MLP 84-X-20-51	Cueva Tixi	3.12	2.08	2.08	2.20	2.72	2.00	—
MLP 95-V-13-1	Fortín Necochea	3.28	2.12	2.16	2.20	—	—	—
MLP 95-V-13-3	Fortín Necochea	3.60	2.24	—	—	—	—	—
MLP s/n	Fortín Necochea	—	2.24	2.40	2.48	2.64	2.32	—
LBII 60-65a/c b	La Bellaca 2	3.30	2.10	2.30	2.10	2.40	2.00	8.20
LBII C1 15-20a	La Bellaca 2	3.50	2.20	2.50	2.20	2.20	2.10	8.70
LBII C1 15-20b	La Bellaca 2	3.30	2.10	2.20	2.20	2.70	2.10	8.50
LBII C1 20-25b	La Bellaca 2	3.20	2.10	2.10	2.20	2.60	2.10	8.50
LBII C1 25-30a	La Bellaca 2	3.30	2.00	2.10	2.20	—	—	—
LBII C1 25-30b	La Bellaca 2	3.40	2.10	2.10	2.10	2.40	2.00	8.40
LBII C1 25-30c	La Bellaca 2	3.20	2.10	2.20	2.10	2.10	2.00	8.10
LBII C2	La Bellaca 2	3.30	2.10	2.20	2.20	2.70	2.00	8.50
LBII C2 13-20	La Bellaca 2	3.40	2.10	2.20	2.20	—	—	—
LBII C4 0-10	La Bellaca 2	3.40	2.00	—	—	—	—	—
LBII C4 10-15	La Bellaca 2	—	—	2.60	2.30	—	—	—
LBII C4 15-20c	La Bellaca 2	3.10	2.00	2.20	2.10	—	—	—
LBII C4 15-20d	La Bellaca 2	3.00	2.10	2.00	2.20	—	—	—
LBII C4 25-30	La Bellaca 2	—	—	2.20	2.20	2.40	1.90	—
LBII C4 30-35a	La Bellaca 2	3.50	2.10	2.10	2.20	2.20	1.90	8.40
LBII C4 30-35b	La Bellaca 2	—	—	2.30	2.10	1.90	2.00	—
LBII T2/4 15-20	La Bellaca 2	—	—	—	—	2.50	2.00	—
LBII T2/4 25-30	La Bellaca 2	3.20	2.10	2.10	2.20	2.60	1.90	8.50
LBII T2/4 30-35	La Bellaca 2	3.30	2.00	2.20	2.20	—	—	—
LG5-CIXb	La Guillerma	—	2.08	2.25	2.24	2.49	2.04	8.54
MLP 95-V-12-4a	La Moderna	—	—	2.44	2.40			—
MLP 95-V-12-4b	La Moderna	—	—	—	—	2.40	2.20	—
MLP 95-V-12-4c	La Moderna	—	—	—	—	2.80	2.20	—
MLP 95-V-12-5	La Moderna	—	—	2.40	2.40	2.84	2.08	—
Lch2 B1C3	Las Chacras 2	—	2.20	2.30	—	2.60	2.40	—
LV1 70-75a/c	Las Vizcacheras	3.60	2.10	2.40	2.10	2.00	2.00	8.20
LV2 10-15	Las Vizcacheras	3.40	2.10	2.30	2.30	2.40	2.00	8.30
LV2 20-25a	Las Vizcacheras	3.20	2.10	2.30	2.20	1.90	1.90	8.20
LV2 25-30	Las Vizcacheras	3.50	2.10	2.40	2.10	2.60	1.90	8.20
LV2 30-35a	Las Vizcacheras	3.50	2.10	2.40	2.30	—	—	—
VZ-2-15-20a	Las Vizcacheras	3.30	2.10	2.40	2.20	—	—	—
VZ-2-15-20b	Las Vizcacheras	—	—	—	—	2.70	1.80	—
MLP 52-X-2-72	Miramar	3.04	2.00	2.24	2.24	—	—	—
MLP 52-X-2-72	Miramar	3.00	2.08	2.20	2.24	—	—	—
UNSGH 485	Napostá Grande	3.40	2.32	2.08	2.48	2.88	2.28	—
UNSGH 492	Napostá Grande	3.32	2.04	2.08	2.40	2.76	2.24	—
UNSGH 493	Napostá Grande	3.48	2.24	2.40	2.40	2.72	2.00	—
PE1 H1C2	Puesto La Esquina 1	3.40	2.30	2.40	2.40	—	—	—
RY11 Sc2	Río Yuspe 11	3.80	2.30	2.50	2.60	2.60	2.20	8.80

Tabla 2 *(continuación)*.—Lower and upper molar measurements of some *Holochilus* and *Lundomys* specimens from Quaternary deposits in Argentina and Uruguay

		m1		m2		m3		m1-m3
Specimen	Locality	length	width	length	width	length	width	length
L. molitor								
MLP 01-III-1-3	Bajo San José	3.65	2.21	2.57	2.22	2.85	2.26	9.01
MLP 95-V-8-3	Paso del Medano	—	—	2.40	2.04	—	—	—

		M1		M2		M3		M1-M3
Specimen	Locality	length	width	length	width	length	width	length
H. brasiliensis								
MSC-C-12	Camet Norte	3.24	2.52	2.20	2.48	2.44	2.20	—
MLP P 028	Centinela del Mar	3.05	2.63	2.27	2.46	—	—	—
MSC-CF-037	Complejo Ferroviario	3.56	2.44	—	—	—	—	—
L. molitor								
MLP 01-III-1-2	Bajo San José	—	2.46	2.41	2.23	—	—	—
FC-DPV-820	Arroyo Malo	3.10	2.70	2.90	2.50	2.40	2.30	8.40
MHD-P323	Río Cuareim	3.60	2.20	2.30	2.90	2.00	1.60	8.40

some beds of the Tarija Basin suggests correlation to magnetic polarity [chron] Clr.1n to early C1n (Matuyama), between 0.7-1.0 myr, but some portion of the Basin may be younger (Steppan, 1996). Detailed description is provided by Steppan (1996).

Genus *Lundomys* Voss et Carleton, 1993
Lundomys molitor (Winge, 1887)
(Figs. 1b and 4, Tables 1 and 2)

Hesperomys molitor (sensu Ameghino, 1889:119)
Holochilus brasiliensis (sensu Mones & Castiglioni, 1979:86; Prado *et al*., 1987:226); Lezcano *et al*., 1992:387)
Holochilus magnus (sensu Bond & Massoia, 1981:8; Pardiñas & Lezcano, 1992:386;
Holochilus sp. (sensu Ubilla, 1985:188)
Lundomys sp. (sensu Pardiñas & Lezcano, 1995:255; Pardiñas & Deschamps, 1996:375)

Recent distribution: Uruguay (González, 2001) and southern Brazil, in the State of Rio Grande do Sul (Marques, 1988; Voss & Carleton, 1993; Fig. 1b).

Fossil record: Middle Pleistocene-Late Pleistocene in central-eastern Argentina; Late Pleistocene-Recent in Uruguay (Figs. 1b and 4, Tables 1 and 2).

Taxonomy: *L. molitor* was originally described based on fossils from Pleistocene-Holocene cave deposits in Minas Gerais, Brazil. Hershkovitz (1955) described extant populations as *Holochilus magnus*, but its synonymy with *molitor* was first suggested by Massoia (1980) and demonstrated by Voss and Carleton (1993). Pardiñas & Lezcano (1995) discussed the reference of Argentinean fossil records to *L. molitor*. The new available material (especially those from Bajo San José; Figs. 3b, 3f, 3g) supports this specific assignation. Mandible morphology and molar measurements of the studied remains are enough to differentiate those from *H. primigenus* (see Steppan, 1996). Both fossil (holotype of *L. molitor* from Lagoa Santa, Minas Gerais, Brazil; see Voss & Carleton, 1993: figure 5A) and recent specimens from Brazil (a sample of rio Ivaí, Tupanciretã, Rio Grande do Sul; see Marques, 1988:Estampa 2) show the presence of a paralophule on M1 typically absent in Argentinean or Uruguayan individuals. The biological meaning of this difference is unknown, but surely merits further studies.

Remarks: The specimen MNHN-DP 599 reported by Mones & Castiglioni (1979) as *Holochilus brasiliensis* from Late? Pleistocene of Uruguay is here referred to *L. molitor* (Figs. 4a, 4e). The mention made by Ameghino (1889) based on a fossil from Late Holocene deposits (Olivera, Buenos Aires, Argentina) must be considered tentative because the material is apparently lost from MACN collections. The Late Pleistocene fossil specimen early reported by Bond & Massoia (1981) is also lost (M. Bond, com. pers.), but in this latter case, unpublished drawings made by Elio Massoia (U. Pardiñas pers. obs.) are enough to support their taxonomical assignation to *L. molitor*. Description is provided by Voss and Carleton (1993).

Discussion

Dental morphology and taxonomy

Today, three species of *Holochilus* are recognized (*H. brasiliensis*, *H. chacarius*, and *H. sciureus*), while *Lundomys* is monotypic, including *L. molitor*. The study of fossil and recent remains of

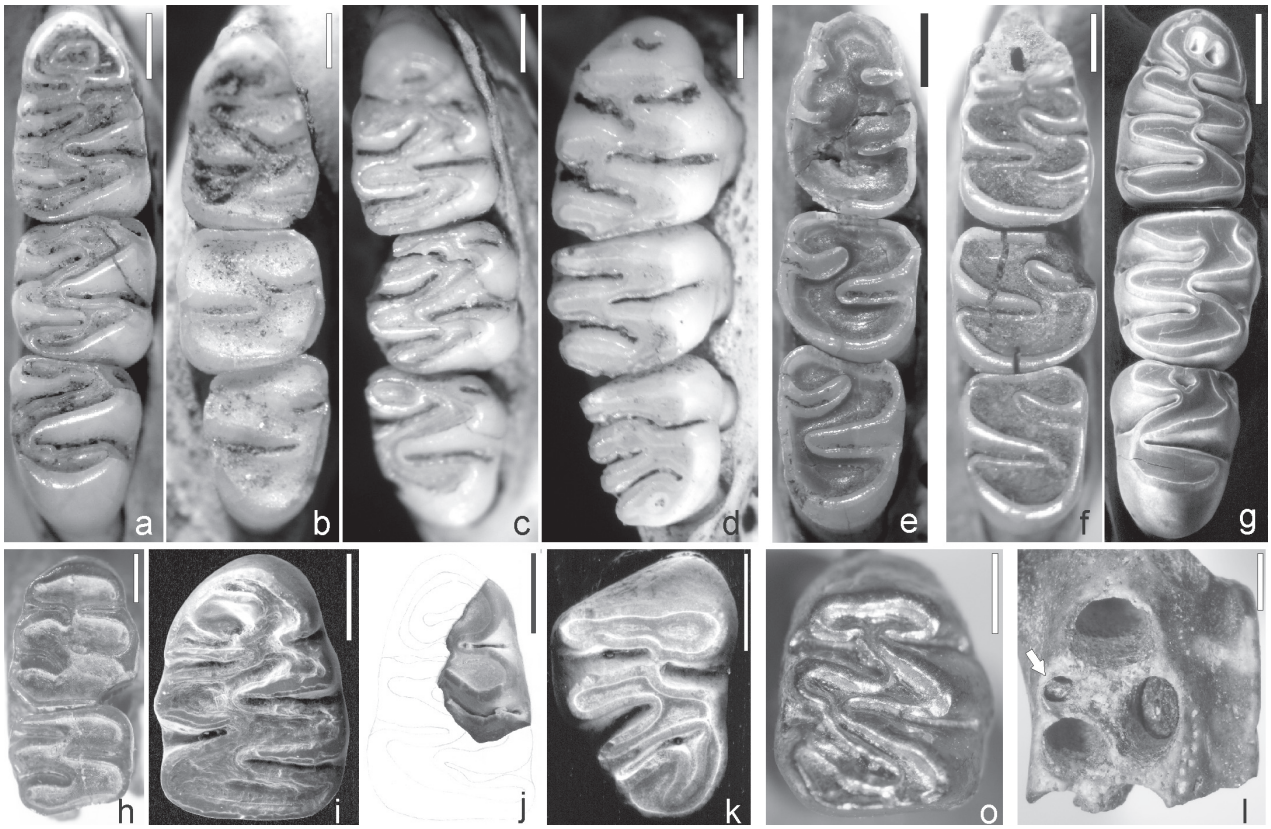

Fig. 3.—Fossil remains of *Holochilus*, upper and lower molars in occlusal view, from Quaternary deposits in Argentina and Bolivia: (a) *H. brasiliensis*, right m1-m3 (Late Holocene, La Higuera, Argentina, C3 #94-239); (b) *H. brasiliensis*, left m1-m3 (Late Holocene, El Gaucho 1, Argentina, AEG1 C2C6); (c) *H. brasiliensis*, right m1-m3 (Late Holocene, C. Pun. 39, Argentina, C3 capa 3); (d) *H. brasiliensis*, right M1-M3 (Late Holocene, El Gaucho 1, Argentina, AEG1 C2C6b); (e) *H. brasiliensis*, right m1-m3 (Late Holocene, La Guillerma, Argentina, LG5-CIXb-level 5); (f) *H. brasiliensis*, left m1-m3 (Late Holocene, La Norma, Argentina, C6 level IV); (g) *H. chacarius*, right m1-m3 (Late Holocene, Lomas del Veinte, Argentina, MLP 79-XI-30-1); (h) *H. brasiliensis*, right M1-M2 (Middle Pleistocene, Centinela del Mar, Argentina, MLP P 028); (i) *H. chacarius*, left m1 (Early to Middle Holocene, Quebrada de Ñuapua, Bolivia, MLP 95-V-26-1); (j) *H. brasiliensis*, fragment of left m1 with schematic design of the missing portion (Late Holocene, Alero Arias, Argentina, MLP 96-V-20-1); (k) *H. brasiliensis*, right M3 (Late Pleistocene, Constitución, Argentina, MLP uncatalogued material); (l) and (o) *H. brasiliensis*, right M1 and its maxillary alveolar portion showing the accessory labial root [arrow], respectively (Middle Pleistocene, Complejo Ferroviario, Argentina, MSC-CF-037). Scale = 1 mm.

Holochilus reveals two different sets of morphological traits that can be identified with the species groups of *H. brasiliensis* and *H. sciureus* (including *chacarius*, see Table 2). The former is characterized by its large size, main molar cusps opposite or slightly alternating, proto- and hypoconid with their posterior faces oriented 45º inwards, typically persistence of mesolophs/ids-like structures, and upper and lower ridges of the masseteric crest confluent at the level of the posterior face of m1 and continuing forward to the mental foramen. In contrast, molar toothrows in *H. chacarius* and *H. sciureus* are smaller than in *H. brasiliensis*, with the main molar cups strongly alternating, proto- and hypoconid with their posterior faces transversally oriented, typical absence of mesolophs/ids-like structures, and upper and lower ridges of the masseteric crest confluent at the level, or slightly above, of the mental foramen. These differences were first recognized by Massoia (1971, 1976) and followed and expanded by Voss & Carleton (1993) and Pardiñas & Galliari (1998). Tooth morphology of lower molars of *Lundomys* and *Holochilus primigenius* includes main cusps arranged in essentially opposite pairs, with lingual and labial margins bluntly rounded; anteroconid of m1 entire (not divided by an anteromedian flexid), but enclosing a large enamel pit; minute anterolophids present on all unworn lower molars; small mesolophids present on unworn m1 and m2, absent on m3; discrete posterolophids pre-

Tabla 3.—First lower molar comparisons among Holochilus living species

Character	H. brasiliensis	H. chacarius	H. sciureus
Molar occlusal design	Main cusps essentially opposite	Main cusps alternating	Main cusps alternating
Form of lophids	Not compressed, rounded outer margins	Compressed, with acute outer margins	Compressed, with strongly acute outer margins (prismatic)
Position of the anteromedian fossetid	Central	Labially displaced	Labially displaced
Form and size of the anteromedian fossetid	Transversally elongated, large to very large	Subcircular, large	Transversally elongated, small
Occlusal development of metaflexid	Well developed, reaching the midline of the tooth	Scarcely developed, not reaching the midline of the tooth	Well developed, freely connected with the protoflexid in subadults
Form of the area in proto- and hipoconid	Subtriangular in outline	Subrectangular in outline	Subrectangular in outline
Orientation of proto- and hypoconid posterior faces	Typically 45°	Transverse	Transverse
Orientation of mesoflexid	Oblique	Transverse	Transverse
Mesolophid	Typically present, although vestigial	Absent	Absent

sent on m1 and m2, usually absent on m3 (Voss and Carleton, 1993; Steppan, 1996).

The alpha taxonomy of *Holochilus* is clearly needed of a major revision. The only available review was made by Hershkovitz (1955), who consolidated 13 extant nominal forms under *H. brasiliensis*. Since then, few studies have been done within specific geographical limits (e. g., those of Massoia [1971, 1976] for Argentinean populations or Aguilera & Pérez-Zapata [1989] for Venezuelan samples). Studies based on morphological features are scarce, while karyological data obtained for some populations are abundant (e. g., Nachman & Myers, 1989; Nachman, 1992). This situation contributes to a poorly resolved taxonomic scenario characterized by partially conventional divisions (see, for example, Barreto & García-Rangel, 2005). A main point of conflict within *Holochilus* alpha taxonomy is the status of several small nominal forms with absent mesolophs and variable karyotypes traditionally included under *H. sciureus*, such as *H. amazonicus* Osgood, 1915, *H. balnearum* Thomas, 1906, *H. berbicensis* Morrison-Scott, 1937, *H. guianae* Thomas, 1901, *H. incarum* Thomas, 1921, *H. nanus* Hershkovitz, 1955 or *H. venezuelae* J.A. Allen, 1904. A large amount of variation in the number of chromosomes was also recorded within the group of *H. brasiliensis*, varying from 2n = 36 in central-eastern Argentina to 2n = 40 or 2n = 48 in Uruguay and southern Brazil, respectively (Aguilera *et al.*, 1993). As has been indicated by Musser and Carleton (2005), the persisting disagreement over number of valid species, uncertain correspondence of karyotypic variants to definable morphologies, and vagueness of distributional limits will only be solved by wholesale generic revision.

Evolutionary timing

The oldest marsh rat recognized in the fossil record is *H. brasiliensis* from Complejo Ferroviario paleontological locality (southeastern Buenos Aires province, Argentina; Pardiñas, 2004; Fig. la). Magnetoestratigraphical data from a profile near the fossiliferous locality indicate that these remains are close to the Brunhes-Matuyama Boundary (0.78 myr). A similar age was initially proposed for *H. primigenus*, but the stratigraphical information associated with the fossil remains of this later species is imprecise (see Steppan, 1996). *H. chacarius* has

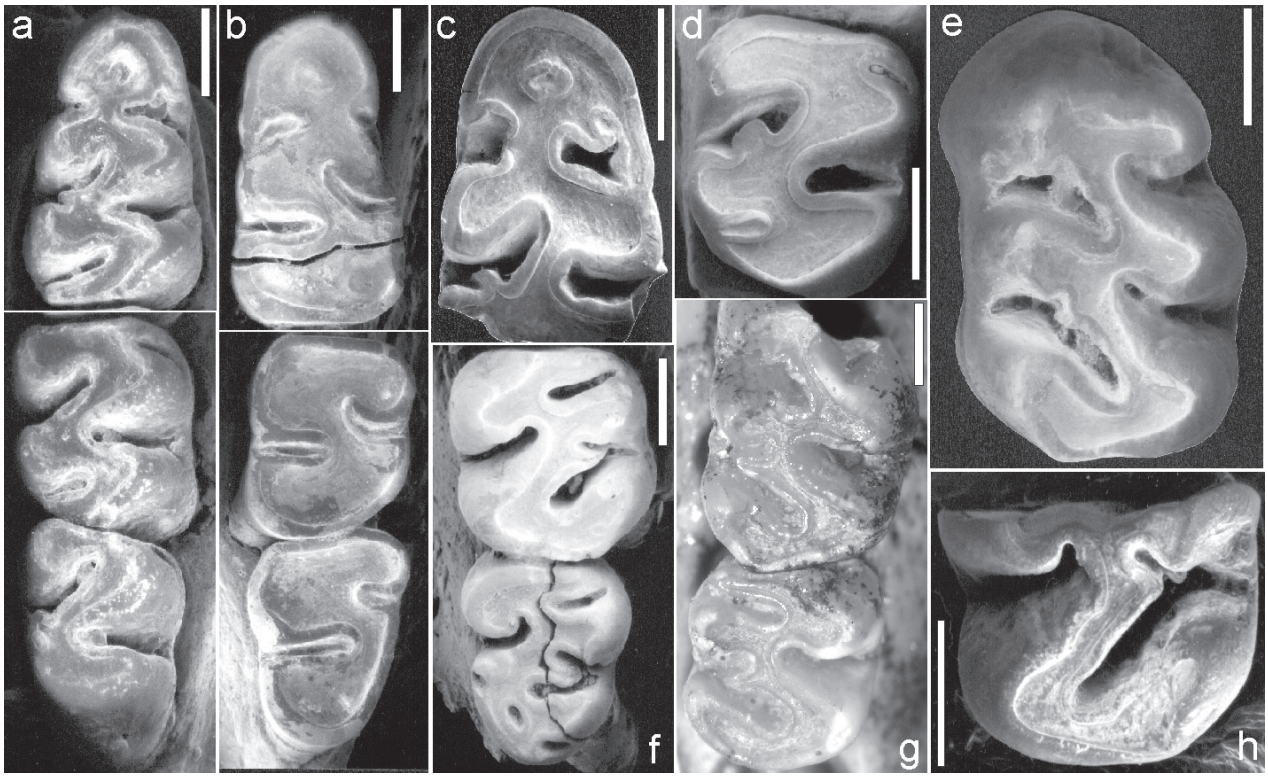

Fig. 4.—Fossil remains of *Lundomys molitor*, upper and lower molars in occlusal view, from Quaternary deposits in Argentina and Uruguay: (a) *L. molitor*, right m1-m3 (Late? Pleistocene, Arroyo Perico Flaco, Uruguay, MNHN-DP 599); (b) *L. molitor*, left m1-m3 (Middle Pleistocene, Bajo San José, Argentina, MLP 01-III-1-3); (c) *L. molitor*, fragmentary right m1 (Late Pleistocene, Paso Otero, Argentina, MLP 80-VIII-13-45h); (d) *L. molitor*, right m2 (Late Pleistocene, Cueva del Tigre, Argentina, MLP 95-V-8-3); (e) *L. molitor*, right M1 (MNHN-DP 599); (f) *L. molitor*, left M2-M3 (Middle Pleistocene, Bajo San José, Argentina, UNSGH 605); (g) *L. molitor*, fragmentary right M1-M2 (Middle Pleistocene, Bajo San José, Argentina, MLP 01-III-1-2); (h) *L. molitor*, fragmentary left M1 (Middle Pleistocene, Pilar, Argentina, MLP 00-II-5-39). Scale = 1 mm

the oldest record in Quebrada de Ñuapua, southern Bolivia, with an Early to Middle Holocene age (Pardiñas & Galliari, 1998). The oldest record for *L. molitor* came from Bajo San José (southwestern Buenos Aires province, Argentina; Pardiñas & Deschamps, 1996; Fig. 4). Verzi *et al*. (2004) and Deschamps (2005) reevaluated the fossil assemblage of Bajo San José and selected this locality and bearing strata as the type of *Ctenomys kraglievichi* Zone, a short biochronological unit tentatively placed in the Early Bonaerian age (0.45 myr; Middle Pleistocene; see also Teta & Pardiñas, 2006). *Lundomys molitor* made its last appearance in the fossil record of Buenos Aires province in sediments of La Chumbiada Member (Luján Formation) probably around 30 kyr ago, becoming extinct slightly before typically Lujanian deposits (Guerrero Member, Luján Formation, ca. 21-13 kyr).

Based on the available evidence, the *Lundomys-Holochilus* split must be fixed at >0.78 myr. (see also Steppan, 1996). According to Steppan, *H. primigenius* is the potential ancestor to living species of the genus *Holochilus*. If this hypothesis is correct or if *H. primigenius* proves to be at least an ancestor both phyletically and temporarily, then the *H. brasiliensis* and *H. sciureus* groups may have split less than 1.0 myr ago (Steppan, 1996). However, based on the suggestions made by Carleton & Olson (1999) and Pardiñas (2008), we think that the generic position of *H. primigenius* needs a reevaluation. As has been highlithed by Pardiñas (2008), the mosaic of characters displayed by *H. primigenius* (combining *Holochilus*-like mandible with *Lundomys*-like molars) is suggestive of generic distinctiveness.

Paleoclimatic significance

Marsh rats of the genus *Holochilus* are narrowly associated with mesic microenvironments, such as

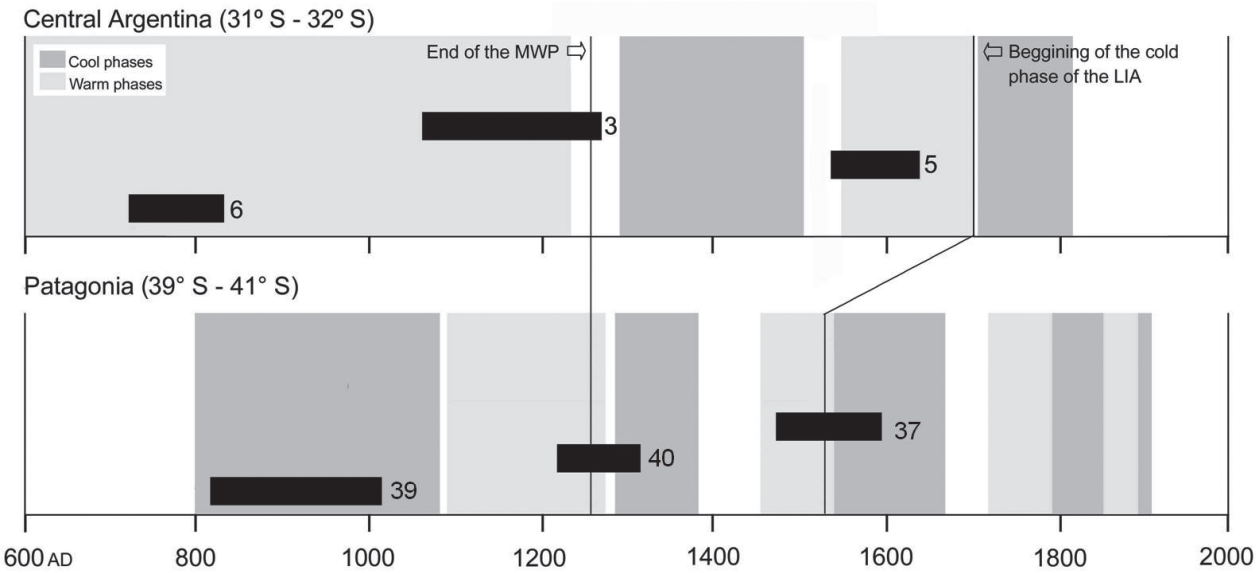

Fig. 5.—Warm and cool phases in central and south-central Argentina during the last 1.4 ry BP (modified from Carignano [1999] and Villalba [1994a, b], respectively). Black bands represent expansion events of the marsh rat *Holochilus brasiliensis* (Desmarest, 1819) according to the fossil record (for the reference number, see Table 1).

moist lowland or tall grasses near streams, grassy marshes, swampy savannas, and gallery forest along watercourses (Barlow, 1969; Massoia, 1976). Recent distribution of *Holochilus* includes temperate, subtropical, and tropical lowland areas of South America between the 10º N and 38º S (Hershkovitz, 1955), while *Lundomys* is more restricted to temperate and subtropical regions between 20° S and 35° S in Uruguay and southern Brazil (Voss & Carleton 1993).

The fossil record of *Holochilus* in southern South America is relatively continuous through the Pleistocene-Holocene. In addition, almost all Pleistocene to Middle Holocene findings are included within the recent range of this genus. In contrast, Late Holocene fossil samples (<3 kyr) include several extra-limital occurrences for *H. brasiliensis* and *H. chacarius* (see Fig. 1). Some of these findings extended the known distribution of the former more than 250 km southwest and 200 km west of its present distribution limits (Fig. 1a). Taking into account the present distribution and environmental requirements of *H. brasiliensis* we hypothesize that the past presence of this species in central and south-central Argentina is associated with the warm and humid pulses that occurred during the Late Holocene. A close inspection of the archeological chronologies and climatic pulses suggests a major correspondence between warm phases of the last 1.4 kyr and the presence of *H. brasiliensis* in central and south-central Argentina (Fig. 5). Paleoclimatic reconstructions for the Southern Hemisphere suggest that the last 1-1.4 ka were highly variable encompassing a period of rapid climatic change around the limit between the Medieval Warm Period [MWP] and the Little Ice Age [LIA] (see Mayewski *et al*., 2004). In central Argentina, several climatic indicators suggest warm and humid conditions for the period 1.4-0.8 ry BP and 0.4-0.3 ry BP (Carignano, 1999; Cioccale, 1999). The first of these two periods was related with a climatic improvement registered by incipient soil development, expansion of the fluvial and lacustrine systems, and formation of swamps in depressions (Carignano, 1999; Cioccale, 1999). This phase, that has been correlated with the MWP, was characterized by a temperate, humid to semi-humid climate, with a pluviothermal regime either similar to the recent or perhaps more humid (Carignano, 1999; Cioccale, 1999). At the same time, tree-ring based reconstructions for northern Patagonia, south-central Argentina, suggest the alternation of warm (1080-1250 [ascribed to the MWP], 1720-1790, and 1850-1890 AD) and cool phases (900-1070, 1270-1380, and 1520-1660 AD) during the last 1.0 kyr (Villalba, 1994a, 1994b). Warm and humid pulses, primarily associated with the MWP, might have allowed the range expansion of this rat through the

major rivers that dissect the middle and south-central latitudes of Argentina (e.g., Primero, Segundo, Tercero and Cuarto, Negro, Colorado), whose roles as faunal corridors could be reinforced during these periods. In addition, fossil remains from Santiago del Estero, central Argentina, indicate that *H. chacarius* also extended its southern distribution range near 1-1.2 ry BP (Cione & Tonni, 1981), occurring in an area where permanent fresh water bodies are absent today.

The fossil record of *L. molitor* includes several Pleistocene extra-limital occurrences in middle latitudes of Argentina (Teta & Pardiñas, 2006; Fig. 1B, Table 1). Even when the climate in this area was mostly arid and relatively cold during most of the Bonaerian and Lujanian Stages (Middle-Late Pleistocene), comparatively wet and warm pulses are suggested by the presence of subtropical mammals (e. g., Echimyidae and Dasyproctidae rodents) and tchernozoid paleosoils (Tonni *et al*., 1999). As has been discussed by Teta and Pardiñas (2006), range expansion events of *Lundomys* through middle latitudes of Argentina were partially synchronous with the marine oxygen isotopic stage (OIS) 11 (see also Verzi *et al*., 2004) and OIS 5 (Pardiñas & Lezcano, 1995; Fucks *et al*., 2005). A third expansion event is related to the OIS 3 (ca. 60 to 35 kyr) or perhaps to the wet and warmer conditions registered in middle latitudes of Argentina near 30 to 25 kyr (Tonni *et al*., 1999). Range expansion of *Lundomys molitor* populations also occurred in northern latitudes, at least up to 19° 38' in central-eastern Brazil (Voss and Carleton, 1993). In fact, the type locality of this species is "Lapa da Escrivania Nr. 5," a cave found in Lagoa Santa (Minas Gerais, Brazil), more than 1,450 km north to its recent distributional range (Winge, 1887). According to Voss and Carleton (1993), such paleontological records suggests that past climates in Minas Gerais were at least periodically more temperate than today. Palynological data from central Brazil provide clear evidences of marked environmental changes in the last 30 kyr, including cold-moist and cold-dry alternate pulses (Ledru, 1993). The uncertainness associated with the exact stratigraphic provenance of *L. molitor* remains from Lagoa Santa (Pleistocene? Early Holocene?) precludes a more detailed inference (Auler *et al*., 2006).

In Southern South America, major regional extinctions seem to occur in two intervals. First, *Lundomys molitor* was extirpated from Buenos Aires province near the Last Glacial Maximum (21-18 kyr), surviving exclusively in Uruguay and Brazil. More recently, *Holochilus brasiliensis* disappeared from south-central (ca. 40º S) and central Argentina (ca. 65º W) during the last hundred years (<0,4 kyr), perhaps with the occurrence of the LIA. Relictual and scattered occurences of *H. brasiliensis* past distribution are not improbable in suitable habitats, such as dense palustrine vegetation in fresh-water bodies, specially taking into account the incomplete mammal surveys in Limay and Negro river system (see Pardiñas *et al*., 2003). The obtaining of molecular data for the southernmost populations of *H. brasiliensis* (around Bahía Blanca, southern Buenos Aires province; see Massoia, 1976) could be useful to refine the changing demographic scenario envisioned through the fossil record.

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Appendix 1

Fossil specimens examined. Acronyms for institutions and archeological collections are as follows: Cátedra de Geología Histórica, Universidad Nacional del Sur, Bahía Blanca, Argentina (UNSGH); Cátedra de Prehistoria y Arqueología, Universidad Nacional de Córdoba, Córdoba, Argentina (AEG1, LCh2, C.Pun.39, RY11, and PE1); Facultad de Ciencias, Universidad de la República, Departamento Paleontología Vertebrados, Montevideo, Uruguay (FC-DPV); Instituto Nacional de Antropología y Pensamiento Latinoamericano, Buenos Aires, Argentina (LBII, and VZ); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Colección Ameghino, Buenos Aires, Argentina (MACN-A); Museo de Ciencias Naturales de Santa Clara del Mar, Buenos Aires, Argentina (MSC); Museo de La Plata, La Plata, Argentina (MLP); Museo de Paleontología de Moreno "Francisco Javier Muñiz," Moreno, Argentina (MFJM); Museo Histórico Departamental de Artigas, Artigas, Uruguay (MHD-P); Museo Nacional Historia Natural, Departamento de Paleontología, Montevideo, Uruguay (MNHN-DP).

Holochilus brasiliensis (n = 93): Argentina: Buenos Aires, Azul, left mandible with m1-m2 (Pleistocene, MACN-A 2207); Playa La Serena (= Balneario Menta), left mandible (Late Holocene, MLP 95-V-1-3); Camet Norte, left mandible with m1-m3 (Lujanian, Late Pleistocene, MSC-C-13), palate fragment with premaxillae and left M1-M3 and right M1-M2 (Holocene, MSC-C-12); Camping Americano, left mandible with m1 (Early Holocene, MLP 95-V-6-1); Centinela del Mar, mandible (Late Holocene, MLP 96-V-16-12), two left premaxillae, five right mandibles and 5 left mandibles (Late Holocene, MLP 96-V-17-7), right maxillary with M1-M2 (Bonarian, Middle Pleistocene, MLP P 028), isolated left M1 and m1 (Late Holocene, MLP 91-IV-15-7); Complejo Ferroviario, right maxillary with M1 (Ensenadan, Middle Pleistocene, MSC-CF-037); Constitución, isolated molars (Late Pleistocene, MLP uncatalogued material); Cueva Tixi archaeological site, mandible (Late Holocene, MLP 84-X-20-51), mandible (Late Holocene, MLP 84-X-20-41), mandible (Late Holocene, MLP 84-X-20-40); Estación Manuel J. García, isolated right M2 (Early Holocene, MLP 94-III-1-13); Fortín Necochea archaeological site, left mandible with incisive and m1-m3 (Holocene, MLP s/n), right mandible with m1-m2 (Holocene, MLP 95-V-13-1), right maxillary (Holocene, MLP 96-V-18-1), isolated m1 (Holocene, MLP 95-V-13-3); La Bellaca 2 archeological site, right maxillary with M1-M2 (Late Holocene, LBII-2-20-25), right maxillary with M1-M2 (Late Holocene, LBII-4-20-25), left maxillary with M1-M2 (Late Holocene, LBII-4-15-20a), left maxillary with M1-M3 (Late Holocene, LBII-4-15-20b), right mandible with m1-m3 (Late Holocene, LBII-1-15-20a), right mandible without tooth (Late Holocene, LBII-1-15-20b), right mandible with incisive and m1-m3 (Late Holocene, LBII-1-25-30d), right mandible with incisive and m1-m2 (Late Holocene, LBII-2-15-20), right mandible with m2-m3 (Late Holocene, LBII-4-20-30), right mandible with m2 (Late Holocene, LBII-4-10-15), right mandible with m1-m3 (Late Holocene, LBII-4-30-35b), right mandible without tooth (Late Holocene, LBII-1-30-35), right mandible with m2-m3 (Late Holocene, LBII-1-35-40), right mandible with m1-m3 (Late Holocene, LBII-A/C-60-65b), right mandible with m1-m2 (Late Holocene, LBII-4-15-20d), right mandible with incisive and m1-m3 (Late Holocene, LBII-s/n), left mandible with incisive and m1-m3 (Late Holocene, LBII-1-20-25), left mandible with m1-m3 (Late Holocene, LBII-1-25-30a), left mandible with m1-m2 (Late Holocene, LBII-1-25-30b), left mandible with m1-m3 (Late Holocene, LBII-1-25-30c), left mandible with m1-m3 (Late Holocene, LBII-1-15-20a), left mandible with m3 (Late Holocene, LBII-2/4-15-20), left mandible with m1-m3 (Late Holocene, LBII-2/4-25-30), left mandible with m1-m3 (Late Holocene, LBII-2/4-30-35), left mandible with incisive

and m1-m3 (Late Holocene, LBII-4-0-10), left mandible with m1-m2 (Late Holocene, LBII-4-15-20c), left mandible with m1-m3 (Late Holocene, LBII-4-30-35a), left mandible without tooth (Late Holocene, LBII-A/C-60-65a); La Guillerma archaeological site, left maxillary with M1 and fragment M2 (Late Holocene, LG5-BIXa-level 3[10-15]), right mandible with m1-m3 (Late Holocene, LG5-CIXb-level 5); La Higuera archaeological site, right maxillary with M1-M3 (Late Holocene, #94-260), left mandible with m1-m3 (Late Holocene, #94-122"), left mandible with m1-m3 and right mandible with m1-m3, same individual (Late Holocene, #94-239); La Moderna archaeological site, left mandible with m2-m3 (Lujanian-Platan transition, Early Holocene, MLP 95-V-12-5), left mandible with m2 (Lujanian-Platan transition, Early Holocene, MLP 95-V-12-4a), isolated left m3 (Lujanian-Platan transition, Early Holocene, MLP 95-V-12-4b), isolated right m3 (Lujanian-Platan transition, Early Holocene, MLP 95-V-12-4c); La Norma archaeological site, left mandible with m1-m3 (Late Holocene, C6-capa IV); Las Vizcacheras archeological site, right maxillary with M1-M3 (Late Holocene, VZ-1-A/C-40-45), left maxillary with M1-M3 (Late Holocene, VZ-1-15-20), left maxillary with M1-M3 (Late Holocene, VZ-2-20-25a), right mandible with m3 (Late Holocene, VZ-2-15-20b), right mandible with incisive and m1-m3 (Late Holocene, VZ-2-20-25a), right mandible with m1-m2 (Late Holocene, VZ-2-30-35a), right mandible with incisive and m1-m3 (Late Holocene, VZ-1-40-45), right mandible with incisive and m1-m3 (Late Holocene, VZ-1-70-75),), left mandible with m1-m3 (Late Holocene, VZ-2-10-15), left mandible with m1-m2 (Late Holocene, VZ-2-15-20a), left mandible with incisive and m1-m3 (Late Holocene, VZ-2-25-30); Miramar, righ and left mandibles with m1-m2 ("Aymaran", Late Holocene, MLP 52-X-2-72); Olivera, left mandible with incisive and m1-m3 (Late Pleistocene, MACN-A 1355, holotype of *H. multannus*), incomplete skull with right M1-M3 and left M1-M2, left mandible with m1-m3 and right mandible with m1-m3, same individual (Late Pleistocene, MACN-A 1348 to 1353); Streets 43 and 122, Ensenada, left m2 (Middle Holocene, MLP 83-XI-10-219). Córdoba, Alero el Gaucho archeological site, left mandible with m1-m3 (Late Holocene, AEG1 C2C6), left mandible with m1-m2 (Late Holocene, AEG1 C2C10); Arroyo Santa Catalina, right mandible with m1 and fragmentary m2-m3 (Holocene, MLP 96-V-26-1); C.Pun.39 archeological site, right mandible with m1-m3 (Late Holocene, C.Pun.39 C3C3), right mandible with m1-m3 (Late Holocene, C.Pun.39 D3C2), right mandible with m1-m2 (Late Holocene, C.Pun.39 D3C3a), left mandible with m2 (Late Holocene, C.Pun.39 D1C1b), left mandible without tooth (Late Holocene, C.Pun.39 D1C1c), isolated left m3 (Late Holocene, C.Pun.39 D1C1d), isolated lower incisive (Late Holocene, C.Pun.39 D3C3b); Las Chacras 2 archeological site, right mandible with m1-m2 (Late Holocene, LCh2 B1C3), incomplete left mandible without tooth (Late Holocene, LCh2 C1C2); Puesto La Esquina 1 archeological site, right mandible with m1-m2 (Late Holocene, PE1 H1C2a), isolated upper incisive (Late Holocene, PE1 H1C2b); Río Yuspe 11 archeological site, right mandible with m1-m3 (Late Holocene, RY11SC2). Río Negro, Alero Arias archaeological site, incomplete mandible with m1 (Late Holocene, MLP 96-V-20-1).

Holochilus chacarius (n = 4): Argentina: Santiago del Estero, Lomas del Veinte archaeological site, skull and right mandible (Late Holocene, MLP 79-XI-30-1). Bolivia: Tarija, Quebrada de Ñuapua, several mandibles (Early to Middle Holocene, MLP 95-V-26-1).

Lundomys molitor (n = 13): Argentina: Buenos Aires, Bajo San José, left mandible with incisive and m1-m3 (Middle Pleistocene, MLP 01-III-1-3), right maxillary with M1-M2 (Middle Pleistocene, MLP 01-III-1-2), left maxillary with M1-M3 (Middle Pleistocene, UNSGH 605), left mandible with m3 (Middle Pleistocene, UNSGH 616); Cueva del Tigre, left mandible with m2 (Middle Pleistocene, Argentina, MLP 95-V-8-3); Paso Otero archaeological site, fragment right m1 (Late Pleistocene, MLP 80-VIII-13-45h); Pilar, partial left M1 (Middle Pleistocene, MLP 00-II-5-39); Río de la Reconquista, left M1 (Bonaerian, Middle Pleistocene, MFJM 683). Uruguay: Artigas, río Cuareim, anterior fragment of skull with both molar series (Late Pleistocene, MHD-P-323); Salto, arroyo Sopas, left mandible with m1 and postcranial remains (Late Pleistocene, FC-DPV-620); Soriano, arroyo Perico Flaco near its mouth, right mandible with incisive and m1-m3, both premaxillae, right maxillary with M1-M3, left maxillary with M2-M3, associated postcranial elements (Late? Pleistocene, MNHN-DP 599); Tacuarembó, arroyo Malo, skull (Late Pleistocene, FC-DPV-820), right mandible with m1-2 and incisor, left mandible with m1-2 (Late Pleistocene, FC-DPV-813).

Appendix 2

Recent specimens examined. Acronyms for institutions are as follows: Colección de Vertebrados del Museo de Historia Natural "Noel Kempff Mercado," Santa Cruz de la Sierra, Bolivia (MNK); Colección Elio Massoia, Buenos Aires, Argentina (CEM); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN); Museo Nacional de Historia Natural y Antropología, Montevideo, Uruguay (MNHN); Museu Nacional, Rio de Janeiro, Brazil (MN).

Holochilus brasiliensis (n = 23): Argentina: Buenos Aires, González Catán (CEM 3482, CEM 3484, CEM 3789, CEM 3795, CEM 3716, CEM 3485), Delta del Paraná, Canal 6 (CEM 4797, CEM 3685, CEM 3296, CEM 3302, CEM 3305, CEM 3307), Mar del Tuyú (CEM 2714), General Lavalle (CEM 2705), Arroyo El Pantanoso, Balcarce (CEM 3331, CEM 3332, CEM 3333), Coronel Dorrego (CEM 3686), Arroyo Grande, Balcarce (CEM 3457, CEM 3458); Corrientes, Bella Vista (MACN 14050); Santa Fe, Santa Fe (MACN 16549); Entre Ríos, Palmar de Colón (MACN 18601).

Holochilus chacarius (n = 19): Argentina: Formosa, Finca Yacaré (CEM 3425, CEM 3426, CEM 3424, CEM 3421, CEM 3422, CEM 3398, CEM 3568, CEM 3560, CEM 3567, CEM 3559, CEM 3564, CEM 3566); Jujuy, San Salvador de Jujuy (MACN 33.24, MACN 33.169); Salta, Tabacal (MACN 33.24, MACN 17885). Bolivia: Santa Cruz, Bañados del Izozog (MNK 2038, MNK 3213), colina Uruma (MACN 13106).

Holochilus sciureus (n = 6): Bolivia: Beni, río Mamoré (MACN 50.376, MACN 50.378); Brazil (MN 4205, MN 4207, MN 4209, MN 4167).

Lundomys molitor (n = 5): Uruguay: Canelones, arroyo Tropa Vieja (CEM 220, CEM 623, CEM 946, CEM 4442, MNHN 780).